25th Lowell Wakefield Fisheries Symposium
Alaska Sea Grant College Program

Biology and Management of Exploited Crab Populations under Climate Change

EDITORS
G.H. KRUSE • G.L. ECKERT • R.J. FOY • R.N. LIPCIUS
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About the Proceedings Book and the Symposium

Twenty-seven peer-reviewed research and review papers are included in this proceedings volume; all were presented at the symposium *Biology and Management of Exploited Crab Populations under Climate Change*, held March 10-13, 2009, in Anchorage, Alaska.

The symposium was convened to look closely at what fisheries researchers have learned about crab population dynamics, resiliency to fishing, climate effects, and the role of habitat in worldwide crab stocks and fisheries, many of which have fluctuated and collapsed due to shifts in climate, fishing, and ecological interactions.

For example, the collapse of red king crab (*Paralithodes camtschaticus*) fisheries in Alaska in the early 1980s led to much speculation about the roles of a climate regime shift from cool to warm conditions in the late 1970s, associated changes in ecosystem structure including increases in groundfish predators, and overfishing or habitat alterations by large fleets of fishing vessels. Despite 25 years of closed fisheries in the Gulf of Alaska, most stocks of red king crabs have not recovered. Progress into understanding the causative mechanisms has been frustratingly slow, prompting recent initiation of a pilot multiagency king crab stock enhancement and rehabilitation effort. For more information on this program, see the AKCRRAB website, http://seagrant.uaf.edu/research/projects/initiatives/king_crab/general.

Fisheries for Dungeness crabs (*Cancer magister*) along the U.S. west coast and blue crab (*Callinectes sapidus*) along the U.S. east coast provide contrasting examples. For many decades, large, fluctuating catches of both species seemed sustainable, despite extremely high exploitation rates by overcapitalized fishing fleets. Whereas this situation generally remains the case for Dungeness crabs, much concern exists for blue crabs following sharp declines in stock abundance and catches along most of the Atlantic coast in the last decade.

Common threads among the papers in this proceedings are the effects of fisheries and climate on crab abundance, both observed in the past and forecasted into the future. Species addressed include snow, blue, king, and other crabs. Specific topics include crab abundance and distribution related to climate variability and future climate change, stock assessment and fishery management, effects of stock size and environmental variability on recruitment, considerations of reproductive biology and reproductive potential, role of disease and other environmental stressors, predation and habitat considerations, and the utility of stock enhancement programs for rehabilitation of depleted crab stocks.

The symposium was coordinated by Sherri Pristash, University of Alaska Fairbanks, Alaska Sea Grant College Program, Fairbanks, Alaska. Steering committee members were:

- Gordon H. Kruse, chair, University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Juneau Center, Juneau, Alaska
- Ginny Eckert, University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Juneau Center, Juneau, Alaska
- Robert Foy, NOAA Fisheries, Alaska Fisheries Science Center, Kodiak Laboratory, Kodiak, Alaska
- Romuald N. Lipcius, Virginia Institute of Marine Science, Gloucester Point, Virginia
- Bernard Sainte-Marie, Fisheries and Oceans Canada, Maurice Lamontagne Institute, Mont-Joli, Quebec, Canada
- Diana Stram, North Pacific Fishery Management Council, Anchorage, Alaska
- Doug Woodby, Alaska Department of Fish and Game, Juneau, Alaska

Symposium sponsors were:

- Alaska Sea Grant College Program
- Alaska Department of Fish and Game
- NOAA Fisheries (National Marine Fisheries Service)
- North Pacific Fishery Management Council
- Wakefield Endowment (University of Alaska Foundation)

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The Lowell Wakefield Symposium Series and Endowment

The Alaska Sea Grant College Program has been sponsoring and coordinating the Lowell Wakefield Fisheries Symposium series since 1982. These meetings are a forum for information exchange in biology, management, and economics of various fish species and complexes, as well as an opportunity for scientists from high-latitude countries to meet informally and discuss their work.

Lowell Wakefield was the founder of the Alaska king crab industry. He recognized two major ingredients necessary for the king crab fishery to survive—ensuring that a quality product be made available to the consumer, and that a viable fishery can be maintained only through sound management practices based on the best scientific data available. Lowell Wakefield and Wakefield Seafoods played an important role in the development and implementation of quality control legislation, in the preparation of fishing regulations for Alaska waters, and in drafting international agreements for the high seas. In his later years, as an adjunct professor of fisheries at the University of Alaska, Lowell Wakefield influenced the early directions of Alaska Sea Grant. The Wakefield Symposium series is named in honor of Lowell Wakefield and his many contributions to Alaska's fisheries. In 2000, Lowell's wife Frankie Wakefield made a gift to the University of Alaska Foundation to establish an endowment to continue this series.

Armstrong, D.A., P.S. McDonald, G.H. Kruse, A.H. Hines, and J.M. Orensanz. 2010. A Crab for all Seasons: The Confluence of Fisheries and Climate as Drivers of Crab Abundance and Distribution. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.05

A Crab for All Seasons: The Confluence of Fisheries and Climate as Drivers of Crab Abundance and Distribution

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Abstract

Abundance and distribution of crab stocks are affected by factors such as habitat quality, community structure, climate variability, and fishing that are interrelated in various ways. We explore the interplay of climate and fishing on crab populations by reviewing several well-known case studies. Snow crab (*Chionoecetes opilio*) in the eastern Bering Sea declined to about 10% of their abundance in the late 1990s. Concurrently, the stock underwent a dramatic distributional shift from southeast to northwest over the continental shelf. Contraction to the northwest during a warming phase perhaps resulted from an “environmental ratchet” whereby crab now occur in northerly areas of colder water, and a large predator guild may limit recruitment in southerly areas. Red king crabs (*Paralithodes camtschaticus*) declined significantly in Alaska following a climate regime shift, but fishing may have also adversely affected stocks. Recovery or ongoing depletion in different areas may reflect variable influence of climate and fishing as causative factors. Dungeness crab *(Cancer magister)* fluctuate widely in abundance and most hypotheses evoke climate-driven oceanographic processes regulating recruitment. The long-term demise of the central California fishery is ascribed to a decadal-long shift in timing of the spring transition. These case studies represent male-only fisheries, but an intriguing fishery that exploits both sexes exists for blue crab (*Callinectes sapidus*) along the U.S. east coast. Crab spawning stock abundance has declined more than 80% in the last decade and habitat degradation and fishing pressure on females appear primarily responsible. Based on our review, we ask: does climate trump fishing as the leading cause of change in distribution and abundance of fished crab populations?

Introduction

The Wakefield Fisheries Symposium series has provided an invaluable forum for discussion of myriad issues related to fisheries and ecosystems that support them. Prominent among the many taxa covered have been decapod crustaceans that comprise some of the most important and intriguing fisheries worldwide. Symposia since the mid 1980s have provided scientists and opportunity to present results, interpretations, and opinions about research on species that embody fascinating stories of life history, population variability, and dramatic shifts in distribution and abundance, which are linked to a spectrum of physical and biological drivers. Building on information from symposia in 1995 and 2001, the collection of papers in this volume is oriented toward the general issue of climate change as it might affect all aspects of life history, community composition, and habitat, with resultant implications for management of commercial species.

As we considered what perspective to emphasize in the present paper, we were intrigued by the notion of interplay between climate change and fishery exploitation as accounting for shifts in distribution and abundance, and resultant trends in landings or need for closures. At one scale, it strikes us that "climate forcing" trumps fisheries as the usual cause for well-documented variability of some species. In this sense, climate change is not necessarily unidirectional as warmer or colder henceforth, but rather the decadal patterns of change in the context of regime shifts (sensu Grebmeier et al. 2006). The literature for the northeastern Pacific has been particularly prolific on these topics over the last 4-5 years, hence the benefit of periodic update provided by the Wakefield symposia. Comprehensive treatises on systems such as the "Pribilof Domain" (e.g., see Hunt et al. 2008, Stabeno et al. 2008) have provided invaluable context for development of hypotheses to explore mechanisms behind some of the most dramatic shifts in decapod distributions and abundance, and striking decrease in fishery production. Regime shifts may modulate weather in ways that profoundly affect recruitment of many species (Bond and Overland 2005). Warming trends (Stabeno et al. 2007) have affected sea ice and bottom temperature that have led to pervasive change in community structure and biogeography (Grebmeier et al. 2006, Aydin and Mueter 2007, Mueter and Litzow 2008), which is consistent with other examples such as northward shift in North Sea fauna (Perry et al. 2005) or the spread of lithodid crabs to Antarctica (Thatje et al. 2005, Aronson et al. 2007).

Fisheries also exert impacts that are well documented, such as for the lithodid red king crab stocks in the eastern Bering Sea (Orensanz et al. 1998, Dew and McConnaughey 2005). Whether the causes that lead to reductions below "overfished" thresholds are due primarily to climate or fisheries themselves is uncertain (e.g., Zheng and Kruse 2006). Dramatic decline in Chesapeake Bay stocks of blue crab to the point of being recruitment-limited has been attributed to overfishing and habitat degradation (Davis et al. 2005, Zohar et al. 2008). The extent to which unidirectional climate change and fisheries interact synergistically to produce non-additive effects should be explored.

We have selected four cases of crab fisheries to briefly explore roles of climate and fisheries as causes of population fluctuations and changes in distribution. The species provide life history contrasts in features like age at maturity and reproductive strategies, but also contrasts in nature and complexity of the fisheries and management. The literature is vast for all; therefore, in this brief coverage tied to climate and exploitation, we attempt to highlight unique, sometimes odd, aspects of life history, ecology, and fishery regulations, management, and history.

Species profiles and discussion

Snow crab (Chionoecetes opilio)

Life history and population dynamics

Snow crabs are widely distributed in subarctic and arctic regions, including the northwestern Pacific, Bering Sea, parts of the Arctic, northwest Atlantic south to Maine, and west coast of Greenland. The species has been introduced to the Barents Sea where there is now a self-sustained population (Alvsvåg et al. 2009). Here we focus on the eastern Bering Sea stock (Fig. 1; see Kruse et al. 2007, for an overview).

Snow crab life history has been well studied in eastern Canada (Sainte-Marie et al. 2008), where the calendar of major life-history events (Table 1) appears to be very similar to the eastern Bering Sea. Males and females stop growing after reaching a terminal molt. Immediately after, females mate for the first time while still in a soft-shell condi-

Table 1. Life history characteristics of focal crab species.

Life history characteristic	Snow crab (Chionoecetes opilio) eastern Bering Sea	Red king crab (Paralithodes camtschaticus)	Dungeness crab (Cancer magister)	Blue crab (Callinectes sapidus) Chesapeake Bay
Larval stages and duration of pelagic larval life	2 zoeae and a megalopa (post-larva); 3-5 months.	4 zoeae and a glaucothoe; 2 months.	5 zoeae and a megalopa (post-larva); 2.5-5 months.	7-8 zoeae and a megalopa (post-larva); 1.5 months.
Settlement period and juvenile habitat	Expected in September-October. Juvenile habitat largely unknown.	May-July; near-shore high-relief habitat.	Peak settlement in May-June through September in higher latitudes. Juvenile survival highest in complex intertidal habitats, such as eelgrass and oyster shell.	August-November; settlement in seagrass beds for ~2 months growth to 5-7 instar (~20mm), then juvenile dispersal to shallow shoreline habitats of sub-estuaries.
Growth	Most individuals growth through instars II and III (~5 and 7 mm CW) during first calendar year after settlement, instars IV and V (~10 and 15 mm CW) during the third, once a year afterward, during winters.	Mean sizes at 1, 2, and 3 years post-settlement are 9-16 mm CL, 23-42 mm CL, and 47-66 mm CL, depending on location.	Rapid growth during first summer following settlement, particularly in estuaries. Individuals grow through instars XII-XIV in two calendar years post-settlement; thereafter molting occurs once a year.	Growth is seasonal in the mid Atlantic; juveniles may reach ~65 mm CW (instar X-XII) within three months after settlement but growth ceases during winter. Individuals molt less frequently as they grow larger.
Growth determinacy	Immature size-at-instar schedule varies little among populations. Male and female have a terminal molt; male transition recognizable in the relative size of claws.	Females molt annually prior to mating and egg extrusion. Males molt annually until maturity, and then do not molt every year.	Size-at-instar and molt frequency affected by temperature. Annual molt upon reaching maturity; no terminal molt.	Size-at-instar and molt frequency affected by temperature. Females have terminal molt to maturity but males continue to molt and grow.
Size/age/stage at maturity, females	Strong clinal variation in size-at-maturity (smaller at higher latitudes), reflecting instar at maturity. Maturity reached over a range of 4 years, starting at ~4.5-5.5 (post-settlement); age-at-maturity is conservative. Most mature at instars IX-XI, but maturity may be earlier in low latitudes (instar VIII or XII).	Mean size of female maturity: 89 mm CL (Bristol Bay) and 102 mm CL (Kodiak).	Most females mature ~100 mm CW. Age-at-maturity shows clinal variation (older at higher latitudes), from ~1 year in central California to 4-5 years in British Columbia. Most females mature at end of second year post-settlement or in third growing season, corresponding to instars XII-XIV.	Size-at-maturity is variable (100-180 mm CW). Sexual maturity occurs at 1-1.5 years, corresponding to instars XVI-XX. Size at maturity is inversely related to water temp at pubertal molt. Size at maturity appears related inversely to both water temperature and salinity.

[a] Adolescents: mature males that have not reached terminal molt; males past terminal molt are known as “adults,” and are all mature.

[b] Oldshell indicates the individual did not molt in the year of mating.

Table 1. (continued)

Life history characteristic	Snow crab (Chionoecetes opilio) eastern Bering Sea	Red king crab (Paralithodes camtschaticus)	Dungeness crab (Cancer magister)	Blue crab (Callinectes sapidus) Chesapeake Bay
Size/age/stage at maturity, males	Males reach maturity at ~35-40 mm CW, but grow longer than females of the same age. Terminal molt during the summers. Males > 100 mm CW undergo terminal molt ~3-4 years after peak of terminal molting of females in the same year class. All males larger than 110 mm (80% of those larger than 100 mm) are adult.	For Kodiak, physiological size at maturity is ~80 mm CL, but functional size at maturity is ~130 mm CL based on studies of mating pairs.	Most males mature at ~116 mm CW after about 2 years but latitudinal variation in age-at-maturity exists.	Size-at-maturity is variable (120-140 mm, with potential post-maturation growth to 250 mm. CW). As with females, sexual maturity occurs at 1-1.5 years, corresponding to instars XVI-XX.
Maximum life span	Estimated maximum life after the terminal molt is on the order of 7 years. Maximum life span 12-14 years for females, 16-18 years for males.	>20 years, based on a captive specimen in Japan.	Maximum life ~8-10 years.	Typical life span is 3-4 yrs, with maximum life span of 6-8 years recorded in rare cases.
Spawning, brooding and hatching	Female terminal molt and primiparous mating occur during the winter, multiparous mating, egg hatching, and subsequent oviposition during the spring. Brooding period is 1-2 years, determined by temperature during early embryogenesis.	Egg hatching occurs in spring (March-May) followed immediately by mating, egg extrusion, and fertilization. Embryos are brooded for 207-305 days, depending on temperature.	Mating occurs offshore April-September. Eggs are extruded September-February. Eggs are fertilized during extrusion. Brooding period is 2-4 months depending on water temperature. Multiple broods may be produced from a single mating without molting (skip-molt).	In Chesapeake Bay, mating occurs May-October. Females mate only once and store sperm in seminal receptacles; multiple clutches of eggs may be produced. Egg extrusion occurs May-August with a brooding period of 1-2 weeks. Females release larvae late July-August.
Mating system	Adolescent males do not develop pre-copulatory behavior when confronted with multiparous females, irrespective of their size. Prospective male mates for the primipara include all mature males (adolescents and adults), while those available to the multipara include only the adults.	In the laboratory, most small (80-89 mm CL) males failed to induce more than one female to ovulate, whereas large (>120 mm CL) males induced ovulation in all four females tested. Among wild mating pairs most (56-61%) males were oldshell or very oldshell.b	Males must be larger than premolt females to successfully initiate pre-copulatory behavior. Mating occurs between hardshell males and newly molted soft females. Males hold females in post-copulatory embrace for ~2 days.	Late molt-stage females initiate pair formation with hardshell males. Copulation occurs following a terminal female molt. Brooding occurs June-September, with egg incubation lasting ~2 weeks and 1-4 broods being produced. Up to 8 broods per year in longer season in Florida.

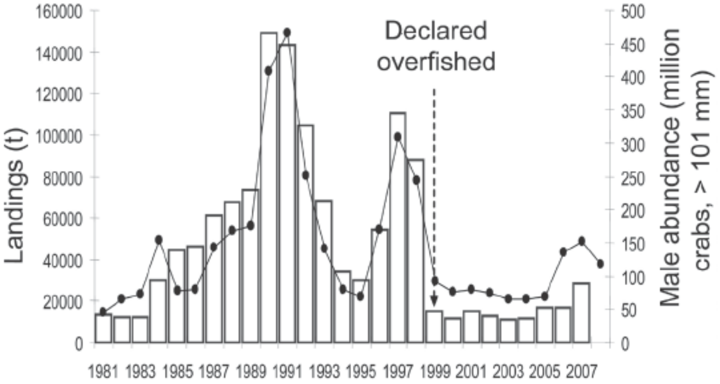

Figure 1. **Trends in landings (bars) and estimated abundance (line) of snow crab of commercial size (males, CW > 101 mm) in the eastern Bering Sea. (Data from NPFMC 2008a; modified from Parada et al. 2010.)**

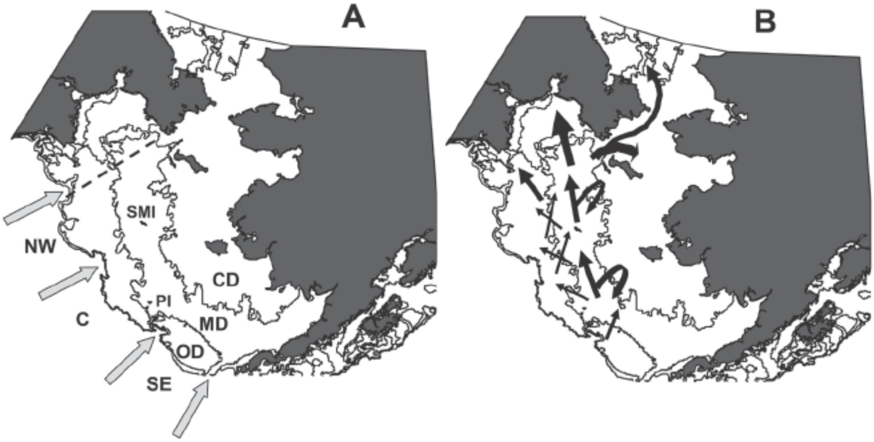

Figure 2. **(A) Eastern and northern Bering Sea, showing major geographic features of significance for snow crab distribution and dynamics. SMI: St. Matthew Island; PI: Pribilof Islands; CD, MD and OU: Coastal, Middle, and Outer Domains; NW, C, and SE: northwest, central, and southeast sections of the shelf; arrows indicate constrictions of the Outer Domain that define natural sections. (B) Major patterns of larval transport based on Regional Ocean Model System (ROMS) and Individual-Based Models (IBM); curved arrows highlight subsystems (northwest and southeast sections of the Middle Domain) with potential for larval retention. (Modified from Parada et al. 2010.)**

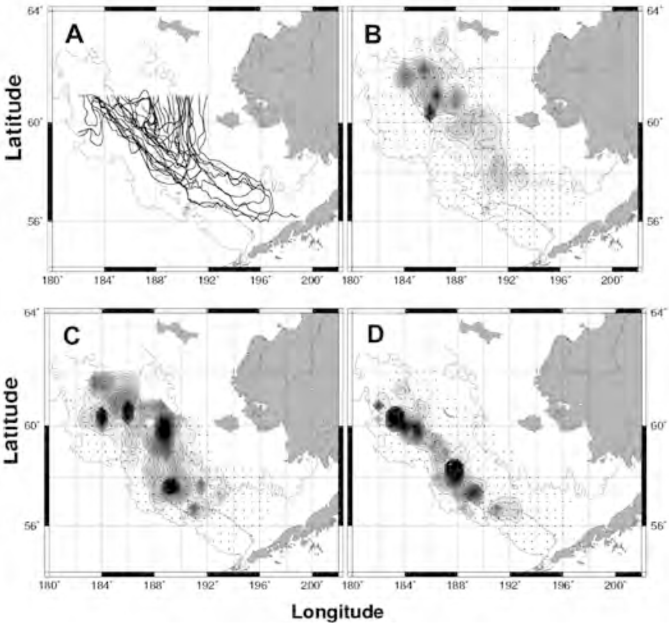

Figure 3. Spatial dynamics of female snow crab in the eastern Bering Sea. (A) Extension of the cold pool (near-bottom termperature, near-bottom temperature <2°C), one line per year. (B-D): Relative abundance (survey CPUE, averaged by station) of different categories of females. (B) Immature females. (C) Primipara. (D) Adult females that underwent terminal molt during the preceding year or earlier. All figures are aggregate data for the interval 1978-2007. Intensity of shading is proportional to CPUE, scale is the same in all cases. (Data from the NMFS annual summer trawl surveys. Modified from B. Ernst et al., Departamento de Oceanografía, Universidad de Concepcion, Concepción, Chile, unpubl.)

tion (“primipara”). In subsequent years (as “multipara”) they spawn and eventually mate while in “hardshell” condition, shortly after eggs hatch. Males mature before reaching terminal molt, at a size (carapace width, CW) of 33-38 mm. After molting into maturity and mating in the “Middle Domain” (50-100 m, Fig. 2A) during the winter, the primipara start a one-year ontogenetic migration toward the “Outer Domain” (100-200 m, Fig. 3C, D; Ernst et al. 2005). Males undergo terminal molt during the summer, when large “softshells” occur in the Middle Domain (Fig. 4A). Hardshell adults (one year or more past-terminal molt) occur primarily in the Outer Domain (Fig. 4C; Orensanz et al. 2004). The ontogenetic migration is likely to be superimposed on a seasonal onshore-offshore

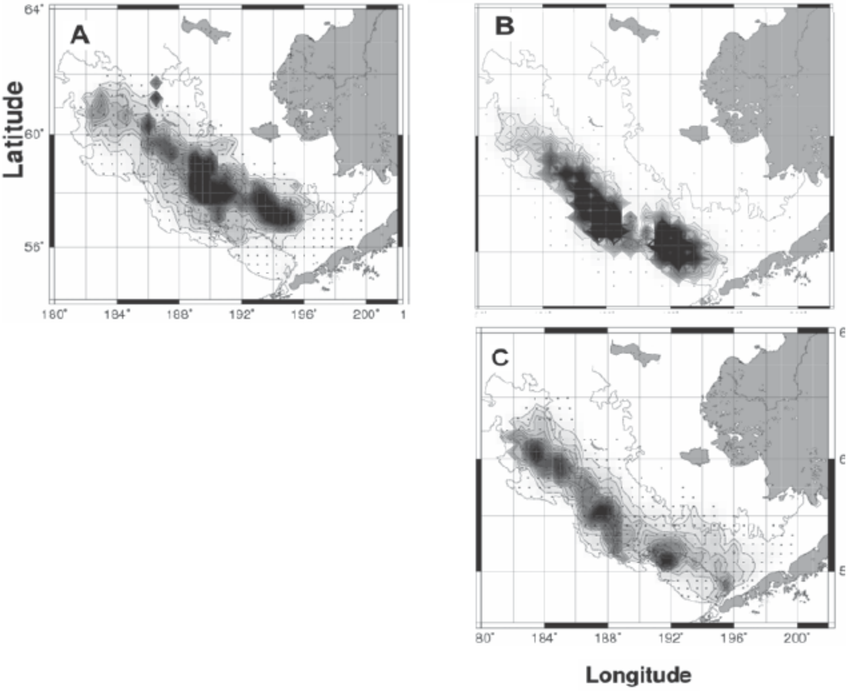

Figure 4. Spatial dynamics of large male snow crab in the eastern Bering Sea. (A) Relative abundance (survey CPUE) of recently molted (softshell) large males (CW > 100 mm) during the summer. Summer: males molt into the "large adult" category, mostly in the Middle Domain. Afterward they migrate offshore during the fall, becoming the "new-shells" available to the winter fishery. (B) Distribution of fishing effort (mostly winter, 1990-1999). Winter: large new-shell males targeted by the fishery in the Outer Domain, but also in the Middle Domain of the southeast shelf. (C) Relative abundance (survey CPUE) of old-shell males during summer. Summer: escapement (large hardshell males) observed by the survey in the same regions where the winter fishery operated. Notice that it is proportionally important in the northwest, where fishing effort is relatively small. Shading is proportional to CPUE in A and C (same scale in both), and to effort intensity in B. (Effort data from Alaska Department of Fish and Game. Distribution data from the NMFS annual summer trawl surveys, 1978-2007. Modified from B. Ernst et al., Departamento de Oceanografía, Universidad de Concepcion, Concepción, Chile, unpubl.)

component (Lovrich et al. 1995), but this has not been confirmed in the eastern Bering Sea.

Because of circulation patterns and the structure of the water column during the summer, it has been hypothesized that the Middle Domain is a suitable environment for the retention, survival, and settlement of pelagic larvae, while the Outer Domain appears to be a much more advective environment. A combination of oceanography and spatial crab dynamics effectively decouples the hatching areas of the primipara and multipara, and, presumably, the fate of their larvae. Modeling results also show that many larvae originating in the northwest section of the shelf are likely to be transported far to the north and northwest, eventually to sink outside the realm of the eastern Bering Sea (Fig. 2B). Settlement regions predicted by coupled Regional Ocean Model System (ROMS) and Individual-Based Models (IBM) match historical regions of abundance of immature crab (Fig. 3B), and are consistent with observed fields of suitable near-bottom temperature (Fig. 3A; Parada et al. 2010).

Four pulses of primipara abundance occurred at approximately seven-year intervals between 1978 and 2005. Spatial coincidence in the Middle Domain of (1) primipara spawning and (2) potential for larval retention prompt an intriguing hypothesis: the regular cycle could be the result of each pulse in the sequence being the maternal stock of the subsequent one. If this were the case, renewal of the stock would depend largely on primipara abundance. Time between egg extrusion by a maternal year class and recruitment of its progeny to the primipara is consistent with the hypothesis. The cycle of recruitment to the reproductive stock can be detected in every indicator of stock status, and ultimately in commercial landings (Fig. 1).

Fishery

Snow crab fishing in the eastern Bering Sea was started by Japanese vessels during the 1960s, but access of foreign fleets was terminated during the 1980s following implementation of the Fishery Conservation and Management Act of 1976. During the 1990s the U.S. snow crab fishery was one the largest and most lucrative crab fisheries in the world, but over the last two decades landings declined dramatically from a maximum of nearly 150,000 t in 1991 to historical lows on the order of 12,000 t during the 2000s (Fig. 1). The eastern Bering Sea snow crab stock was declared “overfished” in 1999 because the survey estimate of mature biomass was below the minimum stock size threshold. A rebuilding plan was implemented in 2000; model estimates of the biomass of commercial size males continued to decline through 2003, then increased after 2006 (Fig. 1; Kruse et al. 2007, NPFMC 2008a). Management regime and regulations are summarized in Table 2.

Peaks in the abundance and catch of large males in 1990-1991and 1997-1998 correspond (with a ca. 3-4 years lag) to the pulses of primipara recruitment centered around 1987 and 1994. Pot CPUE (catch per unit effort) in the commercial fishery also shows the seven-year cycle. The main segment of the male population targeted by the fishery is large adults that molted during the previous summer (Fig. 4:A) and become vulnerable as "new-shells" during the following winter (Orensanz et al. 2004). The fleet, which is variably constrained by the extent of sea ice, operates almost exclusively in the Outer Domain north of the Pribilof Canyon (Fig. 4:B). Hardshell large males observed in the Outer Domain during the summer survey (Fig. 4C) correspond to the escapement from the preceding fishing season.

Due to the complicated reproductive strategy of this species the fishery may affect the operational sex ratios, effective breeding, and the potential for sexual selection (see Sainte-Marie et al. 2008, for a detailed review). Given a combination of (1) pronounced population cycles, (2) different male and female schedules of age-at-adulthood, (3) ontogenetic migrations, and (4) selective fishing, the pattern of spatiotemporal variation in different categories of effective sex ratios (primipara and multipara and adolescent and adult males of variable size) is inevitably complex. This problem has been investigated by Canadian scientists in the Gulf of St. Lawrence (Sainte-Marie et al. 2008). Complexities of the mating system make it difficult to interpret indicators of female per capita and aggregate reproductive activity and output, such as clutch size, fertilization rate, and spermathecae load. These have received considerable attention as possible indicators of overfishing related to sperm limitation in this and other male-only crab fisheries (Sainte-Marie et al. 2002, 2008).

Climate forcing

Shelf waters of the eastern Bering Sea are covered by ice most years from late fall through early spring. As ice melts in spring, the less saline water "floats" over higher salinity marine water. The combination of low salinity water and upper water column heating results in stratification. The stratified water column "traps" an extensive "cold pool" of water (summer near-bottom temperature <2°C) down to the seafloor over a large part of the Middle Domain (Wyllie-Echeverria and Wooster 1998). Following a warm winter, there may be virtually no cold pool over the eastern Bering Sea–Bristol Bay (southeastern Bering Sea) region, or the cold pool may cover most of the Middle Domain following a very cold winter (Ernst et al. 2005). One major consequence of global warming is the poleward retreat of seasonal sea ice cover, with important potential consequences for demersal fish and invertebrate communities (Grebmeier et al. 2006, Mueter and Litzow 2008).

Poleward retreat of ice cover and consequent contractions of the cold pool are of great significance for snow crab. While the thermal preferendum for the stenothermic early benthic instars is in the range 0-2°C in eastern Canada (Dionne et al. 2003), some major predators (most notably cod) are relatively intolerant of the low temperatures that define the cold pool. The southern edge of the cold pool, which defines the ecotone between arctic and subarctic communities, has retreated 230 km northward since the early 1980s (Mueter and Litzow 2008). Over the same period the reproductive female stock has contracted toward the northwest sector of the shelf (Orensanz et al. 2004, Zheng and Kruse 2006) and the amplitude of the recruitment cycle in the southeast has declined. The latest pulse of recruitment to the mature female population was not detected in the southeast shelf, where recruitment of mature females has been minimal since 1997 (Parada et al. 2010). This phenomenon has been addressed by the environmental ratchet hypothesis, broadly framed in the context of the oscillating control hypothesis (Hunt et al. 2002). The environmental ratchet hypothesis claims that the shift in geographic range is an asymmetrical process: contraction to the northwest would be easier than expansion back to the southeast even after the return of favorable conditions (Orensanz et al. 2005, Parada et al. 2010). The rationale for this conjecture is a combination of (1) circulation patterns, (2) decoupling of the hatching regions of the primipara and multipara, (3) deterioration of settlement habitat during warm periods due to an increase of near-bottom temperature beyond the thermal preferendum of stenothermic juvenile crab, and (4) increased fish (mostly cod) predation. Regarding the latter, we should note that spatial dynamics in the geographic distributions of groundfish and crabs over time make it difficult to relate crab recruitment strength to groundfish biomass (Zheng and Kruse 2006).

Trends in environmental variables, particularly near-bottom temperature, in recent years create exceptional conditions to investigate hypotheses on the response of the eastern Bering Sea snow crab stock to climate. A historical maximum in the extension of the cold pool in 1999 was followed by a warming episode between 2001 and 2005, during which near-bottom temperature in the eastern Bering Sea increased ~3°C (Stabeno et al. 2007). More recently (2006-2008) there was a return to an extended cold pool over the central section of the Middle Domain (Boldt 2008, their Fig. 20). This sequence of events is reminiscent of the scenario of changes in the system between the mid 1970s and mid 1980s, which according to the environmental ratchet hypothesis had dramatic and long-lasting consequences. An eventual resurgence of the southeast subsystem sustained by the residual stock of reproductive females, or by larval inputs from other sectors, would be most informative about stock dynamics. A modest pulse of pseudo-cohort recruitment centered northwest of the Pribilof Islands in 2005, for example, could have originated during the cooling event centered around 1999 (B. Ernst et al., Departamento de Oceanografía, Universidad de Concepcion, Concepción, Chile, unpubl.).

While the deterioration of the cold pool and increased cod predation associated with warm periods are likely to have medium- to long-term detrimental effects on recruitment, per-capita contribution of adult females may increase during warm regimes due to larger female size and annual brooding (Sainte-Marie and Gilbert 1998, Orensanz et al. 2007, Sainte-Marie et al. 2008). Subtle effects of climate on operational sex ratio have been discussed by Sainte-Marie et al. (2008). The effects of fishing may be exacerbated or attenuated by climate, depending on the direction of temperature change (Sainte-Marie et al. 2008).

Red king crab

Life history and population dynamics

Unless otherwise specified, the following life history information is abridged from two previous syntheses (Kruse 1993, 2007). Key life history features are summarized in Table 1. Red king crabs *(Paralithodes camtschaticus)* are distributed in the northeast Pacific from British Columbia throughout the Gulf of Alaska, into the eastern and western Bering Sea, and along the northwest Pacific as far south as Japan. Interestingly, red king crabs from Kamchatka were transplanted into the Barents Sea in the northeast Atlantic Ocean in the 1960s. Since then, their abundance has increased in Russian and Norwegian waters, providing for a target fishery, but also becoming a bycatch nuisance to pre-existing longline and gillnet fisheries for cod and other groundfish.

Red king crabs are lithodids and the largest of the four species of crabs considered in our review; for instance, males attain a maximum size of 227 mm carapace length (CL) weighing 11 kg off Kodiak. In contrast to snow, Dungeness, and blue crabs, red king crabs do not possess spermathecae for sperm storage. Therefore, mating occurs just after the female molt, which takes place annually even after maturity (Table 1). Likewise, males continue to molt after maturity, albeit not necessarily every year. Molting is a particularly vulnerable life history stage; in the eastern Bering Sea, most adult red king crabs in cod stomachs are softshell females (Livingston 1989).

During a nearly one-year embryo incubation period, nemertean worms and amphipods feed on egg masses carried by females, inflicting high rates of predation in some areas and years (Kuris et al. 1991). Seasonal migrations are well known for red king crabs. Adult females move into shallow, nearshore waters where embryos hatch in spring (Stone et al. 1992). Larvae are pelagic, primarily in the upper 40 m of the water column, and they molt through four pelagic zoeal stages (Table 1) before transforming into glau-

Table 2. Management characteristics for four focal crab species.

	Snow crab (EBS fishery)	Red king crab (Alaska fisheries)	Dungeness crab (U.S. coastal fisheries)	Blue crab (Chesapeake Bay fishery)
Jurisdictions	Cooperative state-federal management.	State management in GOA, cooperative state-federal management in Bering Sea and Aleutian Islands.	State or DFO (in BC) management. In CA, OR, and WA, cooperation is facilitated by the Tri-State Dungeness Crab Committee, an ad hoc advisory group of commercial crab fishermen and processors sponsored by the Pacific States Marine Fisheries Commission.	Each state has separate management enforcement. In Chesapeake Bay MD, VA, and Potomac River Commission all have independent management oversight and regulation of the stock in their territories.
Access	IQ system for fishermen and processors implemented in 2005; 7.5% of harvest allocated to CDQs starting in 1998.	IQ system for fishermen and processors implemented in 2005; 7.5% of harvest allocated to CDQs starting in 1998.	Open recreational fishery, but limited entry for commercial licenses, with substantial variation in limitations among jurisdictions.	Open recreational fishery, but limited entry for commercial licenses, with substantial variation in limitations among jurisdictions.
Size regulations	78 mm CW, but processors prefer a minimum size of 102 mm.	Minimum size limits vary by stock, generally set one molt increment larger than male size at maturity. For instance, 121 mm CW for Norton Sound to 178 mm CW for Kodiak.	Commercial size limits CW, excluding spines: 158.8 mm in CA, OR, and WA; 165.1 mm in AK; 154.3 mm in BC.	75 mm CW for "peeler crabs" (premolt); 125 mm CW (5 inches) for "hard crabs" (intermolt).
Sex regulations	Males only.	Males only.	Males only.	Male and female but only weak restrictions on females. Recent changes in regulations prohibit taking "dark sponge" (late stage brooding) females in VA. For first time in 2008-2009, mature females were prohibited in MD recreational fishery, commercial season was restricted on mature females during portion of fall migration in MD, and winter dredge fishery was eliminated in VA to restrict take of mature females.

ADFG: Alaska Department of Fish and Game.
CDQ: Community Development Quota.
CW: carapace width
DFO: Department of Fisheries and Oceans Canada.
DNR: Department of Natural Resources
EBS: eastern Bering Sea.
GHL: Guideline Harvest Level.
GOA: Gulf of Alaska.
IQ: Individual Quota.
NMFS: U.S. National Marine Fisheries Service.
SERC: Smithsonian Environmental Research Center
TAC: Total Allowable Catch
VIMS: Virginia Institute of Marine Science
VMRC: Virginia Marine Resources Commission

Table 2. (continued)

	Snow crab (EBS fishery)	Red king crab (Alaska fisheries)	Dungeness crab (U.S. coastal fisheries)	Blue crab (Chesapeake Bay fishery)
Season regulations	Winter fishing to protect crab during the spring mating and summer molting seasons.	Late fall/early winter to protect crab during the spring mating and summer molting seasons.	Early winter (November or December) through summer (July or August) and differs by state in WA, OR, and CA. In AK, June-August and October-February. In BC, typically September or October through February, and closures vary by area.	Pot and trotline fishery restricted to April-November (although crabs can only be caught with this gear in warm months when foraging). Until 2008-2009, dredge fishery was limited to winter months. Beginning in 2008, limited season on mature females.
Gear regulations	Only pots of specific design, equipped with escape rings and biodegradable mechanisms.	Only pots of specific design, equipped with escape rings and biodegradable mechanisms.	Only pots of specific design, equipped with escape rings and biodegradable mechanisms.	Variations among MD, VA, and Potomac Fisheries Commission for restrictions on gear type and gear quantity by location, season, and for recreational versus commercial fishers. Pot design is regulated by mesh size, cull rings, design; trotlines are restricted by length.
Effort regulations	License limitation and pot limits based on vessel size and quota level.	License limitation and pot limits based on vessel size and quota level.	License limitation and pot limits (in WA, OR, and BC). License limitation in CA.	Pot number is limited depending on recreational and commercial fishers; trotline length is limited based on recreational and type of commercial license. Location of effort is also limited, depending on state.
Surveys	Summer trawl systematic surveys conducted by NMFS since mid 1970s.	Summer trawl surveys conducted by NMFS (EBS) and ADFG (GOA), and pot surveys in non-trawlable areas of GOA and EBS by ADFG. Trawl surveys since 1968 (EBS) and 1983 (GOA) and pot surveys since 1970s (GOA).	No formal surveys of abundance. Preseason collections are done in WA, OR, and CA to verify meat yield following male molt. In BC, pot surveys are done by DFO before and after commercial fishery, and an industry service provider collects fishery-independent and fishery-dependent data bimonthly January-June and monthly July-December.	Fishery-independent bay-wide winter dredge survey conducted since 1989 by MD DNR and VMRC throughout bay water deeper than ~3 m; fishery-independent trawl survey of spawning stock conducted by VIMS in spawning sanctuary in summer brooding season since 1960; multi-decadal fishery-independent trawl surveys conducted in summer by MD DNR and SERC.

	Snow crab (EBS fishery)	Red king crab (Alaska fisheries)	Dungeness crab (U.S. coastal fisheries)	Blue crab (Chesapeake Bay fishery)
Assessment	Assessment is based on a size-structured model.	Assessments based on size-structured models for major stocks.	No formal assessment in WA, OR, CA, or AK fisheries. Assessment in BC based on CPUE of pot surveys done by DFO, industry, and First Nation groups.	Annual spatially explicit, life-stage dependent stock assessment updated annually based on exploitation model from data for catch and fishery-independent winter dredge survey.
Catch regulations	Prior to 2000 GHL was 58% of abundance of males >101 mm, estimated from the survey. Target harvest rate reduced to 20% following declaration of stock as overfished in 1999. GHL/TAC since 2000 based on harvest strategy aiming at recovery to proxy for BMSY established in 1998 (921.6 million lbs of total mature biomass).	For major stocks, prior to 1990, 20-60% harvest rate of legal males based on population size, pre-recruit abundance, and relative abundance of post-recruits. In early 1990s, mature male harvest rate of 20%. In 1995, reduced to 10-15% of mature males in 1995 based on effective spawning biomass.	Harvest limits are not imposed in most jurisdictions. In WA, the stock is managed to allocate 50% of landings to treaty tribes. Most landings occur early in season; 80% of CA landings occur during opening month.	Relative exploitation target is 46% of fishable stock, with overfishing at >53% of stock. Absolute lower safe abundance for stock is 86 million "spawning-aged crabs" (based on lowest recorded number in fishery records) and target abundance of 200 million crabs in winter dredge survey.
Bycatch loss	Discard of males below commercial size in the crab pot fisheries (discard mortality of females considered to be minimal); discards in the trawl fisheries targeting flatfish and cod. Discard mortality estimated by observer programs. Bycatch caps in groundfish fisheries.	Discard of males below commercial size in the crab pot fisheries (discard mortality of females considered to be minimal); discards in the trawl fisheries targeting flatfish and cod. Discard mortality estimated by observer programs. Bycatch caps in groundfish fisheries.	Mortality of discarded hardshell females and undersized males is low (2-4%) but softshell (i.e., recently molted crabs) mortality has been reported as high as 22-25%.	Minimal. However, some evidence of bycatch loss of crabs due to handling in fishery. Bycatch of diamondback terrapins in pots is also significant in some places.
Reserves/ sanctuaries	No closure areas designed to protect snow crab. Northern Bering Sea and arctic trawl closures protect habitats that include snow crabs at the northern end of their distribution.	In EBS, trawl closure areas around Pribilof Islands protect crab habitats, Red King Crab Savings Area in Bristol Bay protects adult males, and nearshore Bristol Bay Closure protects juveniles and their habitats. In GOA, trawl closures include state waters (0-3 nm), entire eastern GOA, Yakutat Bay, and seasonal offshore trawl closure areas to protect adult king crabs off Kodiak.	No reserve or sanctuary areas designed to protect Dungeness crab.	Summer spawning sanctuary established throughout most of VA portion of mainstem of bay to protect brooding females. Commercial pot fishing is prohibited/restricted in sub-estuaries of MD.

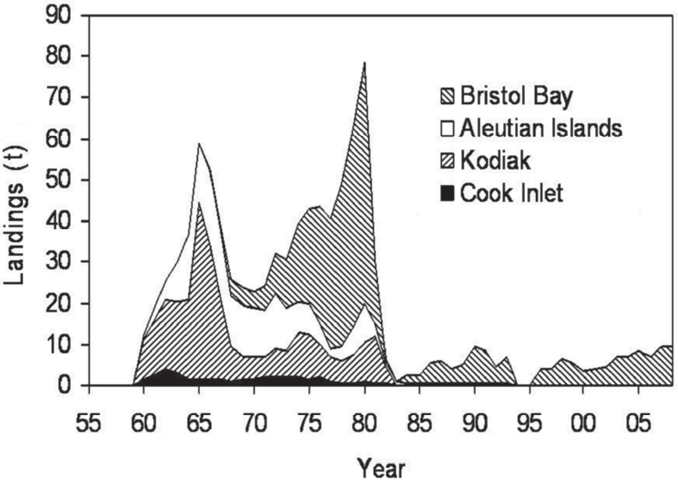

Figure 5. Historical landings of red king crabs from four major commercial fisheries in Alaska from 1960 to 2008. (Data from J. Zheng, Alaska Department of Fish and Game, pers. comm.)

cothoe, an intermediate stage akin to the megalopae of brachyuran (e.g., snow, Dungeness, and blue) crabs. Glaucothoe prefer to settle in structurally complex nearshore nursery areas where they can seek cover among rocks and shell hash or associate with algae or high-profile sessile invertebrates, such as anemones and polychaete tubes (Stevens and Kittaka 1998, Loher and Armstrong 2000). Adults live mainly on sand and mud bottoms at depths of 0 to 200m (but may be distributed as deep as 400 m).

Fishery

Unless otherwise noted, the following review of red king crab fisheries is summarized in Table 2 from the synthesis of Kruse et al. (2000) and updated by Woodby and Hulbert (2006). King crab fisheries in the Gulf of Alaska were initiated by Japanese fishermen in the late 1930s and small domestic catches were also taken. During the late 1950s and 1960s landings in Cook Inlet, Kodiak, and Aleutian Islands fisheries increased rapidly, then declined, eventually closing in the 1980s because of low stock abundance (Fig. 5). After the decline of red king crab harvests in the Gulf of Alaska, fisheries expanded into the Bering Sea and landings grew from 1970 to 1980 followed by an abrupt collapse and fishery closure in 1983 because of low crab abundance. Other small red king crab fisheries have been prosecuted in southeast Alaska, Prince William

Sound, Alaska Peninsula, Aleutian Islands, Pribilof Islands, and Norton Sound (see Orensanz et al. 1998).

King crab fishery management plans and regulations are established by the State of Alaska, even for fisheries in federal waters (Table 2). In the case of resources in the Bering Sea and Aleutian Islands, crab fisheries are managed cooperatively by state and federal agencies under a federal fishery management plan (NPFMC 2008b). There is a long tradition of managing red king crab fisheries in Alaska by size, sex, and season regulations. Seasons are set to avoid molting and mating periods, as well as to accommodate industry preferences for high product quality associated with gain in muscle mass after molting. Females may not be legally harvested, and a minimum size limit is set for males, usually one molt increment larger than size at maturity. Because size at maturity varies by stock, minimum size limits vary from 121 to 178 mm CW for Norton Sound and Kodiak, respectively (Table 2; Donaldson and Donaldson 1992).

It has been suggested that red king crabs were the first of a series of crustacean resources that were serially depleted by overfishing in the Gulf of Alaska (Orensanz et al. 1998). Fishing reduces stock biomass, which has adverse effects on recruitment when stock biomass is depleted to very low levels. Unfortunately, stock-recruit relationships have been evaluated for only two red king crab stocks: Kodiak (Bechtol and Kruse 2009a) and Bristol Bay (Zheng and Kruse 2003). In both cases, there is evidence for a weak to moderate density-dependent relationship between recruitment and stock size. However, recruitment patterns are also consistent with decadal climate shifts (see next section), thus confounding the interpretation of cause and effect.

In the case of Bristol Bay, declines in recruitment in the 1970s prior to the buildup of the commercial fishery set the stage for a stock decline, which was then amplified by high harvest rates (>60%) of legal males in the early 1980s. Dew and McConnaughey (2005) argued that undocumented high crab bycatch mortality during the transition from foreign to domestic groundfish fisheries may have contributed to the decline. For Kodiak, a recent stock reconstruction analysis of red king crab abundance indicates that very high male harvest rates in the late 1960s were not sustainable, likely due to reproductive failure (unmated females) resulting from male-depauperate sex ratios (Bechtol and Kruse 2009b). Although a thorough analysis of historical harvest rates for the major king crab stocks in Alaska has yet to be conducted, it appears that some, but not all, declines in red king crab stocks can be attributed to overfishing. Nevertheless, a general inability to sustain productive crab fisheries over the long term has led to progressively more conservative management strategies in recent decades.

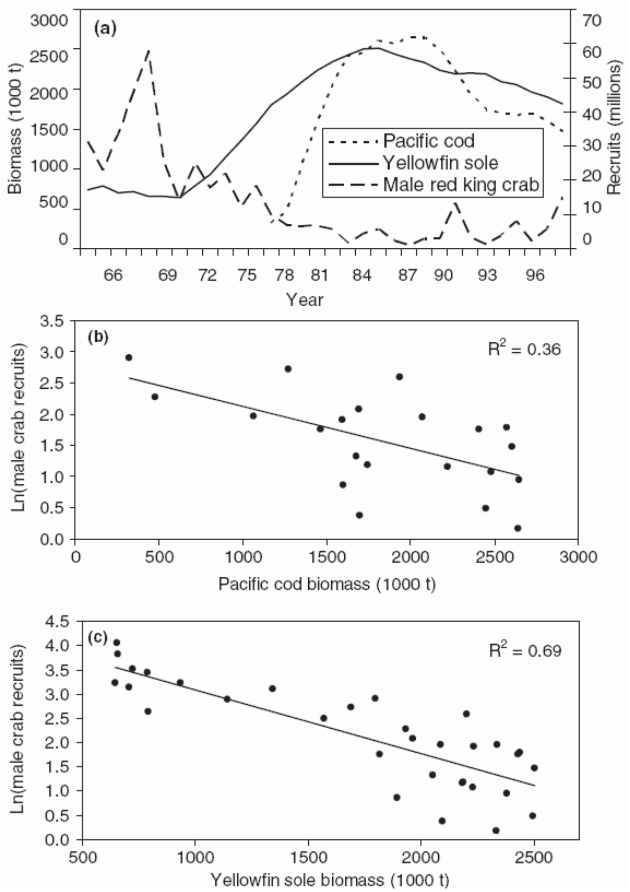

Figure 6. (a) Time series of Pacific cod and yellowfin sole biomass in the eastern Bering Sea and male recruitment of Bristol Bay red king crab, and relationships among log-transformed male king crab recruitment and biomass of (b) cod and (c) yellowfin sole. (Data from Zheng and Kruse 2006.)

Climate forcing

Zheng and Kruse (2000) examined recruitment patterns of 15 Alaska crab stocks from southeast Alaska to the Bering Sea, including seven red king crab stocks. In general, after an increase in the late 1960s, year-class strength declined sharply during the early 1970s for all red king crab stocks in the northern Gulf of Alaska. Red king crabs in Bristol Bay revealed a rather similar pattern. However, trends diverge from this

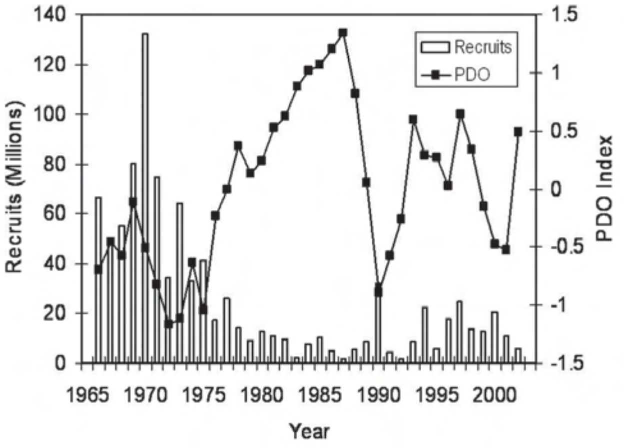

Figure 7. Estimated red king crab recruits (bars) in Bristol Bay and three-year running average anomalies of the Pacific Decadal Oscillation (solid line) over November-March. A seven-year lag from hatching to recruitment was applied to match recruits to climate conditions during hatching. (Crab data from J. Zheng, Alaska Department of Fish and Game, pers. comm.)

typical "gulf" pattern for the southerly and northerly stocks in southeast Alaska and Norton Sound. Red king crab recruitment is periodic, with indications of a decadal signal, which has prompted several retrospective analyses attempting to uncover the responsible mechanisms (Bechtol and Kruse 2009a,b, 2010; Zheng and Kruse 2000, 2006).

A number of hypotheses about climate forcing of red king crab recruitment have been proposed (Zheng and Kruse 2000, 2006; Kruse et al. unpubl.). Some hypotheses about recruitment mechanisms stemmed from the apparent association between the gulf pattern of red king crab recruitment and the strength of the Aleutian low pressure system in winter (Fig. 7). Zheng and Kruse (2000) postulated that years of strong Aleutian lows were associated with stronger winds in spring. A climate regime shift from weak to strong Aleutian lows in winter triggered an ecosystem reorganization in the Gulf of Alaska that led to increases in salmon and groundfish (Fig. 6:A) and declines in shrimp and forage fishes (Anderson and Piatt 1999). In a five-year study in Auke Bay, Alaska, the spring bloom was composed largely of Thalassiosira diatoms in years of light winds and a more diverse phytoplankton species composition in years of strong winds (Bienfang and Ziemann 1995). Red king crab larvae must feed within 2-6 days of hatching in order to survive (Paul and Paul 1980) and their growth is related to concentrations of Thalassiosira (Paul et al. 1990). These findings led Zheng and Kruse to hypothesize that crab larval survival was tied to atmospheric pressure systems that drive phytoplankton community composition and dynamics.

A somewhat related hypothesis, invoked to explain recruitment of many marine fish and invertebrate species, is Cushing's match-mismatch hypothesis (Cushing 1969). It purports that feeding success depends on the timing of larval abundance with the spring bloom. This hypothesis was tested during a study of red king crab recruitment dynamics over 1985-1989 in Auke Bay, southeast Alaska (Shirley and Shirley 1989). However, the lack of a relationship between crab larval survival and synchrony of larval hatching with the spring bloom led to the rejection of the match-mismatch hypothesis in this case (Shirley and Shirley 1989). As the timing of the spring bloom in Auke Bay is determined by day length rather than climate-driven oceanographic conditions, this hypothesis ought to be more broadly tested for other red king crab populations before it is fully rejected.

In Bristol Bay, a 20% reduction in geographic range was accompanied by a 20-fold decrease in abundance since the late 1970s (Loher and Armstrong 2005). Coincidentally, centers of distribution of ovigerous females shifted northeastward to the central portion of Bristol Bay with the exception of a slight return to the south during 1988-1991. The extent of the northeastward shift of crabs was negatively correlated with the geographic extent of the cold pool (Loher and Armstrong 2005). A northeastward shift of ovigerous females reduces the ability of red king crab larvae to settle within preferred nursery areas to the south. Coincidentally, relatively strong 1990 year class resulted during the modest southward shift in the distribution of ovigerous females during 1988-1991 (Zheng and Kruse 2006). A return shift to the south during the late 2000s coincident with recent cold years (J. Zheng, Alaska Department of Fish and Game, pers. comm.) appears to further support this hypothesis.

An oscillating control hypothesis asserts that the pelagic ecosystem of the eastern Bering Sea is controlled by food supply (bottom-up control) in cold regimes and predation (top-down control) in warm regimes (Hunt et al. 2002). During cold regimes, extensive sea ice retreats late (April-May), and ice-edge plankton blooms occur in cold water. As cold temperatures limit zooplankton growth, most primary production falls ungrazed to the seafloor, enhancing benthic production. With a shift to a warm regime, sea ice retreats early (prior to mid March) and the bloom is delayed until May-June in thermally stratified waters. Under such conditions, most production remains in the water column and does not fall to the seafloor because warm water favors growth of zooplankton grazers. Long-term shifts toward warmer conditions may shift energy flow from benthic to pelagic ecosystems (Grebmeier et al. 2006), perhaps adversely affecting the forage base of red king crabs.

In Bristol Bay, a decline of red king crab recruitment in the 1970s was significantly correlated with increases in the biomass of both Pacific cod (*Gadus macrocephalus*) and yellowfin sole (*Pleuronectes asper*) leading Zheng and Kruse (2006) to suggest predation as a mechanism regulating red king crab recruitment (Fig. 6). In another retrospective analysis, a strong negative association existed between biomass of age 3+ Pacific cod and red king crab recruitment off Kodiak Island (Bechtol and Kruse 2010). Yet, an irony of both studies is that cod and sole stomachs do not indicate consumption of large numbers of young red king crabs. However, groundfish stomachs have not been sampled in nearshore waters where most predation on settling glaucothoe or juvenile red king crabs would occur and few stomachs are collected during the male molting period (late winter), so this hypothesis requires further directed field investigations.

Dungeness crab (Cancer magister)

Life history and population dynamics

Dungeness crabs (*Cancer magister*) occur from Unalaska, Alaska, to Santa Barbara, California (Jensen 1995), in bays, estuaries, and nearshore coastal areas. After hatching and spending 3-4 months as planktonic zoea (Table 1; Eggleston and Armstrong 1995), competent megalopae settle broadly in late spring or summer (May-June or August, depending on latitude) nearshore along the coastal shelf and metamorphose to young of the year (YOY) crabs (Tasto 1983; McConnaughey et al. 1992, 1994). YOY crabs recruiting to warm, shallow estuaries grow at nearly twice the rate of conspecifics in adjacent nearshore coastal habitats (Gutermuth and Armstrong 1989, Gunderson et al. 1990). Survival is highest in complex epibenthic substrates, where refuge from predation and abundant prey contribute to increased survival (McConnaughey et al. 1992). Most growth occurs during the warm, highly productive summer months (Stevens and Armstrong 1984, Gutermuth 1987), and juvenile crabs migrate into deeper subtidal areas, or emigrate from estuaries to nearshore habitats, as water temperatures decrease in autumn. Growth is minimal during winter months but resumes the following spring after crabs return to shallow coastal or estuarine waters as subadults (Stevens et al. 1984, McMillan et al. 1995). Subadult crabs are particularly abundant in estuaries, where typical densities range between 600 and 3,000 crabs per ha in sublittoral areas (Rooper et al. 2002, Armstrong et al. 2003). These crabs make intertidal forays to satisfy daily energetic demand (Holsman et al. 2003, 2006) until they approach sexual maturity at about age 2+ (100 mm CW for females, ~130 mm CW for males; Gutermuth and Armstrong 1989) and emigrate

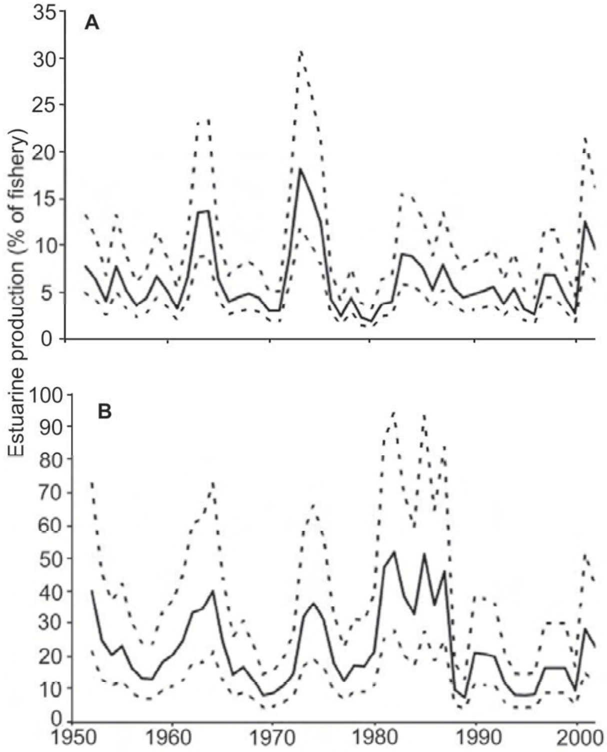

Figure 8. Estimated percent contribution of estuarine production of subadult Dungeness crab to landings in coastal fisheries. Published mortality rates were applied against estuarine subadult abundance for 2.5 years and survivors reduced by 50% to account for male-only landings. The percent annual landings of these estuarine-produced adult males was computed for all ports in small coastal estuaries of Oregon (A) and ports in Willapa Bay, Grays Harbor, and the Columbia River (B). Solid line is contribution based on overall mean subadult abundance; lower and upper dashed lines are the low and high range. (Data from Armstrong et al. 2003.)

to nearshore coastal waters (Collier 1983, Gunderson et al. 1990). As a result of enhanced growth and survival, estuarine populations may contribute significantly and disproportionately to subsequent landings of the coastal fishery (Fig. 8; Armstrong et al. 2003).

In contrast to YOY and subadult age classes, adult crabs are less common in shallow estuaries and scarce in intertidal areas, and generally occupy cooler and deeper coastal habitats and inland waters of

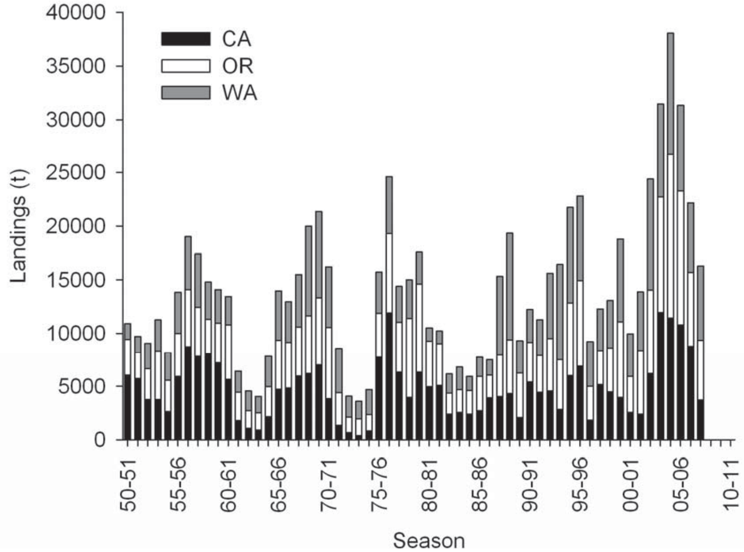

Figure 9. Commercial landings of Dungeness crab in Washington (WA), Oregon (OR), and California (CA) by season (i.e., 1950-51 = 1951). (Data from Didier 2002 and Pacific States Marine Fisheries Commission unpubl.)

Washington, British Columbia, and southeast Alaska. Despite lack of physical barriers to movement, adult crabs have relatively restricted home ranges and only migrate inshore to mate during spring and summer months (Collier 1983), with males and females demonstrating different seasonal patterns (Stone and O'Clair 2001). In general adult female crabs remain inactive during winter months (November to mid April, depending on latitude), abruptly migrate into shallow water to release larvae in spring, and return to cooler deeper foraging areas in summer. Patterns of male crab movement during winter months are similar to females with relative inactivity until early spring followed by spring migrations to shallower water, but in contrast to female crabs, males do not undertake migrations to deeper water until early fall (Diamond and Hankin 1985, Stone and O'Clair 2001).

Fishery

The commercial fishery for Dungeness crab began in San Francisco in 1848 (Dahlstrom and Wild 1983) and presently occurs in nearshore coastal waters (<40 m deep) from Alaska to California. In all jurisdictions, the fishery is regulated under the "three S" strategy (sex, size, and season;

Table 2); only males greater than a minimum size (CW excluding spines: 159 mm in California, Oregon, and Washington; 165 mm in Alaska; 154 mm in British Columbia) are targeted with the intention of allowing most males at least one reproductive season before capture. Moreover, seasonal fishing closures are used to reduce incidental take of soft-shelled male crabs and reduce possible bycatch of ovigerous females. Dungeness crab fisheries are highly cyclic with decadal oscillations in landings (Fig. 9; Methot 1989, Pauley et al. 1989, Armstrong et al. 2003). While Alaska and British Columbia manage their fisheries independently, the Fish and Wildlife agencies of California, Oregon, and Washington consult closely on issues affecting the commercial Dungeness crab fishery. There is no formal survey of crab abundance in any jurisdiction, although pot surveys are used in British Columbia to assess CPUE; therefore, stock assessment for setting quotas is limited (Table 2). Under the Pacific States Marine Fisheries Commission Dungeness Crab Tri-State Process, the fishery agencies of California, Oregon, and Washington conduct a pot survey in late fall to assess only the extent to which legal males have hardened after molt in order to set an opening for the winter fishery. Although exploitation rates are high, and can exceed 90% of legal-size male crabs in some fisheries and years (Gotshall 1978, Methot and Botsford 1982, Hankin 1985; Smith and Jamieson 1989), evidence of recruitment overfishing or detrimental effects on populations is negligible (Hankin 1985). Smith and Jamieson (1991) suggested that intense harvest of legal-size males could potentially limit mating success of females >140 mm in some British Columbia fisheries since assortative mating occurs and males must be larger than females to embrace them. However, Hankin et al. (1997) found no evidence of reduced mating success and/or egg production. Data on the presence of sperm plugs and fullness of spermathecae among females indicates that most mature individuals have mated regardless of fishing pressure (Hankin et al. 1997). Additionally, skip-molt females are capable of storing viable sperm across reproductive seasons, which may further buffer populations from fishing effects. Fishing pressure does not appear to affect population size structure.

Given the important stabilizing influence of estuarine Dungeness crab production to coastal fisheries (Armstrong et al. 2003), regional fishery declines may be related to loss of critical estuarine habitat (Holsman et al. 2006). The collapse of the central California crab fishery in the late 1960s provides a case in point (but see Shanks and Roegner 2007, for an alternative climate-driven hypothesis). Although myriad biotic factors (salmon predation, nemertean worm predators, disease, exotic species) and abiotic forcing factors (water pollution, elevated sea surface temperatures, changes in offshore current regimes) have been proposed, long-term degradation and loss of intertidal habitat may have contributed as well (Wild and Tasto 1983, Botsford et al. 1989). Since European colonization, more than 40% of tidelands and nearly

90% of tidal marsh habitat of the San Francisco Bay estuary have been eliminated. The substantial reduction in habitat and foraging base of juvenile and subadult crabs would have greatly reduced the capacity for crab production (e.g., Eggleston and Armstrong 1995, Holsman et al. 2006), resulting in reduced recruitment to the central California fishery. Loss of estuarine habitat serves as warning for conservation of essential habitat for early life history stages in all estuaries, small or large, and in the inland waters from Washington through Alaska.

Climate forcing

A number of authors have explored physical and climatic factors influencing the commercial fishery for Dungeness crab and have cited variation in ocean circulation and upwelling as potential drivers that result in periodic pulse recruitment events (Wild et al. 1983, McConnaughey et al. 1992) and pre- and post-settlement density-dependent mortality (Botsford 1984, Eggleston and Armstrong 1995, Higgins et al. 1997). Northward wind stress along the west coast of North America causes onshore transport, while southward wind stress moves water masses offshore (Johnson et al. 1986). McConnaughey et al. (1992) suggested that landward surface transport retains Dungeness crab megalopae positioned in near-surface water masses close to shore and directs them toward estuaries and inland waters. Wind stress and Ekman transport toward shore increase the pressure gradient force in that direction; the balance of the Coriolis effect with this force creates a quasi-geostrophic current in shelf waters. Prior to the spring transition, this current flows northward and functionally dominates alongshore transport, especially during winter storms when wind-driven currents are irregular (Hickey 1989).

The climate-ocean phenomenon called El Niño Southern Oscillation (ENSO) also impacts physical transport (Hickey 1989) and hence larval recruitment of benthic invertebrates (Botsford 2001). Two distinct phases of ENSO have been identified: a warm phase called El Niño and a cool phase called La Niña. The alternation between phases generally occurs every three to seven years, and individual events typically last between 8 and 15 months. The two phases of ENSO tend to affect oceanographic conditions in opposite ways. El Niño events are characterized by anomalously weak southward flow in the California Current (Hickey 1989). The spring transition may be weak or delayed in El Niño years, resulting in higher than normal northward transport, decreased upwelling and increased water temperatures. A recent study by Shanks and Roegner (2007) has demonstrated a strong correlation between the timing of spring transition (that drives coastal ocean currents and primary productivity), the abundance of megalopae in light-trap collection boxes, and the magnitude of fishery landings four years later (Fig. 10). Thus, cyclic peaks in catch are likely the result of strong fisheries for

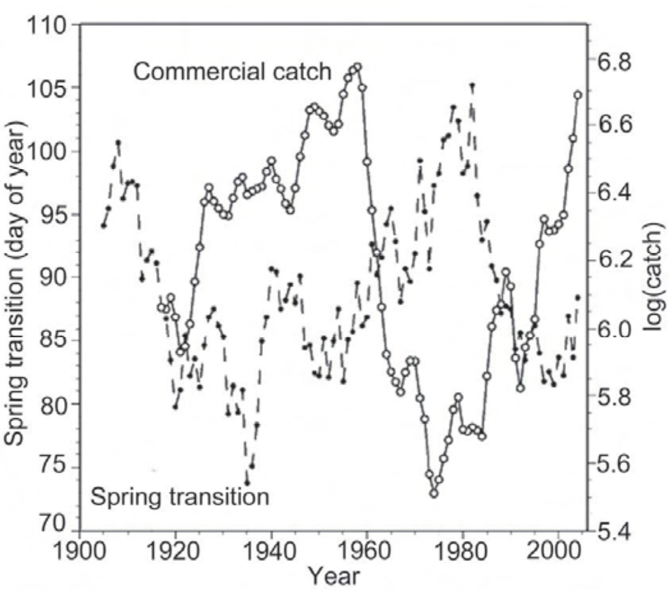

Figure 10. Date of the spring transition as determined from San Francisco sea level data (solid circles, left-hand axis) plotted with the log-transformed commercial catch of *Cancer magister* (originally measured in metric tons) landed in San Francisco (open circles, right-hand axis). Both time series are smoothed with a 9-year running average, and the commercial catch data were lagged 4 years prior to smoothing. (From Shanks and Roegner 2007.)

two or more years on a single large year class that periodically occurs as the result of optimal weather and oceanic circulation.

Blue crab (Callinectes sapidus)

Life history and population dynamics

The life history of the blue crab (Table 1) has been reviewed in detail recently for reproductive biology (Jivoff et al. 2007), larval biology (Epifanio 2007), ecology of post-larvae and early juveniles (Lipcius et al. 2007), and juvenile and adult ecology (Hines 2007). Blue crab larvae hatch from ovigerous females near the mouths of estuaries on nocturnal flood tides that transport zoea out of estuaries and lagoons onto the continental shelf. After developing in the plankton through 7-8 zoeal stages and a post-larva during approximately 45 days, megalopae use tidal transport to re-enter estuaries and lagoons and settle primarily into seagrass beds of high salinity areas. Newly settled blue crabs grow through a series of early juvenile instars within seagrass and other settlement habitats of the lower estuary. They may also move upstream to settle in soft-bottom areas. Upon attaining the 5th to 7th crab instar and ~20 mm CW, juveniles typically disperse from their settlement site to exploit an array of habitats throughout the estuary. Dispersed juveniles use a variety of micro-habitats in lower salinity nursery areas of tributaries, where they forage on diverse food resources and grow for 0.5-1.5 years (depending on temperature and food availability) until they reach sexual maturity in the 16th-20th crab instar at ~110 to 180 mm CW. After mating at the time of their pubertal molt, inseminated mature females cease molting and migrate back to the lower estuary, produce broods, and incubate eggs until larvae are released and transported out of the estuary onto the continental shelf. By contrast, mature males may continue to molt and grow for 1 to 3 additional instars (typical large size is 180 to 200 mm, but occasionally some grow to >250 mm CW). Unlike females, mature males tend to remain dispersed in the upper estuary without migrating directionally along the salinity gradient.

Timing of life history events is markedly regulated by seasonal fluctuations in temperature, especially at higher latitude with longer, colder winters. Settlement occurs in summer and fall, with dispersal of juveniles into nursery areas in fall in mid-Atlantic estuaries, although brood production and settlement may occur 8-10 months of the year in low latitude systems of the Gulf Coast. In the higher latitude Chesapeake Bay, small juveniles remain in nursery areas over winter, but larger juveniles and adults move into deeper water in channels and the main stem of the bay to overwinter. Winter in Chesapeake Bay is a period of little blue crab activity, with movement, feeding, and molting proceeding slowly if at all, especially at temperatures below 9° or 10°C; maturation typically occurs in the second season after settlement. Most blue crabs are thought to die after a life span of about three years, although death in the Chesapeake stock ensues from both a high rate of fishing capture and senescence. In Chesapeake Bay, a small portion of the population lives to be 4 to 5 years old, with individuals rarely (<1%) living to 6 to 8 years (Table 1).

Fishery

The history of the blue crab fishery has been reviewed recently (Kennedy et al. 2007), and the current status of population and fishery dynamics has been summarized by Fogarty and Lipcius (2007). Blue crabs are fished widely in the estuaries and lagoons of the east coast and Gulf Coast of North America, with smaller fisheries for *Callinectes sapidus* and other *Callinectes* species along Central and South America. Historically, Chesapeake Bay has been the dominant producer (more than 60-80%) of the blue crab catch, although other areas are increasingly important as demand and fishing have increased in the southeast and Gulf Coast systems, and as the Chesapeake catch has declined in the past 15 years.

The blue crab fishery is complex with a long history of evolving gear developments, including a variety of baited traps, trotlines, and dredges (Table 2). The fisheries are managed with complicated regulations that vary significantly among states, including variations in temporal (seasonal, weekly) and spatial restrictions within and among them. For example, the large Chesapeake stock is managed by three separate jurisdictions (Maryland Department of Natural Resources, Virginia Marine Resources Commission, and Potomac River Fisheries Commission), each with distinct sets of regulations. The variation in regulations derives from both historical accidents of fishing culture and the temporally and spatially shifting targets of the migratory life-history stages. The single most important gear is the "crab pot," invented in the early 1940s, which led to rapidly increasing commercial catches from the 1950s to 1990 and accounting for more than 80% of the catch. The fishery targets both adult males and females as "hard" (intermolt) crabs larger than 5 inches (125 mm CW). Hard crabs are fished extensively by pots and trotlines in warm months of active foraging; however, "hibernating" buried mature females have been targeted historically by a winter dredge fishery in lower Chesapeake Bay. "Peeler crabs" (premolt stage) as small as 3 inches (75 mm CW) are also fished (1-3% of total catch) by dredging seagrass beds; peeler crabs are then held in flowing water systems (shedding tanks) until they molt and can be sold as "soft crabs" (post-molt stage). The recreational fishery contributes 1-9% of the total catch, although in some local areas it can amount to more than

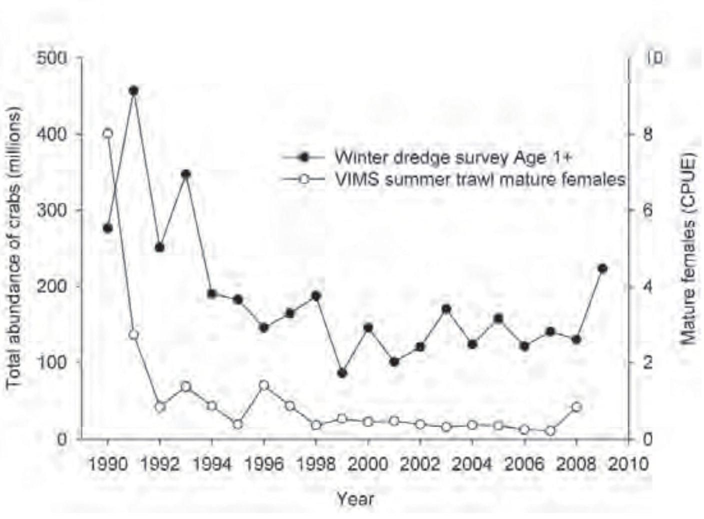

Figure 11. Measures of blue crab population abundance in Chesapeake Bay. Annual estimates of the abundance of total 1+ year-old males (solid circles) and females from fishery-independent dredge surveys in winter (open circles). (Data from CBSAC 2009.)

30% of the catch from a combination of pots and other traps, trotlines, and baited hand-held strings ("chicken necking").

The Chesapeake fishery has declined drastically since 1991 (CBSAC 2009), with a 70% decline in annual catch (CBSAC 2009), a >60% decline in the fishery-independent winter dredge survey of the population throughout the bay (Fig. 11; CBSAC 2009), and >80% decline in the fishery-independent measure of spawning stock biomass (mature females in the spawning area of the lower bay during the summer brooding season (Lipcius and Stockhausen 2002). The population has been sustained at a low level for nearly 10 years. While the population suffers from a combination of negative impacts on habitat and water quality, the decline is probably a consequence of intensive fishing that has resulted in overfishing (defined as annual removal of >53% of the fishable stock) in 9 of the 11 years between 1998 and 2008 (Fig. 12; CBSAC 2009). As a result of low spawning biomass, the population is recruitment limited and below carrying capacity in much of the upper Chesapeake Bay (Hines 2007; E.G. Johnson and A.H. Hines, Smithsonian Environmental Research Center, unpubl.). Recent management efforts to restore the

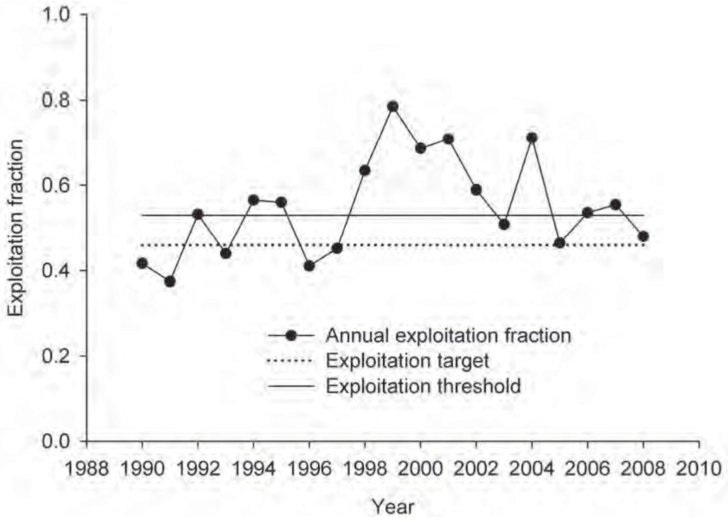

Figure 12. The proportion of Chesapeake Bay blue crab stock harvested each year (annual exploitation fraction), indicating intense fishing pressure. The exploitation target for the fishery take is shown at 46% of the fishable stock, which has been exceeded in 14 of the past 19 years. The exploitation threshold for overfishing is shown at 53% of the stock, which has been exceeded in 11 of the past 19 years. (Data from CBSAC 2009.)

stock focus on reducing fishing pressure on mature females. After more than 10 years of attempting to gradually adjust fishing pressure by small changes in regulations without success, more drastic management restrictions were imposed in 2008-2009. Maryland restricted fishing for migrating mature females along the mainstem migration corridors in the fall, and Virginia eliminated the winter dredge fishery for mature females in the lower bay. The fishery-independent winter dredge survey for 2008-2009 showed a significant increase in abundance of large crabs (Fig. 11; CBSAC 2009), but it is not clear yet whether this will translate into an increase in the summer-time spawning stock.

Climate forcing

The effects of climate forcing on dispersal of larval blue crab in the Middle Atlantic Bight of the east coast of North America have been studied in depth (see review by Epifanio and Garvine 2001). A variety of physical processes, including seasonal winds and river flows, are responsible for transporting early larvae away from natal estuaries, retaining them in shelf waters, and facilitating their reintroduction to estuaries in time to begin their benthic lives. Larvae released on the southern side of Middle Atlantic Bight estuaries (e.g., Hudson, Delaware, and Chesapeake bays) in early spring become entrained in buoyancy-driven currents, which quickly carry them southward away from the estuaries because of high river flow. However, by midsummer, river flow and related buoyancy-driven currents have diminished greatly. Retention occurs as larvae are mixed into weak, wind-driven, northward-flowing water in the mid-shelf region. Periodic episodes of northeasterly winds drive downwelling along the coast, and Ekman transport associated with these events raises sea level and results in strong subtidal flow into the estuaries (Tilburg et al. 2007). Larvae released on the northern side of Middle Atlantic Bight estuaries may be retained near the natal estuary within a null zone, which facilitates reintroduction to the natal habitat (Tilburg et al. 2007).

Tropical cyclones, although less predictable than seasonal winds and precipitation, may also affect recruitment success of blue crab post-larval and juvenile stages, as long as the storm events occur late in the recruitment season. Strong storm events that occur early in the blue crab recruitment season (August) may have little influence on overall recruitment because blue crab post-larvae are less common in shelf waters during this time period as compared with September and October (Etherington and Eggleston 2003). Interestingly, Burkholder et al. (2004) found evidence that declining blue crab numbers in the Neuse River Estuary and Pamlico Sound in 1999 may have been due to the interactive effects of hurricane floodwaters and intensive fishing pressure. High densities of crabs were displaced by hurricane floodwaters and hyper-aggregated in the Pamlico Sound, where they were faced with intensive fishing pressure, and experienced subsequent recruitment failure of early juvenile crabs (Burkholder et al. 2004).

Synthesis

Overfishing

The cases of red king and blue crab give stark evidence that crab stocks can, indeed, be overfished to critically low levels despite the apparent buffer conferred by life history and seemingly conservative management. Exploitation rates on red king crab remained high and increased in the Gulf of Alaska as the population was in decline (Orensanz et al. 1998, Bechtol and Kruse 2009b) leading to collapse of male stocks in the early 1980s. Dew and McConnaughey (2005) concluded that in Bristol Bay (eastern Bering Sea) fishing mortality exceeded a baseline average considered acceptable ($F = 0.24$) by 70%-300% in years leading up to the 1980 collapse. They further contended that climate models explaining a shift in distribution to the Middle Domain (Loher and Armstrong 2005) are misleading and that the present distribution may reflect populations remaining in marginal habitats after an increase in trawl fishery bycatch in the U.S.-Soviet joint-venture fisheries in the late 1970s to early 1980s nearshore in what had previously been a "sanctuary." In the case of blue crab, unlike other crab fisheries in North America, the fishery has targeted females as well as males. The complexity of the fishing systems often led managers to adjust parts of the fishery without effectively reducing the overall fishing effort or catch. However, after the marked recent decline in Chesapeake Bay, as well as North Carolina sounds and less severe declines in other systems, management concerns are shifting to much more stringent regulations. Still, while recent management changes target the protection of females from some gears during certain seasons at some locations, there is still intensive fishing for females, with as much as 70% of females being removed in some sub-estuaries of Chesapeake Bay before new regulatory restrictions.

While fishing-related declines of some stocks are undeniable, disentangling the effects of fishing and environmentally driven variability is a major and elusive problem in most cases. Identification of the signature of climate on the dynamics of crab populations requires contrast in processes with inherently large operational scales. Drastic auto-correlated fluctuations, as experienced in the eastern Bering Sea during the 1999 and 2008 decade (see snow crab section), offer exceptional opportunities. Alternatively, Hines et al. 2010 investigated the potential effects of climate change on blue crab demography and ecology by using latitudinal variation among populations as a surrogate.

Male-only crab fisheries offer an unusual edge to extricate the effects of fishing and climate. First, changes in sex ratio may be informative about male depletion (Orensanz et al. 1998, Dew and McConnaughey 2005). Second, recruitment overfishing must be the result of sperm limitation, which could be diagnosed (at least in principle) through indicators of female reproductive performance (clutch size, fertilization rate, spermathecae load) or mating activity (mating marks, sperm plugs). It has often been assumed that male-only crab fisheries are sheltered from overfishing by virtue of polygyny and sperm storage (in brachyurans), but those ideas have been repeatedly challenged because of demonstrated limits to effective male polygyny and declining potency of stored sperm. For that reason potential polygyny, sex-ratio-dependent fertilization rate, reserves of sperm stored in female spermathecae, and other intricacies of crab reproductive ecology have received considerable attention from fishery scientists and managers, a situation unparalleled in finfish or molluscan fisheries. Overfishing of mature males resulted in a high percentage of unmated female red king crabs in some Kodiak fishing districts during 1966-1967 (McMullen and Yoshihara 1969) and associated reproductive failure that initiated the decline of the Kodiak stock of red king crabs (Orensanz et al. 1998, Bechtol and Kruse 2009b). Mating marks on chelae of male Dungeness crab indicate copulatory activity, and sperm plugs in females indicate actual insemination (Smith and Jamieson 1991), Jensen et al. 1996, Hankin et al. 1997). Metrics of female reproductive viability are routinely collected in assessment surveys for snow and king crab in the eastern Bering Sea, most notably clutch fullness for various shell condition categories. Across such data, and including limited assessment of spermathecal load (Rugolo et al. 2005, Slater et al. 2010, B. Ernst et al., Departamento de Oceanografía, Universidad de Concepcion, Concepción, Chile, unpubl.), there is no conclusive indication of reduction in breeding success of snow crab females in the eastern Bering Sea. In contrast, studies conducted on snow crab in the Gulf of St. Lawrence show compelling evidence that sex ratio is positively correlated with female sperm load that, in turn, corresponds to clutch size (Sainte-Marie et al. 2002, 2008). The history of the red king crab fishery around Kodiak Island reconstructed by Bechtol and Kruse (2009b) points to such overfishing of males that they concluded reproductive failure ensued due to badly skewed sex ratios.

Climate and life history

Perhaps the most obvious of the effects to be expected from climate change are changes in the boundaries of geographic ranges of distribution in response to warming (Gaston 2009). Thermal preferenda can be stage-specific, as in stenothermic juveniles of snow crab (Dionne et al. 2003), species-specific, or even lineage-specific, as well exemplified by monophyletic clades of lithodid crabs (Hall and Thatje 2009). Discussion of the physiological basis of those preferenda is beyond the scope of this review, but can include bioenergetic constraints (e.g., Foyle et al. 1989, in the case of male snow crab) or ionic regulation (Wittmann et al. 2010). It has been hypothesized, for example, that the virtual absence of crabs from the Southern Ocean south of the Antarctic Convergence is due to their reduced ability to regulate Mg^{2+} levels in the haemolymph (Frederich et al. 2000). This hypothesis, however, is contradicted by recent results showing that isopods, which have been successful invaders of the Antarctic, also have high levels of haemolymph magnesium (Wittmann et al. 2010). A corollary of the Mg^{2+} regulation hypothesis is that warming will facilitate the extension of the range of crab species into antarctic waters (Aronson et al. 2007).

Climate change is likely to affect the abundance and distribution of crab stocks through several mechanisms. Based on our overview we emphasize three broad themes: the dislocation of spawning grounds, modification of hydrographic processes driving the dispersal/retention of pelagic larvae, and ecological changes in the benthic boundary layer.

Females of many crab species participate in ontogenetic or seasonal migrations that take them from settling or mating grounds to the regions where eggs hatch. Recruitment success depends on the coupling of the location of ovigerous females at the time of egg hatching and the hydrographic systems that provide for the arrival of settling larvae to regions of essential benthic habitat to ensure successful recruitment and perpetuation of the life history cycle. Several cases of climate-related decline of commercial crab stocks can be traced to dislocation of such cycles. The decline of the Bristol Bay red king crab stock following peak abundance in 1978 was accompanied by shifts in the geographic distribution of ovigerous females, which were negatively correlated with the geographic extent of the cold pool. Loher and Armstrong (2005) hypothesized that the shift reduced the ability of red king crab larvae to settle within preferred nursery areas. Along similar lines, the environmental ratchet hypothesis (Orensanz et al. 2004) implies that resurgence of reproductive female abundance in the productive region northeast of the Pribilof Islands following northward contraction of mature female abundance during warm regimes may be difficult. The reason would be a disruption of a subsystem involving primiparous females and larval retention (Parada et al. 2010). Finally, in the case of blue crab, low oxygen levels resulting from climate change could become a significant barrier to migration of mature females traveling back to the high salinity spawning areas near the mouth of estuaries and lagoons from where nocturnal flood tides transport hatching zoea onto the continental shelf (Tilburg et al. 2007).

Much of the evidence and speculation about the response of crab stocks to climate change revolves around the advective conditions experienced by pelagic larvae. Our overview provides informative examples. In the eastern Bering Sea it appears that recruitment of snow crab depends on retentive cells in the Middle Domain (Parada et al. 2010). Surface transport induced by wind stress (McConnaughey et al. 1992), the El Niño Southern Oscillation (ENSO) (Botsford 2001), and the spring transition, which drives coastal ocean currents and primary productivity (Shanks and Roegner 2007), have been hypothesized to explain the transport, return to the coastal zone, and eventual entry to estuaries of Dungeness crab larvae, driving multiyear cycles in landings. Seasonal winds and river flows transport blue crab larvae away from natal estuaries, retain them in shelf waters, and facilitate their return back to estuaries (Epifanio and Garvine 2001). Retention occurs as blue crab larvae are mixed into wind-driven, northward-flowing water in the mid-shelf region, and return is facilitated by Ekman transport associated with northeasterly winds driving downwelling along the coast, resulting in strong subtidal flow into estuaries (Tilburg et al. 2007). All the hydrographic configurations mentioned above vary on different time scales (year-to-year, decadal, long-term), and are likely to change as climate does.

Unlike fishes, the post-settlement life of most crab species (with the notable exception of some portunids) is constrained to the benthic boundary layer, where they migrate tracking gradients of near-bottom temperature, salinity, depth, and sediment composition. Although the patterns of some near-bottom gradient fields, like salinity along estuaries or near-bottom temperature across shelves (e.g., Ernst et al. 2005), are rather conservative, their steepness and the absolute levels of the respective environmental variables are strongly influenced by climate fluctuations. Crab stocks from subarctic systems, in which successful recruitment is related to the seasonal development of a cold benthic boundary layer environment associated with winter sea ice (e.g., the "cold pool" in the eastern Bering Sea or the "cold intermediate layer" in the Gulf of Saint Lawrence), are particularly vulnerable to warming (see snow crab and king crab sections). In temperate regions climate change can affect conditions in the benthic boundary layer of coastal ecosystems through hydrologic regimes. Predictions for increased, but more episodic, rainfall in the mid-Atlantic estuaries like Chesapeake Bay would lead to higher nutrient inputs, poorer water quality, greater stratification, and low dissolved oxygen. This implies a range of direct and indirect ecosystem impacts for blue crabs (Pyke et al. 2008). Low oxygen levels in deeper water and "spilling" into shallow areas both impact blue crabs directly, but also reduce food resources of benthic communities. Low oxygen could also become a significant barrier to dispersal of small juveniles into nursery habitats, and to migration of mature females traveling back to the high salinity spawning area.

Warming can also favor the intrinsic growth rate of temperate or subarctic populations of commercially valuable crab species. In the case of blue crab, warming will primarily reduce the duration and severity of the cold winter season, thus increasing the duration of the reproductive and growing season, and accelerating rates of growth, maturation, and reproductive output in temperate zone systems like Chesapeake Bay. Climate warming will also reduce winter mortality of blue crabs in Middle Atlantic Bight estuaries, particularly for small juveniles and adult females that are particularly sensitive to fluctuating combinations of cold temperature (<3°C) and low salinity (<8 ppt) at higher latitude sites. External brooding exposes fertilized egg masses of crabs to near-bottom temperature, with consequent variability in the duration of brooding. In the eastern Bering Sea and the Gulf of St. Lawrence, the brooding period can last one or two years depending on near-bottom temperature (Sainte-Marie et al. 2008). Given the determinate life-history schedule of majid crabs, the lifetime reproductive output of female snow crab is radically reduced toward higher latitudes and during cold periods. Besides, females tend to be much larger and their fecundity higher towards relatively low latitudes because size at terminal molt appears to be determined by age and the frequency of molting, which is temperature-dependent (Burmeister and Sainte-Marie 2010). The combined result of brooding time and terminal size is that the effective reproductive output of individual females is much higher toward the upper end of near-bottom temperature thermal habitat.

Climate and biotic interactions

Beyond changes in the life history of crab populations, climate change is expected to affect crab stocks through effects on other components of the ecosystem. These effects can be top-down or bottom-up. Top down effects are perhaps best illustrated by cod predation on snow crab stocks (Chabot et al. 2008, Lang et al. 2006). Cod, as well as other fish predators foraging on juvenile snow crab, are relatively intolerant of the low temperatures that define the cold pool. Cod predation intensifies and expands northward tracking periods of cold pool deterioration and amplifying the effects of the female stock contraction addressed by the environmental ratchet hypothesis (Orensanz et al. 2004, Parada et al. 2010). Cod also prey on red king crab, mostly on softshell females (Livingston 1989), but a causal relation between predation by groundfish and correlated stock declines is not well specified (see king crab section). In Middle Atlantic Bight estuaries like Chesapeake Bay, a warmer climate is likely to promote range extensions for a higher diversity of predators of blue crab, particularly suptropical fishes (Najjar et al. 2010).

The changing range of predatory crab may, in turn, affect other components of benthic ecosystems. As an example, Jørgensen and Primicerio (2007) conducted experiments showing that the range expansion of invasive red king crab may threaten calcified prey species in the Barents Sea, including commercially valuable scallop beds. In the eastern Bering Sea, the northward retreat of the southern edge of the cold pool by 230 km since the early 1980s was accompanied by northward distribution shifts throughout the benthic community (Mueter and Litzow 2008), including snow crab. Consequently, the relative consumption by crabs declined from 27% to 4% between the 1960s and 1980s (Aydin and Mueter 2007).

The most significant climate-related bottom-up processes affecting crab populations correspond to the food supply for pelagic larval stages. This, again, may be most significant in the case of subarctic ecosystems due to the high seasonality of the productive cycle. The oscillating control hypothesis (Hunt et al. 2002) predicts an alternation between primarily bottom-up control in cold regimes and primarily top-down control in warm regimes. According to the model, "the timing of spring primary production is determined predominantly by the time of ice retreat: late

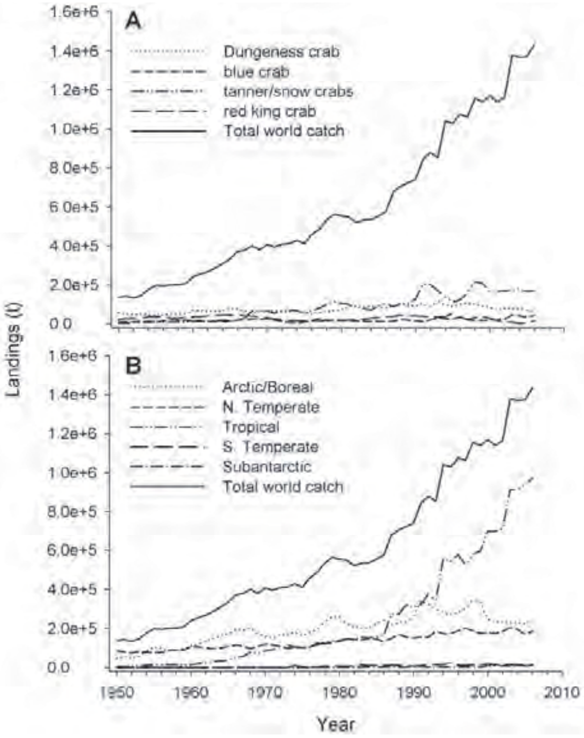

Figure 13. Food and Agriculture Organization (FAO) records of crab catch in metric tons from 1950 to 2006. (A) Catch of focal species compared to total world catch of true crabs and king crabs. (B) Catch of true crabs (Brachyura) and king crabs (Lithodidae) by region. (FishSTAT Fishery Statistical Collections Global Capture Production. http://www.fao.org/fishery/statistics/global-capture-production; accessed Dec. 2010.)

ice retreat (late March or later) leads to an early, ice-associated bloom in cold water, whereas no ice, or early retreat of ice before mid March, leads to an open-water bloom in May or June.” Since the timing of larval hatching in snow crab is constrained by the reproductive cycle of benthic adults, which peaks in April, crab larvae are likely to thrive during cold years. This provides yet another mechanism leading to the poleward contraction of the snow crab stock in a warming climate.

Climate change may affect habitat interactions of benthic stages. The seagrass (*Zostera marina*) meadows that constitute significant blue crab habitat are restricted to colder waters, and may be replaced by *Thalassia testudinum* or other warm-water species in the event of warming. Several oyster species that provide habitat for blue and Dungeness crab may benefit from longer growing seasons associated with mild winters. However, these same species may suffer higher mortality from a variety of pathogens that show increased virulence at higher temperatures (Najjar et al. 2010). Rising sea level associated with climate change will also affect estuarine habitats (Scavia et al. 2002). Accelerated sea level rise may submerge salt marshes that are critical support systems for blue crab nursery areas (Najjar et al. 2010), and habitats utilized by juvenile and subadult Dungeness crab may be similarly impacted.

Global perspective

While in this review we have focused on four examples of subarctic and northern temperate crab fisheries, it is informative to consider their magnitude in the context of world crab landings. Catch from these four fisheries leveled off almost 20 years ago (Fig. 13A), while landings of tropical species have grown steadily (Fig. 13B). For reasons considered above, it seems that climate change, especially warming trends, will have much greater adverse effects on subarctic species than on the tropical ones that now make up most of world landings. The four species considered by us, arguably among the most studied commercial crab, illustrate a comprehensive menu of processes expected to be affected by climate change. Perhaps more significant, they highlight the limitations of current understanding of crab stock dynamics in spite of decades of intensive study.

Tropical fisheries could benefit from both warming and the development of tropical/subtropical aquaculture, as portunid scavengers often thrive in the immediacy of aquaculture operations. Thus, the “tropicalization” of global crab fisheries that started 25 years ago is likely to continue into the future. Despite the inordinate effects on communities of regime shifts that may swing colder or warmer, we contend that longer-term trends in the latter direction will have disproportionately greater adverse impacts on subarctic and temperate crab species and their fisheries than on the tropical guild.

References

Alvsvåg, J., Æ.A.-L. Agnalt, and Æ.K.E. Jørstad. 2009. Evidence for a permanent establishment of the snow crab (*Chionoecetes opilio*) in the Barents Sea. Biol. Invasions 11:587-595. doi:10.1007/s10530-008-9273-7

Anderson, P.J., and J.F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar. Ecol. Prog. Ser. 189:117-123. doi:10.3354/meps189117

Armstrong, D.A., C. Rooper, and D. Gunderson. 2003. Estuarine production of juvenile Dungeness crab (*Cancer magister*) and contribution to the Oregon-Washington coastal fishery. Estuaries 26:1174-1188. doi:10.1007/BF02803372

Aronson, R.B., S. Thatje, A. Clarke, L.S. Peck, D.B. Blake, C.D. Wilga, and B.A. Seibel. 2007. Climate change and invasibility of the antarctic benthos. Ann. Rev. Ecol. Evol. Syst. 38:129-54. doi:10.1146/annurev.ecolsys.38.091206.095525

Aydin, K., and F. Mueter. 2007. The Bering Sea: A dynamic food web perspective. Deep-Sea Res. II 54:2501-2525. doi:10.1016/j.dsr2.2007.08.022

Bechtol, W.R., and G.H. Kruse. 2009a. Analysis of a stock-recruit relationship for red king crab off Kodiak Island, Alaska. Mar. Coast. Fish. Dyn. Manag. Ecosyst. Sci. 1:29-44.

Bechtol, W.R., and G.H. Kruse. 2009b. Reconstruction of historical abundance and recruitment of red king crab during 1960-2004 around Kodiak, Alaska. Fish. Res. 100:86-98.

Bechtol, W.R., and G.H. Kruse. 2010. Factors affecting red king crab recruitment around Kodiak Island, Alaska. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and management of exploited crab populations under climate change. Alaska Sea Grant College Program, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.18

Bienfang, P.K., and D.A. Ziemann. 1995. APPRISE: A multi-year investigation of environmental variation and its effects on larval recruitment. In: R.J. Beamish (ed.), Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. 121:483-487.

Boldt, J. (ed.) 2008. Ecosystem considerations for 2009. Appendix C. 236 pp. Accessed Sept. 2010: http://access.afsc.noaa.gov/reem/ecoweb/content/pdf/AppendixC.pdf.

Bond, N.A., and J.E. Overland. 2005. The importance of episodic weather events to the ecosystem of the Bering Sea shelf. Fish. Oceanogr. 14(2):97-111. doi:10.1111/j.1365-2419.2004.00321.x

Botsford, L.W. 1984. Effect of individual growth rates on expected behavior of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 41:99-107. doi:10.1139/f84-009

Botsford, L.W. 2001. Physical influences on recruitment to California Current invertebrate populations on multiple scales. ICES J. Mar. Sci. 58:1081-1091. doi:10.1006/jmsc.2001.1085

Botsford, L.W., D.A. Armstrong, and J. Shenker. 1989. Oceanographic influences on the dynamics of commercially fished populations. In: M. Landry and B. Hickey (eds.), Coastal oceanography of Washington and Oregon. Elsevier Science Publishing Company, New York, pp. 511-565. doi:10.1016/S0422-9894(08)70355-6

Burkholder, J., D. Eggleston, H. Glasgow, C. Brownie, R. Reed, G. Janowitz, M. Posey, G. Meia, C. Kinder, R. Corbett, D. Toms, T. Alphin, N. Deamer, and J. Springer. 2004. Comparative impacts of two major hurricane seasons on the Neuse River and western Pamlico Sound ecosystems. Proc. Natl. Acad. Sci. U.S.A. 101(25):9291-9296. doi:10.1073/pnas.0306842101

Burmeister, A.D., and B. Sainte-Marie. 2010. Pattern and causes of a temperature-dependent gradient of size at terminal moult in snow crab (*Chionoecetes opilio*) along West Greenland. Polar Biol. 33(6):775-788. doi:10.1007/s00300-009-0755-6

CBSAC. 2009. 2009 Chesapeake Bay blue crab advisory report. Chesapeake Bay Stock Assessment Committee, NOAA Chesapeake Bay Office, Annapolis. 5 pp.

Chabot, D., B. Sainte-Marie, K. Briand, and J.M. Hanson. 2008. Atlantic cod and snow crab predator-prey size relationship in the Gulf of St. Lawrence, Canada. Mar. Ecol. Prog. Ser. 363:227-240. doi:10.3354/meps07384

Collier, P.C. 1983. Movement and growth of post-larval Dungeness crabs, *Cancer magister*, in the San Francisco area. In: P.W. Wild and R.N. Tasto (eds.), Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. Calif. Fish Game, Fish Bull. 172:125-333.

Cushing, D.H. 1969. The regularity of the spawning season of some fishes. J. Cons. Int. Explor. Mer. 33:81-97.

Dahlstrom, W.A., and P.W. Wild. 1983. A history of Dungeness crab fisheries in California. In: P.W. Wild and R.N. Tasto (eds.), Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister,* with emphasis on the central California fishery resource. Calif. Fish Game, Fish Bull. 172:7-23.

Davis, J.L.D., A.C. Young-Williams, A.H. Hines, and Y. Zohar. 2005. Assessing the potential for stock enhancement in the case of the Chesapeake Bay blue crab (*Callinectes sapidus*) Can. J. Fish. Aquat. Sci 62:109-122. doi:10.1139/f04-150

Dew, C.B., and R.A. McConnaughey. 2005. Did trawling on the broodstock contribute to the collapse of Alaska's king crab? Ecol. Appl. 15:919-941. doi:10.1890/03-5231

Diamond, N., and D.G. Hankin. 1985. Movements of adult female Dungeness crabs (*Cancer magister*) in northern California based on tag recoveries. Can. J. Fish. Aquat. Sci. 42:919-926. doi:10.1139/f85-116

Didier Jr., A.J. 2002. The Pacific coast Dungeness crab fishery. Pacific States Marine Fisheries Commission. Submitted to the Committee on Commerce, Science, and Transportation of the U.S. Senate and Committee on Resources of the U.S. House of Representatives. Accessed Dec. 2010: http://www.psmfc.org/publications/WOCCrabReportMarch2002.pdf

Dionne, M., B. Sainte-Marie, E. Bourget, and D. Gilbert. 2003. Distribution and habitat selection of early benthic stages of snow crab *Chionoecetes opilio*. Mar. Ecol. Prog. Ser. 259:117-128. doi:10.3354/meps259117

Donaldson, W.E., and W.K. Donaldson. 1992. A review of the history and justification for size limits in Alaskan king, Tanner, and snow crab fisheries. Alaska Department of Fish and Game, Division of Commercial Fisheries, Fisheries Research Bulletin 92-02. 21 pp.

Eggleston, D.B., and D.A. Armstrong. 1995. Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. Ecol. Monogr. 65:193-216. doi:10.2307/2937137

Epifanio, C.E. 2007. Biology of larvae. In: V.S. Kennedy and L.E. Cronin (eds.), Biology of the blue crab. Maryland Sea Grant College Program, College Park, pp. 513-533.

Epifanio, C.E., and R.W. Garvine. 2001. Larval transport on the Atlantic continental shelf of North America: A review. Estuar. Coast. Shelf Sci. 52:51-77. doi:10.1006/ecss.2000.0727

Ernst, B., J.M. Orensanz, and D.A. Armstrong. 2005. Spatial dynamics of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. Can. J. Fish. Aquat. Sci. 62:250-268. doi:10.1139/f04-201

Etherington, L.L., and D.B. Eggleston. 2003. Spatial dynamics of large-scale, multistage crab (*Callinectes sapidus*) dispersal: Determinants and consequences for recruitment. Can. J. Fish. Aquat. Sci. 60:873-887. doi:10.1139/f03-072

Fogarty, M.J., and R.N. Lipcius. 2007. Population dynamics and fisheries. In: V.S. Kennedy and L.E. Cronin (eds.), Biology of the blue crab. Maryland Sea Grant College Program, College Park, pp. 711-755.

Foyle, T.P., R.K. O'Dor, and R.W. Elner. 1989. Energetically defining the thermal limits of the snow crab. J. Exp. Biol. 145: 371-393.

Frederich, M., F.J. Sartoris, W.E. Arntz, and H.-O. Pörtner. 2000. Haemolymph Mg^{2+} regulation in decapod crustaceans: Physiological correlates and ecological consequences in polar areas. J. Exp. Biol. 203:1383-1393.

Gaston, K.J. 2009. Geographic range limits: Achieving synthesis. Proc. Royal Society (B) 276:1395-1406. doi:10.1098/rspb.2008.1480

Gotshall, D.W. 1978. Catch-per-unit-of-effort studies of northern California Dungeness crabs, *Cancer magister*. Calif. Fish. Game 64:189-199.

Grebmeier, J.M., J.E. Overland, S.E. Moore, E.V. Farley, E.C. Carmack, L.W. Cooper, K.E. Frey, J.H. Helle, F.A. McLaughlin, and S.L. McNutt. 2006. A major ecosystem shift in the northern Bering Sea. Science 311:1461-1464. doi:10.1126/science.1121365

Gunderson, D.R., D.A. Armstrong, Y.B. Shi, and R.A. McConnaughey. 1990. Patterns of estuarine use by juvenile English sole *Parophrys vetulus* and Dungeness crab *Cancer magister*. Estuaries 13:59-71.

Gutermuth, F.B. 1987. Energy budget of the Grays Harbor population of juvenile Dungeness crab (*Cancer magister*) in summer of 1983 and 1984. M.S. thesis, University of Washington, Seattle. 115 pp.

Gutermuth, F.B., and D.A. Armstrong. 1989. Temperature dependent metabolic response of juvenile Dungeness crab *Cancer magister* Dana: Ecological implications for estuarine and coastal populations. J. Exp. Mar. Biol. Ecol. 126:135-144. doi:10.1016/0022-0981(89)90085-3

Hall, S., and S. Thatje. 2009. Global bottlenecks in the distribution of marine Crustacea: Temperature constraints in the family Lithodidae. J. Biogeog. 36:2125-2135. doi:10.1111/j.1365-2699.2009.02153.x

Hankin, D.G. 1985. Proposed explanations for fluctuations in the abundance of Dungeness crabs: A review and critique. In: Proceedings of the Symposium on Dungeness Crab Biology and Management. Alaska Sea Grant College Program, University of Alaska, pp. 305-326.

Hankin, D.G., T.H. Butler, P.W. Wild, and Q.-L. Xue. 1997. Does intense fishing on males impair mating success of female Dungeness crabs? Can. J. Fish. Aquat. Sci. 54:655-669. doi:10.1139/cjfas-54-3-655

Hickey, B.M. 1989. Patterns and processes of circulation over the Washington continental shelf and slope. In: M.R. Landry and B.M. Hickey (eds.), Coastal oceanography of Washington and Oregon. Elsevier Science Publishers, Amsterdam, pp. 41-115. doi:10.1016/S0422-9894(08)70346-5

Higgins, K., A. Hastings, J.N. Sarvela, and L.W. Botsford. 1997. Stochastic dynamics and deterministic skeletons: Population behavior of Dungeness crab. Science 276:1431-1435. doi:10.1126/science.276.5317.1431

Hines, A.H. 2007. Ecology of juvenile and adult blue crabs. In: V.S. Kennedy and L.E. Cronin (eds.), Biology of the blue crab. Maryland Sea Grant College Program, College Park, pp. 565-654.

Hines, A.H., E.G. Johnson, M.Z. Darnell, D. Rittschof, T.J. Miller, L.J. Bauer, and R. Aguilar. 2010. Predicting effects of climate change on blue crabs. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and management of exploited crab populations under climate change. Alaska Sea Grant College Program, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.22

Holsman, K.K., P.S. McDonald, and D.A. Armstrong. 2006. Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. Mar. Ecol. Prog. Ser. 308:183-195. doi:10.3354/meps308183

Holsman, K.K., D.A. Armstrong, D.A. Beauchamp, and J.L. Ruesink. 2003. The necessity for intertidal foraging by estuarine populations of subadult Dungeness crab, *Cancer magister*: Evidence from a bioenergetics model. Estuaries 26:1155-1173. doi:10.1007/BF02803371

Hunt, G.L., P. Stabeno, G. Walters, E. Sinclair, R.D. Brodeur, J.M. Napp, and N.A. Bond. 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Res. II 49:5821-5853. doi:10.1016/S0967-0645(02)00321-1

Jensen, G.C. 1995. Pacific coast crabs and shrimps. Sea Challengers, Monterey. 87 pp.

Jensen, P.C., J.M. Orensanz, and D.A. Armstrong. 1996. Structure of the female reproductive tract in the Dungeness crab (*Cancer magister*) and implications for the mating system. Biol. Bull. 190(3):336-349. doi:10.2307/1543026

Jivoff, P.R., A.H. Hines, and S. Quackenbush. 2007. Blue crab reproductive biology. In: V.S. Kennedy and L.E. Cronin (eds.), Biology of the blue crab. Maryland Sea Grant College Program, College Park, pp. 255-298.

Johnson, D.F., L.W. Botsford, R.D. Methot, and T.C. Wainwright. 1986. Wind stress and cycles in Dungeness crab (*Cancer magister*) catch off California, Oregon, and Washington. Can. J. Fish. Aquat. Sci. 43:838-845.

Jørgensen, L.L., and R. Primicerio. 2007. Impact scenario for the invasive red king crab *Paralithodes camtschaticus* (Tilesius, 1815) (Reptantia, Lithodidae) on Norwegian native epibenthic prey. Hydrobiologia 590:47-54. doi:10.1007/s10750-007-0756-9

Kennedy, V.S., M. Oesterling, and W.A. Van Engel. 2007. History of blue crab fisheries on the U.S. Atlantic and Gulf Coasts. In: V.S. Kennedy and L.E. Cronin (eds.), Biology of the blue crab. Maryland Sea Grant College Program, College Park, pp. 655-709.

Kruse, G.H. 1993. Biological perspectives on crab management in Alaska. In: G.H. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II (eds.), Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations, Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 355-384.

Kruse, G.H. 2007. Ecosystem structure: crabs and shrimps. In: R.B. Spies (ed.), Long-term ecological change in the northern Gulf of Alaska. Elsevier, Amsterdam, pp. 135-145.

Kruse, G.H., A.V. Tyler, B. Sainte-Marie, and D. Pengilly. 2007. A workshop on mechanisms affecting year-class strength formation in snow crabs (*Chionoecetes opilio*) in the eastern Bering Sea. Alaska Fish. Res. Bull. 12:277-290.

Kruse, G.H., F.C. Funk, H.J. Geiger, K.R. Mabry, H.M. Savikko, and S.M. Siddeek. 2000. Overview of state-managed marine fisheries in the central and western Gulf of Alaska, Aleutian Islands, and southeastern Bering Sea, with reference to Steller sea lions. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 5J00-10. 173 pp.

Kuris, A.M., S.F. Blau, A.J. Paul, J.D. Shields, and D.E. Wickham. 1991. Infestation by brood symbionts and their impact on egg mortality of the red king crab, *Paralithodes camtschatica*, in Alaska: Geographic and temporal variation. Can. J. Fish. Aquat. Sci. 48:559-568. doi:10.1139/f91-071

Lang, G.M., P.A. Livingston, K.A. Dodd. 2006. Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1997 through 2001. NOAA Tech. Memo. 158. 254 pp.

Lipcius, R.N., and W.T. Stockhausen. 2002. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. Mar. Ecol. Prog. Ser. 226:45-61. doi:10.3354/meps226045

Lipcius, R.N., D.B. Eggleston, K.L. Heck Jr., R.D. Seitz, and J. van Montfrans. 2007. Ecology of postlarval and young juvenile blue crabs. In: V.S. Kennedy and L.E. Cronin (eds.), Biology of the blue crab. Maryland Sea Grant College Program, College Park, pp. 535-564.

Livingston, P.A. 1989. Interannual trends in Pacific cod, *Gadus macrocephalus*, predation on three commercially important crab species in the eastern Bering Sea. Fish. Bull. 87:807-827.

Loher, T., and D.A. Armstrong. 2000. Effects of habitat complexity and relative larval supply on the establishment of early benthic phase red king crab (*Paralithodes camtschaticus Tilesius*, 1815) populations in Auke Bay, Alaska. J. Exp. Mar. Biol. Ecol. 245:83-109. doi:10.1016/S0022-0981(99)00157-4

Loher, T., and D.A. Armstrong. 2005. Historical changes in the abundance and distribution of ovigerous red king crabs *(Paralithodes camtschaticus)* in Bristol Bay (Alaska), and potential relationship with bottom temperature. Fish. Oceanogr. 14:292-306. doi:10.1111/j.1365-2419.2005.00337.x

Lovrich, G.A., B. Sainte-Marie, and B.D. Smith. 1995. Depth distribution and seasonal movements of *Chionoecetes opilio* (Brachyura: Majidae) in Baie Sainte-Marguerite, Gulf of Saint Lawrence. Can. J. Zool. 73:1712-1726.

McConnaughey, R.A., D.A. Armstrong, B.M. Hickey, and D.R. Gunderson. 1992. Juvenile Dungeness crab (*Cancer magister*) recruitment variability and oceanic transport during the pelagic larval phase. Can. J. Fish. Aquat. Sci. 49:2028-2044. doi:10.1139/f92-226

McConnaughey, R.A., D.A. Armstrong, B.M. Hickey, and D.R. Gunderson. 1994. Interannual variability in coastal Washington Dungeness crab (*Cancer magister*) populations: Larval advection and the coastal landing strip. Fish. Oceanogr. 3:22-38. doi:10.1111/j.1365-2419.1994.tb00045.x

McMillan, R.O., D.A. Armstrong, and P.A. Dinnel. 1995. Comparison of intertidal habitat use and growth rates of two northern Puget Sound cohorts of 0+ age Dungeness crab, *Cancer magister*. Estuaries 18:390-398. doi:10.2307/1352321

McMullen, J.C., and H.T. Yoshihara. 1969. Fate of unfertilized eggs in king crabs *(Paralithodes camtschatica* Tilesius). Alaska Department of Fish and Game, Division of Commercial Fisheries, Inform. Leafl. 127.

Methot, R.D. 1989. Management of a cyclic resource: The Dungeness crab fisheries of the Pacific coast of North America. In: J.F. Caddy (ed.), Marine invertebrate fisheries: Their assessment and management. John Wiley & Sons, Inc., New York, pp. 205-223. doi:10.1139/f82-145

Methot, R.D., and L.W. Botsford. 1982. Estimated preseason abundance in the California Dungeness crab (*Cancer magister*) fisheries. Can. J. Fish. Aquat. Sci. 39:1077-1083. doi:10.1139/f82-145

Mueter, F.J., and M.A. Litzow. 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. Ecol. Appl. 18:309-320. doi:10.1890/07-0564.1

Najjar, R.G., C.R. Pyke, M.B. Adams, D. Breitburg, C. Hershner, M. Kemp, R. Howarth, M.R. Mulholland, M. Paolisso, D. Secor, K. Sellner, D. Wardrop, and R. Wood. 2010. Potential climate-change impacts on the Chesapeake Bay. Estuar. Coast. Shelf Sci. 86:1-20. doi:10.1016/j.ecss.2009.09.026

NPFMC. 2008a. Stock assessment and fishery evaluation (SAFE) report for the king and Tanner crab fisheries of the Bering Sea and Aleutian Islands (BSAI) Regions. North Pacific Fishery Management Council, Plan Team for the King and Tanner Crab Fisheries, Anchorage. 595 pp.

NPFMC. 2008b. Fishery management plan for Bering Sea/Aleutian Islands king and Tanner crabs. North Pacific Fishery Management Council, Anchorage. 118 pp.

Orensanz, J.M., B. Ernst, and D.A. Armstrong. 2007. Variation of female size- and stage-at-maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering Sea. J. Crust. Biol. 27:576-591. doi:10.1651/S-2790.1

Orensanz, J.M., J. Armstrong, D. Armstrong, and R. Hilborn. 1998. Crustacean resources are vulnerable to serial depletion: The multifaceted decline of crab and shrimp fisheries in the greater Gulf of Alaska. Rev. Fish Biol. Fish. 8:117-176. doi:10.1023/A:1008891412756

Orensanz, J.M., B. Ernst, D.A. Armstrong, P. Stabeno, and P. Livingston. 2004. Contraction of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: An environmental ratchet? CalCOFI Rep. 45:65-79

Parada, C., D.A. Armstrong, B. Ernst, S. Hinckley, and J.M. Orensanz. 2010. Spatial dynamics of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: Putting together the pieces of the puzzle. Bull. Mar. Sci. 86(2):413-437.

Paul, A.J., and J.M. Paul. 1980. The effect of early starvation on later feeding success of king crab zoea. J. Exp. Mar. Biol. Ecol. 44:247-251. doi:10.1016/0022-0981(80)90155-0

Paul, A.J., J.M. Paul, and K.O. Coyle. 1990. Growth of stage I king crab larvae of *Paralithodes camtschatica* (Tilesius) (Decapoda: Lithodidae) in natural communities. J. Crust. Biol. 10:175-183. doi:10.2307/1548479

Pauley, G.B., D.A. Armstrong, R.V. Citter, and G.L. Thomas. 1989. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest): Dungeness crab. U.S. Fish and Wildlife Service Biological Report 82 (11.121). U.S. Army Corps of Engineers, TR EL-82-4. 20 pp.

Perry, A.L., P.J. Low, J.R. Ellis, and J.D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. Science 308:1912-1915. doi:10.1126/science.1111322

Pyke, C.R., R.G. Najjar, M.B. Adams, D. Breitburg, M. Kemp, C. Hershner, R. Howarth, M. Mulholland, M. Paolisso, D. Secor, K. Sellner, D. Wardrop, and R. Wood. 2008. Climate change and the Chesapeake Bay: State-of-the-science review and recommendations. A report from the Chesapeake Bay Program Science and Technical Advisory Committee (STAC), Annapolis. 59 pp.

Rooper, C.N., D.A. Armstrong, and D.R. Gunderson. 2002. Habitat use by juvenile Dungeness crabs in coastal nursery estuaries. In: A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, M.B. Sainte, T.C. Shirley, D. Woodby (eds.), Crabs in cold water regions: Biology, management, and economics. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 609-629.

Rugolo, L., D. Pengilly, R. MacIntosh, and K. Gravel. 2005. Reproductive potential and life history of snow crabs in the eastern Bering Sea. Final Comprehensive Performance Report, Bering Sea Snow Crab Fishery Restoration, NOAA Cooperative Agreement NA17FW1274.

Sainte-Marie, B., and D. Gilbert. 1998. Possible effects in CIL temperature and thickness on population dynamics of snow crab, *Chionoecetes opilio*, in the Gulf of Saint Lawrence. Canadian Stock Assessment Secretariat, Research Document 98/38. 19 pp.

Sainte-Marie, B., J.-M. Sévigny, and M. Carpentier. 2002. Interannual variability of sperm reserves and fecundity of primiparous females of the snow crab (*Chionoecetes opilio*) in relation to sex ratio. Can. J. Fish. Aquat. Sci. 59:1932-1940. doi:10.1139/f02-162

Sainte-Marie, B., T. Gosselin, J.-M. Sévigny, and N. Urbani. 2008. The snow crab mating system: Opportunity for natural and unnatural selection in a changing environment. Bull. Mar. Sci. 83:131-161.

Scavia, D., J.C. Field, D.F. Boesch, R. W. Buddemeier, V. Burnett, D.R. Cayan, M. Fogarty, M.A. Harwell, R.W. Howarth, C. Mason, D.J. Reed, T.C. Royer, A.H. Sallenger, and J.G. Titus. 2002. Climate change impacts on U.S. coastal and marine ecosystems. Estuaries 25(2):149-164. doi:10.1007/BF02691304

Shanks, A.L., and G.C. Roegner. 2007. Recruitment limitation in Dungeness crab populations is driven by variation in atmospheric forcing. Ecology 88(7):1726-1737. doi:10.1890/06-1003.1

Shirley, S.M., and T.C. Shirley. 1989. Interannual variability in density, timing, and survival of Alaskan red king crab *Paralithodes camtschatica* larvae. Mar. Ecol. Prog. Ser. 54:51-59. doi:10.3354/meps054051

Slater, L.M., K.A. MacTavish, and D. Pengilly. 2010. Preliminary analysis of spermathecal load of primiparous snow crabs (*Chionoecetes opilio*) from the eastern Bering Sea, 2005-2008. In: Kruse, G.H., G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and management of exploited crab populations under climate change. Alaska Sea Grant College Program, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.10

Smith, B.D., and G.S. Jamieson. 1989. Exploitation and mortality of male Dungeness crabs (*Cancer magister*) near Tofino, British Columbia. Can. J. Fish. Aquat. Sci. 46:1609-1614.

Smith, B.D., and G.S. Jamieson. 1991. Notes: Possible consequences of intensive fishing for males on the mating opportunities of Dungeness crabs. Trans. Am. Fish. Soc. 120:650-653. doi:10.1577/1548-8659

Stabeno, P.J., N.A. Bond, and S.A. Salo. 2007. On the recent warming of the southeastern Bering Sea shelf. Deep-Sea Res. II 54:2599-2618. doi:10.1016/j.dsr2.2007.08.023

Stabeno, P.J., N.K. Kachel, C. Mordy, D. Righi, and S.A. Salo. 2008. An examination of the physical variability around the Pribilof Islands in 2004. Deep-Sea Res. II 55:1701-1716. doi:10.1016/j.dsr2.2008.03.006

Stevens, B.G., and D.A. Armstrong. 1984. Distribution abundance and growth of juvenile Dungeness crabs *Cancer magister* in Grays Harbor estuary Washington USA. Fish. Bull. 82:469-484.

Stevens, B.G., and J. Kittaka. 1998. Postlarval settling behavior, substrate preference, and time for metamorphosis for red king crab *Paralithodes camtschaticus* (Tilesius, 1815). Mar. Ecol. Prog. Ser. 167:197-206. doi:10.3354/meps167197

Stevens B.G., D.A. Armstrong, and J.C. Hoeman. 1984. Diel activity of an estuarine population of Dungeness crabs, *Cancer magister*, in relation to feeding and environmental factors. J. Crust. Biol. 4:390-403. doi:10.2307/1548039

Stone, R.P., and C.E. O'Clair. 2001. Seasonal movements and distribution of Dungeness crabs *Cancer magister* in a glacial southeastern Alaska estuary. Mar. Ecol. Prog. Ser. 214:167-176. doi:10.3354/meps214167

Stone, R.P., C.E. O'Clair, and T.C. Shirley. 1992. Seasonal migration and distribution of female red king crabs in a southeast Alaskan estuary. J. Crust. Biol. 12:546-560. doi:10.2307/1548836

Tasto, R.N. 1983. Juvenile Dungeness crab, *Cancer magister*, studies in the San Francisco Bay area. In: P.W. Wild and R.N. Tasto (eds.), Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. Calif. Fish Game, Fish Bull. 172:135-333.

Thatje, S., K. Anger, J.A. Calcagno, G.A. Lovrich, H.-O. Portner, and W.E. Arntzi. 2005. Challenging the cold: Crabs reconquer the Antarctic. Ecology 86:619-625. doi:10.1890/04-0620

Tilburg, C.E., A.I. Dittel, and C.E. Epifanio. 2007. Retention of crab larvae in a coastal null zone. Estuar. Coast. Shelf Sci. 72:570-578. doi:10.1016/j.ecss.2006.11.030

Wild, P.W., and R.N. Tasto. 1983. Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. Calif. Fish Game, Fish Bull. 172. 352 pp.

Wild, P.W., P.M.W. Law, and D.R. McLain. 1983. Variations in ocean climate and the Dungeness crab fishery in California. In: P.W. Wild and R.N. Tasto (eds.), Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister,* with emphasis on the central California fishery resource. Calif. Fish Game, Fish Bull. 172:175-188.

Wittmann, A.C., C. Held, H.-O. Pörtner, and F.J. Sartoris. 2010. Ion regulatory capacity and the biogeography of Crustacea at high southern latitudes. Polar Biol. 33(7):919-928. doi:10.1007/s00300-010-0768-1

Woodby, D., and L. Hulbert. 2006. Updated overview of state-managed marine fisheries in the central and western Gulf of Alaska, Aleutian Islands, and southeastern Bering Sea, with reference to Steller sea lions. Alaska Department of Fish and Game, Division of Commercial Fisheries, Special Publication 06-23, Anchorage. 110 pp.

Wyllie-Echeverria, T., and W.S. Wooster. 1998. Year-to-year variations in Bering Sea ice cover and some consequences for fish distributions. Fish. Oceanogr. 7:159-170. doi:10.1046/j.1365-2419.1998.00058.x

Zheng. J., and G.H. Kruse. 2000. Recruitment patterns of Alaskan crabs and relationships to decadal shifts in climate and physical oceanography. ICES J. Mar. Sci. 57:438-451. doi:10.1006/jmsc.1999.0521

Zheng, J., and G.H. Kruse. 2003. Stock-recruitment relationships for three major Alaskan crab stocks. Fish. Res. 65:103-121. doi:10.1016/j.fishres.2003.09.010

Zheng, J., and G.H. Kruse. 2006. Recruitment variation of eastern Bering Sea crabs: Climate-forcing or top-down effects? Prog. Oceanogr. 68:184-204.

Zohar, Y., A.H. Hines, O. Zmora, E.G. Johnson, R.N. Lipcius, R.D. Seitz, D.B. Eggleston, A.R. Place, E.J. Schott, J.D. Stubblefield, and J.S. Chung. 2008. The Chesapeake Bay blue crab (*Callinectes sapidus*): A multidisciplinary approach to responsible stock replenishment. Rev. Fish. Sci. 16(1-3):25-35.

Murphy, J.T., A.B. Hollowed, and J.J. Anderson. 2010. Snow Crab Spatial Distributions: Examination of Density-Dependent and Independent Processes. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.19

Snow Crab Spatial Distributions: Examination of Density-Dependent and Independent Processes

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Abstract

The spatiotemporal distributions of the benthic stages of eastern Bering Sea snow crab (*Chionoecetes opilio*) have been considered previously, but principally in qualitative and non-statistical frameworks. Using spatial indices, tests of habitat associations, correlation analyses, and regression modeling, the spatiotemporal distributions of snow crab from 1982-2008 by ontogenetic stage and sex are analyzed to consider the role of density-dependent, density-independent, and ontogenetic factors as mechanisms for the observed distributions. Males and females have different spatial dynamics, with males becoming increasingly dispersed as they age while females become increasingly aggregated. Female spatial distributions can be broadly categorized into immature–newly mature distributions and older mature distributions. Male distributions differ across life stages but not as distinctly as with females. Regression models indicate that temperature is a more important explanatory variable for younger than older crabs and spatial autocorrelation is an important factor in general for all ontogenetic categories of each sex.

Regression models of spatial abundances explain less variation for older crabs than younger crabs, potentially indicating differential influences of environmental factors in structuring spatial distributions across life stages. Correlation and regression models reveal that abundance levels explain much more variation in area occupied than temperature.

Introduction

Biologists and natural resource managers have long recognized that animal populations are not homogeneously distributed entities within their ranges or specified management jurisdictions (Wiens 1976, Tilman and Kareiva 1997, Pelletier and Mahevas 2005). Habitat preferences and tolerances determine the suitability of particular areas for occupancy and utilization. Behavior, especially behaviors associated with dispersal and migration, which may be functions of factors such as size, sex, maturity, and environmental factors, can determine spatial distributions of individual life-history stages (Bowler and Benton 2005). Spatial environmental variability or gradients may result in heterogeneous growth and maturation rates within a population (Brander 1995). The mechanisms responsible for the observed spatial structure, the consequences of the spatial structure on overall population dynamics, and the implications for managing a spatially structured population are the focus of an increasing amount of ecological and natural resource management research, especially for exploited marine species (Rose et al. 2000, Ciannelli et al. 2008).

Spatial structure is of particular importance to the eastern Bering Sea snow crab population (*Chionoecetes opilio*, family Oregoniidae, formerly Majidae; see De Grave et al. 2009), which supports an industrial-scale male-only fishery that annually removes a substantial proportion of large males from the population (Turnock and Rugolo 2008). The eastern Bering Sea snow crab population (snow crab hereafter) has undergone large variations in population sizes in the last 25 years and is currently at low levels (Zheng and Kruse 2006, Turnock and Rugolo 2008). The stock was declared overfished in 1999 and a rebuilding plan was implemented in 2001 (Turnock and Rugolo 2008). Contemporaneous with the decline in abundance in the late 1990s, the population shifted northward in distribution (Zheng et al. 2001), and the eastern Bering Sea underwent a change in oceanographic conditions due to effects of low levels of winter sea ice and warmer water temperatures (Overland and Stabeno 2004). Identifying the mechanisms responsible for the abundance decline is a high priority for fishery managers and industry. Recent studies have focused on how changing oceanographic conditions of the eastern Bering Sea may influence recruitment patterns through reduction in settlement habitat or decreased larval survival and on the impact of groundfish predation on juveniles (Orensanz et al. 2004, Zheng and Kruse 2006).

The spatial structure of the snow crab population has been documented in previous studies (Somerton 1981, Zheng et al. 2001, Ernst et al. 2005). Juvenile crabs occur in high abundances in the shallow waters northeast of the shelf and undergo ontogenetic migrations across the shelf to deeper waters in the outer shelf, where the fishery removes large males (Zheng et al. 2001). Latitudinal variation in size (most prominently in females) occurs with mean size generally decreasing northward and toward shallower depths (Somerton 1981, Otto 1998, Zheng et al. 2001, Orensanz et al. 2007). This occurs partially because younger crabs are more abundant in the north and shallower depths and due to a northward latitudinal trend in maturation at smaller sizes, when molting ceases (Zheng et al. 2001).

As with other demersal and benthic marine species (e.g., Nakken and Raknes 1987), bottom temperatures have been identified as one of the most significant habitat variables for the snow crab, potentially influencing settlement habitat, movement, duration of egg brooding, and growth rates (Moriyasu and Lanteigne 1998, Dionne et al. 2003, Ernst et al. 2005, Rugolo et al. 2005). The correlation between the overall warming of the eastern Bering Sea and the northward shift in geographic range hints at the potential for changing oceanographic conditions as an important mechanism in snow crab population dynamics (Orensanz et al. 2004). The high bottom temperatures of 2001-2005 and the potential for an increasing frequency of high temperatures (Overland and Stabeno 2004) reinforce the need to understand how bottom temperatures influence the spatial distributions and population dynamics of the snow crab.

Impacts of environmental variability, such as changes in bottom temperatures, have been used to assess environmentally driven recruitment hypotheses, with pelagic larvae and early post-settlement crabs being the implicit critical life-history stages (Orensanz et al. 2004, Zheng and Kruse 2006). The influence of environmental variability on adolescent and mature crabs (i.e., crabs at least several years post settlement) has not been closely examined. Ernst et al. (2005) concluded that newly mature females followed bottom temperature gradients during movement from the shallow waters of the middle shelf to the deeper waters of the outer shelf; however, they did not examine how temperature variability (e.g., warm vs. cold years) influenced this presumed behavior. Given that temperature and environmental variability likely have much different consequences for pelagic larvae than benthic adolescents and mature crabs, consideration of these life stages is required as well when evaluating environmental influences on snow crab spatial distributions and population dynamics.

The purpose of this study is to update previous analyses of snow crab spatial distributions (Otto 1998, Zheng et al. 2001, Orensanz et al. 2004) and to analyze spatial distributions in a more rigorous statistical and hypothesis testing framework. Motivating questions are (i) How do temperature and abundance influence occupied area? (ii) What are the differences in aggregation and dispersion between life stages? (iii) What are the differences in habitat distributions within and between life stages over time? (iv) Can environmental variables explain observed spatial distributions and does their significance change over time?

Methods

Data sources and organization

The data source for this study is the annual National Marine Fisheries Service (NMFS) eastern Bering Sea summer bottom trawl survey from 1982-2008. While NMFS eastern Bering Sea surveys have occurred since 1971, the current survey gear and sampling station regime were implemented in 1982. A total of 356 standard stations are sampled between 54.5°N and 60.8°N latitude and between the 20 m and 200 m isobaths. Survey trawls occur for each station at the center of a grid of 20 by 20 nautical miles (1,372 km^2) (Fig. 1). Individual hauls last 30 minutes at a rate of 1.5 m per second. For stations with more than one haul, abundance data were averaged across hauls. Mesh size of the survey net is 10 cm in the body and 8 cm in the codend. The summer trawl survey is a general purpose groundfish and crab survey and the mesh size results in very low capture rates of juvenile crabs less than 30-35 mm. Net selectivity for snow crab increases with increasing crab size (Turnock and Rugolo 2008).

Carapace sizes are measured for each sampled crab. For females, maturation status (immature or mature) is recorded. Males have two maturity states: an adolescent stage with viable sperm products but without enlarged claws, and an adult or morphometrically mature stage marked by the presence of enlarged claws attained at the terminal molt (Conan and Comeau 1986, Sainte-Marie et al. 1995). Use of the word maturity for males is hereafter used to mean morphometric maturity. Allometric relationships between chela (claw) height and carapace width determine the maturity status of an individual male. Since 1989, paired chela height and carapace width measurements have been taken for a subset of males sampled in the survey; these chela height measurements are used to estimate the proportion mature by carapace width.

For each haul in the survey, bottom temperatures were recorded. Sometimes bottom temperatures were not recorded for a station due to equipment malfunction. For these hauls, bottom temperatures were estimated by the average of the bottom temperatures from the immediately adjacent stations in the four cardinal directions (depending on the location of a station, less than four stations may have been used at the edge of the survey grid.) Temperature is hereafter inter-

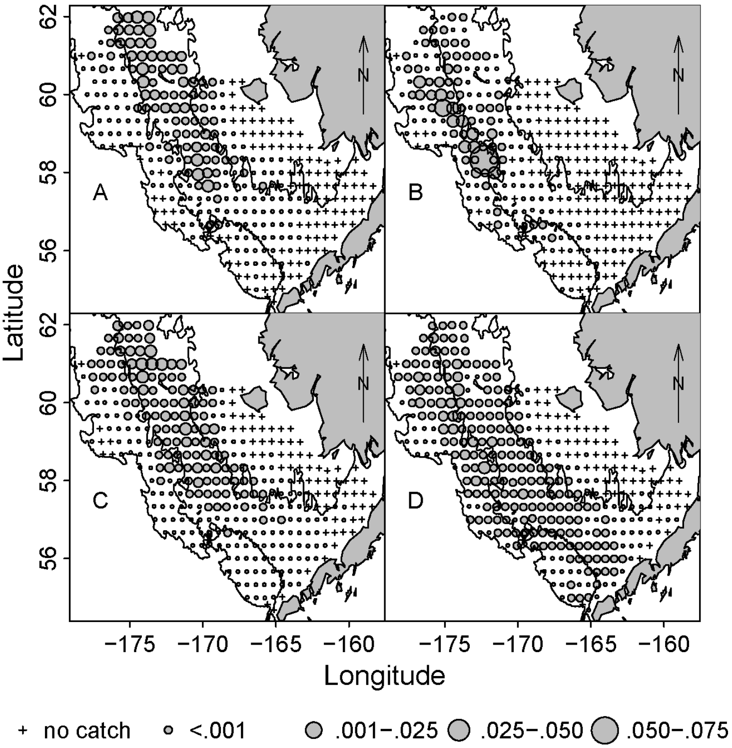

Figure 1. 1999-2008 cumulative spatial proportions of snow crab abundances in the eastern Bering Sea. A: immature and shell 2 mature females. B: shell 3 and shell 4 mature female abundances. C: shell 2 males ≥50 mm carapace width. D: shell 3 males ≥50 mm. From left to right: 200 m, 100 m, 50 m isobaths.

changeable with bottom temperature. An annual bottom temperature index was calculated by averaging temperature values from all survey stations >40 m depth and >56°N latitude.

A classification system describes the snow crab shell condition (Fonseca et al. 2008). As mature crabs do not molt, their shell condition is used as a rough proxy for age since maturation. Shell 1 refers to a crab in the process of molting; few molting crabs are captured by the survey as molting typically occurs in winter and spring for those crabs captured by the survey. Shell 2 is a clean, hard shell that a crab has within one year of molting; almost all crabs between molts and before their terminal molt will have shell 2 condition. Immature crabs that are still molting annually (all crabs that have not undergone their terminal molt) and newly mature crabs will typically have shell 2 condition at the time of the survey. Shell 3 and 4 are slightly to moderately fouled shells typical of mature crabs that are at least one year beyond the terminal molt for shell 3 and likely two to three years for shell 4. Shell 5 crabs have very fouled shells ("graveyard" crabs). Shell 5 crabs are thought to contribute little to reproduction and are much less common in survey catches. Until recently the general assumption was that after the terminal molt, shell condition changes from 2 to 3 to 4 in approximate one year intervals. However, a tagging study from eastern Canada indicates that this progression between adjacent shell conditions does not occur solely at annual time steps but over a range of one to four years (Fonseca et al. 2008).

Snow crab survey data were organized into ten different size and life-history categories, four female categories, and six male categories. The presumed age ranges for the different categories are based on eastern Canadian studies (Comeau et al. 1998, Hebert et al. 2002) and must be considered speculative; few growth data exist for the eastern Bering Sea snow crab and the duration of each shell condition post-terminal molt is uncertain. The female categories are f2: shell 2 immature females, 35-65 mm carapace width (for those captured in the survey), 4-6 years in age; F2: shell 2 mature females, 45-75 mm carapace width, 5-7 years in age; F3: shell 3 mature females, same size as F2, 7-9 years in age; and F4: shell 4 mature females, same size as F2 and F3, 7- 11 years in age. Male categories are Mi2: (i = intermediate), shell 2 males 50-74 mm carapace width, 6-7 years in age; Ml2: (l = large), shell 2 males 75-101 mm carapace width, 7-9 years in age; Mc2: (c = commercial), shell 2 males >101 mm carapace width, 9-12 years in age; Mi3: shell 3 males 50-74 mm carapace width, 7-9 years in age; Ml3: shell 3 males 75-101 mm carapace width, 8-10 years in age; Mc3: (c = commercial), shell condition 3 males >101 mm carapace width, 10-13 years in age. While males >78 mm carapace width can be legally harvested and retained, processing facilities typically only accept males >101 mm. Shell condition 2 males (Mi2, Ml2, and Mc2) are of unknown maturity status, though most shell 2 commercial males are likely mature due to their size. Male shell 2 categories thus contain mature and immature males; shell 2 mature males have undergone their molt-to-maturity only a few to several months prior to their capture in the summer survey and likely have very similar distributions as immature shell 2 males of similar sizes. Shell 3 commercial males are presumed to be mature due to their older shell condition (at least one year past terminal molt).

Analyses

Abundance indices

To give an overview of abundance trends and examine relationships between abundance and occupied area, a time-series of relative abundance was calculated based on NMFS survey data. Following the reasoning of Conners et al. (2002) for dealing with highly skewed fisheries data, relative abundance indices for each category were calculated from the geometric mean multiplied by the number of positive density stations for each year-category combination.

D95

Swain and Benoit (2006) detailed a comprehensive approach to analyze occupied area in relation to temperature and abundance and their methods are closely followed in this analysis. Using cumulative distribution functions, the minimum number of stations occupied by 95% of a specific category abundance (D95 hereafter) were estimated according to the method outlined in Swain and Benoit (2006). With this method, the most sparsely distributed areas representing 5% of the population abundance were subtracted from the total area occupied. Given that each NMFS station represents the same amount of area, trends in occupied stations and occupied area are identical. To maintain continuity with previous studies, the term “occupied area” is employed though occupied stations is the metric estimated in this study.

Relationships between D95 and abundance (per category) and temperature (mean shelf bottom temperature) were initially assessed with calculation of Pearson correlation coefficients, modifying the test for significance due to autocorrelation with the method of Pyper and Peterman (1999). Simple linear regressions were calculated to examine the level of variation explained by abundance levels (of the category examined) and mean shelf bottom temperatures. Total variation explained was partitioned into orthogonal components for each of the two examined factors and into a third component that represented confounded variation explained by both factors (Swain and Benoit 2006, Spencer 2008). If only one of the variables was significant, then the regressions were re-run with the nonsignificant variable removed from the model. Due to prevalent autocorrelation in the time-series considered and residuals of simple linear regressions, linear regressions were also run with the lag 1 autocorrelation parameter in the error estimated (Swain and Benoit 2006) with both temperature and abundance as explanatory variables and the significance of the regression coefficients assessed relative to simple linear regressions. For all regressions, the alpha value for determining significance of parameter estimates was 0.05 unless otherwise stated.

Spreading area ratios

Spreading area (Woillez et al. 2007) represents twice the area under the cumulative distribution functions of areas with positive abundances (sorted from smallest to largest abundances) (see Woillez et al. 2007 for methodology). If abundances are evenly distributed across all occupied stations then the cumulative distribution function is linear and spreading area is maximized and is equal to the total occupied area. However, if only a small portion of the total occupied area has the total abundance, then the cumulative distribution function is highly concave and spreading area is minimized. Thus, the spreading area is inversely related to the level of aggregation within a category's total occupied area. As spreading area values for a particular crab category are more readily interpretable relative to that category's total occupied area, spreading area values here are standardized by total occupied areas to allow for comparisons across categories and years and reported as spreading area ratios. With this standardization, spreading area ratio values closer to 0 represent increased aggregation and values closer to one represent more even distribution within occupied areas.

Habitat distributions: latitude, depth, temperature

Annual distributions by bottom temperature, depth, and latitude were assessed by the randomization test of Perry and Smith (1994). While latitude is not a typical "habitat" variable, for the snow crab latitude distribution contains important information regarding settlement areas and ontogenetic movement. This randomization method tests the null hypothesis of occupied habitat being the same as available habitat, by assessing differences in observed cumulative distribution functions of abundance by habitat variable with the distribution of cumulative distribution functions generated from abundance data randomly distributed across sampling stations (see Perry and Smith 1994 for methodology). For each combination of crab category, habitat variable, and year combination, 3,000 randomizations were performed. The alpha value for determining significance of randomization tests was 0.05.

Spatial regression modeling

Annual regression models for each crab category were constructed with depth (with linear and quadratic terms), bottom temperature, abundance of the congeneric Tanner crab (*Chionoecetes bairdi*), temperature-depth interaction, and spatial eigenvectors (explained below) as explanatory variables for snow crab spatial distributions across survey stations. Tanner crab distributions overlap partially with snow crab distributions and their inclusion as an explanatory variable was used to examine whether potentially antagonistic or competitive interactions occur between the species. Exploratory analyses showed that snow crab spatial abundance data are strongly skewed due to the high number of zero values (zero inflation) (Stefansson 1996) and strongly spatially autocorrelated, based on the calculation of Moran's index for presence-absence and abundance data with latitude and depth trends removed (Fortin and Dale 2005). Spatial autocorrelation results in non-independent data (violating a fundamental assumption of standard regression models) and inflated estimates of significance for the predictor variables (increased Type I errors) (Dormann et al. 2007, Griffith and Peres-Neto 2006). Though spatial autocorrelation was present, geostatistical methods, which explicitly account for spatial autocorrelation (e.g., Jensen and Miller 2005), were not considered due to the skewed, nonstationary data and the large and uniform spacing of the survey data. See Vining and Watson (1996) for further discussion of issues pertaining to geostatistical analysis of eastern Bering Sea crab data.

To account for the zero inflation, two-stage regression models were constructed (Stefansson 1996, Brynjarsdóttir and Stefánsson 2004, Jensen et al. 2005) using generalized linear models. (Generalized additive models were also considered [e.g., Jensen et al. 2005] but they were not found to adequately account for the spatial autocorrelation in the data using latitude and longitude as spatial variables and the smoothed variable functions for bottom temperature and depth did not exhibit strong nonlinear trends.) The first stage modeled only presence-absence over all sampling sites with a binomial error distribution (P-A model). The second stage modeled only positive abundances (log scale) with a Gaussian error distribution (abundance model). For each stage, models with all possible subsets of variable combinations were developed; this procedure helped minimize any bias resulting in stepwise regression (Whittingham et al. 2006). Variance inflation factors (vif) were estimated to identify collinear terms (vif > 3, Fox 2002). Collinear terms were sequentially removed starting with the highest vif values and the models re-run. Akaike Information Criteria (AIC) were used to identify the most parsimonious and efficient model and the model with the lowest AIC value was chosen as the final model for the particular combination of year and crab category.

If model residuals had significant Moran's index values, then spatial eigenvectors were calculated and added as explanatory variables (Griffith and Peres-Neto 2006). Spatial eigenvectors are calculated from the decomposition of a spatial geographic matrix. They capture hierarchical spatial patterns and they can be included in regression models to reduce spatial autocorrelation in model residuals and explain the amount of spatial autocorrelation in the dependent variable (Griffith and Peres-Neto 2006). Selection of spatial eigenvectors for inclusion in the model followed the methods of Griffith and Peres-Neto (2006). Amount of deviance explained by each variable was examined with ANOVA ($p < 0.05$). The "spdep" package for the program R was used to calculate spatial eigenvectors and Moran's index values.

Receiver operating characteristic (ROC) curves were used to assess the model fit of the first stage P-A binomial models (Jensen et al. 2005). ROC curves are a plot of sensitivity (the fraction of correctly predicted presences) against 1-specificity (the fraction of correctly predicted absences) with changing values of the critical probability (the probability above which presence is predicted) (Jensen et al. 2005). ROC curves are used to calculate the area under the ROC curve (AUC), which ranges from 0 to 1 depending on the discriminatory power of the model. Hosmer and Lemeshow (2000, as stated in Jensen et al. 2005) report the following values to evaluate binomial models: 0.7 to 0.8 as acceptable, 0.8 to 0.9 as excellent, and >0.9 as outstanding. The ROC analysis estimates an optimal probability value, a threshold value above which denotes presence and maximizes the number of correct predictions. The "PresenceAbsence" package for the program R was used for the ROC and AUC analyses.

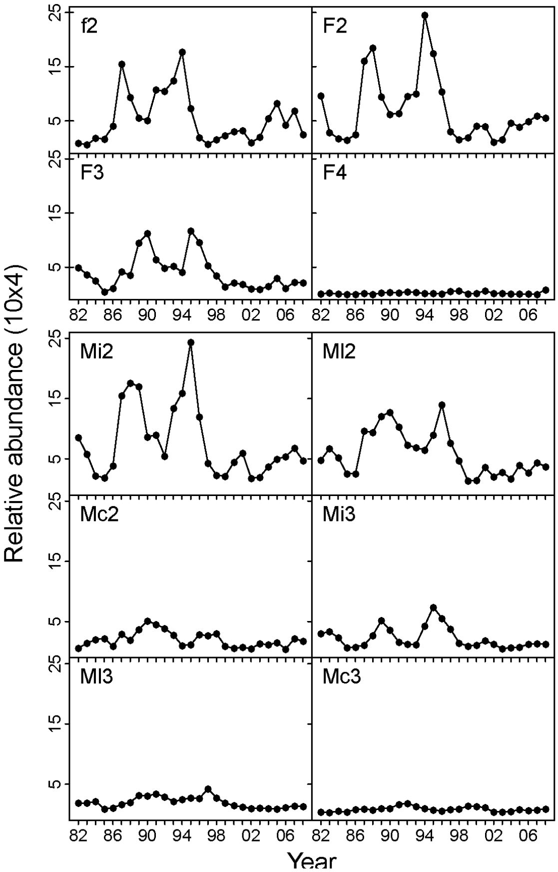

Figure 2. 1982-2008 relative abundance indices for 10 snow crab categories based on geometric mean. See text for category definitions. Top: female results. Bottom: male results.

Results

Abundance indices

High levels of abundances occurred across categories from the late 1980s to mid 1990s with large decreases thereafter (Fig. 2). Shell 3 and shell 4 categories have much lower abundances than shell 2 categories as expected due to their older ages.

D95

The calculated D95 values (Fig. 3) quantify the spatial patterns in Fig. 1. The older females occupy less area than the younger females, and older males occupy more area than younger males. Female D95 values

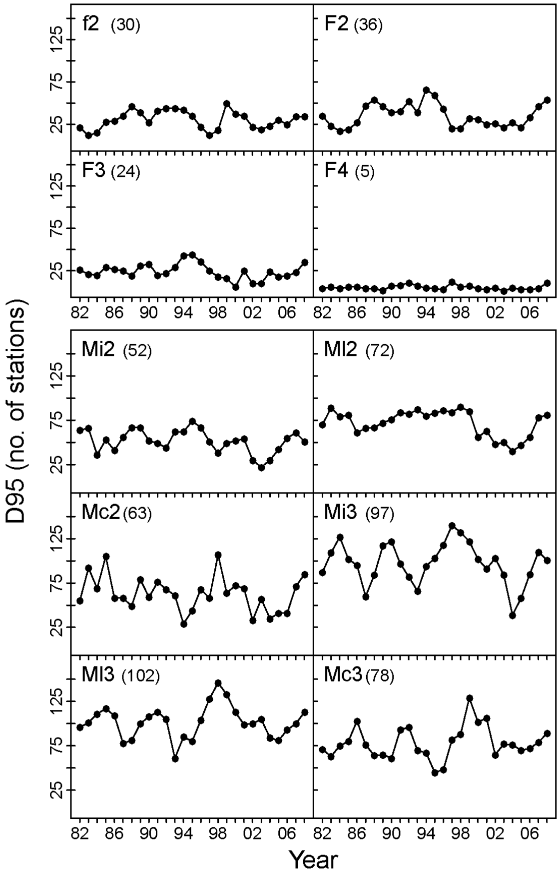

Figure 3. 1982-2008 D95 values, mean values in parentheses. Top: female results. Bottom: male results. D95 is the minimum number of stations occupied by 95% of a specific category abundance.

Table 1. D95 correlation results.

category	*N*		*T*	
	r	*p*	*r*	*p*
f2	0.64	0.00	-0.22	0.27
F2	0.86	<.001	-0.20	0.31
F3	0.60	0.00	0.02	0.90
F4	0.57	0.00	-0.04	0.84
Mi2	0.75	<.001	-0.07	0.72
Ml2	0.46	0.03	0.11	0.58
Mc2	0.37	0.06	0.06	0.78
Mi3	0.40	0.05	-0.05	0.81
Ml3	0.26	0.21	-0.09	0.66
Mc3	0.54	0.01	-0.37	0.06

N is category abundance, *T* is annual mean shelf bottom temperature, *r* is correlation coefficient, and *p* is significance level. D95 is the minimum number of stations occupied by 95% of a specific category abundance

Table 2. D95 regression results

Category	Total R^2	Partial R^2			*p*: AC(1)	
		T	*N*	*Unaccounted*	*T*	*N*
f2	0.51	0.06	0.17	0.28	0.04	<0.01
F2	0.81	0.07	0.56	0.18	0.03	<0.01
F3	0.45	0.04	0.16	0.25	0.07	<0.01
F4	0.48	0.08	0.15	0.26	0.01	<0.01
Mi2	0.56	-	0.56	-	0.41	<0.01
Ml2	0.36	0.05	0.09	0.22	0.28	0.06
Mc2	0.14	-	0.14	-	0.32	0.04
Mi3	0.16	-	0.16	-	0.31	0.09
Ml3	0.00	-	-	-	0.34	0.18
Mc3	0.30	-	0.30	-	0.05	<0.01

N is category abundance, *T* is annual mean shelf bottom temperature, *Unaccounted* is interaction of abundance and temperature, *p*: AC(1) is significance level for regression coefficients of linear regressions with first order autocorrelation in the error. Dashes indicate nonsignificant results. All significant regression coefficients are positive for abundance and negative for temperature. D95 is the minimum number of stations occupied by 95% of a specific category abundance.

increased slightly from f2 to F2, then decrease from F2 to F3,with a sharp drop from F3 to F4. F4 values are quite small with a mean value of 4. Male D95 values increase from Mi2 to Ml2 but Mc2 have more variable values and a lower mean value (63) relative to Ml2 (72), possibly because of fishery removals. Shell 3 males have larger D95 values than their shell 2 counterparts of the same size class, especially between intermediate and large males, which contrast sharply with trends between F2, F3, and F4. D95 is significantly correlated with abundance for all categories except for Ml3 and Mc2 ($p = 0.06$) (Table 1). F2 ($r = 0.86$) and Mi2 ($r = 0.75$) have the largest correlation values. No significant correlations were found between D95 and temperature (with Mc3 almost significant, $p = 0.06$). Total variation explained (R^2 values) from the simple linear

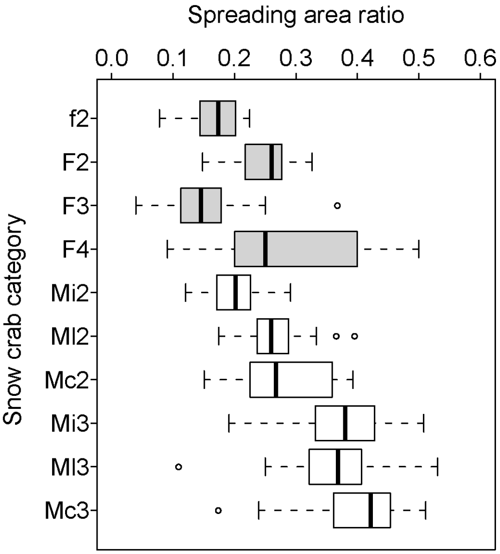

Figure 4. Boxplot summaries of 1982-2008 spreading area ratios (spreading area to total occupied area). Female values in gray, males white.

regressions range from 0 for Ml3 (neither temperature nor abundance were significant) to 0.81 for F2 (Table 2). For all female categories abundance explains a significant amount of variation in D95 values relative to temperature. Abundance was a significant explanatory variable for all male categories except for Ml3, and temperature was not significant for any male categories except for Ml2. For all categories having temperature as a significant covariate, the amount of variation explained by temperature ranged from 12 to 60% of total variation explained. The lag 1 autocorrelation parameters were significant ($p < 0.05$) for all the autoregressive regressions with a value range of 0.30 to 0.44 (results not shown). Accounting for autocorrelation changed the results slightly relative to the simple linear regressions, with temperature becoming nonsignificant for F3 ($p = 0.07$) and Ml2 ($p = 0.28$) and becoming marginally significant for Mc2 ($p = 0.05$) (Table 2).

Spreading area ratios

Spreading area ratios increase from f2 to F2, then decrease to F3, but then increase strongly for F4 (Fig. 4). F4 have the largest range of values of all female and male categories. The spreading area ratio values for F4 indicate these females become more evenly distributed among occupied areas than F3 females; however, the variability of values relative to the other crab categories indicate that these values may be more a function of the quite small values of occupied area for these females. Male

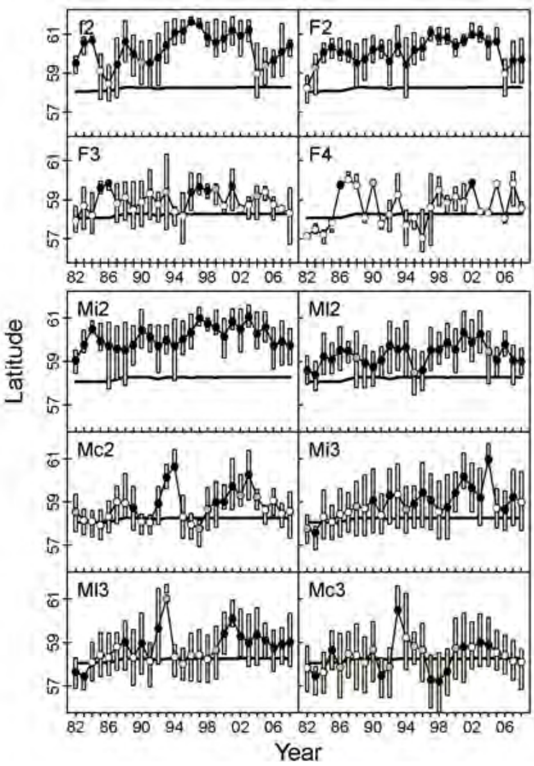

Figure 5. Results of significance testing of latitude distributions (black circle, $p < 0.01$; gray circle, $p < 0.05$; open circle, $p > 0.05$). Boxes are interquantile ranges of distributions. Thick black line is mean survey latitude. Top: female results. Bottom: male results.

spreading area ratio values increase across shell 2 categories; male shell 3 values are similar across size categories but generally larger than their shell 2 counterparts of the same size and larger than female values.

Latitude distributions

Females show a consistently more southern latitude distribution from f2 to F2 to F3 categories (Fig. 5). F2 and f2 occupy significantly different latitude distributions than the mean latitude distributions. F3 latitude centroids are mostly more northern than the mean survey latitude but not always significantly so. F4 depth distributions show the most variability with large interannual fluctuations. Noticeably, some years the F4 latitude centroid appears much different from the mean survey latitude but not significantly so. This phenomenon is likely due to the

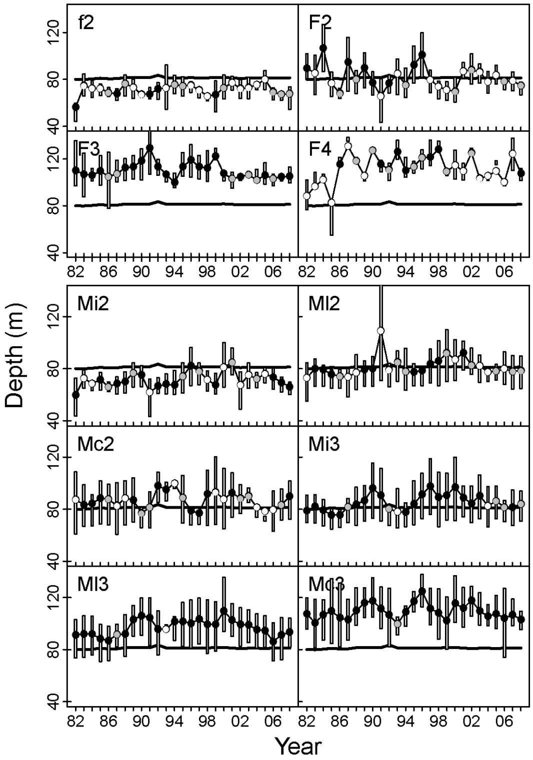

Figure 6. Results of significance testing of depth distributions (black circle, $p < 0.01$; gray circle, $p < 0.05$; open circle, $p > 0.05$). Boxes are interquantile ranges of distributions. Thick black line is mean survey depth. Top: female results. Bottom: male results.

relatively low number of occupied stations by these females as the randomization test produces fewer significant results as the occupied area decreases. Two trends within these latitude distributions are of particular interest. The first is that the late 1990s–early 2000s was a time of particularly northern latitude distributions for all females. However, a large drop in latitude distribution occurred from 2003 to 2004 for f2, which was followed by a similar change in F2 in 2005-2006. A sudden drop is not noticeable for F3 and F4, though these females exhibited less pronounced northward shifts in distributions compared to f2 and F2.

Mi2, Ml2, and Mc2 exhibit similar trends to f2, F2, and F3 females, with a consistent decrease in latitude between categories. Shell 3 males (Mi3, Ml3, and Mc3) have more widely distributed latitude distribution relative to shell 2 males (as seen by the consistently larger interquantile ranges). Mi3 and Ml3 appear to have similar latitude distributions while Mc3 have the most southern distributions. The noticeable drop in latitude seen for f2 and F2 around 2003-2006 are not evident in the shell 2 males (the closest in age to those females) but a more gradual decrease in latitude distribution is present. The large drop in latitude distribution for Mi3 from 2004 to 2005 appears to be a part of a variable spike and then drop in latitude. An obvious trend seen in males but not females is the large increase in latitude distribution in the early 1990s for Mc2, Ml3, and Mc3; this trend is not seen in the other male categories. The similarity of this spike between the different categories indicates this is not likely a chance sampling event. The lack of similar trends in the smaller and younger males indicates the potential for harvest removals as a mechanism responsible for this trend.

Depth distributions

Female depth distributions consistently shift ontogenetically to deeper waters from f2 to F2 to F3 (Fig. 6). F4 distributions are more variable but appear quite similar to F3 females; the occurrence of nonsignificant differences between occupied depth distributions and mean depth values even when large differences are apparent is again likely due to the low number of occupied stations by these females influencing the findings of the randomization tests. F3 and f2 have reasonably consistent depth distributions.

Mi2 has the most shallow and most narrow male depth distribution. Ml2, Mc2, and Mi3, have similar depth distributions; Ml3 has an intermediate distribution between those males and Mc3 males, which have the deepest distributions. Male depth distributions have different dynamics than for females. Large overlap in depth distributions occurs between most male categories. While females have two general categories of depth distributions, f2-F2 and F3-F4 distributions, males have broader depth distributions with more gradual ontogenetic changes. Only Mc3, the largest and oldest males, have depth distributions most similar to F3 and F4 females.

Temperature distributions

F2 and f2 females occupy significantly colder temperatures than the annual mean on the shelf while F3 and F4 distributions are typically centered around the mean temperature (Fig. 7). Analogous to female depth distributions, female temperature distributions have two categories: a colder distribution for f2 and F2 and a warmer distribution for F3 and F4. All male categories except for Mc3 generally occupy significantly colder temperatures than the mean, though all male distributions appear correlated with mean temperature values. Mi2 have the most similar temperature distributions to f2 and F2. Mc3 distributions appear most similar to the F3 and F4 temperature distributions.

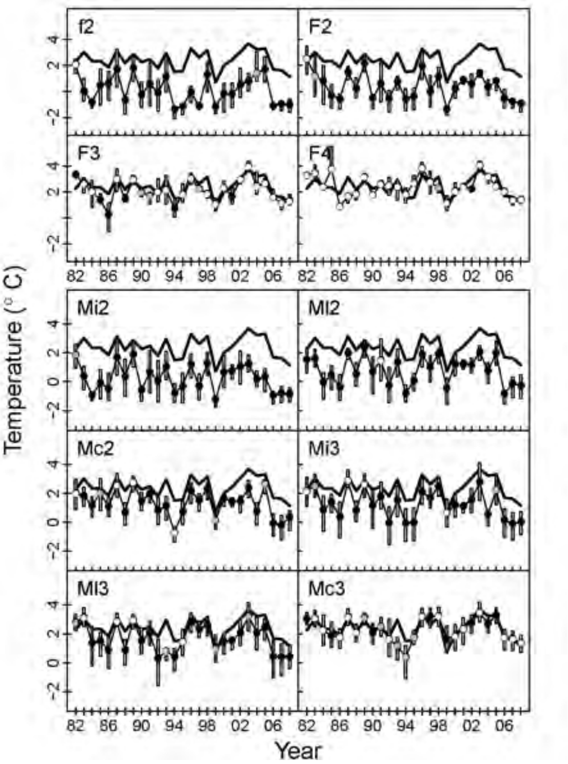

Figure 7. Results of significance testing of temperature distributions (black circle, $p < 0.01$; gray circle, $p < 0.05$; open circle, $p > 0.05$). Boxes are interquantile ranges of distributions. Thick black line is mean survey temperature. Top: female results. Bottom: male results.

Regression models

Results from the ROC analysis indicate that the P-A model performed well (Table 3). Mean AUC values (the average for each category over the 1982-2007 time period) ranged from 0.85 (F4) to 0.94 (F2). The mean optimal probability value that resulted in the maximization of correct number of predicted absences-presences was near 0.50 for all categories, though values ranged approximately between 0.30 and 0.65. The range of annual percent correct ranged from the mid 70s to the low 90s across most categories. The amount of deviance explained by each significant variable in the final model was calculated with ANOVA and is used as an approximate measure of the amount of variation that each significant variable explains. The models for the youngest crab categories for each

Table 3. Results of the ROC analysis.

Category	AUC (mean)	AUC (range)	Optimal prob. (mean)	Optimal prob. (range)	% Correct (mean)	% Correct (range)
f2	0.92	0.83 - 0.97	0.51	0.30 - 0.64	0.87	0.81 - 0.95
F2	0.94	0.91 - 0.98	0.48	0.28 - 0.74	0.90	0.86 - 0.95
F3	0.92	0.87 - 0.95	0.52	0.41 - 0.66	0.88	0.83 - 0.91
F4	0.85	0.50 - 0.95	0.57	0.13 - 0.74	0.96	0.91 - 0.99
Mi2	0.93	0.83 - 0.97	0.51	0.34 - 0.66	0.86	0.76 - 0.91
Ml2	0.92	0.79 - 0.95	0.50	0.36 - 0.64	0.86	0.73 - 0.90
Mc2	0.89	0.77 - 0.95	0.51	0.34 - 0.61	0.84	0.76 - 0.91
Mi3	0.90	0.85 - 0.96	0.47	0.30 - 0.62	0.83	0.77 - 0.89
Ml3	0.92	0.86 - 0.95	0.50	0.36 - 0.67	0.85	0.79 - 0.91
Mc3	0.90	0.83 - 0.95	0.50	0.38 - 0.66	0.84	0.78 - 0.91

ROC = receiver operating characteristic. AUC = area under the ROC curve. See text for further definitions.

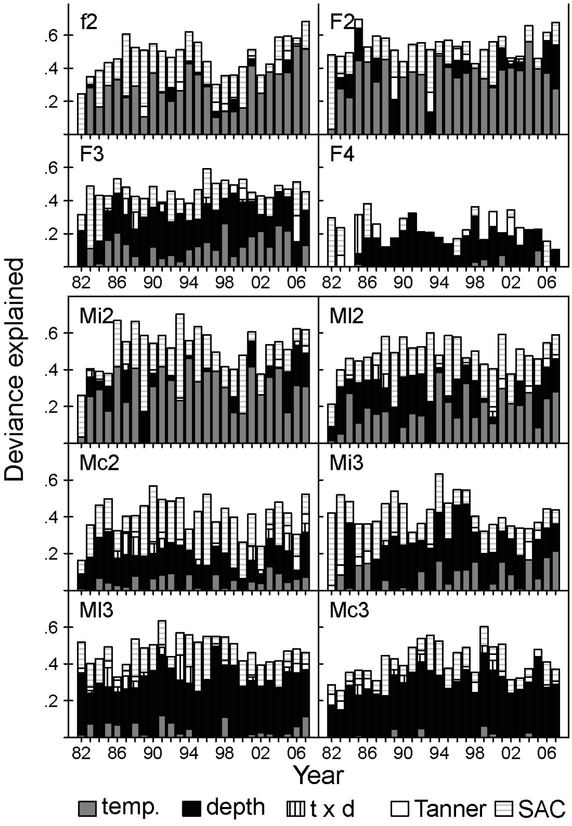

Figure 8. Deviance explained for presence-absence regression model by temperature (dark gray), depth (black), temperature-depth interaction (t × d, vertical lines), Tanner crab abundance (white), and spatial autocorrelation (SAC, horizontal gray lines). Top: female results. Bottom: male results.

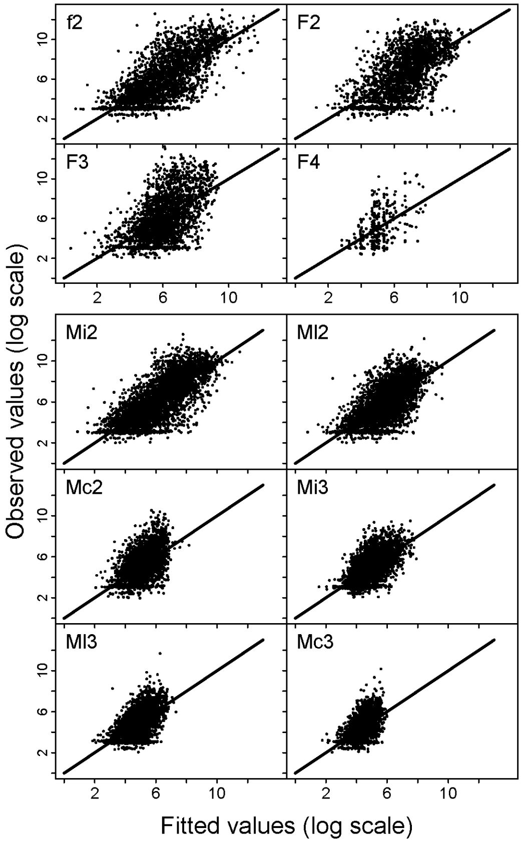

Figure 9. Observed versus fitted residuals for abundance regression model by crab category. Residuals for all years combined. Top: female results. Bottom: male results.

sex (f2, F2, Mi2, Ml2) had the largest amount of deviance explained with a gradual decrease across the other male categories but with a large drop from F3 to F4 (Fig. 8). Temperature explains the most deviance for the same younger crab categories, but becomes much less important for the older crab categories with depth explaining much more deviance for older crabs of both sexes, especially for Ml3 and Mc3. Spatial autocorrelation explains a substantial portion of deviance for most categories for most years except for F4. The temperature-depth interaction explains significant deviance in a sporadic number of years across categories, though mostly for males. Abundance of Tanner crab explains only a small amount of deviance in a sporadic number of years across categories.

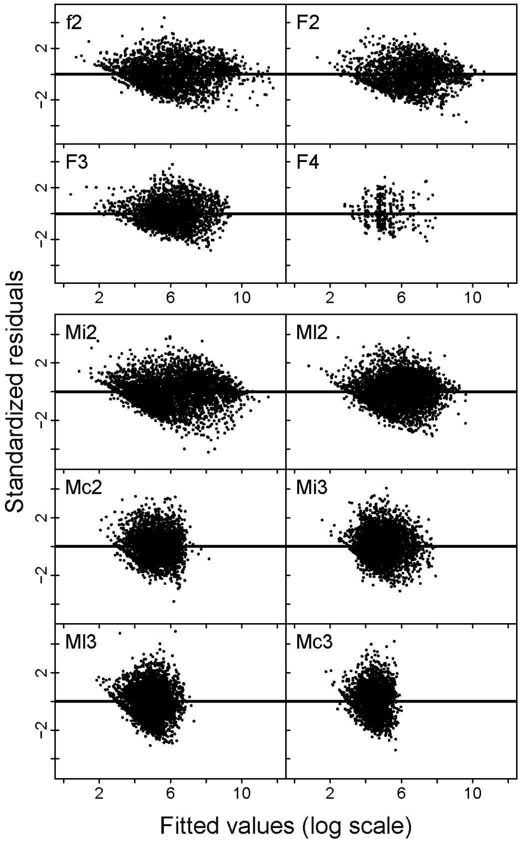

Figure 10. Fitted values versus standardized residuals for abundance regression model by crab category. Residuals for all years combined. Top: female results. Bottom: male results.

Plots of observed vs. fitted values (Fig. 9) and standardized residuals vs. fitted values (Fig. 10) were used to assess the performance of the abundance regression models. The standardized residuals indicate lack of a major trend but do show the models overestimate smaller abundances (corresponding mostly to stations where only one crab for the specified category was captured) and underestimate larger abundances. Even with these trends, however, the models appear to perform satisfactorily. The amount of deviance explained is generally less than for the P-A models, especially for the older categories (Fig. 11). F4 has significant covariates for only a handful of years. Similar to the P-A models, temperature is the dominant explanatory variable for

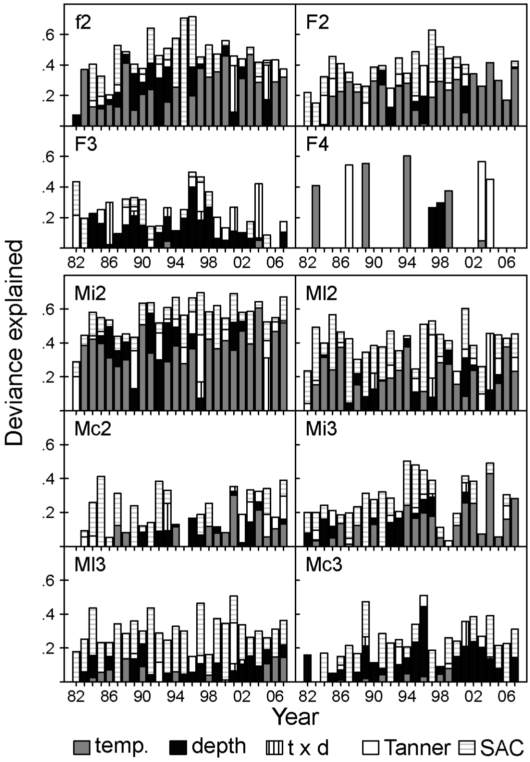

Figure 11. Deviance explained for abundance regression model by temperature (gray), depth (black), temperature-depth interaction (t × d, vertical lines), Tanner crab abundance (white), and spatial autocorrelation (SAC, horizontal gray lines). Top: female results. Bottom: male results.

f2, F2, and Mi2 but mostly drops out as an explanatory variable for F3 relative to the P-A model. For the male categories other than Mi2 and Ml2, temperature still explains only a small portion of deviance as in the P-A models. Depth in general becomes much less important in the abundance models while the amount of deviance explained by spatial autocorrelation increases.

The values of regression coefficients for temperature, depth, and Tanner crab abundance when they occurred in the final model are summarized with boxplots in Fig. 12. For both the P-A and abundance models, temperature coefficients are most strongly negative (i.e., temperature is inversely related to probability of occurrence or abundance) for the younger crabs of both sexes and then increase in

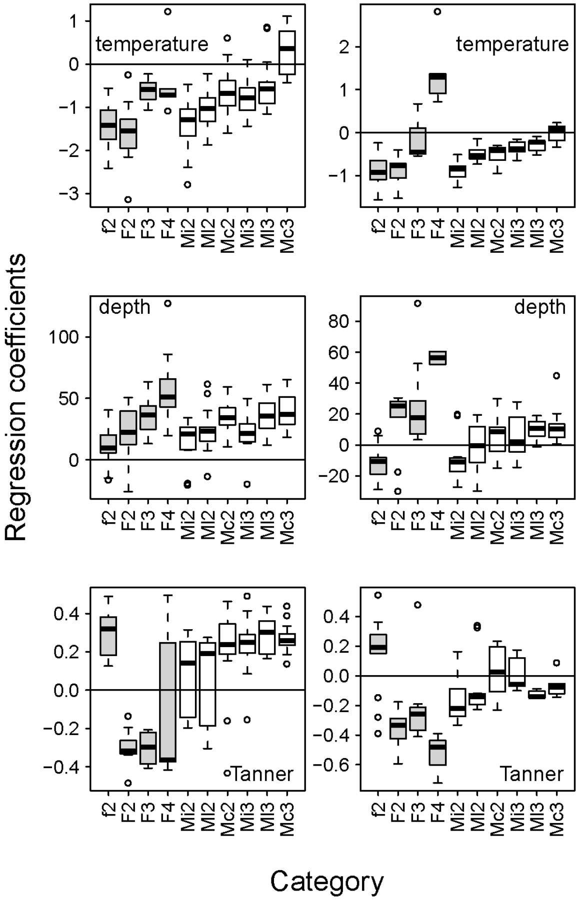

Figure 12. **Boxplots of regression coefficients for presence-absence (left column) and abundance (right column) regression models for final models that contained temperature, depth, and Tanner crab biomass as explanatory variables. Female values in gray, males in white.**

value across older categories. Depth coefficients show a similar trend for both models, increasing in value from younger to older crabs of each sex, indicating a stronger association of older crabs with deeper depth. Interpretation of the coefficients for Tanner crab abundance is not straightforward; except for f2, female crabs have mostly negative coefficients for both model types but males have mostly positive for the P-A model and mostly negative for the abundance model. These trends may indicate a mostly negative relationship between Tanner crabs and female snow crabs, while males have more association with Tanner crabs but do not occur in high abundances in their presence.

Discussion

This study both confirms previous findings regarding snow crab spatial distributions (e.g., the more dispersed distributions of older males relative to females by Zheng et al. 2001), and provides a suite of quantitative and statistical analyses to broaden and clarify earlier insights. The time-series of D95 values and spreading area ratio values highlight the different spatial dynamics of males and females as well as ontogenetic stages within sexes. Females are maximally dispersed as newly mature shell 2 females (F2). Given that F2 are likely undergoing a substantial cross-shelf migration at their time of capture from the upslope habitat of f2 and F2 to the down-slope habitat of F3 and F4, the large dispersion of F2 relative to f2 follows. The decrease in D95 values and spreading area ratio values from F2 to F3 indicates a shift from a more dispersed to more aggregated spatial distribution within approximately one to two years. Natural mortality does not appear to be a significant factor if it can be assumed that males and females have similar natural mortality rates during the transition between shell 2 and shell 3 conditions, because male dispersion increases between these shell conditions (e.g., from Mi2 to Mi3).

Environmental forcing or behavioral mechanisms are two potential explanations for the decrease in D95 values and spreading area from F2 to F3 (i.e., the apparent increased aggregation from F2 to F3). Temperature is a possible environmental mechanism but does not appear to be an important factor because it is not significantly correlated with F3 D95 values, does not explain substantial variation in the F3 D95 simple linear regressions, is a nonsignificant variable in the F3 regression with autocorrelation, and while temperature is a consistent though minor explanatory variable in the spatial regression models for F3, it is mostly a nonsignificant variable in the abundance models. Behavioral mechanisms may be another plausible explanation for the changes in D95 values and spreading area from F2 to F3. Snow and Tanner crabs and other spider crab species are known to be gregarious. Podding behavior of female Tanner crabs in the Gulf of Alaska, and of mature female snow crabs in eastern Canada, have been documented during the mating season with mature males congregating around the pods (Stevens et al. 1993). While the summer survey occurs after the winter-spring mating period, the aggregation caused by podding, if it occurs, still may be prevalent at the time of the survey.

Whatever the mechanisms responsible for the aggregation of F3 females, these same mechanisms are not operating on shell 3 males, which all have higher D95 and spreading area values than their shell 2 counterparts of the same size class and much higher values than for F3 females. A plausible expectation is that shell 3 mature males and mature females have the same spatial dynamics (e.g., same D95 and spreading area trends) in response to increased mating probabilities. One possible explanation is that the annual "snapshot" that the NMFS survey provides is an incomplete view of male and female spatial distributions. If males undergo a seasonal migration between the summer survey to be in proximity of the mature females during the winter-spring breeding period, then the male distribution at the time of mating may be more congruent with the female distribution than is observed from the summer survey. Tagging studies could provide useful information to resolve this issue.

Analyses of the latitude, depth, and temperature distributions emphasize the relatively rapid shift for the female population from more northern, shallower, and colder waters of the middle shelf to the more southern, deeper, and warmer waters of the outer shelf. The male population does not have such a pronounced shift but a more gradual dispersal of longer duration across the shelf. Only Ml3 and Mc3 males have distributions similar to F3 and F4 females. The age difference between these males and F3 females is not known, but it probably spans 2-6 years (by assuming shell 3 crabs are at least one year past maturation and synthesizing growth data from Hebert et al. 2002 and Comeau et al. 1998). Thus, it takes males of the same year class longer than females to reach the outer shelf. While some aspects of crab distributions appear associated with mean shelf temperature (some female D95 values), the shift to southern, deeper, and warmer waters appears persistent over a range of shelf temperature regimes.

Latitudinal distributions showed the northern shift in the population in the 1980s and 1990s previously noted by Zheng et al. (2001) and Orensanz et al. (2004), but more recent trends for 2006-2008 indicate a southward shift. Orensanz et al. (2004) speculated that the latitudinal increase of the snow crab population in the 1980s and 1990s resulted from a decrease in cold water settlement habitat. Mueter and Litzow (2008) described a northward shift of the eastern Bering Sea demersal community in recent decades and attributed it to warmer bottom temperatures of the eastern Bering Sea. If bottom temperatures are an important determinant of spatial recruitment patterns, then the early benthic distributions will likely continue to shift variably along the northwest-southeast shelf axis as seen for 1982-2008 (using f2 as a rough proxy for settlement distributions). However, the cross-shelf movement patterns do not appear to be strongly influenced by latitudinal distributions. Further, ontogenetic and sex-specific patterns in spatial distributions were persistent through a variety of bottom temperature regimes and abundance levels (e.g., the relative constancy of the depth distributions). Whether during "cold" or "warm" years or during years of low abundances or high abundances, younger crabs are found consistently in shallower depths on the middle shelf and older crabs are found in deeper and more southern waters.

Analysis of spatial distributions from 1982 to 2008 revealed that snow crab response to environmental variability and climate change will likely differ from that of eastern Bering Sea groundfish species and other invertebrates. Spencer (2008), Ciannelli and Bailey (2005), and Wyllie-Echeverria and Wooster (1998) correlated variable interannual north-south shifts in distributions of eastern Bering Sea species with the extent of the summer cold pool (the shelf region with bottom temperatures <2°C). For snow crab, however, major interannual shifts of the population do not typically occur, though spatial settlement patterns are likely variable due to climate effects and population abundances and distributions. Using multivariate analyses of benthic invertebrate survey data, Yeung and McConnaughey (2006) correlated several expansions of the "offshore" eastern Bering Sea epibenthic invertebrate community into more shallow waters with periods of warmer temperatures. Little evidence indicates snow crab movement to more shallow depths, so the expansion of the offshore epibenthic community into more shallow waters during warmer years documented by Yeung and McConnaughey (2006) would not appear to have involved snow crab.

Bottom temperatures have been one of the principal metrics in discussion of impacts of climate change and environmental variability on the snow crab and other eastern Bering Sea benthic and demersal species (Orensanz et al. 2004, Mueter and Litzow 2008). The spatial regression models indeed showed that bottom temperatures were the dominant covariate of the distributions of younger crabs but were not as important for older crabs. Field and laboratory studies have indicated upper and lower temperature thresholds and preferences for snow crab, but how these may change ontogenetically have not been described in detail. Dionne et al. (2003) showed how temperature preferences in a laboratory increased from 0.0-1.5°C to 1.0-4.5°C for very early benthic snow crab instars (<16 mm carapace width) but these crabs were much younger (within two years of benthic settlement) and smaller than those analyzed in this study. Foyle et al. (1989) calculated a negative energy budget for water temperatures above 7.0°C. Conversely, very cold bottom temperatures have been implicated in the decline of a snow crab population. Taylor et al. (1994) concluded that the snow crab population at the Avalon Peninsula in southeastern Newfoundland collapsed due to the mean bottom temperature declining from –0.6°C to –1.4°C, which interrupted the molt cycle of the snow crab and caused cessation of growth. Additional physiological and temperature preference studies could further refine knowledge of suitable temperature ranges. Such knowledge will be critical in assessment of climate change impacts on the snow crab.

The snow crab fishery is mostly centered in the southwest portions of the eastern Bering Sea shelf (Turnock and Rugolo 2008), and the persistent southwesterly ontogenetic movement pattern explains why commercial-size males are more common in that region and the spatial distribution of the fishery. While the spatial extent of the fishery can be constrained by ice cover, even in years not constrained by ice cover the majority of the catch occurs south of 58.5°N, in the southern portion of the snow crab range (Turnock and Rugolo 2008). Fishing locations are not only determined by the crab distributions but also by financial decisions of the fleet; the principal fishing port of Dutch Harbor and the major processing facilities are located in the Aleutians and along the Alaska Peninsula on the southern border of the eastern Bering Sea, providing an economic incentive for the fishery to operate in more southern waters. Given the distributions of the fishery of the past two decades (Zheng et al. 2001, Turnock and Rugolo 2008) through varying abundance and temperature regimes, the spatial distributions of the fishery will not likely vary considerably in the near future and remain centered below 58.5°N and on the deeper portions of the shelf.

The significance of spatial-autocorrelation as an explanatory variable in the regression models strongly implies that other unexamined variables are important in explaining spatial distributions. Variables related to physical (e.g., substrate composition) and biogenic habitat (e.g., biomass of other benthic organisms) may also be important and their influences should be examined in future spatial distribution models. A large northward spike in distribution of males vulnerable to the fishery (large and commercial-size males) occurred during the time of large harvests in the early 1990s. This observation should be explored further to determine whether fishery removals are correlated to spatial shifts in distribution. Fishery removals were not considered in this analysis. Behavioral mechanisms such as intra-species competition may be important, though examination of such mechanisms on spatial distributions of crabs entails more complex, mechanistic models that are beyond the scope of statistical regression models (e.g., Huse et al. 2004).

This study provides baseline analyses to further spatial and mechanistic modeling of the eastern Bering Sea snow crab. Before detailed spatial and mechanistic models can be constructed, patterns in the available data need to be well described and elucidated (Grimm et al. 2005). Ongoing work is focused on spatial population modeling and how benthic spatial distributions and fishing removals influence population dynamics and potential management scenarios (e.g., Miller 2003). Integrating behavioral mechanisms will require further field and experimental studies but may be a fruitful research avenue to understand spatial distributions and their impact on population dynamics.

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References

Bowler, D.E., and T.G. Benton. 2005. Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. Biol. Rev. 80:205-225. doi:10.1017/S1464793104006645

Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES J. Mar. Sci. 52:1-10. doi:10.1016/1054-3139(95)80010-7

Brynjarsdóttir J., and G. Stefánsson. 2004. Analysis of cod catch data from Icelandic groundfish surveys using generalized linear models. Fish. Res. 70:195-208. doi:10.1016/j.fishres.2004.08.004

Ciannelli, L., and K.M. Bailey. 2005. Landscape dynamics and underlying species interactions: The cod-capelin system in the Bering Sea. Mar. Ecol. Prog. Ser. 291:227-236. doi:10.3354/meps291227

Ciannelli, L., P. Fauchald, K.S. Chan, V.N. Agostini, and G.E. Dingsør. 2008. Spatial fisheries ecology: Recent progress and future prospects. J. Mar. Syst. 71:223-236. doi:10.1016/j.jmarsys.2007.02.031

Comeau, M., G.Y. Conan, F. Maynou, G. Robichaud, J.C. Therriault, and M. Starr. 1998. Growth, spatial distribution, and abundance of benthic stages of the snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland, Canada. Can. J. Fish. Aquat. Sci. 55:262-279. doi:10.1139/cjfas-55-1-262

Conan, G.Y., and M. Comeau. 1986. Functional maturity and terminal molt of male snow crab, *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci. 43:1710-1719. doi:10.1139/f86-214

Conners, M.E., A.B. Hollowed, and E. Brown. 2002. Retrospective analysis of Bering Sea bottom trawl surveys: Regime shift and ecosystem reorganization. Prog. Oceanogr. 55:209-222. doi:10.1016/S0079-6611(02)00079-4

De Grave, S., N.D. Pentcheff, S.T. Ahyong, T.Y. Chan, K.A. Crandall, P.C. Dworschak, D.L. Felder, R.M. Feldmann, C.H.J.M. Fransen, L.Y.D. Goulding, R. Lemaitre, M.E.Y. Low, J.W. Martin, P.K.L. Ng, C.E. Schweitzer, S.H. Tan, D. Tshudy, and R. Wetzer. 2009. A classification of living and fossil genera of decapod crustaceans. Raff. Bull. Zool. Suppl. 21:1-109.

Dionne, M., B. Sainte-Marie, E. Bourget, and D. Gilbert. 2003. Distribution and habitat selection of early benthic stages of snow crab (*Chionoecetes opilio*). Mar. Ecol. Prog. Ser. 259:117-128. doi:10.3354/meps259117

Dormann, F.C., J.M. McPherson, M.B. Araújo, R. Bivand, J. Bolliger, G. Carl, R.G. Davies, A. Hirzel, W. Jetz, W.D. Kissling, I. Kühn, R. Ohlemüller, P.R. Peres-Neto, B. Reineking, B. Schröder, F.M. Schurr, and R. Wilson. 2007. Methods to account for spatial autocorrelation in the analysis of distributional species data: A review. Ecography 30:609-628. doi:10.1111/j.2007.0906-7590.05171.x

Ernst, B., J.M. Orensanz, and D.A. Armstrong. 2005. Spatial dynamics of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. Can. J. Fish. Aquat. Sci. 62:250-268. doi:10.1139/f04-201

Fonseca, D.B., B. Sainte-Marie, and F. Hazel. 2008. Longevity and change in shell condition of adult male snow crab *Chionoecetes opilio* inferred from dactyl wear and mark-recapture data. Trans. Am. Fish. Soc. 137:1029-1043. doi:10.1577/T07-079.1

Fortin, M.J., and M.R.T. Dale. 2005. Spatial analysis: A guide for ecologists. Cambridge University Press, Cambridge. 356 pp. doi:10.1017/CBO9780511542039

Foyle, T.P., R.K. O'Dor, and R.W. Elner. 1989. Energetically defining the thermal limits of the snow crab. J. Exp. Biol. 145:371-393.

Fox, J. 2002. An R and S-plus companion to applied regression. Sage, Thousand Oaks, California. 312 pp.

Griffith, D.A., and P.R. Peres-Neto. 2006. Spatial modeling in ecology: The flexibility of eigenfunction spatial analyses. Ecology 87:2603-2613. doi:10.1890/0012-9658(2006)87[2603:SMIETF]2.0.CO;2

Grimm, V., E. Revilla, U. Berger, F. Jeltsch, W.M. Mooij, S.F. Railsback, H. Thulke, J. Weiner, T. Wiegand, and D.L. DeAngelis. 2005. Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. Science 310:987-991. doi:10.1126/science.1116681

Hebert, M., K. Behalima, G. Miron, and M. Moriyasu. 2002. Moulting and growth of male snow crab, *Chionoecetes opilio* (O. Fabricius, 1788) (Decapoda, Majidae) in the southern Gulf of St. Lawrence. Crustaceana 75:671-702. doi:10.1163/156854002760202679

Huse, G., G.O. Johansen, B. Bogstad, and H. Gjosaeter. 2004. Studying spatial and tropic interactions between capelin and cod using individual based modeling. ICES J. Mar. Sci. 6:1201-1213. doi:10.1016/j.icesjms.2004.06.011

Jensen, O.P., and T.J. Miller. 2005. Geostatistical analysis of the abundance and winter distribution patterns of the blue crab *Callinectes sapidus* in Chesapeake Bay. Trans. Am. Fish. Soc. 134:1582-1598. doi:10.1577/T04-218.1

Jensen, O.P., R. Seppelt, T.J. Miller, and L.J. Bauer. 2005. Winter distribution of blue crab (*Callinectes sapidus*) in Chesapeake Bay: Application and cross-validation of a two-stage generalized additive model (GAM). Mar. Ecol. Prog. Ser. 299:239-255. doi:10.3354/meps299239

Miller, T.J. 2003. Incorporating space into models of blue crab populations. Bull. Mar. Sci. 72:567-588.

Moriyasu, M., and C. Lanteigne. 1998. Embryo development and reproductive cycle in the snow crab, *Chionoecetes opilio* (Crustacea: Majidae), in the southern Gulf of St. Lawrence, Canada. Can. J. Zool. 76:2040-2048. doi:10.1139/cjz-76-11-2040

Mueter, F.J., and M.A. Litzow. 2008. Warming climate alters the demersal biogeography of a marginal ice sea. Ecol. Appl. 18:309-320. doi:10.1890/07-0564.1

Nakken, O., and A. Raknes. 1987. The distribution and growth of northeast arctic cod in relation to bottom temperatures in the Barents Sea, 1978-1984. Fish. Res. 5:243-252. doi:10.1016/0165-7836(87)90044-0

Orensanz, J.M., B. Ernst, and D.A. Armstrong. 2007. Variation of female size and stage at maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering Sea. J. Crust. Biol. 27:576-591. doi:10.1651/S-2790.1

Orensanz, J., B. Ernst, D.A. Armstrong, P. Stabeno, and P. Livingston. 2004. Contraction of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: An environmental ratchet? CalCOFI Reports 45:65-79.

Otto, R.S. 1998. Assessment of the eastern Bering Sea snow crab, *Chionoecetes opilio*, stock under the terminal molting hypothesis. In: Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Can. Spec. Publ. Fish. Aquat. Sci. 125:109-124.

Overland, J., and P.J. Stabeno. 2004. Is the climate of the Bering Sea warming and affecting the ecosystem? EOS 85:309-316. doi:10.1029/2004EO330001

Pelletier, D., and S. Mahevas. 2005. Spatially explicit fisheries simulation models for policy evaluation. Fish Fish. 6:307-349. doi:10.1111/j.1467-2979.2005.00199.x

Perry, R.I., and S.J. Smith. 1994. Identifying habitat associations of marine fishes using survey data: An application in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 51:589-602. doi:10.1139/f94-061

Pyper, B.J., and R.M. Peterman. 1999. Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon, 1967-1997. Can. J. Fish. Aquat. Sci. 56:1716-1720. doi:10.1139/cjfas-56-10-1716

Rose, G.A., B. deYoung, D.W. Kulka, S.V. Goddard, and G.L. Fletcher. 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): A view from the ocean. Can. J. Fish. Aquat. Sci. 57:644-664. doi:10.1139/cjfas-57-3-644

Rugolo, L.J., D. Pengilly, R. MacIntosh, and K. Gravel. 2005. Reproductive dynamics and life- history of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. Final completion report to the Alaska Department of Fish and Game under NOAA award NA17FW1274. National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle.

Sainte-Marie, B., S. Raymond, and J.C. Brethes. 1995. Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura, Majidae). Can. J. Fish. Aquat. Sci. 52:903-924. doi:10.1139/f95-091

Somerton, D.A. 1981. Life history and population dynamics of two species of Tanner crab, *Chionoecetes bairdi* and *C. opilio* in the eastern Bering Sea with implications for the management of the commercial harvest. Ph.D. thesis, University of Washington, Seattle. 220 pp.

Sousa, P., R. Lemos, M. Gomes., and M. Azevedo. 2007. Analysis of horse mackerel, blue whiting, and hake catch data from Portuguese surveys (1989-1999) using an integrated GLM approach. Aquat. Living Resour. 20:105-116. doi:10.1051/alr:2007021

Spencer, P. 2008. Density-independent and density-dependent factors affecting temporal changes in spatial distributions of eastern Bering Sea flatfish. Fish. Oceanogr. 15:396-410. doi:10.1111/j.1365-2419.2008.00486.x

Stefánsson, G. 1996. Analysis of groundfish survey abundance data: Combining the GLM and delta approaches. ICES J. Mar. Sci. 53:577-588. doi:10.1006/jmsc.1996.0079

Stevens, B.G., W.E. Donaldson, J.A. Haaga, and J.E. Munk. 1993 . Morphometry and maturity of paired Tanner crabs, *Chionoecetes bairdi*, from shallow- and deepwater environments. Can. J. Fish. Aquat. Sci. 50:1504-1516. doi:10.1139/f93-172

Swain, D.P., and H.P. Benoit. 2006. Change in habitat associations and geographic distribution of thorny skate (*Amblyraja radiata*) in the southern Gulf of St Lawrence: Density-dependent habitat selection or response to environmental change? Fish. Oceanogr. 2:166-182. doi:10.1111/j.1365-2419.2006.00357.x

Taylor, D.M., P.G. O'Keefe, and C. Fitzpatrick. 1994. A snow crab, *Chionoecetes opilio* (Decapoda, Majidae), fishery collapse in Newfoundland. Fish. Bull. 92:412-419.

Tilman, D., and P. Kareiva (eds.) 1997. Spatial ecology: The role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton.

Turnock, B.J., and L.J. Rugolo. 2008. Stock assessment of eastern Bering Sea snow crab (*Chionoecetes opilio*). Report to the North Pacific Fishery Management Council, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle. 81 pp.

Vining, I., and L.J. Watson. 1996. Application of kriging to trawl survey data to estimate red king crab distribution and abundance in Bristol Bay, Alaska. In: High latitude crabs: Biology, management, and economics. Alaska Sea Grant, University of Alaska Fairbanks, pp. 255-282.

Whittingham, M.J., P.A. Stephens, R.B. Bradbury, and R.P. Freckleton. 2006. Why do we still use stepwise modelling in ecology and behaviour? J. Anim. Ecol. 75:1182-1189. doi:10.1111/j.1365-2656.2006.01141.x

Wiens, J.A. 1976. Population responses to patchy environments. Ann. Rev. Ecol. Syst. 7:81- 120. doi:10.1146/annurev.es.07.110176.000501

Woillez, M., J.C. Poulard, J. Rivoirard, P. Petitgas, and N. Bez. 2007. Indices for capturing spatial patterns and their evolution in time with application to European hake (*Merluccius merluccius*) in the Bay of Biscay. ICES J. Mar. Sci. 64:537-550. doi:10.1093/icesjms/fsm025

Wyllie-Echeverria, T., and W.S. Wooster. 1998. Year-to-year variations in Bering Sea ice cover and some consequences for fish distributions. Fish. Oceanogr. 7:159-170. doi:10.1046/j.1365-2419.1998.00058.x

Yeung, C., and R.A. McConnaughey. 2006. Community structure of eastern Bering Sea epibenthic invertebrates from summer bottom-trawl surveys 1982 to 2002. Mar. Ecol. Prog. Ser. 318:47-62. doi:10.3354/meps318047

Zheng, J., and G.H. Kruse. 2006. Recruitment variation of eastern Bering Sea crabs: Climate- forcing or top-down effects? Prog. Oceanogr. 68:184-204.

Zheng, J., G.H. Kruse, and D.R. Ackley. 2001. Spatial distribution and recruitment patterns of snow crabs in the eastern Bering Sea. In: G.H. Kruse, N. Bez, A. Booth, M.W. Dorn, S. Hills, R.N. Lipcius, D. Pelletier, C. Roy, S.J. Smith, and D. Witherell (eds.), Spatial processes and management of marine populations. Alaska Sea Grant, University of Alaska Fairbanks, pp. 233-256.

Agnalt, A.-L., K.E. Jørstad, V.A. Pavlov, and E. Olsen. 2010. Recent Trends in Distribution and Abundance of the Snow Crab (*Chionoecetes opilio*) Population in the Barents Sea. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.23

Recent Trends in Distribution and Abundance of the Snow Crab (*Chionoecetes opilio*) Population in the Barents Sea

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Abstract

The snow crab (*Chionoecetes opilio*) is distributed in the Bering Sea (North Pacific) and the northwestern Atlantic, including Canada and West Greenland. A few specimens were first recorded in the northeast Atlantic in 1996. Since 2004 snow crabs have been recorded routinely during annual bottom-trawl surveys (winter and autumn) in the Barents Sea. These investigations confirmed previous fishery observations of snow crabs in the northern region of Goose Bank, but also detected snow crabs over a much broader geographic area. The crabs were found at depths of 40-380 m, with a majority between 100 and 300 m. In 2008, a total of 664 snow crabs were captured during the autumn survey, suggesting that the abundance is increasing. In total, about 40% of the snow crabs consisted of juveniles under 50 mm carapace width (CW), providing evidence for successful recruitment. These small-sized crabs were exclusively found in eastern Barents Sea, indicating this to be the main nursery area. Egg-bearing females have been found since 2004. The smallest female with extruded eggs measured 65 mm CW; all females >80 mm CW were ovigerous. Collectively, these data demonstrate the successful establishment of a snow crab population in the Barents Sea.

Comparative genetic studies are needed to identify the source population of this species introduction, and extensive sampling of size, sex, maturity status, distribution, and abundance are necessary to monitor the potential growth of this new snow crab population.

Introduction

The first five specimens (one female, four males) of snow crab (*Chionoecetes opilio*) in the Barents Sea were captured by Russian fishermen in the eastern Barents Sea (Goose Bank) in 1996. The sizes ranged from 41 mm carapace width (CW) to 123 mm CW; crabs were captured at depths from 100 to 280 m (Kuzmin et al. 1999). It is believed that the snow crab invaded the Barents Sea via ballast water from unknown areas where the species is commercially abundant (Kuzmin et al. 1999). Since 1996, additional crabs were reported, mainly as bycatch in bottom trawl fishery in the Barents Sea. Species identifications and samples have been collected during the annual bottom trawl surveys by the Institute of Marine Research (Norway) and the Polar Research Institute of Marine Fisheries and Oceanography (Russia) since 2004.

In the Barents Sea, another large-bodied crab species, the red king crab (*Paralithodes camtschaticus*) was successfully introduced from waters off the Kamtschatka Peninsula for purposes of establishing a new commercial fishery (Orlov and Ivanov 1978, Sundet and Hjelset 2002). Possible negative ecological consequences of the red king crab introduction are, however, poorly understood. In contrast, negative impacts of other introduced crab species, such as European green crab *(Carcinus maenas)*, have been documented in other regions of the world (e.g., Grosholz and Ruiz 1995, Griffen and Byers 2009).

As a precursor to studies of potential impacts of the non-native snow crab in the Barents Sea, the purpose of this paper is to summarize the distribution and abundance of snow crab from trawl surveys conducted during 2004-2008.

Materials and methods

Norway and Russia have established a long-term joint research and monitoring program of fishery resources in the Barents Sea, including annual hydroacoustic and bottom trawl surveys for demersal fish, mainly targeting Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). The combined surveys are conducted in autumn (August-September), with two or three large research vessels participating each year (*G.O. Sars, J. Hjort, F. Nansen,* or *Smolensk*) to cover this large geographic area. All surveys are conducted with a Campelen 1800 shrimp trawl with 80 mm (stretched) mesh size in the front, and a 20 mm codend with a 116 mm cover net (Alvsvåg et al. 2009). Norway also conducts a survey in winter (February-March). Annual survey effort has typically been 10-14 vessel-weeks and about 450 bottom-trawl hauls. Depth was recorded at all trawling stations. In some years (e.g., 2007) the survey area during winter was reduced mainly due to ice cover or administrative obstacles to gaining access to Russian waters. The autumn survey, on the other hand, covers almost the entire area of the Barents Sea (Stiansen and Filin 2008).

Crab abundance was estimated as number of crabs per nautical mile of trawl tow distance for each winter and autumn survey over 2004-2008. The observations obtained during the winter surveys over 2004-2006 were reported by Alvsvåg et al. (2009) and are mainly used here as reference for evaluating recent changes in the crab population. Snow crabs were identified based on morphological characteristics described by Jadamec et al. (1999). Since 2004, a large fraction of the crabs was frozen onboard and brought back to the laboratory in Bergen for further analysis. In the laboratory, CW and body weight were recorded to the nearest mm and gm, respectively. Sex was determined according to the shape of the abdomen (Jadamec et al. 1999). Brood development of egg-bearing female snow crabs was estimated using the criteria of Sainte-Marie (1993).

Results

The total annual number of captured snow crab in the Barents Sea steadily increased from 39 in 2004 to 720 in 2008, except in 2007 when only 66 crabs were captured (Table 1). In 2008, 93 of the trawl hauls captured snow crabs, and as many as 79 crabs were found in one trawl haul (Russian vessel) at 111 m depth, while 28 crabs (all >50 mm CW) were captured in a single trawl haul at the Central Bank (Norwegian vessel). Trends over time were consistent for both autumn and winter surveys, although fewer crabs were captured during winter surveys compared with autumn surveys. In general, one to three crabs were captured per nautical mile; however, in autumn 2008 catches averaged >11 crabs per nautical mile (Table 1). Snow crabs were captured at depths of 40-380 m, with the majority between 80 and 300 m depth (Fig. 1). During autumn 2008 crabs were found at bottom temperatures of 0.7-4.1 (Fig. 2). Although most snow crabs were captured in the eastern Barents Sea, a large number of crabs also were captured in the central Barents Sea. In 2007 most crabs were distributed in northeastern regions, whereas crabs were found over much larger areas in subsequent years, including south of Novaya Zemlya.

During 2004-2008 biological information was collected from 239 crabs (161 males and 78 females) by Norwegian surveys. In general, males were larger than females (Fig. 3). The largest female measured 93 mm CW, and the largest male was 136 mm CW. About 40% of the males were larger

Table 1. Total number of bottom-trawl stations at each survey, number of stations with captured snow crabs (*Chionoecetes opilio*), estimated number of crabs per nautical mile trawling (CPUE), and total number of crabs captured. Note that snow crabs were captured as bycatch in the surveys targeting cod and haddock.

Year, month	Number of stations	Number of stations with crabs	Number of crabs per nmi trawl (CPUE)	Number of crabs
2004 Feb-March	517	13	1.66	37
2004 Aug-Sep	825	1	2.00	2
2005 Feb-March	493	19	2.66	85
2005 Aug-Sep	646	3	3.06	5
2006 Feb-March	298	17	3.43	95
2006 Aug-Sep	663	21	2.24	31
2007 Feb-March	339	6	1.04	11
2007 Aug-Sep	581	23	2.83	55
2008 Feb-March	481	19	1.78	56
2008 Aug-Sep	412	74	11.32	664
2009 Feb-March	407	13	3.0	30

than 90 mm CW, but only two females were found at these sizes. A significant fraction of crabs of both sexes was small, between 10 to 30 mm CW. These small crabs were found during both February/March and August/September surveys in 2006 and 2008, respectively. Peaks in the overall size distribution occurred at 22 mm CW and 30 to 32 mm CW for both sexes.

Ovigerous females (N = 23) were found throughout the entire investigative period. Females with recently extruded eggs (bright orange in color) were captured during winter and autumn surveys, but females with eggs close to hatching (dark brown coloration) were found in February only. The smallest and largest female with extruded eggs measured 65 mm and 93 mm CW (Fig. 4), respectively. No females <55 mm CW were ovigerous, but all females >80 mm CW were ovigerous. Size at which 50% of females were ovigerous was 66 mm CW.

Discussion

The presence of snow crab was discovered in the Barents Sea in 1996 when five specimens were captured in a Russian trawler (Kuzmin et al 1999). In the 1990s, occasional individuals started being captured in

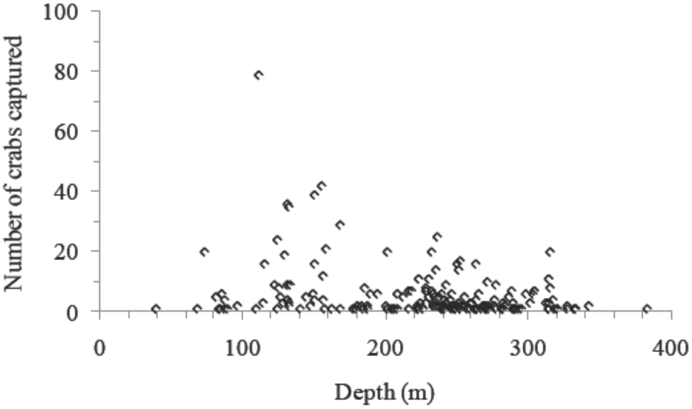

Figure 1. Depths at which snow crabs (*Chionoecetes opilio*) were captured in the Barents Sea during surveys from 2004 to 2008.

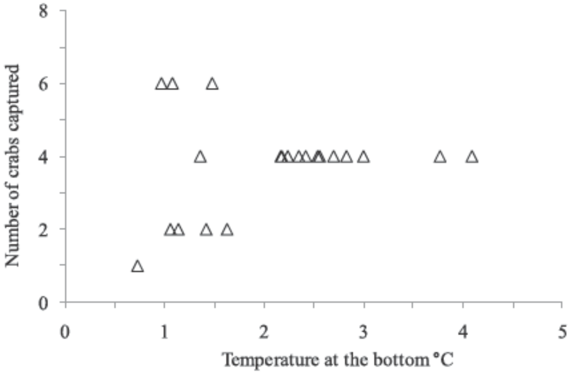

Figure 2. Bottom temperature at stations where snow crabs were captured during the 2008 autumn survey.

bycatch of the commercial cod fishery in Norway and Russia (Alvsvåg et al. 2009). Since 2004, snow crabs have been recorded as part of the bycatch in annual bottom trawl surveys run by the Institute of Marine Research in Norway and the Polar Research Institute of Marine Fisheries and Oceanography in Russia. Catch observations during 2004-2006 suggested an increase in abundance and size of the area occupied by snow crabs (Alvsvåg et al. 2009). Findings during the survey run in autumn 2008 suggested a further increase in number of crabs in the Barents Sea.

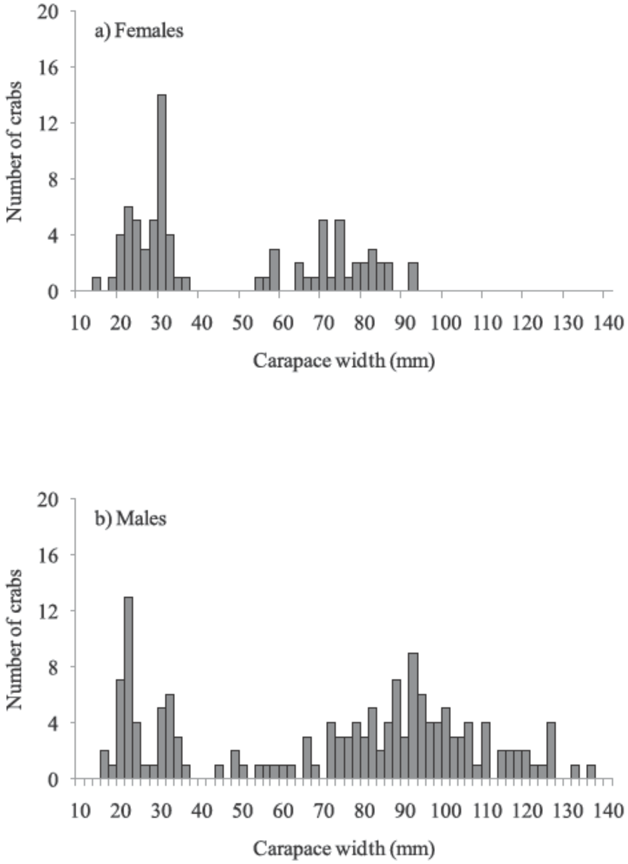

Figure 3. **Size frequency distributions of (a) female and (b) male snow crabs (*Chionoecetes opilio*) captured in the Barents Sea from 2004 to 2008.**

The preponderance of small crabs (10 to 40 mm CW) of both sexes indicates recruitment. The peak in size distribution in the Barents Sea population at 22 mm CW corresponds to instar VI, and the peak at 30 to 32 mm CW to instar VII (Alunno-Bruscia and Sainte-Marie 1998), with corresponding ages of 28 months and 3.3 years, respectively. However, research trawls may select for specific size groups. Small crabs bury in muddy sediments and as crabs become larger they become more susceptible to capture by trawls.

The presence of a significant number of ovigerous females and small juveniles was interpreted as evidence for a reproductively viable population of this non-native crab species in the Barents Sea (Alvsvåg et al.

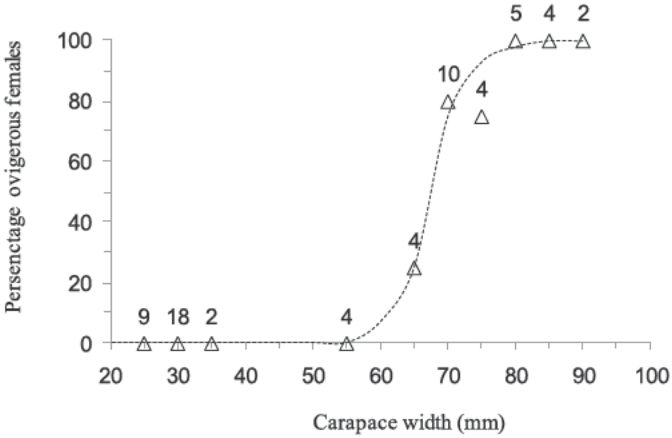

Figure 4. Percentage of ovigereous female snow crabs (*Chionoecetes opilio*) with size. Observations come from all surveys were combined. Sample size is given above each triangle.

2009). To date, the reproduction area seems to be established only in the eastern part of the Barents Sea, a conclusion also drawn by Alvsvåg et al. (2009). The size at which 50% of the females are ovigerous (~66 mm CW) and size (80 mm CW) above which all females are ovigerous is much larger than those (50 and 60 mm CW, respectively) in the Gulf of St. Lawrence (Watson 1970, Jewett 1981, Elner and Beninger 1995). Minimum size at maturity in male snow crab in the Barents Sea was estimated by to be 45 mm CW, and all males above 55 mm CW were mature (E.A. Filina and V.A. Pavlov, Polar Research Institute of Marine Fisheries and Oceanography, Murmansk, pers. comm., 2009).

Although snow crab appear to have been unintentionally introduced to the Barents Sea, possibly through ballast water (Kuzmin et al. 1999), there are substantial distances to important fishing areas, such as the northern Bering Sea and northwest Atlantic (Canada and West-Greenland). Little information is available about ship traffic in the most eastern and remote part of the Barents Sea, where the first known crabs were reported. An alternative possibility is that the appearance of snow crab in the Barents Sea is from a trans-arctic interchange. About 3.5 million years ago the Bering Strait, between Alaska and the Russian Far East, was open during a warm period, and species could move between the Atlantic and Pacific oceans (e.g., Reid et al. 2007, Vermeij and Roopnarine 2008). Examples of arctic invasive species are Pacific herring (Jørstad 2004), the gadoid fish *Theragra finmarchica* (Christiansen et al. 2005), the Pacific copepod *Calanus marshallae* (Sundt and Melle 1998), and bivalve mollusks (Väinölä 2003, Nikula et al. 2007). The Bering Strait also has been ice free in this century (Gerland et al. 2008, Reid et al. 2010), and another species interchange could possibly have taken place.

In other areas snow crab distribution seems to be controlled by bottom substrate and temperature (Coulombe et al. 1985, Robichaud et al. 1991, Dawe and Colbourne 2002). Hence, further expansion of this new snow crab population in the Barents Sea will possibly be closely linked to climatic conditions as this species prefers temperatures below 5°C. Extensive monitoring programs in Norwegian and Russian areas should be established. Since 2007, Russia has conducted annual assessment surveys during August to September (Pavlov 2008). Based on these assessments, Pavlov (2009) estimated that the population consisted of 7.7 million individuals. This estimate appears high and needs to be reevaluated by more comprehensive surveys. Comparative genetic studies are needed to identify the source of this species introduction, and extensive sampling of size, sex, maturity status, distribution, and abundance are necessary to monitor the potential growth of this new snow crab population.

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References

Alunno-Bruscia, M., and B. Sainte-Marie. 1998. Abdomen allometry, ovary development, and growth of male snow crab, *Chionoecetes opilio* (Brachyura, Majidae), in the northwestern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 55:459-477. doi:10.1139/cjfas-55-2-459

Alvsvåg J., A.-L. Agnalt, and K.E. Jørstad. 2009. Evidence for a permanent establishment of the snow crab (*Chionoecetes opilio*) in the Barents Sea. Biol. Invasions 11:587-595. doi:10.1007/s10530-008-9273-7

Christiansen, J.S., S.E. Fevolden, and I. Byrkjedal. 2005. The occurrence of *Theragra finmarchica* Koefed 1956 (Teleostei, Gadidae), 1932-2004. J. Fish. Biol. 66:1193-1197. doi:10.1111/j.0022-1112.2005.00682.x

Coulombe, F., J.-C. Brêthes, R. Bouchard, and G. Desrosiers. 1985. Segregation édaphique et bathymétrique chez le crabe des neiges, *Chionoecetes opilio* (O. Fabr.), dans le sud-ouest du golfe du Saint-Laurent. Can. J. Fish. Aquat. Sci. 42:169-180. doi:10.1139/f85-021

Dawe, E.G., and E.B. Colbourne. 2002. Distribution and demography of snow crab (*Chionoecetes opilio*) males on the Newfoundland and Labrador Shelf. In: A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley, and D. Woodby (eds.), Crabs in cold water regions: Biology, management and economics. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 577-594.

Elner, R.W., and P.G. Beninger. 1995. Multiple reproductive strategies in snow crab, *Chionoecetes opilio*: Physiological pathways and behavioral plasticity. J. Exp. Mar. Biol. Ecol. 193:93-112. doi:10.1016/0022-0981(95)00112-3

Gerland, S., A.H.H. Renner, F. Godtliebsen, D. Divine, and T.B. Løyning. 2008. Decrease of sea ice thickness at Hopen, Barents Sea, during 1966-2007. Geophys. Res. Lett. 35:1-5. doi:10.1029/2007GL032716

Griffen, B.D., and J.E. Byers. 2009. Community impacts of two invasive crabs: The interactive roles of density, prey recruitment, and indirect effects. Biol. Invasions 11:927-940. doi:10.1007/s10530-008-9305-3

Grosholz, E.D., and G.M. Ruiz, 1995. Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. Mar. Biol. 122:239-247.

Jadamec, L.S., W.E. Donaldson, and P. Cullenberg. 1999. Biological field techniques for *Chionoecetes* crabs. Alaska Sea Grant College Program, University of Alaska Fairbanks. 89 pp.

Jewett, S.C. 1981. Variation in some reproductive aspects of female snow crabs *Chionoecetes opilio*. J. Shellfish Res. 1:95-99.

Jørstad, K.E. 2004. Evidence for two highly differentiated herring groups at Goose Bank in the Barents Sea and the genetic relationship to Pacific herring, *Clupea pallasi*. Environ. Biol. Fishes 69:211-221. doi:10.1023/B:EBFI.0000022878.90511.88

Kuzmin, S.A., S.M. Akhtarin, and D.T. Menis. 1999. The first findings of the snow crab *Chionoecetes opilio* (Decapoda, Majidae) in the Barents Sea. Can. Transl. Fish. Aquat Sci. 5667. 5 pp.

Nikula, R., P. Strelkov, and R. Väinöä. 2007. Diversity and trans-arctic invasion history of mitochondrial lineages in the North Atlantic *Macoma balthica* complex (Bivalvia: Tellinidae). Evolution 61:928-941. doi:10.1111/j.1558-5646.2007.00066.x

Orlov, Yu.I., and B.G. Ivanov. 1978. On the introduction of the Kamchatka king crab *Paralithodes camtschatica* (Decapod: Anomura: Lithodidae) into the Barents Sea. Mar. Biol. 48:373-375. doi:10.1007/BF00391642

Pavlov, V.A. 2008. Snow crab: Expected state of biological fishery resources in the Barents Sea and North Atlantic in 2008. PINRO Press Murmansk, pp. 50-51. (In Russian)

Pavlov, V.A. 2009. Snow crab: Expected state of biological fishery resources in the Barents Sea and North Atlantic in 2009. PINRO Press Murmansk, pp. 51-52. (In Russian)

Reid, P.C., M. Edwards, and D.G Johns. 2010. Trans-arctic invasion in modern times. Science 322:528-529. doi:10.1126/science.322.5901.528c

Reid, P.C., D.G. Johns, M. Edwards, M. Starr, M. Poulin, and P. Snoeijs. 2007. A biological consequence of reducing arctic ice cover: Arrival of the Pacific diatom *Neodenticula seminae* in the North Atlantic for the first time in 800,000 years. Global Change Biology 13:1910-1921. doi:10.1111/j.1365-2486.2007.01413.x

Robichaud, D.A., R.W. Elner, and R.F.J. Bailey. 1991. Differential selection of crab *Chionoecetes opilio* and *Hyas* spp. as prey by sympatric cod *Gadus morhua* and thorny skate *Raja radiata*. Fish. Bull. 89:669-680.

Sainte-Marie, B. 1993. Reproductive cycle and fecundity of primiparous and multiparous female snow crab, *Chionoecetes opilio*, in the northwest Gulf of Saint Lawrence. Can. J. Fish. Aquat. Sci. 50:2147-2156. doi:10.1139/f93-240

Stiansen, J.E., and A.A. Filin (eds.) 2008. Joint PINRO/IMR report on the state of the Barents Sea ecosystem in 2007, with expected situation and considerations for management. Institute of Marine Research, Bergen, Norway, IMR-PINRO Joint Report Series 2008(1), ISSN 1502-8828. 185 pp.

Sundet, J.H., and A.M. Hjelset. 2002. The Norwegian red king crab (*Paralithodes camtschaticus*) fishery: Management and bycatch issues. In: A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley, and D. Woodby (eds.), Crabs in cold water regions: Biology, management and economics. Alaska Sea Grant Collage Program, University of Alaska Fairbanks, pp. 681-692.

Sundt, R., and S. Melle. 1998. Atlantic observations of *Calanus marshallae* (Copepoda; Calanoida). Mar. Ecol. Prog. Ser. 166:207-210. doi:10.3354/meps166207

Väinölä, R. 2003. Repeated trans-arctic invasions in littoral bivalves: Molecular zoogeography of the *Macoma balthica* complex. Mar. Biol. 143:935-946. doi:10.1007/s00227-003-1137-1

Vermeij, G.J., and P.D. Roopnarine. 2008. The coming arctic invasion. Science 321:780-781. doi:10.1126/science.1160852

Watson, J. 1970. Maturity, mating, and egg laying in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 27:1607-1616.

Rittschof, D., M.Z. Darnell, K.M. Darnell, M. Goldman, M.B. Ogburn, and R. McDowell. 2010.
Estimating Relative Abundance of the Female Blue Crab Spawning Stock in North Carolina.
In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby
(eds.), Biology and Management of Exploited Crab Populations under Climate Change.
Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.21

Estimating Relative Abundance of the Female Blue Crab Spawning Stock in North Carolina

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Abstract

Accurate assessment of the spawning stock should be important in informing fisheries management decisions. The life history and behavior of blue crabs *(Callinectes sapidus)* makes assessment of the spawning stock complex. In North Carolina, female blue crabs undergo their terminal molt and mate from March through November. After a variable amount of time, their ovaries mature and they extrude their first clutch of eggs. Crabs that mature in the upper estuary move from low salinity (<20 ppt) to high salinity (>22 ppt) to release their first clutch of eggs. Crabs in good habitat then forage and produce subsequent clutches of eggs, continuing to move seaward with each subsequent clutch. Thus, at any particular location, different spawning crabs will be seen each month and will build up in high salinity areas in the sounds and in the coastal ocean. The spawning population peaks in number in August/September with some crabs releasing their first clutch and others releasing their second or higher clutch. Using blue crab bycatch data from Division of Marine Fisheries monthly gill net surveys may be helpful in estimating blue crab spawning stock. Gill net data show the monthly pattern of spawning stock movement from low to high salinity and the

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buildup of spawning stock in high salinity waters. The pattern in spawning females is correlated with the return of settlement-stage crab larvae from the coastal ocean to a tidally driven estuary.

Introduction

The blue crab *(Callinectes sapidus)* fishery is North Carolina's most valuable fishery, with an average annual commercial harvest value of $35 million during 1996-2005. According to the 2004 stock assessment, the population is declining, with a reduction in spawning stock biomass of 74% since 1999 (Eggleston et al. 2004). Commercial landings increased from 1986 to 1996, followed by a period of reduced landings in 2000-2002 and in 2004-2007. The 2007 fishery yielded the lowest landings since 1977 (9,707 metric tons compared to an average of 20,638 t), though landings increased in 2007 in part of the state. The North Carolina Division of Marine Fisheries lists the current stock status as "of concern." Although there is great uncertainty regarding current maximum sustainable yield (MSY) estimates due to modeling limitations and the influence of environmental variables on the population, estimates of MSY range from 11,793 t to 23,586 t per year. Despite modeling limitations, fishery-dependent and fishery-independent data indicate that current fishing pressure exceeds MSY (NCDMF 2007). At this point, the blue crab is on the brink of being considered overfished (NCDMF 2007).

Although regulators acknowledge that management of fisheries requires a thorough understanding of the species' life history, key features of blue crab life history are missing (NCDMF 2004). It is known that females experience a terminal molt to maturity, mate, and store sperm. Females forage, mature their ovaries, and then extrude and attach a clutch of fertilized eggs to their abdomens where they are brooded until hatching. Little is known about individual female movements before or after hatching of a clutch of eggs. Most of the work on large-scale female movements has been done in the very large Chesapeake Bay and Albemarle Pamlico Estuarine System, where size, geometry, and huge numbers of crabs make following of individuals difficult. It is known that females with mature eggs undergo a spawning migration, in which they migrate seaward on ebb tides at night.

The initial hypothesis that females return to the upper estuary after spawning (Tankersley et al. 1998) has been rejected (Forward et al. 2005). The work of Forward et al. (2005), Hench et al. (2004), Darnell (2009), and Darnell et al. (2010a) indicates that crabs do not return to the low-salinity areas of the upper estuary. Rather, spawning female crabs forage in high-salinity habitat (inlets, sounds, coastal ocean) until they gain sufficient energy to extrude an additional clutch of eggs. These crabs continue to be most active on falling tides, which ensures that they continue to move seaward throughout the spawning season.

In a small, tidally driven estuary, the spawning migration moves females seaward throughout the spawning season (Rittschof 2004). We hypothesize that the spawning migration similarly moves females seaward throughout the entire spawning season in other locations. We postulate that crabs rapidly exit low-salinity habitat following oviposition and then have punctuated movements seaward. They may, for example, remain in an area foraging for several weeks while they build up energy stores, mature their ovaries, and extrude an additional clutch of eggs.

The migratory nature of the blue crab life cycle makes assessment of the spawning stock a complex task. Presently in North Carolina, June and September trawl surveys in the Pamlico Sound are used to assess spawning stock biomass. The survey is inadequate in many regards, including the following: (1) less than 1% of the female crabs captured in either trawl survey are ovigerous females; (2) most crabs captured in the September survey will not spawn until the following year (Darnell et al. 2009); (3) the survey is fixed in one area, independent of salinity, and not in blue crab habitat; (4) there are fisheries to the ocean side of the survey area; and (5) the survey does not take into account that crabs mature continuously from early spring (March) to late fall (November) (Dickinson et al. 2006; Ramach et al. 2009).

Our objectives are threefold. First, we develop a conceptual model for the female blue crab spawning migration based upon a mark-recapture study in a small, tidally driven estuary. We use mark-recapture approaches to understand these features of the life history that would be costly and virtually impossible in larger estuaries. Second, we apply that natural history information to examine two different methods (the standard trawl survey and monthly gill net bycatch data) of assessing the blue crab spawning stock in the Albemarle Pamlico Estuarine System (APES) of North Carolina. The APES is a vast (second largest estuary in the United States), mainly wind-driven estuarine system (Roelofs and Bumpus 1953, Luettich et al. 2002). Third, we use return of megalopae to Beaufort Inlet, North Carolina, as a measure of efficacy of a proposed method of sampling the spawning stock. Megalopal (settlement stage crabs) data from this inlet has a strong correlation with fisheries yields (Ogburn and Forward 2009). Two hypotheses have been put forth concerning the spawning stock/recruitment relationships to explain the timing of megalopal recruitment. The first hypothesis is that high crab settlement in North Carolina estuaries in the fall is due to peak spawning of blue crabs in the estuary in late summer/early fall. The alternative hypothesis is that peak settlement in the fall is due to continual spawning of blue crabs from spring to fall, with oceanographic conditions most favorable for inshore transport only in the fall (Eggleston et al. 2004). Given recent information on spawning biology of blue crabs (Darnell 2009, Eggleston et al. 2010), it is likely that peak spawning and oceanographic conditions are both involved. We assess these two

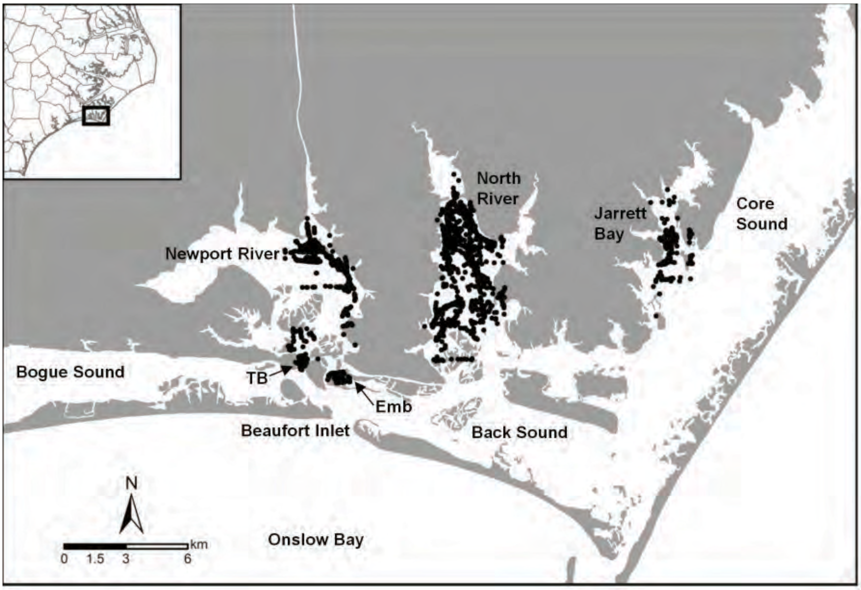

Figure 1. Map of Beaufort Inlet drainage showing locations of crabs tagged in 2001 and 2002. Each dot represents the location of one tagged crab. TB: turning basin. Emb: embayment.

hypotheses using Pamlico Sound gill net CPUE data and megalopal recruitment data from Beaufort Inlet. We stress that our goal is to provide insights to stock assessment scientists and fishery managers; we do not to attempt such stock assessments here.

Materials and methods

Beaufort Inlet drainage

The Beaufort Inlet drainage is an estuarine and sound system that makes up an area of approximately 225 square miles. Major features of this study area include the Newport River, North River, Jarrett Bay, Port of Morehead City turning basin, a high-salinity embayment in the Rachel Carson National Estuarine Research Reserve, Onslow Bay, and two fishing piers to the west of the inlet (Fig. 1). Beaufort Inlet drains to the south between Shackleford Banks and Bogue Banks into Onslow Bay. Approximately 85% of the flow in the drainage is due to tidal forcing (Hench and Luettich 2003).

In 2001 and 2002, mature female blue crabs were captured in the upper estuary bays (Newport River, North River, Jarrett Bay) and off

Table 1. Numbers of crabs marked and recaptured for each of the tagging locations in 2001 and 2002.

Year	Location	Marked	Recaptured	Recapture rate
2001	Embayment	667	297	44.53%
	Newport River	779	33	4.24%
	North River	456	105	13.89%
2002	Embayment	923	311	33.69%
	Jarrett Bay	1,235	60	4.86%
	Newport River	951	49	5.15%
	North River	930	70	7.53%

the Onslow Bay fishing piers. Migrating ovigerous crabs were captured in the turning basin and in Radio Island channel from a boat as they swam at the surface. Mature females were also captured in the Rachel Carson embayment around the times of nocturnal low tides using a dip net. Egg stage was noted for each crab, and for crabs captured in the three main bays and the embayment, each crab was marked with uniquely numbered across-the-back tags composed of a poker chip with 18 g plastic-coated copper wire looped around the large lateral spines. A total of 5,941 female crabs were tagged and released immediately at the location of capture (Fig. 1). Recapture data were obtained from local fishermen, crabbers, and other scientists working in the area. Returns were monitored and documented. A total of 925 crabs were recaptured, for a total recapture rate of 15.6% (Table 1). Additionally, in collaboration with an offshore fisherman, pots were set offshore and egg status was recorded for female crabs caught in 10 to 15 meters of water in Onslow Bay. Egg state was noted at times of capture.

Program 915 gill net survey

To better understand the distribution and abundance of the blue crab spawning population, data were obtained and analyzed from the North Carolina Department of Marine Fisheries Pamlico Sound Independent Gill Net Survey (Program 915; Paramore 2009). Field sampling for this survey began in May 2001 with four objectives: (1) calculate annual indices of abundance for Pamlico Sound for Atlantic croaker (*Micropogonias undulatus*), bluefish (*Pomatomus saltatrix*), red drum (*Sciaenops ocellatus*), southern flounder (*Paralichthys lethostigma*), spot (*Leiostomus xanthurus*), weakfish (*Cynoscion regalis*), spotted seatrout (*Cynoscion *nebulosus*), and striped bass (*Morone saxatilis*); (2) supplement samples for age, growth, and reproduction studies; (3) identify bycatch problems in Pamlico Sound; and (4) characterize habitat utilization in Pamlico Sound. Sampling was originally conducted in all 12 months of the year but due to extremely low catches and unsafe working conditions the sampling season was shortened in 2002 with sampling no longer occurring between December 15 and February 14.

The gill net survey employs a stratified random sampling design and the sampling area consists of two regions: eastern Pamlico Sound adjacent to the Outer Banks from southern Roanoke Island to the northern end of Portsmouth Island, and western Pamlico Sound from Stumpy Point Bay to Abel's Bay. The area extends into both the Oregon and Hatteras Inlet blue crab spawning sanctuaries, but lies completely outside the Ocracoke Inlet sanctuary. Twice monthly from March to November, and once per month in February and December, four areas within the grid were sampled in both the eastern and western regions. For each area selected, both shallow (≤1.8 m) and deep (>1.8 m) strata were sampled with a separate array of nets, each array consisting of 27.3 m segments of 7.6, 8.9, 10.2, 11.4, 12.7, 14, 15.2, and 16.5 cm stretched mesh webbing, totaling 218.4 m of gill nets. Each month, a total of 16 core samples were collected in each region (eight in February and December).

Gill net survey data on female crabs caught in east and west Pamlico Sound, from May 2001 to November 2006, were extracted from the survey database, and the numbers of immature, non-ovigerous mature, and ovigerous crabs were calculated for each month of each year. Ovigerous crabs caught on the east side were further classified by the stage of embryonic development, which can be inferred from the color of the egg mass. The survey recorded egg mass color as either yellow-orange (early stage embryos) or brown-black (late-stage embryos). Female crabs were coded by maturity stage and their locations mapped using ArcMap 9.2. To investigate temporal and spatial trends in mature female crabs caught in the gill net survey, mean catch per unit effort of immature, mature, and ovigerous crabs was calculated for each month by dividing the number of crabs caught by the number of samples taken that month (number of crabs caught per month per number of samples per month). Several months were short of the full sixteen samples (i.e., eight samples in February and eight in December), most likely due to weather conditions (K. West, North Carolina Division of Marine Fisheries, pers. comm.). Bottom salinity was also measured in collected samples.

Post-larval (megalopae) settlement data

To test the two hypotheses concerning the blue crab spawning stock/recruitment relationship and the timing of blue crab post-larval (megalopae) recruitment, settlement was quantified at the Duke University Marine Laboratory dock, located approximately 3 km inshore of

Beaufort Inlet, daily from June 2 to November 15 in 2004 and 2005 and from June 1 to November 15 in 2006. Biweekly settlement numbers were compared to CPUE of mature females in east Pamlico Sound during 2004, 2005, and 2006.

To quantify settlement, cylindrical "hogs hair" collectors (Metcalf et al. 1995) were utilized. These collectors consisted of PVC pipe weighted with concrete to insure the pipe hung vertically. Collectors were submerged 1 m below mean low water for approximately 24 hours. Following retrieval, they were soaked in freshwater for a minimum of 20 minutes and sprayed with freshwater to remove megalopae, which were identified and quantified using a dissecting microscope.

If the first hypothesis (that fall settlement is due to peak spawning in the estuary in late summer/early fall) is correct, we expect megalopal return to be related to monthly ovigerous female CPUE one to two months earlier. Alternatively, if the second hypothesis (that peak settlement in the fall is due to continual spawning of blue crabs from spring to fall, with oceanographic conditions most favorable for inshore transport only in the fall) is correct, we expect cumulative CPUE to peak in late summer/early fall, one to two months before settlement peaks in the estuary.

Results

Mark-recapture in Beaufort Inlet drainage

We compared recapture rates of ovigerous crabs marked and released in the upper estuary and ovigerous crabs marked and released in the high salinity embayment for three months. During each month, crabs were tagged in one of the three upper estuary areas (Newport River, North River, Jarrett Bay), and in the embayment. Recaptures of crabs in the upper estuary were between 4% and 14%, while recaptures in the embayment for the same time intervals were between 33% and 45% (Fig. 2). Of 1,590 crabs marked in the high salinity embayment, seven crabs (0.4%) were recaptured in the upper estuary areas. Even though we had 30-50% recapture in the high salinity embayment, essentially all of the female crabs left the embayment when embryos reached the late stages of development.

We next compared two years of data for crabs migrating at the surface at night in the turning basin (Fig. 3). One year (2001) had normal rainfall, whereas the other (2002) experienced a drought. In the year with normal rainfall over 90% of the crabs captured while migrating had late-stage egg masses. In contrast, approximately 50% of the crabs migrating during the drought year were not ovigerous.

We traveled the region in the vicinity of the Beaufort Inlet at night on ebb tides looking for migrating crabs at the surface. We found the

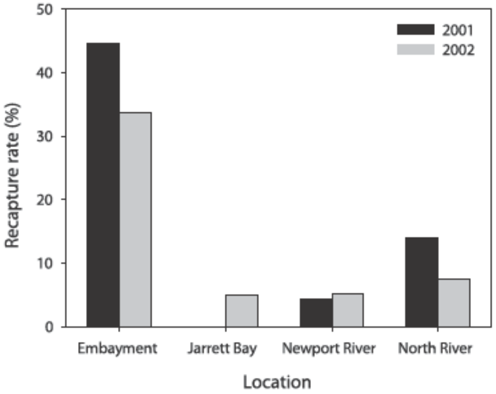

Figure 2. **Recapture rates of female crabs tagged in the high-salinity embayment and the three upper estuary bays. Note that no crabs were tagged in Jarrett Bay in 2001. Effort was approximately equal in all areas.**

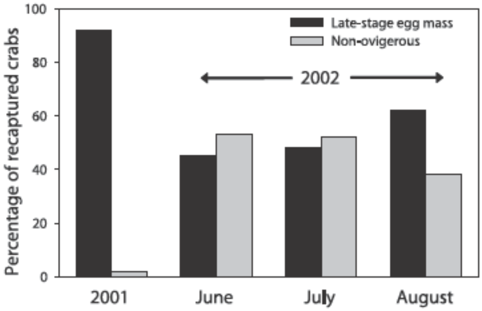

Figure 3. **Percent of crabs migrating with a late-stage egg mass and with no egg mass during a normal rainfall year (2001), and during 3 months of a drought year (2002).**

locations where sightings were relatively common: the Port of Morehead City turning basin, the Pivers Island Bridge (Tankersley et al. 1998), and Radio Island channel. All crabs found swimming at the surface were females, and in two nights of traveling the same areas on flood tides, no crabs were observed migrating on the surface. The only ovigerous crabs marked in the upper estuary and recaptured after larval release were crabs recaptured in the turning basin while migrating and in foraging habitat in the Rachel Carson embayment.

At the start of the study, the lore was that a female blue crab had a single clutch of eggs. Subsequently Hines et al. (2003), Hench et al.

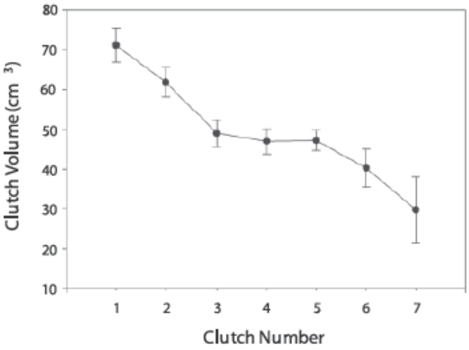

Figure 4. Mean clutch volume (±SE) over successive clutches for blue crabs producing more than two clutches in captivity. All stages of embryonic development and all crab sizes are included. Crabs were retained in the field individually in submerged minnow traps. (From Dickinson et al. 2006; axis labels have been redrawn.)

(2004), Dickinson et al. (2006), and Darnell et al. (2009) reported that blue crabs had multiple clutches of eggs, often in rapid succession. Female blue crabs confined individually in the field as described by Dickinson et al. (2006) and Darnell et al. (2009) produced multiple clutches of eggs, up to seven clutches in a single season, and some crabs spawned during two spawning seasons (Darnell et al. 2009). In all recent studies of blue crab clutch production, clutch volume was correlated with crab size, but decreased with clutch number for all size classes of crabs (Dickinson et al. 2006; Darnell et al. 2009, 2010b) (Fig. 4).

In the summer, it generally takes about 12 days for blue crab embryos to develop. Development within an egg mass is synchronous. Newly extruded egg masses are yellow, and the egg mass color progresses to orange, brown, and finally black as the embryos develop. Egg mass color was recorded for all areas where crabs were caught (Fig. 5). All developmental stages were observed at all locations except the fishing piers, the turning basin, and Radio Island channel. At the fishing piers, primarily orange egg masses were seen, with some brown and black egg masses. No yellow egg masses were seen at the fishing piers. The turning basin had no yellow egg masses and only a few orange and brown egg masses. The vast majority of egg masses captured in the turning basin were black. For the very small number of crabs (<20) observed in the Radio Island channel region, only black egg masses were observed.

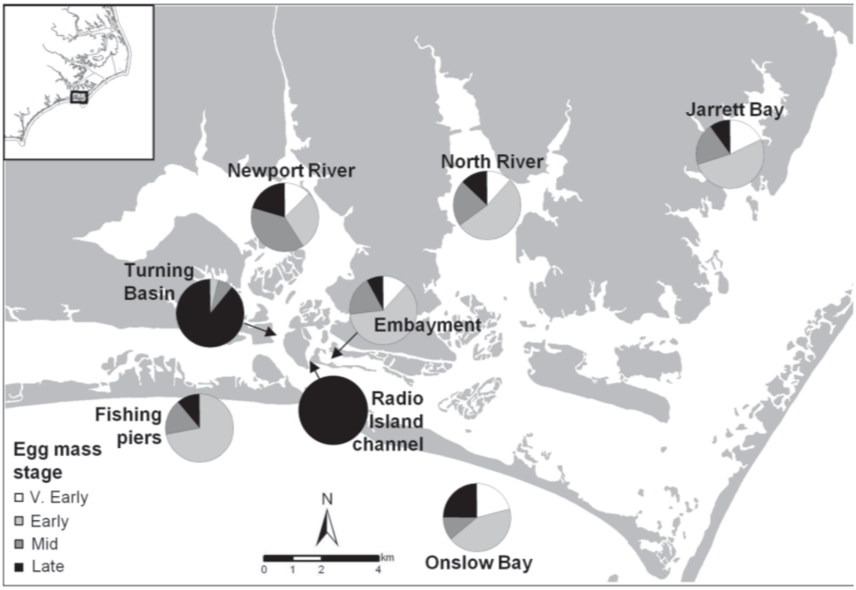

Figure 5. Distribution of egg mass stages at each capture location in 2001 and 2002.

Pamlico Sound gill net survey

The Division of Marine Fisheries gill net survey captured large numbers of female crabs as bycatch. The nets were set in crab habitat on the west and east sides of Pamlico Sound (Fig. 6). Salinity on the west side of the sound was usually less than 21 ppt while the salinity on the east side of the sound was 30-35 ppt. The gill net survey caught predominantly immature females in west Pamlico Sound and mature females in east Pamlico Sound (Fig. 7). On the east side, the percentage of mature females with eggs varies from month to month, but in the spring and summer months the percentage of ovigery can be as high as 96%. On the west side, mature females rarely have eggs. The presence of ovigerous crabs on the west side was correlated with salinity conditions. Ovigerous crabs were caught on the west side in three of the six years surveyed (15 in 2001, 14 in 2002, and 3 in 2004.) Their presence was likely due to low freshwater runoff, providing the salinity conditions necessary for embryonic development, ~20-25 ppt (Warner 1976, as cited in Ballance and Ballance 2004). Ovigerous crabs were found on average at salinity of 21 ppt.

Of all females caught in the gill net survey (approximately 1,000 on each side), 2.4% of those caught on the west side were ovigerous and

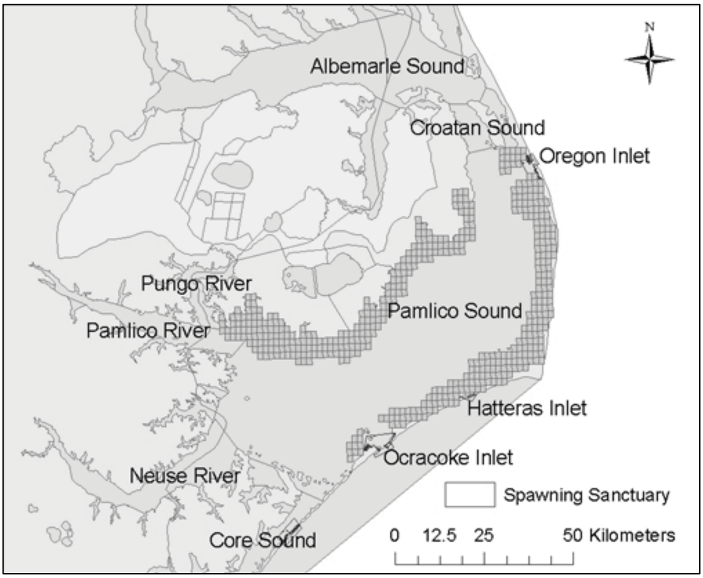

Figure 6. Sampling locations (squares) for North Carolina Division of Marine Fisheries Program 915 gill net survey in Pamlico Sound. The locations of the spawning sanctuaries are shown around Oregon, Hatteras, Ocracoke, and Drum inlets.

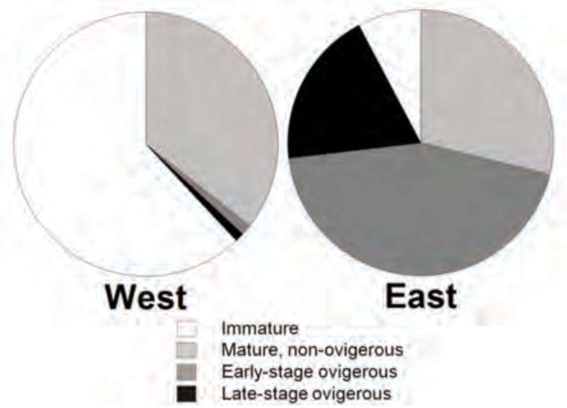

Figure 7. Proportion of females by maturity and egg mass stage for the east Pamlico Sound and west Pamlico Sound Program 915 gill net survey from 2001-2006.

65% of those caught on the east side were ovigerous (Fig. 7). On the east side, ovigerous crabs with early stage embryos occurred about twice as frequently as ovigerous crabs with late-stage embryos. As predicted, the east gill net survey caught the highest percentage of mature and ovigerous females.

Three years of megalopal abundance data collected at the Duke Marine Lab dock were compared with mature female CPUE from the gill net survey on the east side of the sound (Fig. 8). These three years were used because they were the only years for which we had a complete megalopal data set for the entire spawning season. In the gill net survey, seasonal peaks in abundance of mature females on the spawning grounds have varied from year to year, generally occurring in April/May and/or July. When cumulative CPUE is calculated, it levels off in late summer/early fall. Total numbers of mature females were highest in 2004, intermediate and ~34% of the 2004 levels in 2005, and ~28% of 2004 levels in 2006. Megalopal abundance lagged behind mature female abundance, was highest in 2005, ~85% of 2005 abundance in 2004, and approximately 50% of 2005 megalopal abundance in 2006.

Discussion

Based upon our results of several years of capturing, marking, and recapturing crabs throughout the Beaufort Inlet drainage, we propose an operational model of the female blue crab spawning migration. We suggest that the specified components of our model could form the basis for developing a future stock assessment to estimate the spawning stock biomass of blue crab. In addition, interpreting data in the context of the model would be a starting point for a life history based fishery management strategy. However, both of these future important activities are beyond the scope of this study.

In the model females molt to maturity and mate during all months when blue crabs are active. In North Carolina, females reach maturity, usually in water between 0 and 20 ppt salinity and mate from mid-March to mid-November. In the spring, molting is relatively synchronous and becomes less synchronous as the season progresses. Maximum numbers of females molt from April to October (Darnell et al. 2009, Ramach et al. 2009). A smaller number of crabs mature and mate in high salinity water (Ramach et al. 2009). Depending on the time of year and temperature, females forage in the vicinity of where they mated for 3 to 12 weeks in the summer and potentially longer in cooler seasons or regions (Darnell 2009).

Around the time of extrusion of the first clutch of eggs, crabs move to salinity of approximately 21 ppt or higher. Crabs in lower salinity and in non-foraging habitat migrate rapidly seaward until they encounter foraging habitat. When crabs are in foraging habitat, swimming fre-

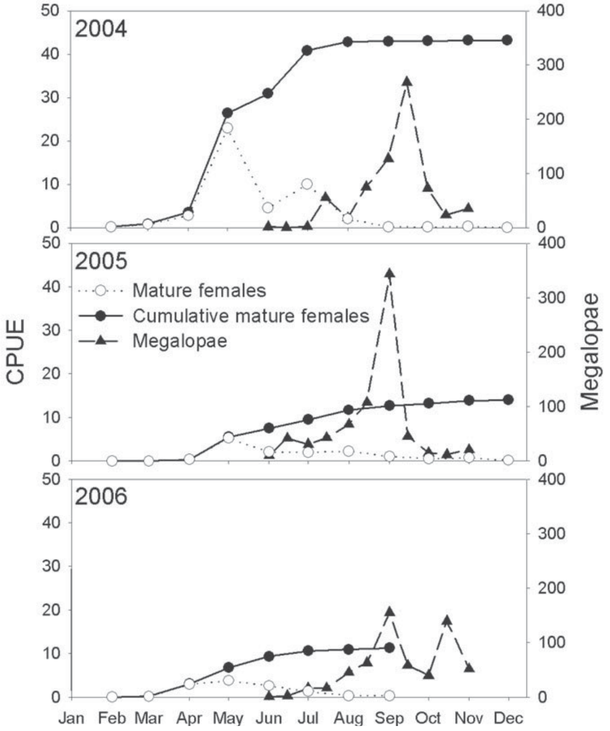

Figure 8. Monthly CPUE of mature females, cumulative total CPUE of mature females, and biweekly megalopal settlement for three years. Mature female data are from the Program 915 eastern Pamlico Sound gill net survey. Megalopal data are from the Duke Marine Lab dock.

quency decreases dramatically and they forage until embryos mature and eggs are close to hatching (Rittschof 2004, Darnell 2009, Ramach et al. 2009). Seaward movement activity increases as the embryos mature (Hench et al. 2004, Darnell 2009). Crabs leave foraging habitat when eggs are within 1-2 days of hatching. Ebb tide transport is obvious down migration corridors, areas of high ebb current velocity, to the next foraging habitat (Hench et al. 2004, Rittschof 2004, Darnell 2009).

Due to short distances and multiple clutches of eggs in the small strongly tidal Beaufort Inlet drainage, most female crabs have migrated out of the estuary and into the ocean by September (Rittschof 2004). In a huge system like the Albemarle Pamlico Estuarine System, crabs migrate to the high salinity waters on the inside of the barrier islands and the probably into and through the spawning sanctuaries to the coastal ocean. Crabs do not discriminate between sounds and the coastal ocean. Where crabs end up depends upon currents and the quality of the foraging habitat.

Thus, in the model, spawning female blue crabs are continuously migrating seaward throughout the blue crab's active season (Hench et al. 2004, Forward et al. 2005). Movement in high-salinity water is into and out of foraging habitats and depends on currents. Because of production of multiple clutches, spawning female crabs accumulate in high salinity water over time.

The spawning stock for the present year is composed of crabs that matured from the previous fall until the beginning of September (Darnell et al. 2009). Relatively few crabs spawn over two seasons (mainly those that mature in late July and August) (Darnell et al. 2009). Their contribution in the second spawning season is made early in the spring and is relatively low because fecundity drops with each successive clutch. Thus, in most years the east Pamlico Sound gill net survey should be useful in estimating spawning stock biomass and the cumulative CPUE of mature females caught in the survey should be useful in predicting recruitment. In years of extreme drought, the western Pamlico Sound gill net survey would also add information. If the high salinity water on the east side of the sound were closed to crab fishing, the eastern Pamlico Sound gill net survey would be a reliable estimate of the post-fishery spawning stock. Thus, the cumulative total of mature females spawning that season and their total fecundity is the spawning stock biomass. By totaling monthly CPUE from the eastern Pamlico Sound gill net survey over time, one could obtain an estimate of the total number of spawning crabs. Using mature size and time of year, fecundity could be estimated.

Presently, spawning stock biomass is estimated in North Carolina using a fishery-independent trawl survey. While trawl surveys are often used to assess blue crab spawning stocks (e.g., Lipcius and Van Engel 1990, Lipcius and Stockhausen 2002, Kahn and Helser 2005), the trawl survey used in North Carolina may not be adequate for assessing the spawning stock in Pamlico Sound. The trawl survey is a fixed location on the west side of Pamlico Sound, is poorly timed conducted only in June and September each year, ignores the spawning biology of blue crabs, and is taken in the middle of the fishery. Trawls take place in relatively deep water that is usually low-salinity, and the trawls yield less than 1% ovigerous females at both time intervals. The June census misses the spring (March to June) pulse of ovigerous crabs that have already moved to high-salinity water. Because they will have multiple clutches of eggs and many will finish spawning in October (Dickinson et al. 2006, Darnell et al. 2009) these crabs may be major contributors to the spawning stock. The September trawl survey measures some percentage of crabs that will spawn that year and some proportion of the next year's spawning stock. Crabs that molt to maturity in September do not extrude their first clutch until the following year (Darnell et al. 2009). Thus, some proportion of females captured by the trawl survey in September is females that molted to maturity prior to September and the rest are crabs that molted to maturity in September and will contribute to spawning stock for the subsequent year. We estimate that less than 1% of the present year's spawning stock is represented in the September trawl survey. Thus, if the trawl survey were to be a useful starting point it would need to be adjusted to account for these shortcomings. We suggest that an alternative starting point might be blue crab bycatch data from monthly gill net surveys. Using information from the west and east sides of the survey separately enables a continuous assessment of spawning stock in relation to the proposed conceptual model.

After release, larvae develop on the continental shelf through seven zoeal stages in four to five weeks (Epifanio 1995). Settlement stage larvae re-enter the estuary and settle in benthic habitats such as seagrass or shallow detrital habitats (Etherington and Eggleston 2003). Re-entrance into the estuary is associated with southward, alongshore wind events, and occurs in discrete pulses and does not necessarily occur in parent estuaries (Epifanio 1995). In North Carolina, post-larval settlement is highest in Pamlico Sound in the fall (Eggleston et al. 2004) and dependent upon storm forcing (Eggleston et al. 2010). Near Beaufort Inlet, peak settlement occurs in September/October (Dudley and Judy 1971, Forward et al. 2004). In 2004, 2005, and 2006, settlement in the Newport River Estuary near Beaufort Inlet remained low until mid August, with peak settlement in September/October. Peak spawning is predicted to occur 4-5 weeks before this, in August (Eggleston et al. 2004).

As already discussed, CPUE of mature females in the east side gill net survey peaked in May of these years. Cumulative CPUE, on the other hand, indicates peak numbers of spawning females in late summer/early fall. High settlement in the fall may also be attributed to retention of settlement-stage larvae in coastal waters during the summer (Tilburg et al. 2007) and oceanographic conditions most favorable for inshore transport in the fall (Eggleston et al. 2004). This supports the hypothesis that patterns in settlement are a function of continual spawning from spring to fall, with peak numbers of spawning females in late summer/early fall and reentrance of settlement stage larvae about four weeks later during favorable wind and tidal conditions (Epifanio 2003; Eggleston et al. 2004, 2010).

In order to sustainably manage the blue crab fishery, an accurate spawning stock assessment would be helpful. Methods for such a stock assessment could be based on the life history and spawning biology of the species and detailed data already collected as part of finfish management programs. Those interested in modeling blue crab spawning stock might consider this proposal as an option.

Acknowledgments

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References

Ballance, E.S., and E.B. Ballance. 2004. Blue crab sampling in the vicinity of the Ocracoke and Hatteras Inlet blue crab sanctuaries using crab pots. Final report for contract 02-POP-03 to the Blue Crab Research Program, North Carolina Sea Grant. 18 pp. Unpublished.

Darnell, M.Z. 2009. Spawning biology of female blue crabs, *Callinectes sapidus*. Ph.D. dissertation, Duke University, Durham.

Darnell, M.Z., D. Rittschof, K.M. Darnell, and R.E. McDowell. 2009. Lifetime reproductive potential of female blue crabs *Callinectes sapidus* in North Carolina, USA. Mar. Ecol. Prog. Ser. 394:153-163. doi:10.3354/meps08295

Darnell, M.Z., D. Rittschof, and R.B. Forward Jr. 2010a. Endogenous swimming rhythms underlying the spawning migration of the blue crab, *Callinectes sapidus*: Ontogeny and variation with ambient tidal regime. Mar. Biol. 157(11):2415-2425. doi:10.1007/s00227-010-1506-5

Darnell, M.Z., K.M. Darnell, R.E. McDowell, and D. Rittschof. 2010b. Postcapture survival and future reproductive potential of ovigerous blue crabs *Callinectes sapidus* caught in the central North Carolina pot fishery. Trans. Am. Fish. Soc. 139:1677-1687.

Dickinson, G.H., D. Rittschof, and C. Latanich. 2006. Spawning biology of the blue crab, *Callinectes sapidus*, in North Carolina. Bull. Mar. Sci. 79:273-285.

Dudley, D.L., and M.H. Judy. 1971 Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina. NOAA Technical Report, NMFS SSRF-637. 10 pp.

Eggleston, D.B., E.G. Johnson, and J.E. Hightower. 2004. Population dynamics and stock assessment of the blue crab in North Carolina. Final report for contracts 99-FEG-10 and 00-FEG-11 to the North Carolina Fisheries Resource Grant Program, North Carolina Sea Grant. 230 pp. Unpublished.

Eggleston, D.B., N.B. Reyns, L.L. Etherington, G.R. Plaia, and L. Xie. 2010. Tropical storm and environmental forcing on regional blue crab (*Callinectes sapidus*) settlement. Fish. Oceanogr. 19:89-106. doi:10.1111/j.1365-2419.2009.00530.x

Epifanio, C.E. 1995. Transport of blue crab (*Callinectes sapidus*) larvae in the waters off mid-Atlantic states. Bull. Mar. Sci. 57:713-725.

Epifanio, C.E. 2003. Spawning behavior and larval ecology: A brief summary. Bull. Mar. Sci. 72:322-330.

Etherington, L.L., and D.B. Eggleston. 2003. Spatial dynamics of large-scale, multistage crab *(Callinectes sapidus)* dispersal: Determinants and consequences for recruitment. Can. J. Fish. Aquat. Sci. 60:873-887. doi:10.1111/j.1365-2419.2009.00530.x

Forward, R.B., J.H. Cohen, M.Z. Darnell, and A. Saal. 2005. The circatidal rhythm in vertical swimming of female blue crabs, *Callinectes sapidus*, during their spawning migration: A reconsideration. J. Shellfish Res. 24:587-590.

Forward, R.B., J.H. Cohen, R.D. Irvine, J.L. Lax, R. Mitchell, A.M. Schick, M.M. Smith, J.M. Thompson, and J.I. Venezia. 2004. Settlement of blue crab *Callinectes sapidus* megalope in a North Carolina estuary. Mar. Ecol. Prog. Ser. 269:237-247. doi:10.3354/meps269237

Hench, J.L., and R.A. Luettich. 2003. Transient tidal circulation and momentum balances at a shallow tidal inlet. J. Phys. Oceanogr. 33:913-932. doi:10.1175/1520-0485(2003)33<913:TTCAMB>2.0.CO;2

Hench, J.L., R.B. Forward, S.D. Carr, D. Rittschof, and R.A. Luettich. 2004. Testing a selective tidal-stream transport model: Observations of female blue crab (*Callinectes sapidus*) vertical migration during the spawning season. Limnol. Oceanogr. 49:1857-1870. doi:10.4319/lo.2004.49.5.1857

Hines, A.H., P.R. Jivoff, P.J. Bushmann, J. van Montfrans, S.A. Reed, D.L. Wolcott, and T.G. Wolcott. 2003. Evidence for sperm limitation in the blue crab, *Callinectes sapidus*. Bull. Mar. Sci. 72:287-310.

Kahn, D.M., and T.E. Helser. 2005. Abundance, dynamics and mortality rates of the Delaware Bay stock of blue crabs, *Callinectes sapidus*. J. Shellfish Res. 24:269-284.

Lipcius, R.N., and W.T. Stockhausen. 2002. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. Mar. Ecol. Prog. Ser. 226:45-61. doi:10.3354/meps226045

Lipcius, R.N., and W.A. Van Engel. 1990. Blue crab population dynamics in Chesapeake Bay: Variation in abundance (York River, 1972-1988) and stock-recruit functions. Bull. Mar. Sci. 46:180-194.

Luettich, R.A., S.D. Carr, J.V. Reynolds-Fleming, C.W. Fulcher, and J.E. McNinch. 2002. Semi-diurnal seiching in a shallow, micro-tidal lagoonal estuary. Cont. Shelf Res. 22:1669-1681. doi:10.1016/S0278-4343(02)00031-6

Metcalf, K.S., J. von Montfrans, R.N. Lipcius, and R.J. Orth. 1995. Settlement indices for blue crab megalopae in the York River, Virginia: Temporal relationships and statistical efficiency. Bull. Mar. Sci. 57:781-792.

NCDMF. 2004. North Carolina fishery management plan: Blue crab. North Carolina Division of Marine Fisheries, Morehead City. 134 pp.

NCDMF. 2007. Stock status of the blue crab in North Carolina, 2007. North Carolina Division of Marine Fisheries. Accessed Dec. 2010: http://www.ncfisheries.net/stocks/index.html.

Ogburn, M.B., and R.B. Forward. 2009. Ingress of brachyuran crab post-larvae to the Newport River estuary. Estuar. Coasts 32:309-318. doi:10.1007/s12237-009-9136-1

Paramore, L. 2009. Pamlico Sound independent gill net survey. North Carolina Division of Marine Fisheries final report for grant F-70 to the U.S. Fish and Wildlife Service. 47 pp. Unpublished.

Ramach, S.M., M.Z. Darnell, N.G. Avissar, and D. Rittschof. 2009. Habitat use and population dynamics of blue crabs, *Callinectes sapidus*, in a high-salinity embayment. J. Shellfish Res. 28:635-640. doi:10.2983/035.028.0328

Rittschof, D. 2004. Migration and reproductive potential of mature female blue crabs. Final report for contract 02-Biol-04 to the North Carolina Fisheries Blue Crab Research Grant Program, North Carolina Sea Grant. 53 pp. Unpublished.

Roelofs, E.W., and D.F. Bumpus. 1953. The hydrography of Pamlico Sound. Bull. Mar. Sci. Gulf Carib. 3:181-205.

Tankersley, R.A., M.G. Wieber, M.A. Sigala, and K.A. Kachurak. 1998. Migratory behavior of ovigerous blue crabs *Callinectes sapidus*: Evidence for selective tidal-stream transport. Biol. Bull. 195:168-173. doi:10.2307/1542824

Tilburg, C.E., A.I. Dittel, and C.E. Epifanio. 2007. Retention of crab larvae in a coastal null zone. Estuar. Coast. Shelf Sci. 72:570-578. doi:10.1016/j.ecss.2006.11.030

Warner, W.W. 1994. Beautiful swimmers: Watermen, crabs, and the Chesapeake Bay. Little, Brown and Company, New York.

Hines, A.H., E.G. Johnson, M.Z. Darnell, D. Rittschof, T.J. Miller, L.J. Bauer, P. Rodgers, and
R. Aguilar. 2010. Predicting Effects of Climate Change on Blue Crabs in Chesapeake Bay. In:
G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby
(eds.), Biology and Management of Exploited Crab Populations under Climate Change.
Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.22

Predicting Effects of Climate Change on Blue Crabs in Chesapeake Bay

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Abstract

Callinectes sapidus populations support fisheries extending over a broad range of latitude from the species' tropical origins into the temperate zone. We analyzed latitudinal patterns of survival, reproduction, growth and maturation of blue crab populations in Florida, North Carolina, and Maryland/Virginia to project demographic effects of climate warming and certain other potential climate changes on the Chesapeake blue crab population. Field surveys and laboratory experiments indicate that harsh winters (<3°C, <8 ppt salinity) cause significant mortality in small (10 mm) juveniles and mature females. Brooding in populations at lower latitudes begins 3-4 months earlier than at high latitudes, allowing more broods per season. Cold winter temperature also restricts the growing season and inserts a prolonged period of suspended activity compared to lower latitudes, where juveniles grow rapidly to mature in one season rather than two at higher latitudes. However, tethering experiments indicate predation and cannibalism on juveniles is much higher during the warm season than spring and fall. Although there are not clear trends across latitude, size at maturity is inversely correlated with temperature within a site. While small females may molt to maturity and mate sooner, small size increases vulnerability to predation and diminishes fecundity per brood. Thus, cold winter temperatures and a short growing and reproducing season restrict the species' northward distribution from its tropical origins. Climate change reducing the severity of winters is predicted to increase winter survival and to promote rapid growth and brood production. However, warmer temperatures may promote increased juvenile mortality and may reduce size at maturity. Demographic schedules for fishery models will need to consider complex effects of warming.

Introduction

Blue crab (*Callinectes sapidus*) populations support lucrative fisheries and blue crabs are important predators in estuaries and lagoons extending across a broad range of latitudes of the western Atlantic Ocean (Fogarty and Lipcius 2007, Hines 2007). Although blue crabs have tropical evolutionary origins, their geographic range extends into the temperate zones of both South America and North America (Williams 2007). Despite a long history of sustained high productivity, fishery stocks in Chesapeake Bay and the North Carolina sounds, as well as other locations to a lesser extent, have suffered serious declines in the past decade. These declines appear to be associated with both intensive fishing and multiple environmental stressors, ranging from poor water quality to impacts of major hurricanes.

The blue crab life cycle (Fig. 1) is complex, encompassing a larval phase of 8 zoeal stages and a post-larval megalops, followed by 16-20 juvenile instars, before molting to maturity, followed by mating and egg production (Jivoff et al. 2007, Epifanio 2007, Hines 2007). Like many estuarine species, habitat use shifts markedly as life stages disperse and migrate across the salinity gradient of the estuary to offshore. Females produce and incubate a series of egg batches in the high salinity waters near the mouth of estuaries. Larvae hatch and are advected in the plume of the estuary offshore onto the continental shelf. Post-larvae use tidal stream transport to re-enter the estuary and then settle in seagrass beds, where they metamorphose and grow for approximately seven instars to 20 mm juveniles. Juveniles then disperse into lower salinity, shallow nursery habitats throughout the estuary, where they grow to maturity and mate. Females mate only once in their lifetime, while males may mate multiple times. Following mating, inseminated females migrate back to high salinities of the estuary to produce eggs. In small estuaries, mature females may move outside the estuarine

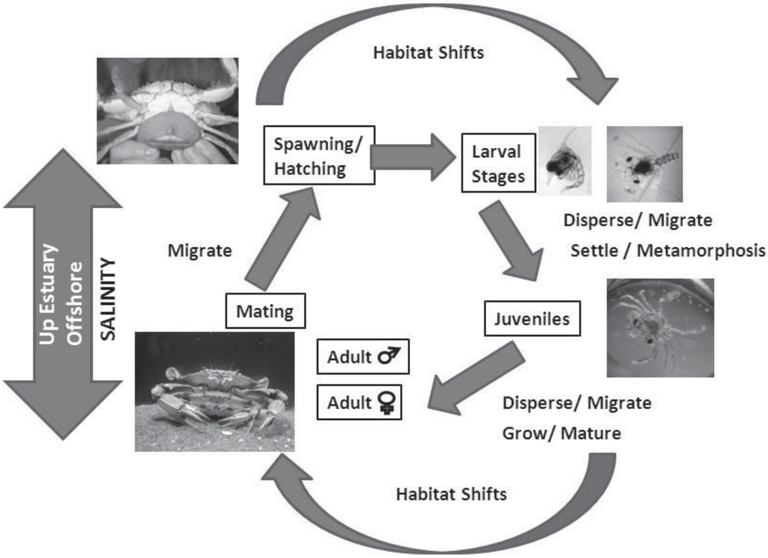

Figure 1. Schematic of blue crab life cycle showing life history stages and events, emphasizing habitat shifts and migration.

mouth, while in large systems like Chesapeake Bay they remain in the area of the bay mouth.

The blue crab life cycle is markedly affected by the seasonal cycle of temperature (Jivoff et al. 2007, Epifanio 2007, Hines 2007). Egg production and brooding occur in the warm season, and feeding and movement cease below 10°C, as does molting. Thus, in estuaries where winter water temperatures drop below 10°C, blue crabs undergo a period of suspended activity, which can markedly increase the blue crab generation time. Conversely, longer warm seasons may affect demographic variables with rapid growth, development, and reproduction. Crustaceans, including brachyuran crabs, exhibit geographic variation in reproductive traits (Lonsdale and Levinton 1985, Reaka 1986, Hines 1989, Dugan et al. 1991, Lardies and Castilla 2001, Brante et al. 2003, Castilho et al. 2007, Rodgers 2010). Because seasonal cycles vary predictably with latitude, we may reasonably infer effects of climate change on seasonal features of reproduction, settlement, and growth.

In this paper we consider how climate change may affect the important economic and ecological roles of blue crabs in these systems. We use latitudinal variation in demography of blue crab populations to project the probable effects of climate change on the blue crab population in Chesapeake Bay. We also review potential effects of climate change

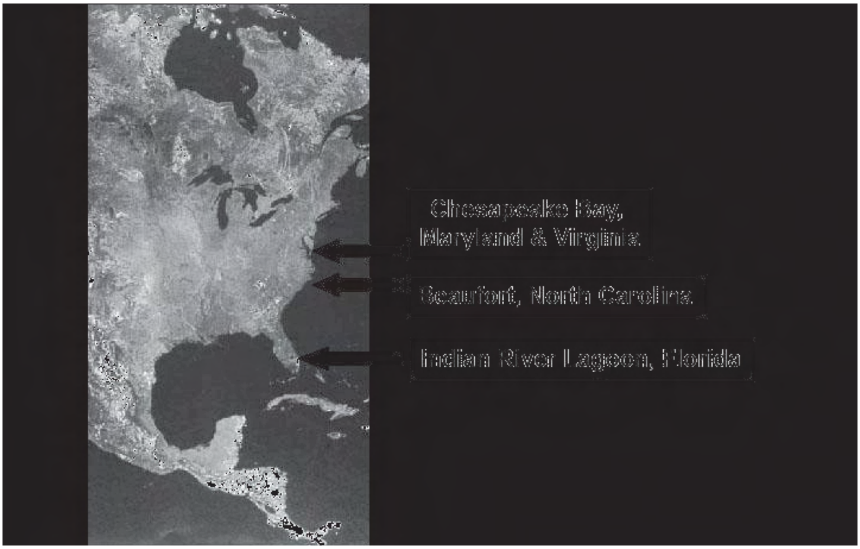

Figure 2. Locations of three study sites for demographic variables of blue crab life histories along the east coast of North America. The range of latitude provides a surrogate for climate change.

on community and ecosystem ecology for blue crabs, incorporating observed impacts of seasonal and annual variation in weather to highlight complex, often indirect consequences for blue crabs that make the impacts of climate change uncertain.

Approach and methods

To examine effects of climate change on demography, we document patterns of latitudinal variation in reproduction, growth, and maturity based on published information (see recent reviews: Jivoff et al. 2007, Epifanio 2007, Lipcius et al. 2007, Hines 2007) and our own extensive unpublished observations of blue crab biology at three main locations along the east coast of North America (Fig. 2): (1) Chesapeake Bay, Maryland, and Virginia (centered at 38°5'0"N, 76°20'0"W); (2) Beaufort Inlet, North Carolina (34°41'38"N, 76°39'59"W); and (3) Indian River Lagoon, Florida, particularly the Sebastian Inlet (27°51'30"N, 80°27'30"W). The decrease in latitude across these sites represents major climatic warming and associated seasonal variation. Plots of monthly mean water temperatures for the three main locations indicate that the major difference in the seasonal pattern is that lower latitudes have much

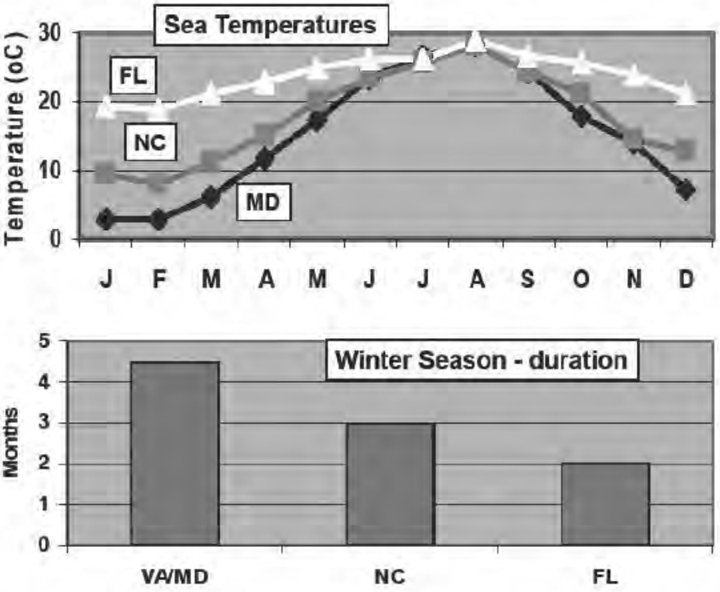

Figure 3. Seasonal variation in water temperature (top) and duration of winter (bottom) at three locations shown in Fig. 2. Sea temperatures from NOAA monitoring stations at each site.

warmer winters, but not substantially hotter summers (Fig. 3A). Given that blue crab movement and foraging ceases at temperatures below approximately 10ºC (Hines 2007), the duration of their winter shutdown of activity in Chesapeake Bay is more than 4 months, or twice as long as the short winter season in the Indian River Lagoon (Fig. 3B).

In addition, we consider impacts of interannual variation in winter temperature and salinity on blue crabs in Chesapeake Bay as a means of predicting effects of climate change on an important source of mortality for populations near the edge of their geographic range (Rome et al. 2005, Bauer and Miller 2010a,b). We also consider how climate changes in prevailing oceanographic conditions might affect larval recruitment dynamics (Epifanio 2007) for the three main locations.

To examine effects of climate changes in community and ecosystem interactions, we also compare ecology of blue crabs (Hines 2007) among the three main locations (Indian River Lagoon, Beaufort Inlet, Chesapeake Bay). We consider the probable or potential effects of climate warming and seasonal changes on other key species in Chesapeake ecosystems.

Results

Latitudinal variation in demography

Season

Seasonal durations of blue crab life history phases increased markedly with decreasing latitude (Fig. 4). The brooding season increased from 4 months in Chesapeake Bay (late May through September) to about 9 months in Florida (February through October). Mating season increased twofold from 3.5 months in mid Chesapeake Bay (late May to early September) to about 8 months in the Indian River Lagoon (April to October/November). Duration of the post-larval settlement season also increased about twofold from about 3.5 months (mid-August through October) in Chesapeake Bay to 7 months in Florida (May through November).

Growth rates and time to maturity

Growth of juvenile blue crabs was markedly affected by seasonal variation in temperature, with seasonal growth rates increasing in warm summer temperatures and dropping to zero in winter (Fig. 5). Time to reach critical juvenile size, maturity, and generation time were much shorter at lower latitudes with longer warm seasons (Fig. 6). Depending on seasonal timing of settlement and thus whether they ceased

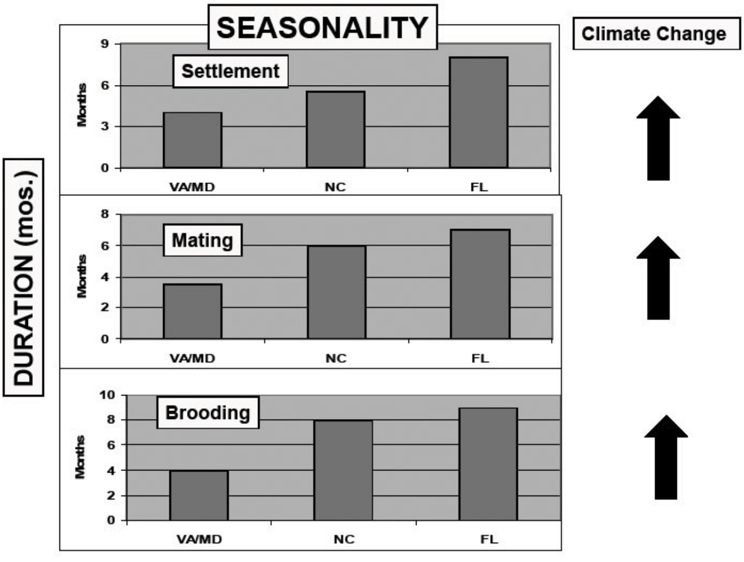

Figure 4. Variation in seasonal duration of settlement, mating, and brooding for blue crabs sampled at three locations shown in Fig. 2. Arrows indicate direction of effect of climate warming on the variable.

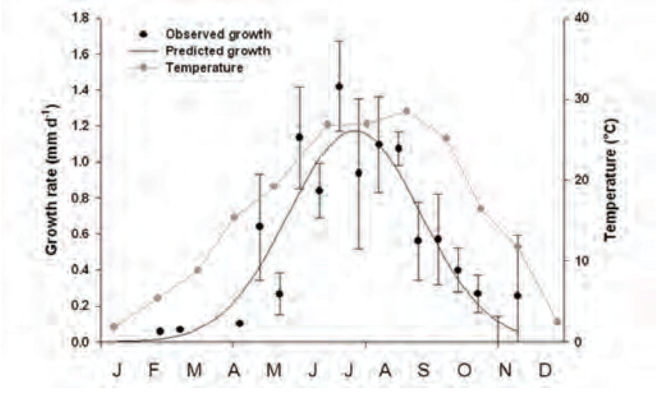

Figure 5. Seasonal variation in growth rate of juvenile blue crabs and in water temperature in the Rhode River in upper Chesapeake Bay. Mean and standard errors are indicated for growth rates. E.G. Johnson et al. (unpubl.)

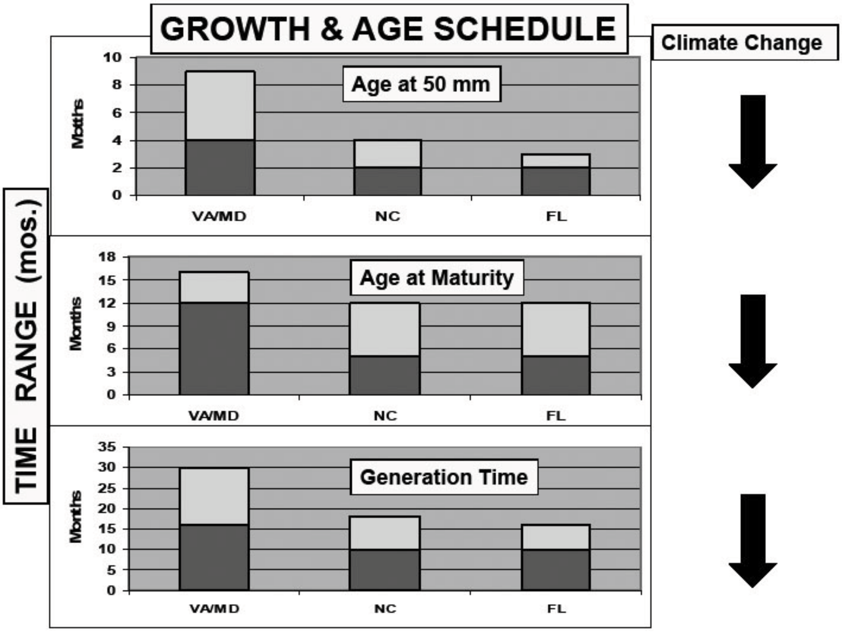

Figure 6. Schedule for growth and maturity for blue crabs sampled at three locations indicated in Fig. 2. Axes show estimated times to grow to 50 mm (carapace width) juveniles, age at maturity, and generation time. Shaded bars indicate ranges in lower and upper time durations (months) for each variable. Arrows indicate direction of effect of climate warming on the variable.

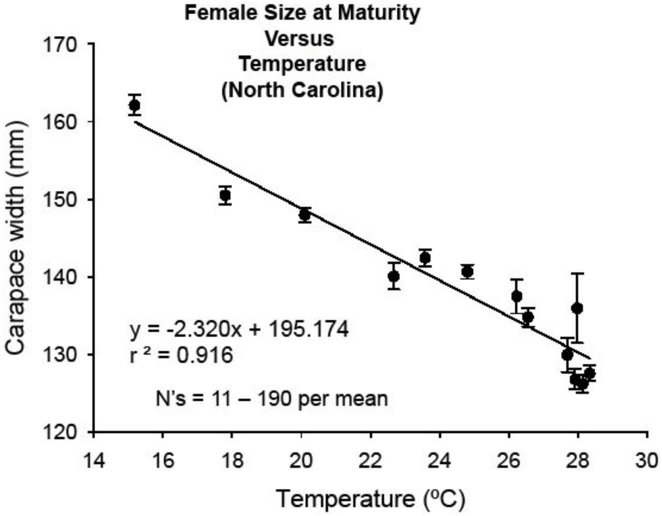

Figure 7. **Correlation of female blue crab size at maturity versus water temperature. Females molting to maturity were measured in locations that varied naturally in water temperature in the vicinity of Beaufort Inlet, North Carolina.**

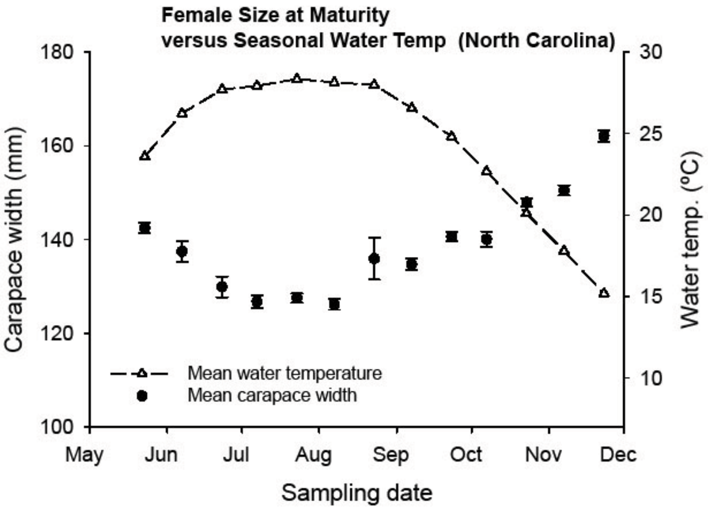

Figure 8. **Seasonal variation in female blue crab size at maturity and water temperature at Beaufort Inlet, North Carolina. Solid symbols show mean and standard error of carapace width. Triangles show mean water temperature.**

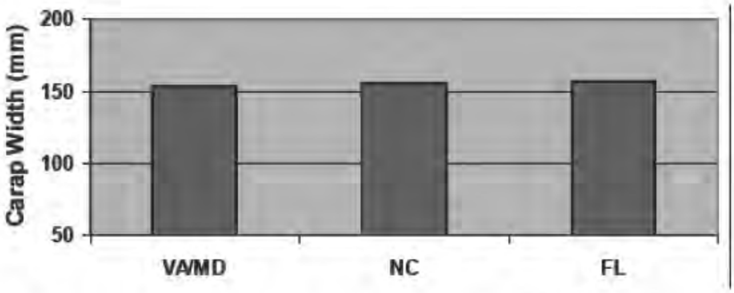

Figure 9. Mean size at maturity for females at three sampling locations shown in Fig. 2.

growing over winter, juveniles reached 50 mm size in 4-9 months in Chesapeake Bay but 2-3 months in Florida. Age at maturity ranged from 12-16 months in Chesapeake Bay but 5-12 months in Florida. Similarly, generation time decreased from 16-30 months in Chesapeake Bay to 10-16 months in Florida.

Temperature and female size at maturity

Female size at maturity was negatively correlated with temperature at the habitat site of molting, when salinity was constant (Fig. 7). Female size at maturity was also inversely related to seasonal variation in water temperature when salinity was constant (Fig. 8). However, mean size of mature females did not appear to exhibit latitudinal variation (Fig. 9), because other factors, such as salinity, also affected size at maturity and confounded latitudinal comparison.

Egg size, brood production, and fecundity

Egg diameter appeared to decrease from Chesapeake Bay to Florida, and fecundity per brood appeared to increase concomitantly (Fig. 10) (Rodgers 2010). However, these patterns may have been confounded by seasonal effects, because broods at lower latitudes were collected later in series of broods produced over a longer brooding season that started at an earlier month than broods collected in the same month in Chesapeake Bay. Broods produced later in the season may have had smaller, less yolky eggs, resulting in more eggs per brood, even if late season broods are smaller than early season broods (Prager et al. 1990, Dickinson et al. 2006). Because the brooding season increased in duration (Fig. 4), the number of broods produced per year by a female increased from 3-4 broods in Chesapeake Bay to 6-8 broods in Florida (Fig. 11); and annual fecundity also increases from 9-12 million eggs in

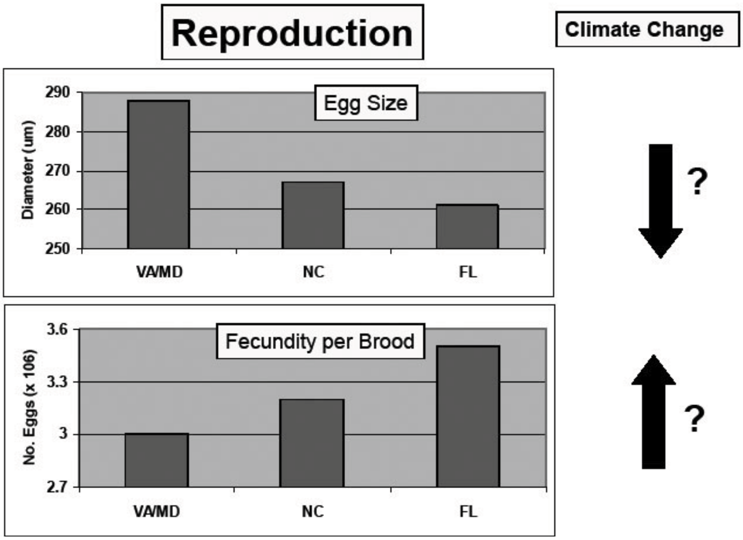

Figure 10. Average egg size and fecundity per brood at three sampling locations shown in Fig. 2. Arrow and ? indicate uncertainty in direction of effect of climate warming on the variable because of differences in seasonal timing of sampling among locations (see text).

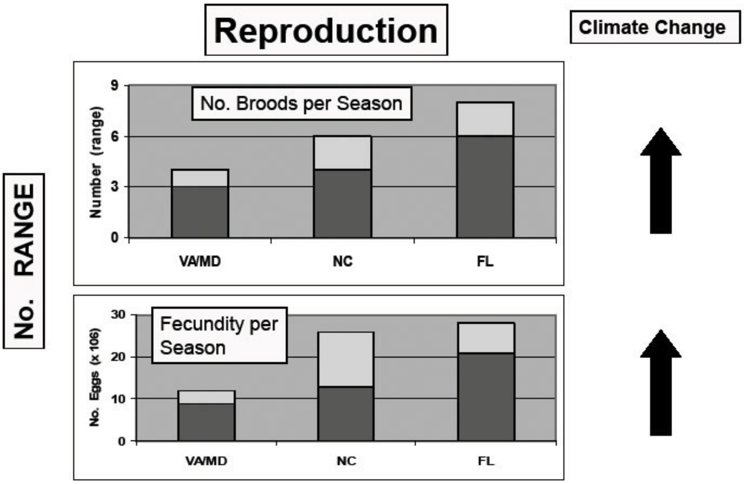

Figure 11. Reproductive output per female blue crab at three sampling locations shown in Fig. 2. Range in number of broods and in number of eggs produced per season are indicated. Bar shading indicate lower and upper levels of the variables. Arrows indicate direction of effect of climate warming on the variable.

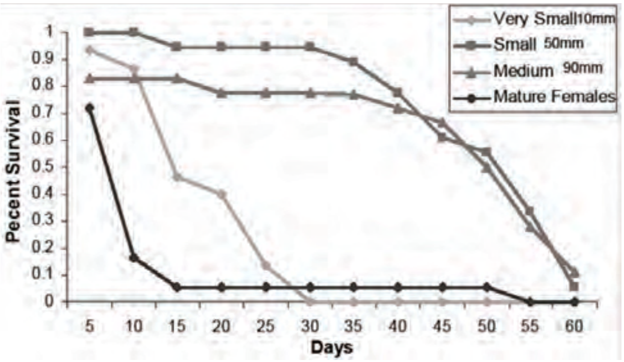

Figure 12. Survival of blue crabs exposed in the laboratory to harsh winter conditions of 3°C and 8 ppt salinity. Size and life stage of crabs are indicated: very small = 10-15 mm; small = 30-50 mm; medium = 70-90 mm; mature females ≥130 mm. From Rome et al. (2005).

Chesapeake Bay to 21-28 million eggs in Florida. Although we have recorded females that lived to age 5 years, longevity of most females in the intensively fished Chesapeake Bay population was about 1-3 years (Fogarty and Lipcius 2007), resulting in a lifetime fecundity of 9-24 million eggs in that system. Longevity in Florida was uncertain. If it were the same as Chesapeake Bay, lifetime fecundity would be 42-56 million eggs. However, if longevity were shorter at warmer, lower latitudes (averaging, say, 1 year in Florida), then lifetime fecundity would approach the annual values.

Mortality related to climatic conditions

Blue crab survival at higher latitudes in the temperate zone was limited by winter severity, with harsh winters determined as combinations of cold water temperatures (<3°C) and low salinity (<8 ppt) causing markedly increased mortality, especially for small juveniles and mature females (Rome et al. 2005; Bauer and Miller 2010a,b) (Fig. 12). Winter mortality also varied with the duration of the exposure to the harsh conditions of low temperature-salinity combinations (Rome et al. 2005, Bauer and Miller 2010a,b). In Chesapeake Bay mature females migrate in the fall from low salinity nursery and mating areas to higher salinities of the lower bay in preparation for brood production. Tagging studies (Aguilar et al. 2005) and winter dredge surveys (Jensen et al. 2005) indicate that some females may stop partway down the salinity gradient as cold temperatures interrupt their migration, resulting in females being distributed along the estuarine range of salinities and winter temperatures (Fig. 13). In Chesapeake Bay, interannual fluctuations in

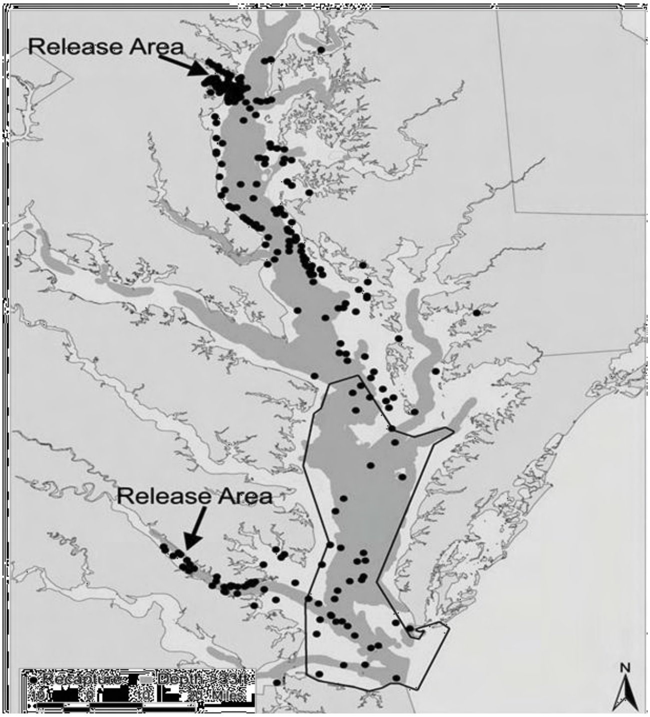

Figure 13. Recapture sites of migrating mature female blue crabs in Chesapeake Bay. Mature females were tagged with numbered plastic Floy tags attached to their dorsal carapace and released in the Rhode River (upper) and York River (lower). Data on location of capture were provided by commercial and recreational fishers, who were compensated with rewards. Revised from Aguilar et al. (2005).

winter severity affected both the level of mortality (ranging from 0 to 70% in certain harsh winters) and the spatial extent of mortality in the bay, with harsh conditions extending well down below mid bay in cold, low-salinity winters, and lasting more than 5 months in the upper half of the bay (Figs.14-15) (Bauer and Miller 2010 a,b). Thus, climate change is predicted to result in warmer, shorter winters, reducing winter mortality (Najjar et al. 2010). However, if climate change also imposes wetter winters (Najjar et al. 2010), then lower salinities may increase mortality during cold periods.

Changes in coastal currents and weather patterns along the east coast may have marked effects on larval survival and blue crab recruitment due to shifts in current systems (Epifanio 2007). However, it is

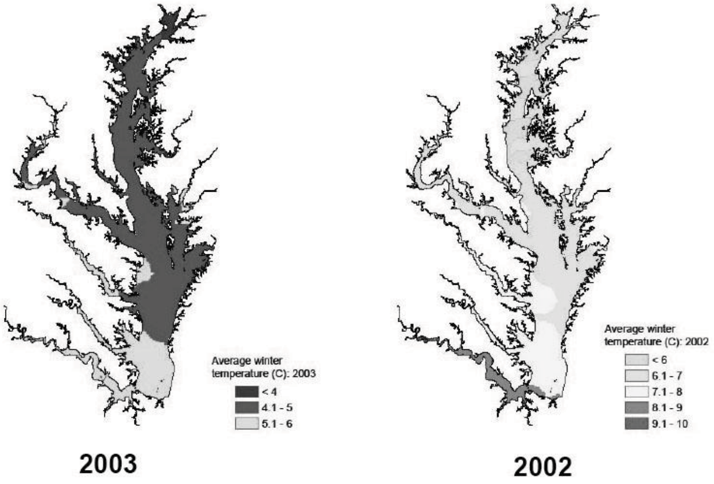

Figure 14. **Average winter water temperature distribution for November 1 through April 30 for Chesapeake Bay for contrasting years 2003 and 2002. From Bauer and Miller (2010).**

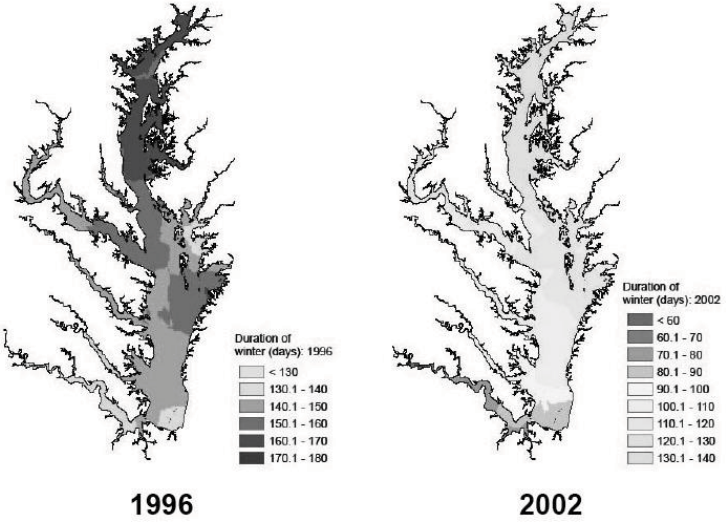

Figure 15. **Winter duration of cold water temperatures below 10°C during November 1 through April 30 in Chesapeake Bay for contrasting years 1996 and 2002. From Bauer and Miller (2010).**

difficult to predict the effects of potential climate changes in nearshore southward flowing currents and gyres that seem to supply larvae to estuaries in the regions of the mid-Atlantic and south-Atlantic bights of North America (Epifanio 2007).

Climate change is predicted to increase the frequency and intensity of tropical storms (Karl et al. 2009). Much of blue crab larval settlement occurs in late summer and fall for northern estuaries, which coincides with hurricane season (Epifanio 2007). These storms may affect larval recruitment in systems like Chesapeake Bay, if these storms cause major disturbance of offshore surface currents and tidal surge, but storms can also cause huge runoff and flushing problems within the estuaries (Najjar et al. 2010) (see also "Dead zones" below).

Habitat impacts of climate change in Chesapeake Bay

Climate change is likely to affect the geographic distribution of key habitat-forming species and trophic interactions that are critical for various blue crab life stages, especially near their latitudinal limits, such as Chesapeake Bay (Pyke et al. 2008, Najjar et al. 2010).

Seagrasses and submerged vegetation

Eelgrass (*Zostera marina*) exhibited a major die off in 2005 in the lower Chesapeake Bay, which was attributed to high summer temperatures (Orth and Moore 2008). Eelgrass was critical habitat for juvenile blue crab abundance, survival, distribution, and foraging biology (Lipcius et al. 2007). Changes in rainfall that alters estuarine salinities also may have affected other species of submerged vegetation.

Emergent vegetation

Salt marshes provided crucial resources for juvenile blue crabs in adjacent unvegetated bottom (King et al. 2005). Marshes provided detritus that fuels infaunal prey resources for juvenile crab nursery habitat. With sea-level rise by the year 2100, at least 161,000 acres of salt marsh are predicted to be lost in Chesapeake Bay (Pyke et al. 2008). Mangroves have been important structural habitat along tropical shorelines, and juvenile blue crabs derived nursery habitat value from mangroves in Florida. Cold winter temperatures (freezing) limit the northern distribution of mangroves along the east coast of North America, and warming appeared to allow the northward spread of this habitat, now extending beyond Cape Canaveral. However, it is not likely that climate change will allow mangroves to spread to Chesapeake Bay in the coming century.

Oyster reefs

Oysters were often considered to create valuable habitat for blue crabs. However, there was very little empirical or experimental evidence that the oyster reefs per se were utilized extensively by blue crabs (Hines 2007). Rather, epifaunal and infaunal organisms associated with oyster reefs seemed to provide food resources, especially for larger crabs. Oysters were at record low levels in Chesapeake Bay, with almost no viable oyster reefs remaining. They have been decimated by overfishing and by disease, which is especially intense at higher salinities of Chesapeake Bay. In lower latitude estuaries, oysters in the intertidal zone often have had less disease due to warm temperatures and sustained air exposure. However, in much of Chesapeake Bay, intertidal oysters were killed by low winter temperatures. With warming, intertidal oysters may persist and provide a spawning stock that may help restore reefs as a habitat.

"Dead zones"

Low dissolved oxygen develops in deeper waters of eutrophic estuaries that are stratified by warmer temperatures and freshwater runoff. Thus, if climate change results in warming and higher rainfall in estuaries like Chesapeake Bay (Pyke et al. 2008), then stratification and low dissolved oxygen will increase in extent and duration, potentially killing blue crabs. Not only can low oxygen affect survival of crabs, but such dead zones will also reduce foraging resources and distribution of blue crabs (Hines 2007). Low oxygen also may regulate their movement as juvenile crabs dispersing up-estuary and mature females migrating down-estuary encounter deeper, low oxygen waters (Aguilar et al. 2005, Johnson and Hines unpubl. data). Even if the timing of the female migration occurs after the fall turnover of the water column, low oxygen would reduce the availability of benthic prey that fuels the crabs' movement.

Trophic interactions

Populations in the Gulf of Mexico and Florida encounter a high diversity of predatory fish and crustaceans feeding on post-larval and juvenile blue crabs, resulting in intense predation rates and low survival (Hines 2007). Climate warming is likely to allow more predator species to extend into Chesapeake Bay in greater abundance and for longer periods of time (Najjar et al. 2010). Certain key prey species for blue crabs are near their biogeographic limit in Chesapeake Bay. For example, the southern limit of the tellinid bivalve *Macoma balthica* is in Chesapeake Bay, and this species is a major component in the diet of blue crabs. If climate warming pushes *M. balthica* farther north, blue crabs will have to shift to other prey species, perhaps those spreading from the south. The effects of such species substitutions may or may not balance out in the food web.

Discussion

As a species of tropical origin, the geographic range of blue crabs is limited in higher latitudes by cold winter temperatures, especially at low salinities in estuaries. Severe winters can cause as much as 70% mortality of blue crabs in key areas of Chesapeake Bay, especially for the most sensitive life stages/sizes (Rome et al. 2005; Bauer and Miller 2010a,b). Warming winter temperatures are expected to result in reduced winter mortality of blue crabs at higher latitudes and to allow northward range expansion of fishable blue crab stocks.

Effects of climate change on blue crab demography are also expected to promote increased fishery production. Our latitudinal comparisons predict that warming climate will extend the length of the seasons for reproduction, settlement, and growth. Growth rates and maturation/generation times should also shorten the life cycle. Reproductive output should increase for the population.

Due to an array of environmental stresses, many habitat-forming species have undergone serious declines in Chesapeake Bay, including submerged vegetation due to eutrophication and increased water turbidity and epiphytes; oysters due to overfishing and disease; and salt marshes due to habitat destruction and increasingly inundation. Further stresses of climate change may push these habitats past a threshold of sustainability, and losses of such species are already occurring in some particularly warm years. If these species are not replaced by functionally similar species the consequences may be large and complex. However, because these habitat functions are generally intact at lower latitudes, “replacement species” may extend their range and sustain the ecosystem functions. Range extensions have been documented for invasive species into Chesapeake Bay, including for some habitat-forming species like the red alga *Gracilaria vermiculophylla* (Falls 2008). However, it remains to be seen if similar range extensions will occur for native species, or whether the effects of climate change with multiple environmental stressors will result in major losses of habitats. These uncertainties are further complicated by management’s restoration efforts. For example, oyster reef habitats in Chesapeake Bay are at unprecedented low levels due to fishing, shell removal and disturbance, and invasive diseases. Climate warming may promote improved winter survival of intertidal oysters, helping to restore a larger spawning stock that persists in more southern parts of the species range.

In light of the recent major decline and overfishing in the Chesapeake Bay stock of blue crabs (CBSAC 2009), especially the sharp decline in mature females in the summer spawning stock (Lipcius and Stockhausen 2002), management decisions for the fishery are ever more precarious. The complex, often interactive effects of climate change add uncertainty to these decisions. Effects of climate change are already evident in systems like Chesapeake Bay (Pyke et al. 2008), but it remains difficult to partition population fluctuations among intense fishing, a myriad of human impacts on the nearshore environment, and climate change. While variations in weather have always been a factor of uncertainty in fishery management, the projected acceleration of climate change impacts for systems like Chesapeake Bay is certain to make these effects a focus for the future.

Acknowledgments

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References

Aguilar, R., A.H. Hines, T.G. Wolcott, D.L. Wolcott, M.A. Kramer, and R.N. Lipcius. 2005. The timing and route of movement and migration of postcopulatory female blue crabs, *Callinectes sapidus* Rathbun, from the upper Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 319:117-128. doi:10.1016/j.jembe.2004.08.030

Bauer, L.J., and T.J. Miller. 2010a. Spatial and annual variability in winter mortality of the blue crab (*Callinectes sapidus*) in the Chesapeake Bay. Estuar. Coasts 33:678-687. doi:10.1007/s12237-009-9237-x

Bauer, L.J., and T.J. Miller. 2010b. Temperature, salinity, and size-dependent winter mortality of juvenile blue crabs (*Callinectes sapidus*). Estuar. Coasts 33:668-677. doi:10.1007/s12237-010-9277-2

Brante, A., M. Fernández, L. Eckerle, F. Mark. H.-O. Portner, and W. Arntz. 2003. Reproductive investment in the crab *Cancer setosus* along a latitudinal cline: Egg production, embryo losses and embryo ventilation. Mar. Ecol. Prog. Ser. 251:221-232. doi:10.3354/meps251221

Castilho, A.L., M.A. Gavio, R.C. Costa, E.E. Boschi, R.T. Bauer, and A. Fransozo. 2007. Latitudinal variation in population structure and reproductive pattern of the endemic South American shrimp *Artemesia longinaris* (Decapoda: Penaeoidea). J. Crustacean Biol. 27:548-552. doi:10.1651/S-2788.1

CBSAC (Chesapeake Bay Stock Assessment Committee). 2009. 2009 Chesapeake Bay blue crab advisory report. NOAA Chesapeake Bay Office, Annapolis. 5 pp.

Dickinson, G.H., D. Rittschof, and C. Latanich. 2006. Spawning biology of he blue crab, *Callinectes sapidus*, in North Carolina. Bull. Mar. Sci. 79:273-285.

Dugan, J.E., A.M. Wenner, and D.M. Hubbard. 1991. Geographic variation in the reproductive biology of the sand crab *Emerita analoga* (Stimpson) on the California coast. J. Exp. Mar. Biol. Ecol. 150:63-81. doi:10.1016/0022-0981(91)90106-7

Epifanio, C.E. 2007. Biology of larvae. In: V.S. Kennedy and L.E. Cronin (eds.), Biology of the blue crab. Maryland Sea Grant College Program, College Park, pp. 513-533.

Falls, J.A. 2008. The survival benefit of benthic macroalgae *Gracilaria vermiculophylla* as an alternative nursery habitat for juvenile blue crabs. M.S. thesis. Virginia Institute of Marine Science, College of William and Mary. 69 pp.

Fogarty, M.J., and R.N. Lipcius. 2007. Population dynamics and fisheries. In: V.S. Kennedy and L.E. Cronin (eds.), Biology of the blue crab. Maryland Sea Grant College Program, College Park, pp. 711-755.

Hines, A.H. 1989. Geographic variation in size at maturity of brachyuran crabs. Bull. Mar. Sci. 45:356-368.

Hines, A.H. 2007. Ecology of juvenile and adult blue crabs. In: V.S. Kennedy and L.E. Cronin (eds.), Biology of the blue crab. Maryland Sea Grant College Program, College Park, pp. 565-654.

Jensen, O.P., R. Seppelt, T.J. Miller, and L.J. Bauer. 2005. Winter distribution of blue crab *Callinectes sapidus* in Chesapeake Bay: Application and cross-validation of a two-stage generalized additive model. Mar. Ecol. Prog. Ser. 299:239-255. doi:10.3354/meps299239

Jivoff, P.R., A.H. Hines, and S. Quackenbush. 2007. Blue crab reproductive biology. In: V.S. Kennedy and L.E. Cronin (eds.), Biology of the blue crab. Maryland Sea Grant College Program, College Park, pp. 255-298.

Karl, T.R, J.M. Melillo, and T.C. Peterson (eds.) 2009. Global climate change impacts in the United States. Cambridge University Press. 196 pp. Accessed Dec. 2010: www.globalchange.gov/usimpacts.

King, R.S., A.H. Hines, F.D. Craige, and S. Grap. 2005. Regional, watershed and local correlates of blue crabs and bivalves in subestuaries of Chesapeake Bay, USA. J. Exp. Mar. Biol. Ecol. 319:101-116. doi:10.1016/j.jembe.2004.05.022

Lardies, M.A., and J.C. Castilla. 2001. Latitudinal variation in the reproductive biology of the commensal crab *Pinnaxodes chilensis* (Decapoda: Pinnotheridae) along the Chilean coast. Mar. Biol. 139:1125-1133. doi:10.1007/s002270100661

Lipcius, R.N., and W.T. Stockhausen. 2002. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. Mar. Ecol. Prog. Ser. 226:45-61. doi:10.3354/meps226045

Lipcius, R.N., D.B. Eggleston, K.L. Heck Jr., R.D. Seitz, and J. van Montfrans. 2007. Ecology of postlarval and young juvenile blue crabs. In: V.S. Kennedy and L.E. Cronin (eds.), Biology of the blue crab. Maryland Sea Grant College Program, College Park, pp. 535-564.

Lonsdale, D.J., and J.S. Levinton. 1985. Latitudinal differentiation in copepod growth: An adaptation to temperature. Ecology 66:1397-1407. doi:10.2307/1938002

Najjar, R., C.R. Pyke, M.B. Adams, D. Breitburg, C. Hershner, M. Kemp, R. Howarth, M. Mulholland, M. Paolisso, D. Secor, K. Sellner, D. Wardrop, and R. Wood. 2010. Potential climate-change impacts on the Chesapeake Bay. Estuar. Coast. Shelf Sci. 86:1-20. doi:10.1016/j.ecss.2009.09.026

Orth, R.J., and K.A. Moore. 2008. Effects of salinity and water temperature on the ecological performance of *Zostera marina*. Aquat. Bot. 88:239-246.

Prager, M.H., J.R. McConaugha, C.M. Jones, and P.J. Greer. 1990. Fecundity of blue crab, *Callinectes sapidus*, in Chesapeake Bay: Biological, statistical and management considerations. Bull. Mar. Sci. 46:170-179.

Pyke, C.R., R.G. Najjar. M.B. Adams, D. Breitburg, M. Kemp, C. Hershner, R. Howarth, M. Mulholland, M. Paolisso, D. Secor, K. Sellner, D. Wardrop, and R. Wood. 2008. Climate change and the Chesapeake Bay: State-of-the-science review and recommendation. Report from the Chesapeake Bay Program Science and Technology Advisory Committee (STAC), Annapolis. 59 pp.

Reaka, M.L. 1986. Biogeographic patterns of body size in stomatopod Crustacea: Ecological and evolutionary consequences. In: R.H. Gore and K.L. Heck, Jr. (eds.), Crustacean biogeography. Balkema Press, Rotterdam, pp. 209-235.

Rodgers, P.J. 2010. A comparative analysis of sperm storage in six brachyuran superfamilies: Mating behavior, ecological variation and phylogenetic patterns. Ph.D. thesis, University of Maryland, College Park. 189 pp.

Rome, M.S., A.C. Young-Williams, G.R. Davis, and A.H. Hines. 2005. Linking temperature and salinity tolerance to winter mortality of Chesapeake Bay blue crabs (*Callinectes sapidus*). J. Exp. Mar. Biol. Ecol. 319:129-145. doi:10.1016/j.jembe.2004.06.014

Williams, A.B. 2007. Systematics and evolution. In: V.S. Kennedy and L.E. Cronin (eds.), Biology of the blue crab. Maryland Sea Grant College Program, College Park, pp. 1-21.

Dew, C.B. 2010. Podding Behavior of Adult King Crab and Its Effect on Abundance-Estimate Precision. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks, Fairbanks. doi:10.4027/bmecpcc.2010.24

Podding Behavior of Adult King Crab and Its Effect on Abundance-Estimate Precision

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Abstract

The Alaska red king crab, *Paralithodes camtschaticus*, is a major target of the Bristol Bay stock assessment bottom-trawl survey conducted annually by the U.S. National Marine Fisheries Service. Because of the difficulty of sampling extremely patchy spatial distributions, it is important to know whether the podding behavior documented for juvenile red king crab continues into adulthood. A common assumption is that adults are not podding crab. I present data from in situ investigations at Kodiak and adaptive cluster sampling in Bristol Bay, which demonstrates that adults are podding crab whose behavior results in discrete aggregations that can cover more than 370 km^2. Because of this behavior, and because historical estimates of precision were based on a flawed method (post-stratification), the uncertainty of annual abundance estimates, and their association with climate changes, is greater than previously thought.

Introduction

Podding is an intensely gregarious behavior unique to red king crab (*Paralithodes camtschaticus*) (Dew 1990, Dew et al. 1992, Dew and McConnaughey 2005). The behavior causes the crab to be spatially distributed throughout the year in extremely dense clusters or aggregations known as pods. Unlike the transitory mating and molting aggregations of sexually mature crab reported for several species in

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the family Majidae, e.g., spider crab (*Libinia emarginata*) (Degoursey and Stewart 1985, Degoursey and Auster 1992), opilio crab (*Chionoecetes opilio*) (Hooper 1986), lyre crab (*Hyas lyratus*) (Stevens et al. 1992), and Tanner crab (*Chionoecetes bairdi*) (Stevens et al. 1994), red king crab podding is the persistent, year-round, day-to-day, social functioning of cohesive, identifiable population units composed of juvenile, subadult, and adult red king crab of both sexes. While the quotidian aspect of red king crab podding distinguishes it from the occasional aggregative behavior observed for other crab species, it also results in population-abundance estimates that are considerably less precise than equivalent estimates for other major crab (Tanner and opilio crab) and fish (walleye pollock [*Theragra chalcogramma*], Pacific cod [*Gadus macrocephalus*], and yellowfin sole [*Limanda aspera*]) species targeted by the annual NMFS multispecies bottom-trawl survey of the eastern Bering Sea (Dew and Austring 2007).

Early research resulted in a circumscribed definition of podding behavior that led to the misconception that adult red king crab do not form pods. For example, Powell and Nickerson (1965) defined a pod by its size (no more than 3,000 crab), shape (spherical), and activity (resting). Under this definition, foraging aggregations were not pods; and adults, which had been observed to form piles or aggregations but not "spherical" pods, were assumed to have outgrown their podding behavior early in their fourth year of life (age 3). However, trying to define a pod (or a flock, herd, or school) solely by its structure rather than its function (e.g., social organization) has not proven to be particularly useful. Also, Powell and Nickerson's (1965) definition was based on daytime-only observations of a pod's resting phase—observations that led them to conclude, incorrectly, that the observed pod remained in the same location for days or even weeks without foraging. Some 25 years later the discovery of a diel podding cycle, whereby the crab dispersed from the resting pod each evening, foraged as a cohesive unit throughout the night, and reconstituted the resting pod each morning (often in the same location), revealed the structural fluidity and organizational persistence of podding behavior (Dew 1990). Now it could be understood that a pod has a continuously changing structure, and that pod members often alternate each day between a resting phase and a foraging phase, with little to be gained by differentiating among piles, pods, and aggregations (e.g., Powell and Nickerson 1965, Stone et al. 1993), all of which may be manifestations of the same, cohesive population unit.

Based largely on Powell and Nickerson (1965), a consensus hypothesis underlying the management of the Bristol Bay red king crab stock is that podding is specific to juveniles only, and that podding behavior ceases after red king crab attain a size of 60-65 mm CL at age 4 (e.g., Incze et al. 1986, Otto 1986, Armstrong et al. 1993, Witherell 1998, Ackley and Witherell 1999). The question of whether podding continues into adulthood is of more than academic interest. Incze et al. (1986, p. 375) commented that if adult red king crab were podding crab, "a tremendous sampling effort would be required to obtain reasonable estimates" of their abundance, suggesting that the precision of population estimates based on sample sizes typical of the NMFS Bristol Bay survey might be unacceptably low for podding crab.

The consensus hypothesis implies that red king crab discontinue podding and disperse to a more tractable, less aggregated spatial distribution at about the time they become a target of the NMFS stock-assessment survey as subadult and adult crab. This is the hypothesis favored by resource managers responsible for estimating red king crab abundance each year. Consistent with this hypothesis, Otto (1986) reported rather precise 95% confidence intervals of ±12-27% for abundance estimates of legal crab (males with carapace length (CL) ≥135 mm) in Bristol Bay during the years leading to the collapse of the stock (1975-1983). Because podding is associated with low abundance–estimate precision, investigators (e.g., Incze et al. 1986, Armstrong et al. 1993) interpreted the relatively high precision reported by Otto (1986) as evidence that adults, unlike juveniles, are not podding crab. However, overlooked by investigators is the fact that the precision reported for adult red king crab was inflated by an invalid stratification method: "In each year . . . this area is stratified on the basis of large [red king crab] males . . ." (Otto 1986, p. 93). This method, known as post-stratification, is a scheme in which stratum formation is based on the spatial distribution of the survey target as determined from the current year's sampling. Post-stratification is a form of data mining that results in an artificially low estimate of variance that is unsuitable for calculating a useful estimate of precision (Cochran 1977, Hilborn and Walters 1992, McConnaughey and Conquest 1993, Gunderson 1993, Skalski 1997).

According to the consensus hypothesis, red king crab engage in podding behavior temporarily, for a 2- to 3-year period during their 15-20 year life span. However, the inception of podding at about 1.5 years of age (Powell and Nickerson 1965, Dew 1990) represents a sharp, apparently advantageous, discontinuity in the behavioral ecology of juvenile red king crab. Pre-podding, early benthic–phase juveniles display a cryptic, solitary existence that is behaviorally distinct from older, podding individuals (Loher 2001). Podding juveniles, no longer reliant on complex habitat to provide individual niches for protection, expand their foraging time and space to include daylight hours and featureless silt or mud bottoms (Dew 1990, 1991). Implausibly, the consensus hypothesis proposes that age-4, subadult red king crab abandon their newly adopted podding strategy and revert to less organized, more solitary behavior, shortly before they attain sexual maturity and begin to reproduce.

The objective of this work is to present evidence that disproves the long-held hypothesis that podding is strictly a juvenile phenomenon, dwindling to insignificance after age 3. Instead, the intensity of podding appears to increase as discrete cohorts, approximately midway through the fourth and fifth years of life (age 3-4), proceed to mix and coalesce into a single, larger, multi-age aggregation (Dew et al. 1992). Once we accept the evidence that adult crab are highly aggregated podding crab, we are faced with the Incze et al. (1986) observation that it is extremely difficult to obtain reasonably precise abundance estimates for podding crab. In turn, we might begin to suspect that the confidence intervals published since 1975 are overly precise, and that red king crab abundance estimates presented to and used by managers are likely to be more uncertain and unreliable than claimed. Finally, we should reevaluate all analyses and conclusions that rely on and assume reasonably precise abundance estimates—e.g., stock-recruitment relationships (e.g., Zheng et al. 1995), the calculation of utilization rates (e.g., Dew and Austring 2007), and the effect of climate change on abundance (e.g., Tyler and Kruse 1996).

Methods

Kodiak

Observations of red king crab podding behavior were made in situ by divers during a 12-year (1985-1996) study focused primarily on Womens Bay (57.7208°N, 152.5250°W), a 490-hectare embayment contiguous with Chiniak Bay and the Gulf of Alaska, and 14.5 km south of the city of Kodiak, Alaska. Most of the dive effort was directed to Womens Bay because information from a 1990-1991 study showed red king crab to be substantially more abundant there than in two other local bays (e.g., Anton Larsen Bay and Trident Basin) (Dew 1991). Investigators used scuba to locate crab pods, and then tagged one or two pod members with a sonic pinger to track the pods from a small boat equipped with a directional hydrophone and a global positioning system receiver. To forestall the possibility that investigators were either tracking a few tagged stragglers instead of thousands of podding crab, or dealing with stationary tags shed during the winter molt and lying on the bottom, divers made frequent, in situ observations to document the behavior of the pods and to periodically collect (and replace) podding crab for length measurements, from which crab ages were estimated. Observations and counts were recorded on writing slates during the dive, and depth profiles were recalled from diver-carried computers that recorded depth at three-minute intervals. Data from more than 500 dives (>280 hours underwater, including approximately 50 hours of night diving) provided information with which to define diurnal and seasonal activity cycles and foraging habits, and to quantify seasonal variations in depth, habitat usage, mobility, dispersion, mixing, and year-class integrity of the aggregations. Additional details of this multiyear study can be found in Dew (1990, 1991) and Dew et al. (1992).

Bristol Bay

The NMFS annual survey in Bristol Bay and adjoining waters (to 166°W) collects bottom-trawl samples at approximately 120 geographically fixed stations, each representing a grid square of 1,372 km^2 (400 nm^2). Although commercial-size (legal) male red king crab have been collected since 1975 at some 117 of 120 regularly sampled Bristol Bay stations east of 166°W, only 24 of these stations have produced legal males more than 80% of the time (in at least 20 of 24 years) from 1975 through 1998. The location, starting point, and time of sampling are nonrandom, remaining approximately the same from year to year.

The sampling is designed to be unstratified and distributed systematically (evenly) over a uniform grid of stations, but this design is often unbalanced by nonrandom sampling that directs extra effort to areas of high crab abundance. These ad hoc, extra samples, sometimes resulting in more than twice the total number of design-based samples (Table 1), are included in population-size estimates. From as early as 1975 (Reeves 1975, Pereyra et al. 1976, Reeves et al. 1976) through at least 2008 (Chilton et al. 2008), NMFS has employed post-stratification to address the analytical complications that result from unbalancing the systematic design with extra sampling. NMFS stratification is an a posteriori stratification of the sampling area after each year's survey, using knowledge of the target species' spatial distribution in the current survey to define the strata; but then NMFS uses the standard formula for a priori stratification to calculate variance, as follows:

$$Var(\bar{x}_{str}) = \frac{a_1^2\left(\frac{s_1^2}{n_1}\right) + a_2^2\left(\frac{s_2^2}{n_2}\right) + \ldots + a_i^2\left(\frac{s_i^2}{n_i}\right)}{(\sum a_i)^2}$$

where $\bar{x}_{str}$ = the stratified arithmetic mean density (crab per km^2), a_i = the area (km^2) in stratum *i*, s^2_i = the variance in stratum *i*, and n_i = the sample size in stratum *i*. Additional details of the Bristol Bay crab survey can be found in Chilton et al. (2008). Also, Otto (1986, p. 93) describes the process of "gerrymandering" strata after a survey, based on red king crab catches in the same survey.

Adaptive cluster sampling

The adaptive cluster sampling (ACS) conducted in 1995 was part of a bottom-trawl special study, which sampled on a relatively fine scale (3.7

Table 1. As part of the NMFS Bristol Bay trawl survey to estimate red king crab abundance, extra trawl sampling was conducted in areas of relatively high legal-male abundance during a period of apparently increasing abundance, after which the population collapsed.

Year	N	n	Extra tows (%)
1975	77	77	0
1976	80	137	71
1977	77	98	27
1978	82	124	51
1979	82	190	132
1980	82	95	16

N = number of grid squares (stations).
n = number of tows (samples) at the stations.

km intervals) within a 27,440 km^2 area of Bristol Bay (Fig. 1). In the 1995 experiment, each of 20 Bristol Bay standard-survey grid squares (37 by 37 km) was subdivided into a 10 by 10 grid yielding 100 possible sampling units (3.7 by 3.7 km). Three of these 100 units were selected randomly from an initial grid square, and this triplet was replicated throughout the remaining 19 grid squares, resulting in a total of 60 ACS sampling units, each to be sampled by a single tow of 30 minutes duration. The "neighborhood" of each of these units was defined as the adjacent units to the north, south, east, and west. If the number of red king crab caught at a unit was equal to or greater than a predetermined threshold value (C), then the unit's neighborhood was added to the sample, and so on until a cluster of units (a network) was formed in which the boundary or edge units were less than C (Thompson and Seber 1996). The initial choice of $C = 18$ adult egg-bearing females was based on data from the standard survey, which had passed through the 20-station ACS survey area several days earlier. The ACS emphasis on females was a response to a lack of mature females in two previous NMFS standard surveys—a lack that, despite being an artifact of survey timing (Dew 2008), caused the cancellation of the Bristol Bay red king crab fishery in 1994 and 1995.

Statistics

Checking and recalculating confidence intervals

By 1992, it was evident that there were inconsistencies between the extremely clumped spatial distribution of the crab, as observed in situ, and the rather precise estimates of their (post-stratified) Bristol Bay abundance, as published by NMFS (e.g., Otto 1986). For each year from 1975 through 1980, I checked the confidence level of the pub-

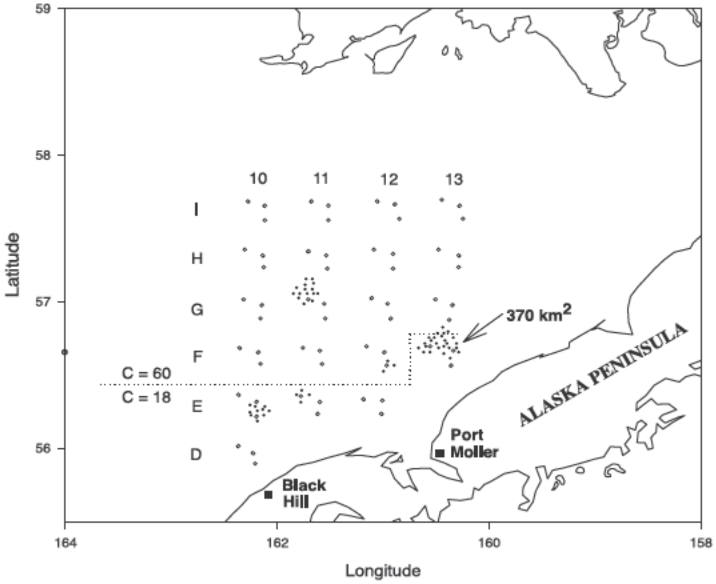

Figure 1. The 1995 Bristol Bay adaptive cluster sampling, with 60 sampling stations shown as open circles and crab aggregations shown as small points. The largest aggregation at F13 was continuous over more than 90,000 acres. The dotted line shows where, after the F13 encounter, investigators increased the threshold value from *C* = 18 to *C* = 60 egg-bearing females.

lished intervals (e.g., Abell et al. 1999) by resampling the NMFS trawl survey data, rebalanced to account for extra sampling (e.g., Dew and McConnaughey 2005, Table 2). For each random resample I obtained the mean and then constructed symmetric intervals of the same ± percent width (relative to the mean) as the published intervals. After repeating this operation 3,000 times, I calculated the proportion of these symmetric intervals that failed to include the "population" mean of the original sample. This proportion was an estimate of α, the type I error rate (nominally $\alpha = 0.05$); conversely, $1 - \alpha$ was an estimate of the confidence level or quality of the interval. If the confidence level of the published interval proved to be much less than the 95% routinely stated by investigators, then the interval was unrealistically precise (too narrow).

Next, in order to determine the effect of post-stratification, I calculated symmetric 95% confidence intervals for each of 3,000 random resamples from the unstratified (but rebalanced) NMFS data. The average limits of these 3,000 intervals formed a symmetric confidence interval, which was then evaluated as to confidence level, as outlined above.

Finally, because symmetric normal-based 95% confidence intervals fail to cover the means of highly skewed catch distributions more often than the expected 5% of trials (Mandel 1964), I used Efron's original percentile method (Efron and Tibshirani 1993; Mooney and Duval 1993; Manly 1997, p. 339) to evaluate the improvement that might be gained by using asymmetric vs. symmetric confidence intervals. To do this, I again resampled the rescaled data to obtain 3,000 resample means. Using a sorted list of the 3,000 resample means for each year, a count up 2.5% to the 75th lowest value and down 2.5% to the 75th highest value gave the endpoints of a 95% bootstrap confidence interval for the mean estimated from the trawl survey.

Randomization tests

I used 5,000-trial randomization tests (Manly 1997) to test whether the legal-male red king crab population size was changing significantly ($P < 0.05$) year-over-year during 1975-1980, and whether significant differences existed among any of the 15 year-pairs between 1975 and 1980. Unlike *t*-tests or ANOVA, randomization tests are valid even when sampling is nonrandom, data are non-normal, variances are heterogeneous among years, and independence of observations is suspect (Prager and Hoenig 1989).

Results

Disproving the consensus hypothesis

Kodiak

In situ research on the diel activity and foraging dynamics of podding red king crab at Kodiak, Alaska, during 1987-1993 led to the conclusion that most age 1-6 red king crab exist as pod members. For example, of the 11,600 age 2-3 crab counted in 1990-1991 during a 116-dive census in Womens Bay (Dew 1991), 97% were found in aggregations of ≥500 crab. Of the estimated 101,000 age 4-6 crab observed in 1993 (36 dives, January-September), 98% were found in aggregations of ≥1,000 crab. These data indicate that podding behavior continued and may have even intensified as the crab grew beyond age 3.

In 1990, investigators at Kodiak began to affix sonic tags to the carapaces of crab from the 1987 and 1988 cohorts (Dew et al. 1992). While tracking the crab and observing them in situ over the next several years, it became clear that red king crab continued their highly aggregative podding behavior until at least age 6, when they moved out of Womens Bay to waters >100 m deep, well beyond diving depths. Rather than becoming more randomized with time, as suggested in the litera-

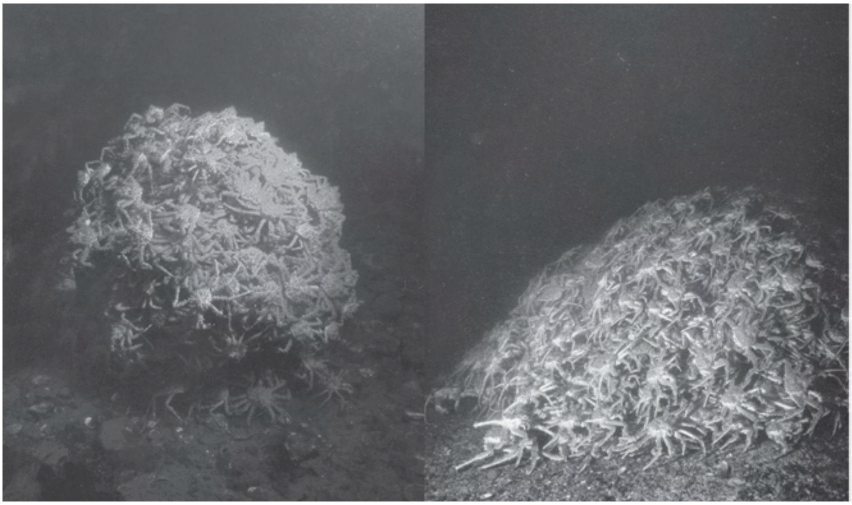

Figure 2. Composite photo showing the similarity between a juvenile resting pod of age-1 red king crab (left) and one composed of adult and subadult crab estimated to range between ages 5 and 12. The juvenile pod of 500-800 crab, each about the size of a U.S. fifty cent piece (30-40 mm CL), is about 0.5 m high. The adult/subadult pod, estimated to contain 8,000-10,000 crab ranging in size from 60 to 165 mm CL (mean = 103 mm CL), is about 2.5 m high. (Photos by B. Dew.)

ture (Incze et al. 1986, Otto 1986, Dew 1990), their distribution over the grounds grew more contagious as the discrete cohorts, approximately midway through their fourth and fifth years of life (age 3-4), proceeded to mix and coalesce into a single, larger aggregation (Dew et al. 1992).

Direct evidence that podding behavior continues into adulthood can be seen in a composite photograph (Fig. 2) documenting the similarity between juvenile and adult resting pods, where the primary difference between the two is the scale of the phenomenon. This photograph modifies the observation by Stone et al. (1993, p. 755) that "Adult pods were not similar to pods of juveniles. [Adult] pods were typically asymmetrical, and crab were usually stacked only three or four individuals deep." Because adult red king crab spend considerably more of their time foraging than resting (Dew 1990), evidence for the adult resting phase is rare compared to that for juveniles (Fig. 2 is the only known photograph of a multi-age, mixed-sex, resting pod of adult and subadult red king crab). The pod was photographed at midday on 26 September 1993 in Chiniak Bay (57.7445°N, 152.4227°W) at a depth of 22 m. The numbers of male (48%) and female (52%) crab were nearly

Figure 3. Members of the (Fig. 2) adult resting pod, now in foraging mode, moving directionally in a tight group, similar to the foraging behavior documented by Dew (1990) for podding juveniles. Note the sharp delineation between areas of high and low (no) density, a behavioral feature that contributes to the low precision of abundance estimates from the NMFS Bristol Bay trawl survey. (Photo by B. Dew.)

equal, and the mean size of the crab was 103 mm CL. The average male was 110 mm CL (range 79-165 mm), and 21% were ≥123 mm CL, which is the size reported for males of grasping pairs at Kodiak (Powell et al. 1973). Females averaged 96 mm CL, and 12% were carrying uneyed egg clutches. The egg-bearing females ranged in size from 99 to 131 mm CL. This resting pod was only a portion of the entire aggregation, which I previously estimated to be 20,000-30,000 crab on 9 September while still in Womens Bay (57.7262°N, 152.4825°W) but moving toward the more open water of Chiniak Bay.

Rather than dispersing over a wide area when foraging, an adult pod forages as a tightly knit, single-layer unit, maintaining a distinctly contagious distribution delimited by sharp transitions from approximate densities of >5 crab per m^2 to densities of 0 crab per m^2 (e.g., Fig. 3). The movement of such "knife-edges" into or out of a fixed sampling location (e.g., the fixed sampling stations of the NMFS Bristol Bay survey)

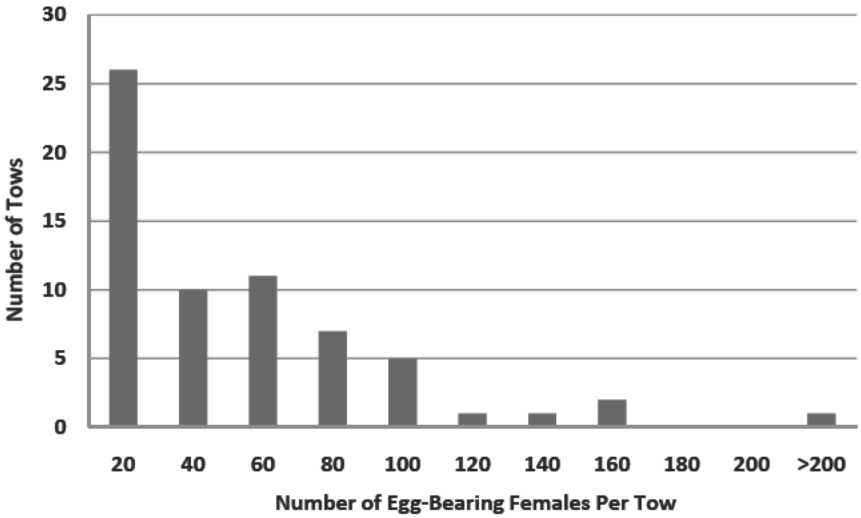

Figure 4. Distribution of catches within aggregations at stations E10, E11, F12, F13, and G11, where predetermined threshold values were triggered. Low threshold values are likely to find even small aggregations but may be impractical given the size of the larger aggregations.

would be an abrupt, all-or-none phenomenon, likely to be interpreted as a profound change in abundance instead of a minor change in location.

Bristol Bay

There are no direct, in situ observations of podding behavior in the southeastern Bering Sea, either for juvenile or adult red king crab, nor have any NMFS studies been designed to make such observations. The standard NMFS assessment survey, with its grid-square arrangement of trawl stations spaced at regular 37 km intervals and collecting a single 0.04-0.05 km² sample every 1,372 km², is likely to be a coarse sieve with which to capture a relatively small-scale phenomenon like podding (Vining and Watson 1996).

More useful was the adaptive cluster sampling (ACS) conducted in 1995 and designed to sample rare, clustered populations (Thompson and Seber 1996) with distributions similar to that expected for podding red king crab. This NMFS special study sampled on a relatively fine scale (3.7 km intervals) to reveal the nonrandom spatial distribution of red king crab in a 27,440 km² area of Bristol Bay (Fig. 1). The adaptive survey began on 10 June 1995 within grid square D10, and by 13 June, at grid square F13, the survey had encountered an aggregation so large that the

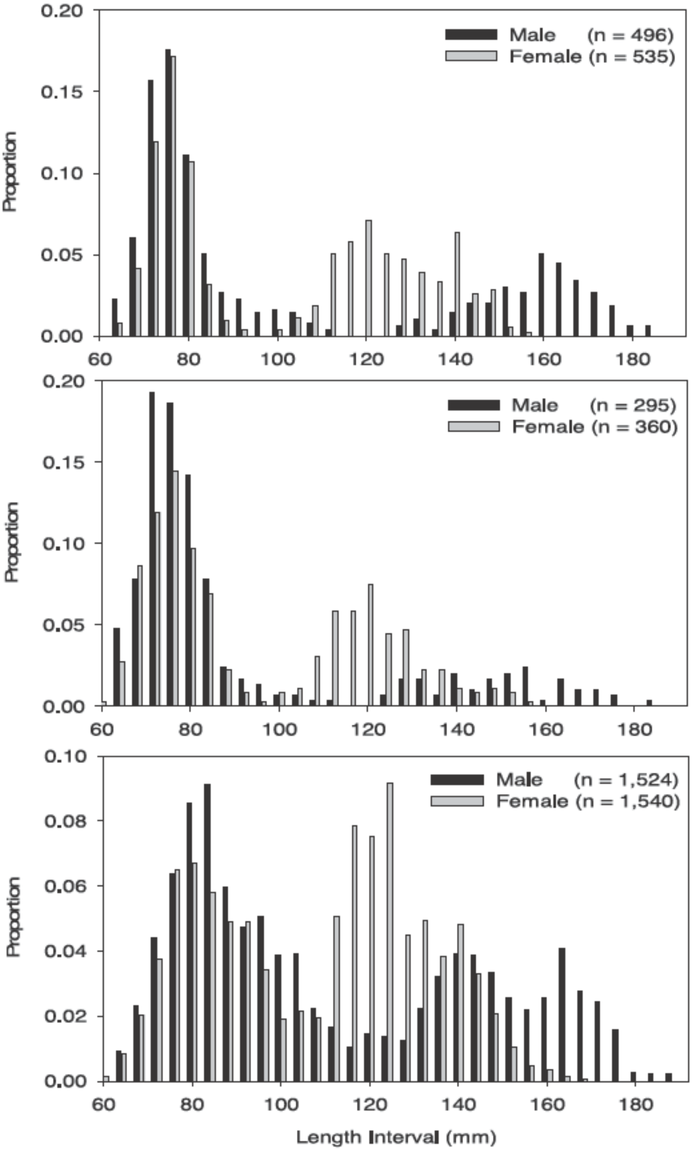

Figure 5. Length composition of 4,750 red king crab within the F13 aggregation: the highest-density catch (top), the second-highest-density catch (mid), and the remaining 25 catches combined (bottom).

threshold value of *C* = 18 was still being triggered after 27 tows and several days of sampling (Fig. 1). Sampling was abandoned before the boundaries of the F13 aggregation were established, but even this incomplete sampling showed the presence of a continuous distribution of crab over an area of 370 km^2, or more than 90,000 acres. Because 85% of the 27 tows within the F13 aggregation met or exceeded the initial threshold value of *C* = 18, the criterion was increased to *C* = 60 to reduce the chances of getting stalled for several days in another aggregation. Even with a *C*-value more than three times the original, the adaptive survey encountered a second large aggregation at grid square G11, 83 km to the northwest of F13, where 16 tows were completed before the effort to define the boundaries of the aggregation, now continuous over an area of 219 km^2, was abandoned because of time constraints.

To set meaningful and practical *C*-values, it would help to know the catch distribution within aggregations encountered in past surveys. Based on the 1995 results (Fig. 4), a criterion of *C* = 18 was useful because even small aggregations were discovered; but it was impractical given the resources allocated to the study. The criterion of *C* = 60, while more practical, probably would not have discovered the aggregation at E10 (Fig. 1), where the highest catch in 12 tows was 20 mature females.

Of the 11,470 crab collected in 117 ACS trawl samples, 78% were from aggregations occupying grounds that represent only 3% of the total sampling area. Of the 5,768 adult crab collected, 82% were from aggregations, and more than half (53%) of the crab in aggregations were adults (males ≥120 mm CL, females ≥90 mm CL, e.g., Zheng et al. 1995). The average density of aggregated adults (1,360 per km^2) was three times the average density of non-aggregated adults (438 per km^2). The largest aggregation, encountered at F13 with an average density of 4,074 per km^2, was estimated to include more than 1.5×10^6 adult and subadult crab within the area sampled. Another large aggregation at G11, with an average density of 4,614 per km^2, was estimated to include more than 1.0×10^6 crab. These estimates understate the number of red king crab in the aggregations at F13 and G11 because sampling was halted before the boundaries of these large aggregations were ascertained.

Length-frequency analysis indicates that the size variation within aggregations was less than the variation between aggregations. The length-frequency distributions within the F13 aggregation were bimodal, with a male-female mode at 70-90 mm and a female mode at 110-150 mm (Fig. 5). These modes were present in each of the two largest F13 catches, which were 5 km apart, and in the remaining 25 F13 catches combined. The G-11 aggregation was distinguishable by its single, male-female mode at 85-120 mm, which was present in each of the two largest catches (4 km apart) and in the remaining 14 catches combined (Fig. 6). Distinctive length-frequency signatures

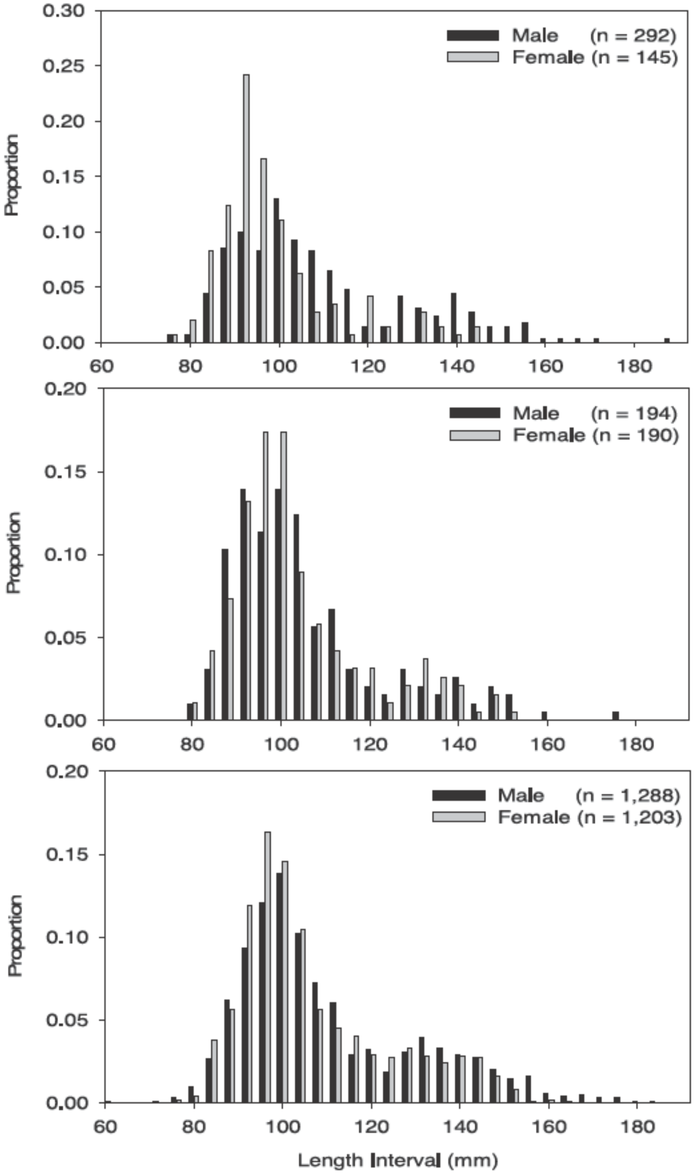

Figure 6. **Length composition of 3,312 red king crab within the G11 aggregation: the highest-density catch (top), the second highest density catch (mid), and the remaining 14 catches combined (bottom).**

throughout each of these two large aggregations, indicating that the crab were well-mixed within but not between aggregations, suggest that each aggregation was a demographically discrete, nonrandom subset of the red king crab population within the ACS area.

Precision

The high levels of precision reported for red king crab abundance estimates are inconsistent with data and observations indicating that Bristol Bay adult, subadult, and juvenile red king crab are podding crab whose behavior results in extremely clumped, contagious spatial distributions. Re-evaluation of the NMFS post-stratified confidence intervals using resampling methods demonstrated that the post-stratified intervals, averaging ±18% of the mean during 1975-1980 (Otto 1986), overstated the precision of abundance estimates to a degree that may have adversely affected the management process. Comparable symmetric intervals without post-stratification, averaging ±39%, were more than twice as wide as the NMFS intervals, and asymmetric bootstrap intervals were, on average, –35% to +44% (Table 2).

Confidence intervals that are too narrow to be realistic will fail to achieve the confidence level claimed by investigators (e.g., 95%). I used resampling methods (e.g., Abell et al. 1999) to demonstrate that the confidence level of the NMFS-published (post-stratified) intervals was closer to 60% (range = 50-73%) than the stated 95% (Table 2). Of the 3,000 confidence intervals for the resampled means ($\bar{x}$), the proportion that did not include the original sample mean ($\hat{\mu}$) ranged from 27% to 50%, or 5 to 10 times the $\alpha = 0.05$ error rate expected for 95% confidence

Table 2. Comparison of three types of confidence interval. Interval widths are expressed as ±% of the mean (legal-male density). Actual (vs. nominal) α-levels, and interval quality ($1 - \alpha$) are shown for post-stratified (PS) and non-stratified (NS) intervals.

	NMFS Poststratified (PS)[a]			No Stratification[a]			Bootstrap[b]	
Year	±%	α	$1 - \alpha$	±%	α	$1 - \alpha$	-%	+%
1975	15	0.39	0.61	34	0.08	0.92	33	36
1976	16	0.35	0.65	33	0.11	0.89	29	39
1977	20	0.27	0.73	34	0.09	0.91	32	38
1978	27	0.31	0.69	50	0.11	0.89	43	58
1979	13	0.49	0.51	35	0.10	0.90	33	42
1980	15	0.50	0.50	46	0.08	0.92	40	50
Avg	18	0.39	0.61	39	0.10	0.90	35	44

PS interval widths (±%) from Reeves (1975), Pereyra et al. (1976), Reeves et al. (1976), Otto (1981, 1986), and Larkin et al. (1990).

[a] Normal-based intervals. Nominal rates: $\alpha = 0.05$ $1 - \alpha = 0.95$

[b] Asymmetric intervals based on resampling from rescaled data.

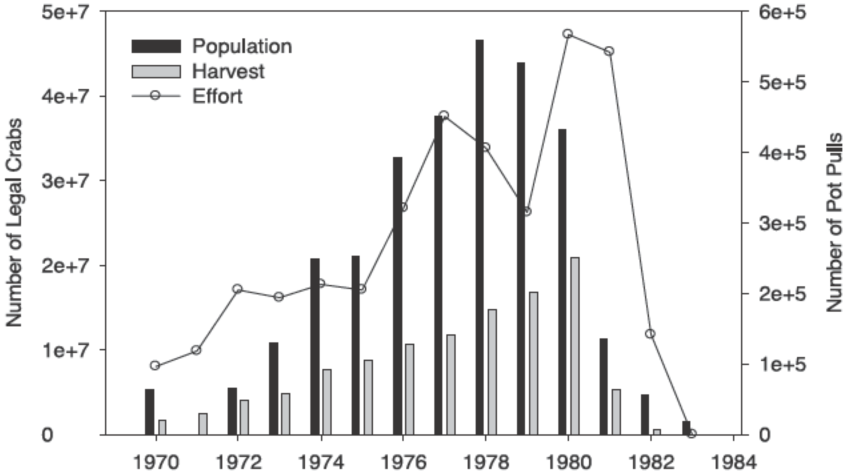

Figure 7. Trends in population size, harvest, and effort, 1970-1983. The 1970-1980 harvest trend can be approximated by the relationship $H_t = 2.22 \times 10^6 e^{0.24t}$ ($r^2 = 0.986$), where H_t = the harvested number of crab in year t (with 1970 being $t = 0$). This represents a doubling of the harvest every 2.9 years. There were no significant ($p \leq 0.05$) differences among population estimates during 1975-1980 (survey data by tow not available for years prior to 1975).

intervals. Thus, instead of the stated 1-in-1/α (1-in-20) chance that the confidence interval for an estimate of mean crab abundance was wrong (i.e., that it failed to include $\hat{\mu}$), there was an average 1/0.38 or a 1-in-2 to 1-in-3 chance. Clearly, there was more uncertainty associated with the NMFS population estimates than was presented to resource managers engaged in an exponential expansion of the Bristol Bay red king crab harvest during 1970-1980 (Fig. 7).

The fact that the post-stratified intervals overstate the reliability and understate the uncertainty of the NMFS population estimates, to a degree that they should not be used as an approximation of survey precision, raises the question of whether the trend of increasing population size (Fig. 7) relied upon by managers was sufficiently dependable to justify the exponentially increasing harvest during 1970-1980. Using 5,000-trial randomization tests (Manly 1997), I tested whether it was reasonable to assume that the population was increasing year-over-year during 1975-1980. Consistent with the wide, overlapping confidence intervals in Fig. 8, the randomization tests suggest that the size of the Bristol Bay red king crab population changed little, if at all, from year to

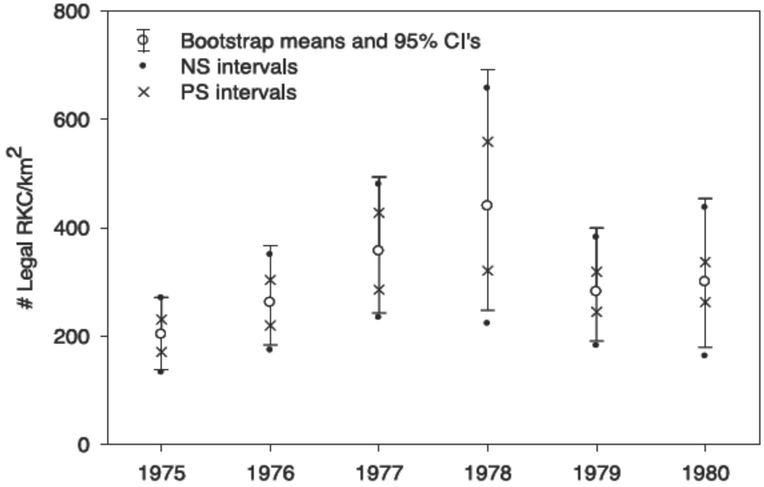

Figure 8. Comparison of NMFS post-stratified (PS) confidence intervals with symmetric intervals without post-stratification (non-stratified, NS intervals) and 95% bootstrap (asymmetric) intervals. There were no significant differences among any of the 1975-1980 abundance estimates (open circles), although the harvest more than tripled during this time.

Table 3. Results of randomization tests comparing densities ($\bar{X}$= mean number per km^2, n = sample size) of legal male red king crab between consecutive years, 1975-1982. During the 1975-1980 period leading up to the population collapse, abundance did not change significantly ($p \leq 0.05$), although changes after 1980 were highly significant ($p \leq 0.005$).

Years	$\bar{X}_i$	(n)[a]	$\bar{X}_{i+1}$	(n)[a]	p	% change
1975-76	202.5	(77)	263.1	(80)	0.287	+30
1976-77	263.1	(80)	357.5	(77)	0.245	+36
1977-78	357.5	(77)	438.3	(82)	0.568	+23
1978-79	438.3	(82)	282.8	(82)	0.235	–35
1979-80	282.8	(82)	301.6	(82)	0.825	+7
1980-81	301.6	(82)	89.2	(82)	0.005	–70
1981-82	89.2	(82)	35.9	(82)	0.000	–60

[a] (n) is the design-based sample size; multiple tows at a station are represented by their mean.

year during the 1975-1980 period of increasing exploitation (Table 3). Not only were there no significant ($P < 0.05$) differences among consecutive years, there were no differences among any of the 15 year-pairs between 1975 and 1980. The only significant differences occurred as the population collapse accelerated during 1980-1982. Apparently the commercial catch swelled to record levels independent of any detectable or statistically significant change in the source population during the six years preceding its collapse.

Discussion

An assumption of assessment surveys such as the Bristol Bay red king crab survey is that an observed trend in annual population estimates is reasonably well-correlated with a real abundance trend in the underlying population. However, without some idea of the precision of each annual population estimate, the reliability of a survey-derived abundance trend cannot be evaluated. In fact, if confidence intervals around the annual estimates are wide enough (i.e., if the uncertainty of the survey estimates is great enough), the survey-derived trend may bear little or no resemblance to the actual abundance changes in the population. In the face of high population-estimate uncertainty, there may be little chance of finding a meaningful link between climate change and abundance trends. Thus it is imperative for scientists and managers to have a full understanding of the reliability of their survey population estimates.

According to the generalized behavioral model taken from the literature, red king crab move through an ontogenetic continuum (Dew 1990) from podding juveniles with an extremely patchy distribution (Otto 1986) that requires a tremendous sampling effort (Incze et al. 1986), to age-4 crab larger than 69 mm CL that have ceased podding (Powell and Nickerson 1965, Incze et al. 1986, Otto 1986, Armstrong et al. 1993, Witherell 1998, Ackley and Witherell 1999), and on to a mature population that is "extremely amenable" to trawl surveys (Otto 1986, p. 98). Upon examination of data collected from Kodiak and Bristol Bay, it becomes clear that older red king crab (subadults and adults greater than age 4) do not conform to this model. Instead, in situ observations, photographic evidence, and the results from adaptive cluster sampling indicate that the podding behavior documented for juveniles (Dew 1990) continues into adulthood for red king crab from Kodiak and Bristol Bay. This information is consistent with the findings of Dew and Austring (2007) that red king crab, when compared to five other major species in the NMFS bottom-trawl survey of the eastern Bering Sea, occupied an extreme position within the spectrum of spatial distribution and statistical intractability, and was the species with the greatest patchiness and the lowest abundance-estimate precision.

It appears that large-scale podding of adult and subadult red king crab, rather than being a rare and unrepresentative event (e.g., Stevens et al. 1991), is a behavioral norm for the species throughout its Alaska range from Bristol Bay and Kodiak to southeast Alaska (Stone et al. 1992, 1993). This observation has implications beyond the category of interesting animal behavior. During the 1970s the red king crab fishery was the most valuable single-species fishery in Alaska, and from 1970 to 1980 the Bristol Bay harvest biomass increased steadily by more than 1400% to all-time record levels. Then, in 1981, after a male-only harvest of 130 million pounds, the Bristol Bay red king crab population abruptly collapsed in one of the more precipitous declines in the history of U.S. fisheries management. It is reasonable to assume that managers who annually recommended an exponentially increasing harvest, doubling every three years for more than a decade, were confident that the exploited population was increasing during this time. Judging from the population estimates derived from the NMFS annual stock- assessment surveys (estimates biased by repeated, nonrandom sampling in areas of high crab abundance, Table 1), the estimated number of legal male red king crab in Bristol Bay appeared to increase by nearly an order of magnitude from 1970 to 1978, after which the population began to decline (Fig. 7). However, without a realistic idea of the precision of each annual population estimate, the reliability of the late-1970s trend of increasing population size cannot be evaluated.

With respect to evaluating the precision of the 1975-1980 legal-male population estimates, the information in Table 2 provides us with three choices (not intended to be the only choices). First, we can use the published NMFS confidence intervals, averaging ±18% of the mean only if we keep in mind that these are, on average, 61% intervals rather than 95% intervals. That is, the NMFS confidence intervals, biased by post-stratification, are likely to be wrong nearly 40% of the time rather than 5%, as claimed. Next, we can forego post-stratification, rebalance the sample list to account for the extra tows (e.g., Table 1), and calculate symmetric, normal-based confidence intervals. These intervals, averaging ±39% of the mean and with an average confidence level of 90% ($\alpha = 0.10$), are more than twice as wide as the NMFS low-quality 61% intervals. This represents a substantial improvement over the NMFS intervals, whose quality is degraded by post-stratification. Last, we can achieve some additional improvement in the quality of the intervals by accounting for the fact that typical red king crab survey data are highly skewed (non-normal), and that the precision of skewed data is better evaluated with asymmetric bootstrap confidence intervals, rather than with symmetric, normal-based intervals. The average limits of the asymmetric intervals are −35% to +44%, with a confidence level of 95% (by definition). With regard to the task of differentiating between climate change and fishing effects, we should recall that if a stock-size estimate is highly uncertain, even less will be known about the fishing pressure on the stock. For example, using an interval width of ±40% for a population-size estimate, the corresponding interval width for the utilization (harvest) rate is ±95% (Dew and Austring 2007).

Understanding that the confidence intervals around the individual population estimates during 1975-1980 are on the order of ±35-50% instead of ±15-20% as published, it is prudent to question whether the 1975-1980 data can be used to define a trend (e.g., Fig. 7), or whether such a trend tells us much, if anything, about actual abundance changes in the underlying population. Upon statistical examination (randomization tests), there were no significant ($P < 0.05$) differences among consecutive years between 1975 and 1980, nor were there significant differences among any of the 15 year-pairs (e.g., 1975 vs. 1978, a period during which the population ostensibly increased by >100%). However, the statistical power of the tests was sufficient to show highly significant differences as the population collapsed after 1980. Unfortunately, the best climate data in the world might not be particularly enlightening when plotted against red king crab data points, none of which can be differentiated by statistical testing, and whose uncertainty is quantified by confidence intervals of ±35% to ±50%.

References

Abell, M.L., J.P. Braselton, and J.A. Rafter. 1999. Statistics with Mathematica. Academic Press, New York. 632 pp.

Ackley, D., and D. Witherell. 1999. Development of a marine habitat protection area in Bristol Bay, Alaska. In: Ecosystem approaches for fisheries management. Alaska Sea Grant, University of Alaska Fairbanks, pp. 511-526.

Armstrong, D.A., T.C. Wainright, G.C. Jensen, P.A. Dinnel, and H.B. Anderson. 1993. Taking refuge from bycatch issues: Red king crab (*Paralithodes camtschaticus*) and trawl fisheries in the eastern Bering Sea. Can. J. Fish. Aquat. Sci. 50:1993-2000. doi:10.1139/f93-223

Chilton, E.A., C.E. Armistead, and R.J. Foy. 2008. The 2008 eastern Bering Sea continental shelf bottom trawl survey: Results for commercial crab species. NOAA Tech. Memo. NMFS-AFSC-187. 88 pp. Accessed Dec. 2010: http://www.afsc.noaa.gov/Publications/AFSC-TM/NOAA-TM-AFSC-187.pdf.

Cochran, W.G. 1977. Sampling techniques, 3rd edn. John Wiley and Sons, New York. 428 pp.

Degoursey, R.E., and P.J. Auster. 1992. A mating aggregation of the spider crab (*Libinia emarginata*). J. Northw. Atl. Fish. Sci. 13:77-82. doi:10.2960/J.v13.a6

Degoursey, R.E., and L.L. Stewart. 1985. Spider crab podding behavior and mass molting. Underwater Naturalist 15:12-16.

Dew, C.B. 1990. Behavioral ecology of podding red king crab, *Paralithodes camtschatica*. Can. J. Fish. Aquat. Sci. 47:1944-1958. doi:10.1139/f90-219

Dew, C.B. 1991. Characterization of preferred habitat for juvenile red king crab in three Kodiak bays. Final report to the Kodiak Island Borough. Contract No. 89-226. 49 pp. Available from Kodiak Island Borough, 710 Mill Bay Road, Kodiak, Alaska 99615.

Dew, C.B. 2008. Red king crab mating success, sex ratio, spatial distribution, and abundance estimates as artifacts of survey timing in Bristol Bay, Alaska. N. Am. J. Fish. Manage. 25:1618-1637. doi:10.1577/M07-038.1

Dew, C.B., and R.G. Austring. 2007. Alaska red king crab: A relatively intractable target in a multispecies trawl survey of the eastern Bering Sea. Fish. Res. 85:165-173. doi:10.1016/j.fishres.2007.02.001

Dew, C.B., and R.A. McConnaughey. 2005. Did trawling on the brood stock contribute to the collapse of Alaska's king crab? Ecol. Appl. 15:919-941. doi:10.1890/03-5231

Dew, C.B., P.A. Cummiskey, and J.E. Munk. 1992. The behavioral ecology and spatial distribution of red king crab and other target species: Implications for sampling design and data treatment. In: L. White and C. Nielsen (eds.), Proceedings of the International Crab Rehabilitation and Enhancement Symposium, Kodiak. Alaska Department of Fish and Game, Fisheries Rehabilitation and Enhancement Division, Juneau, pp. 39-67.

Efron, B., and R.J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York. 436 pp.

Gunderson, D.R. 1993. Surveys of fisheries resources. John Wiley and Sons, New York. 248 pp.

Hilborn, R., and C.J. Walters. 1992. Quantitative fisheries stock assessment: Choice, dynamics, and uncertainty. Chapman and Hall, New York. 570 pp.

Hooper, R.G. 1986. A spring breeding migration of the snow crab, *Chionoecetes opilio* (O. Fabr.), into shallow water in Newfoundland. Crustaceana 50:257-264. doi:10.1163/156854086X00287

Incze, L.S., R.S. Otto, and M.K. McDowell. 1986. Recruitment variability of juvenile red king crab, *Paralithodes camtschatica*, in the southeastern Bering Sea. In: G.S. Jamieson and N. Bourne (eds.), North Pacific workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92:370-378.

Larkin, P.A., B. Scott, and A.W. Trites. 1990. The red king crab fishery of the southeastern Bering Sea. Submitted to D.L. Alverson, executive director of the Fisheries Management Foundation, Seattle. 66 pp. (Available from University of Washington Libraries.)

Loher, T. 2001. Recruitment variability in southeast Bering Sea red king crab (*Paralithodes camtschaticus*): The roles of early juvenile habitat requirements, spatial population structure, and physical forcing mechanisms. Ph.D. thesis, University of Washington. 436 pp.

Mandel, J. 1964. The statistical analysis of experimental data. Dover Publications, New York. 410 pp.

Manly, B.F.J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall, New York. 399 pp.

McConnaughey, R.A., and L.L. Conquest. 1993. Trawl survey estimation using a comparative approach based on lognormal theory. Fish. Bull. 91:107-118.

Mooney, C.Z., and R.D. Duval. 1993. Bootstrapping: A nonparametric approach to statistical inference. Sage University Paper series on Quantitative Applications in the Social Sciences, 07-095. Newbury Park, California. 73 pp.

Otto, R.S. 1981. Eastern Bering Sea crab fisheries. In: D.W. Hood and J.A. Calder (eds.), The eastern Bering Sea shelf: Oceanography and resources. Vol. 2. Office of Marine Pollution Assessment, Juneau, Alaska, pp. 1037-1066.

Otto, R.S. 1986. Management and assessment of eastern Bering Sea king crab stocks. In: G.S. Jamieson and N. Bourne (eds.), North Pacific workshop on stock assessment and management of invertebrates. Can. Spec. Pub. Fish. Aquat. Sci. 92:83-106.

Pereyra, W.T., J.E. Reeves, and R.G. Bakkala. 1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975. NOAA Northwest and Alaska Fisheries Center Processed Report. 619 pp.

Powell, G.C., and R.B. Nickerson. 1965. Aggregations among juvenile king crabs (*Paralithodes camtschatica*, Tilesius) Kodiak, Alaska. Anim. Behav. 13(514):2-3.

Powell, G.C., B. Shafford, and M. Jones. 1973. Reproductive biology of young adult king crabs, *Paralithodes camtschatica* (Tilesius) at Kodiak, Alaska. Proceedings of the National Shellfisheries Association 63:77-87.

Prager, M.H., and J.M. Hoenig. 1989. Superposed epoch analysis: A randomization test of environmental effects on recruitment with application to chub mackerel. Trans. Am. Fish. Soc. 118:608-618. doi:10.1577/1548-8659(1989)118<0608:SEAART>2.3.CO;2

Reeves, J.E. 1975. King and Tanner crab research in the Bering Sea. NOAA, National Marine Fisheries Service, Seattle, unpublished manuscript. 25 pp. (Cited in Pereyra et al. 1976.)

Reeves, J.E., R.N. McBride, and N. Newcome. 1976. King and Tanner crab research in the eastern Bering Sea, 1976. International North Pacific Fisheries Commission (INPFC) Document 1926.

Skalski, J.R. 1997. Sampling theory for biologists. Lectures in Quantitative Science 480. University of Washington School of Fisheries, Seattle.

Stevens, B.G., W.E. Donaldson, and J.A. Haaga. 1992. First observations of podding behavior for the Pacific lyre crab, *Hyas lyratus* (Decapoda: Majidae). J. Crust. Biol. 12:193-195. doi:10.2307/1549074

Stevens, B.G., J.A. Haaga, and W.E. Donaldson. 1994. Aggregative mating of Tanner crab, *Chionoecetes bairdi*. Can. J. Fish. Aquat. Sci. 51:1273-1280. doi:10.1139/f94-127

Stevens, B.G., R.A. MacIntosh, and J.A. Haaga. 1991. Report to industry on the 1991 eastern Bering Sea crab survey. NOAA Alaska Fisheries Science Center (AFSC) Processed Report 91-17. 53 pp. (Available from R.A. MacIntosh, AFSC/NMFS, P.O. Box 1638, Kodiak, Alaska 99615.)

Stone, R.P., C.E. O'Clair, and T.C. Shirley. 1992. Seasonal migration and distribution of female red king crabs in a southeast Alaskan estuary. J. Crust. Biol. 12:546-560. doi:10.2307/1548836

Stone, R.P., C.E. O'Clair, and T.C. Shirley. 1993. Aggregating behavior of ovigerous female red king crab, *Paralithodes camtschaticus*, in Auke Bay, Alaska. Can. J. Fish. Aquat. Sci. 50:750-758. doi:10.1139/f93-086

Thompson, S.K., and G.A.F. Seber. 1996. Adaptive sampling. John Wiley and Sons, New York. 265 pp.

Tyler, A.V., and G.H. Kruse. 1996. Conceptual modeling of brood strength of red king crabs in the Bristol Bay region of the Bering Sea. In: High latitude crabs: Biology, management and economics. Alaska Sea Grant, University of Alaska Fairbanks, pp. 511-543.

Vining, I., and L.J. Watson. 1996. Application of kriging trawl survey data to estimate red king crab distribution and abundance in Bristol Bay, Alaska. In: High latitude crabs: Biology, management, and Economics. Alaska Sea Grant, University of Alaska Fairbanks, pp. 255-282.

Witherell, D. 1998. King and Tanner crabs of the Bering Sea and Aleutian Islands area: Species profiles. Report to the North Pacific Fishery Management Council, 605 West 4th Avenue, Suite 306, Anchorage, Alaska 99501.

Zheng, J., M.C. Murphy, and G.H. Kruse. 1995. A length-based population model and stock-recruitment relationships for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. Can. J. Fish. Aquat. Sci. 52:1229-1246. doi:10.1139/f95-120

Morado, J.F., E.G. Dawe, D. Mullowney, C.A. Shavey, V.C. Lowe, and R.J. Cawthorn. 2010. Climate Change and the Worldwide Emergence of *Hematodinium*-Associated Disease: Is There Evidence for a Relationship? In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.08

Climate Change and the Worldwide Emergence of *Hematodinium*-Associated Disease: Is There Evidence for a Relationship?

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Abstract

Over the past 20 years, many scientific publications have expressed a growing concern about the apparent increase of marine diseases in relation to climate change. Unfortunately, the data on this potential association are not clear; diseases of some marine taxa appear to have increased during the past two decades while diseases of other marine taxa appear to be stable or on the decline. The ambiguous nature of the data is a general result of inadequate historical or baseline data, and failure to measure and include environmental data in disease investigations. However, these findings are not unique as human health specialists are also confounded in their attempts to draw clear examples of human diseases that are only influenced by climate.

Diseases caused by parasitic dinoflagellates of the genus *Hematodinium* have literally exploded across the Northern Hemisphere since 1985. Coincidentally, the rapid expansion of *Hematodinium*-like diseases appears to have co-occurred or closely followed warming trends in both the North Atlantic and Pacific oceans. We will examine this apparent relationship and discuss elements that support or fail to confirm the relationship.

Background

Available evidence indicates that the earth's climate is changing; it is warming as a result of increased amounts of greenhouse gases and, in particular, anthropogenic carbon dioxide (IPCC 2007, Relman et al. 2008). Atmospheric and ocean temperatures are expected to increase resulting in the rise in sea level and unpredictable weather patterns. Concerns associated with climate change were the basis for the creation of the Intergovernmental Panel of Climate Change (IPCC) in 1988. Today, various other organizations are also involved in providing updates and projections on the potential impacts of climate change on human health and ecosystems. Notable publications that discuss possible effects of climate change on human health include *Global Climate Change and Extreme Weather Events* (Relman et al. 2008), *Climate Change and Human Health-Risks and Responses* (WHO 2003), and *Understanding and Responding to Climate Change* (NRC 2008).

In contrast, the literature on the effects of climate change on other animals is less extensive and often incomplete. The World Organization for Animal Health (OIE) has taken a leadership role and coordinates programs for monitoring terrestrial and aquatic animal diseases. Similar in function to the Institute of Medicine (IOM) and World Health Organization (WHO), OIE synthesizes and disseminates information on selected animal health issues and recently, the potential impact of climate change on disease prevalence and distribution (de la Rocque et al. 2008). However, the current data do not permit confirmation of a direct correlation between the occurrence of marine diseases and climate change, even for OIE reportable diseases (http://www.oie.int/).

Over the past decade, many papers have been published on the potential relationship between climate change and an increase in diseases of aquatic organisms. Williams and Bunkley-Williams (1990) proposed that the worldwide coral reef bleaching events of 1979-80, 1982-83, and 1986-88 were caused by warming periods that preceded the anomalies. They further suggested that a number of other diseases of marine organisms shared some of the same features with the observed coral epizootics. Epstein et al. (1998) proposed an ocean health framework, similar to one used by epidemiologists and public health specialists, that would generate early warning signs of conditions favoring disease emergence in response to climate change. Harvell et al. (1999) raised alarms by linking mass mortalities in a limited number of economically and ecologically important marine taxa to climate change. Harvell et al. (2002, 2004) later expanded their discussion on the climate-disease link, but acknowledged that technological and data collection issues existed. In an opposing view, Ward and Lafferty (2004) and Lafferty et al. (2004) indicated that the climate–marine disease link was not entirely clear. They reported that disease was not increasing across all marine taxa and concluded that the disease-environmental link was complex. Lafferty (2009) later offered keen insight on the ecology of climate change and infectious diseases, and suggested that some factors that affect the distribution and occurrence of infectious disease could overshadow the effects of climate. In similar fashion, Kim et al. (2005) noted that an absence of long-term baseline data made it difficult to gauge the significance of recent disease outbreaks.

In light of similar uncertainties, in the proceedings the IOM workshop on Global Climate Change and Extreme Weather Events, Relman et al. (2008) noted that, “In the specific case of the relationship between climate and infectious disease, it is important to recognize that a complex ‘web of causation’ determines the distribution and transmission of infectious disease agents.” Citing additional factors that influence the prevalence and distribution of human disease (i.e., land-use patterns, a variety of social, demographic and geographical factors, trade and transportation, human and animal migration, and public health interventions), workshop participants could not develop a consensus statement on the role of climate change as the sole driver of human diseases. Workshop participants apparently adopted a research framework initially proposed by Haines et al. (2006) and modified by MacPerson and Gushulak (2008; Table 1) that emphasized the collection of climate data in association with epidemiological data to better address a potential health-climate connection. We believe that these research tasks are relevant to the study of marine diseases and will address each topic in

Table 1. Research framework tasks for studying climate change and human health impacts.

- Examine past associations between climate variability and health.
- Determine climate's role in present-day trends in disease transmission and geographical range.
- Create predictive models for future diseases that account for a changing climate, as well as for other influential factors.
- Recognize and address the contribution of human behavior to global climate change and its further effects on infectious disease emergence.

Tasks 1-3 were proposed by Haines et al. (2006); task 4 was submitted by MacPerson and Gushulak (2008).

our review of *Hematodinium*-associated diseases and their potential relationship to climate change.

Climate change and *Hematodinium*-associated disease associations

Task 1. Examine past associations between climate variability and health

Major health events occur during both cooling and warming events (Table 2). Since the last ice age approximately 20,000 years ago, the earth has warmed considerably. During this era, mankind has experienced periods of affluence as well as hardship, particularly during the cool centuries known as the Little Ice Age (LIA) (Fig. 1). The LIA lasted from approximately 1300 to 1850, during which the European human population experienced major epidemics, population shifts, and failed agriculture and fisheries (Lamb 1979, Jónsson 1994, Fagan 2000). After the LIA, another small cooling event occurred prior to 1940, but for a period after 1940, mean global temperatures remained stable. The rise in mean surface temperatures is a recent event, a phenomenon that is projected to continue to rise (WHO 2003). It should be noted that after 1850 and the end of the LIA, significant human and other animal health anomalies have occurred as well (Table 2).

In addressing the first Haines task (Table 1), is it possible to identify a disease of an aquatic organism where a relationship between climate change and its occurrence can be documented? The response is equivocal. Even coral bleaching, which is a disease complex having both infectious (Kushmaro et al. 1996, Brown 1997) and non-infectious (De'ath et al. 2009) etiologies, cannot be solely aligned with climate change. In addition, the historical record indicates that the staghorn coral,

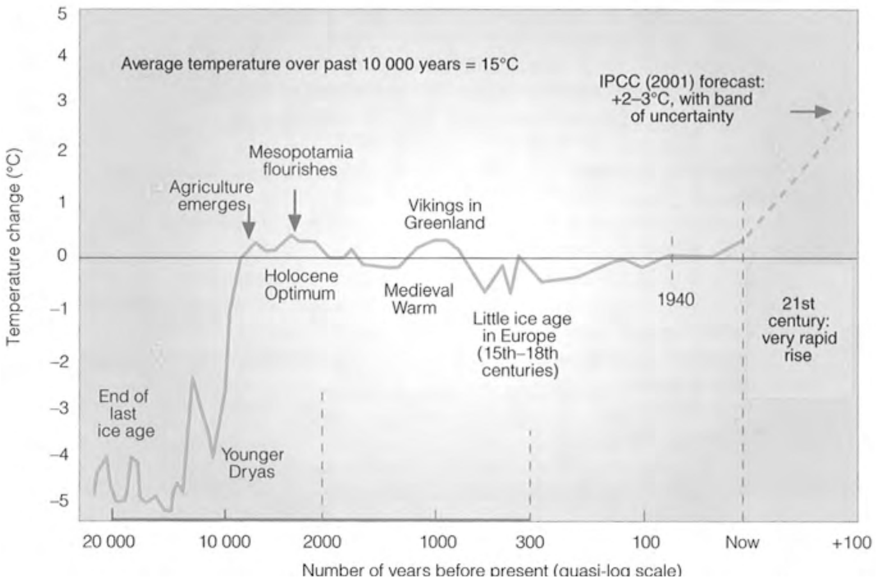

Figure 1. Variations in the earth's average surface temperature over the past 20,000 years. Prior to 1860, analogue measures of temperature are necessary (tree rings, oxygen isotope ratios in ice cores and lake sediments, etc.). Note the substantial natural fluctuations throughout the period. (WHO 2003, with permission.)

Table 2. Major health or cultural events occur during both major cooling and warming events.

Events of Little Ice Age: 1300-1850
1315-1321: The Great Famine
1348: Black Plague
1350: Vikings abandon western Greenland settlement
~1400: Vikings abandon eastern Greenland settlement
1469: Wine cultivation abandoned in England
1700: Faeroe Island cod fishery failure
1845: Irish potato famine
Post Little Ice Age events
1918: Spanish flu pandemic
1988: North Sea seal mortality
1992: Amphibian epizootics
1998: Worldwide coral bleaching events

Cited events for the Little Ice Age are from Fagan 2000.

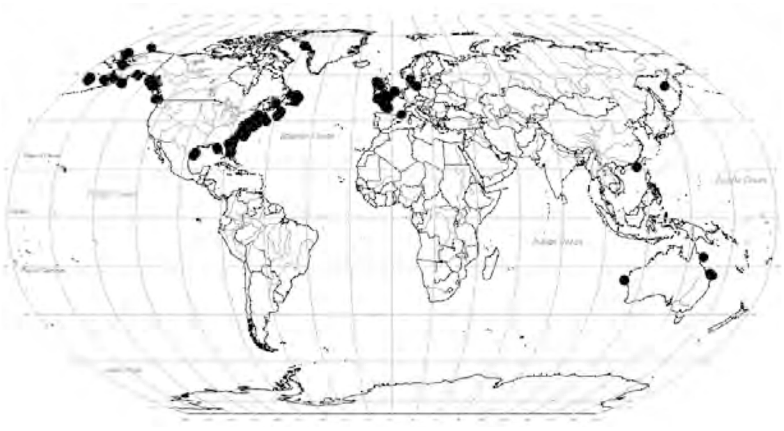

Figure 2. Global distribution of *Hematodinium*-associated disease. Note the rare occurrence of disease in the Southern Hemisphere. Blue dots represent most recent reports.

Acropora cervicornis, survived large-scale climate and environmental changes during the Holocene era (Greer at al. 2009).

Members of the genus *Hematodinium* are parasitic dinoflagellates that produce significant disease and mortality. Common names for resulting diseases include bitter crab syndrome, bitter crab disease, and pink crab disease. However, these common names are misleading as lobsters and amphipods are also known hosts. As a result, we refer to these diseases as *Hematodinium*-associated diseases.

In total, 40 crustacean species from around the world are known to be infected, the majority of which are in the Northern Hemisphere. The type species was described from the Brittany Coast of France in *Polybius depurator* (Chatton and Poisson 1931). When the parasite was described, the investigators noted that based on their data, *Hematodinium* infections were likely rare. Gallien (1940) gave the first indication that infections could be significant as he reported prevalences of 22.5% in *Portumnus latipes*. Thirty-five years later *Hematodinium* infections were reported from the east coast of the United States and upon occasion, at remarkable prevalences (Newman and Johnson 1975). From 1931 to 1985, the number of reports citing infections of the parasitic dinoflagellate totaled six.

However, after 1985, the frequency and number of reported *Hematodinium*-associated epizootics literally exploded. Today, *Hematodinium*-associated infections are common along the coasts of eastern Canada and the United States, Western Greenland, and Europe

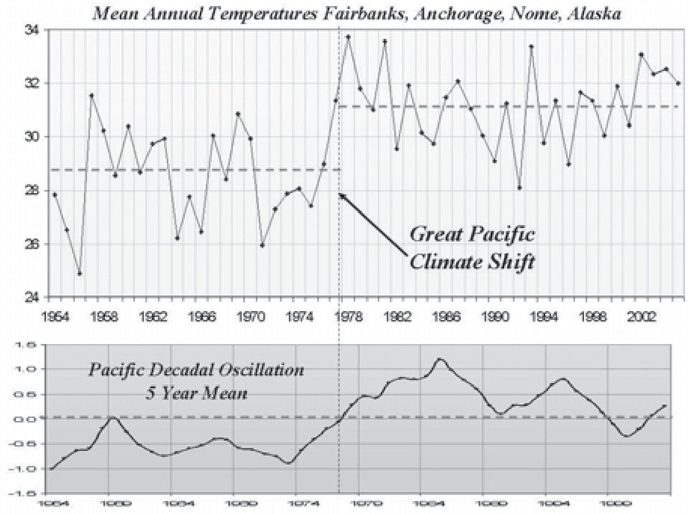

Figure 3. The last major change in the Pacific Decadal Oscillation (PDO) was in 1977. Called the Great Pacific Climate Shift, it produced a sudden change in temperature in Alaska and western North America. Alaska temperatures have been steady since then. (J. D'Aleo, http://icecap.us/docs/change/OceanMultidecadalCyclesTemps.pdf, with permission.)

(France, United Kingdom, Denmark, Norway) and throughout the North Pacific (Vancouver Island, Canada, Gulf of Alaska, Bering Sea, Chukchi Sea, Beaufort Sea, and Sea of Okhotsk) (Fig. 2). Prevalences are generally higher nearshore than offshore and in small, new-shelled crabs than in larger, old shelled crabs, although infections first became and, in some areas, continue to be a concern in crab and lobster fisheries. Until recently infections were limited to high salinity areas (>11‰), but within the past year, *Hematodinium*-like infections were reported in a low salinity aquaculture facility (<9‰) in China (Li et al. 2008).

Regional climate changes and Hematodinium spp. epizootics

The North Pacific

The Pacific climate is dominated by the El Niño–Southern Oscillation (ENSO), which is a global atmospheric-ocean coupled phenomenon. An effective measure of climate variability in the Pacific is the Pacific Decadal Oscillation (PDO) which displays a pattern shift on at least an inter-decadal time scale, and usually about 20-30 years. The data indicate that in 1977, a climate shift occurred in the North Pacific (Fig. 3).

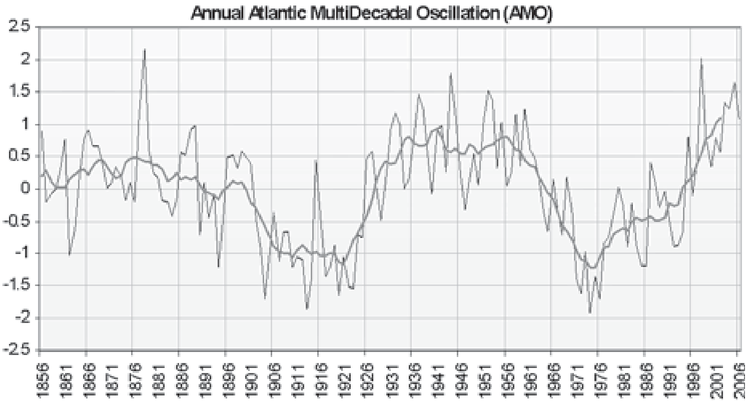

Figure 4. The Atlantic Multidecadal Oscillation (AMO), showing mean ocean temperature from 0 to 70°N. The data show a warming trend since the early 1970s. (J. D'Aleo, http://icecap.us/images/uploads/HF_CLIMATE_FINAL.pdf, with permission.)

In 1985, *Hematodinium* infections were encountered at significant prevalences in the southeast Alaska Tanner crab (*Chionoecetes bairdi*) fishery (Meyers et al. 1987). Prior to 1985, there was no pre-existing evidence of *Hematodinium* in any crab stock throughout the North Pacific. There is anecdotal evidence that a disease of unknown identity was present in southeast Alaska Tanner crabs prior to 1985, but the description of that unknown anomaly is not similar to the visual signs presented by crabs infected by the parasitic dinoflagellate. *Hematodinium* sp. has subsequently been encountered in Tanner crabs from the eastern Bering Sea, and in snow crabs (*C. opilio*) from the eastern Bering and Chukchi seas (Meyers et al. 1996) and most recently from the Beaufort Sea (E.F. Morado, unpubl.). *Hematodinium* infections in southeast Alaska Tanner crabs continue to be a concern with visual prevalence varying with survey area (Bednarski et al. 2010). Within the past year, *Hematodinium* sp. infections were encountered in Sea of Okhotsk red (*Paralithodes camtschaticus*) and blue (*P. platypus*) king crabs at low prevalences (Ryazanova 2008) and in the mud crab, *Scylla serrata*, from a low salinity aquaculture facility in China (Li et al. 2008).

The North Atlantic

The North Atlantic climate is dominated by the North Atlantic Oscillation; unlike the ENSO, the NAO is largely atmospheric in nature. Since 1970, the NAO has generally been in a positive mode (warmer rather than colder, Fig. 4).

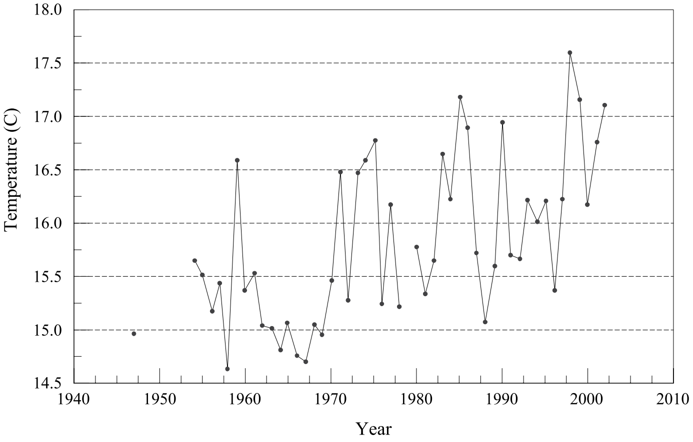

Figure 5. **Annual average surface temperature from the mouth of the York River (VIMS pier). (Austin 2002. Data from Gary Anderson, VIMS Scientific Data Archive, Virginia Institute of Marine Science, College of William and Mary.)**

The Chesapeake. Annual surface temperatures for Chesapeake Bay (Fig. 5), not surprisingly, closely parallel the NOA and show a general warming after 1970 (Austin 2002). In 1975, the parasitic dinoflagellate was encountered in the blue crab, *Callinectes sapidus*, from the eastern United States for the first time (Newman and Johnson 1975). The parasitic dinoflagellate is routinely encountered in several species of crustaceans along the eastern U.S. coast, but especially in Chesapeake Bay blue crabs (Messick 1994). Examination of the possible relationship between temperature and *Hematodinium* epizootics suggests that the majority of events have occurred when surface temperatures of the Chesapeake exceed 16°C (Fig. 5). Interestingly, Messick et al. (1999) determined that low water temperature (<16°C) and salinity (<10‰) limited or delayed disease progression in laboratory-held, but naturally infected blue crabs.

Eastern Canada. Eastern Canada has a long history of water temperature data. Mean vertical water temperatures for the Newfoundland continental shelf show that 1994 was the last cold year and a general warming is now occurring (Fig. 6). Although *Hematodinium*-infected snow crabs were visually observed by fishers and biologists in Newfoundland coastal waters in the early 1990s, it was first microscopically detected in less than 0.1% of crabs examined during a 1992-1993 pot survey (Taylor and Khan 1995). Visual diagnosis of 1998 trawl and

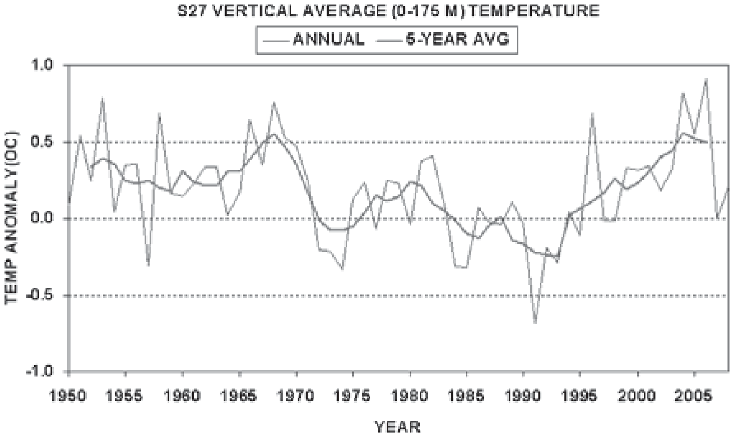

Figure 6. Temperature anomalies and derived indices from data collected during spring and fall multispecies surveys on the Newfoundland and Labrador Shelf. The anomalies are normalized with respect to their standard deviations over the indicated base period. The smoothed line represents a mean 5-year average. (From Colbourne et al. 2008, Table 5).

trap collected snow crabs presented a corrected prevalence of 4.25% from Conception Bay, Newfoundland (Pestal et al. 2003). From 1996 to 2000, continental shelf prevalences of *Hematodinium* in trawl assessed snow crab populations fluctuated between 0.7% and 2.6% (Dawe 2002). In recent years, *Hematodinium* infections have continued to exist at higher prevalences than previously observed in coastal (Shields et al. 2007) and offshore Newfoundland snow crab populations (Dawe 2002), but prevalences do vary from year to year and the disease shows evidence of "pulsing" or cycling in both coastal and continental shelf snow crab populations. Such a pulse may partially explain the anomalous shift in disease from small to large size crab in Conception Bay, Newfoundland (Shields et al. 2007). It is believed that the apparent pulsing may be host density dependent and may moderate large crab recruitment classes, but of course environmental conditions can certainly moderate or cause changes in observed disease patterns.

For *Hematodinium*-associated diseases, low salinity is traditionally acknowledged as a disease-limiting factor in coastal environments, except for the recent report by Li et al. (2008). However, Briggs and McAliskey (2002) demonstrated that over a very narrow salinity range (<1‰), disease prevalence was highly correlated with an increase in salinity in the Irish Sea. Although a similar correlation was not observed

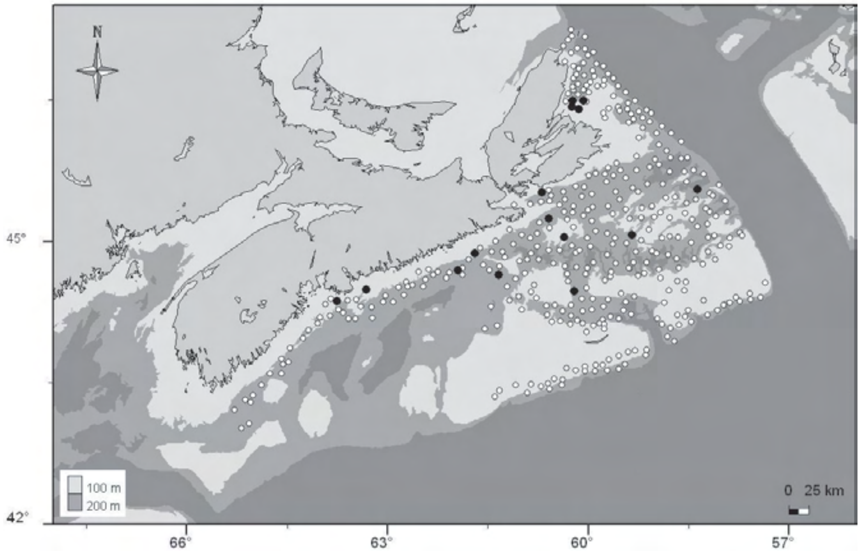

Figure 7. **Map showing the distribution of visually positive diseased snow crabs of the Scotian Shelf. A subset of visually positive crabs was identified as positive via a DNA-based assay.**

over the Newfoundland-Labrador Shelf, Dawe et al. (2010) noted that *Hematodinium* infections were virtually absent from water where salinity was less than 33‰. They also noted that infections were rare in the warmest (>4°C) and most saline (>35‰) waters of the shelf.

The disease continues to spread southward from Newfoundland and within the past year, it was visually detected and confirmed by polymerase chain reaction (PCR) in Nova Scotia snow crab populations. Infections are at visual trace levels throughout the survey area (Fig. 7), primarily occurring in small, new-shelled, coastal crabs. The disease was not visually present in Nova Scotia prior to 2008, thus it is possible that ocean currents played a role in this latest southerly expansion.

Western Greenland. Snow crab are located along western Greenland, from Disco Bay south. The snow crab fishery began in 1997, the same year that a rapid acceleration of Jakobshavn Isbrae (a glacier in western Greenland) was noted (Thomas et al. 2003). The rapid acceleration was later attributed to the arrival of relatively warm water that originated from the Irminger Sea near Iceland (Holland et al. 2008). In 2003, several years after the warming trend, visually positive *Hematodinium* infected snow crabs were encountered at trace levels. From 2003 to 2007, visual prevalences remained low (<0.2%). In an effort to gauge the potential impact of *Hematodinium*-associated disease on Greenland snow crabs, greater effort was directed at a more detailed monitoring program (Eigemann et al. 2008). A comparison study involving both visual and PCR detection was carried out during the fishery. Visual inspection failed to detect the disease in more than 1,000 crabs. However, a smaller subset of visually examined snow crabs was examined by PCR; 40% of that subset was positive for the disease.

Task 2. Determine climate's role in present-day trends in disease transmission and geographical range

Despite the presumptive evidence as presented earlier, it is impossible to properly address this task. Clearly, the susceptible host list and the distribution and prevalence of *Hematodinium*-associated disease have increased and expanded their range since general warming trends have occurred in both the North Pacific and Atlantic oceans. Few monitoring programs have been continuous or conducted on a routine schedule once *Hematodinium* is identified in a crustacean population. In addition, many monitoring programs only recently began recording temperature data in association with prevalence and distribution of *Hematodinium*-associated diseases. Other types of data that should be captured during disease monitoring programs are salinity, depth, and ocean currents, especially when reports suggest that some of these factors may influence or limit spread of the disease. Indeed, the recent report of *Hematodinium* in Nova Scotia snow crab stocks was not a complete surprise given the prevailing ocean currents of the area.

In regard to the parasite, much is still unknown. Critical aspects of the parasite's life history are unknown as is the method of infection. Although some research has been conducted on parasite-host interaction, much still needs to be investigated (see Stentiford and Shields 2005). For example, it is uncertain whether the disease progresses at the same rate in both large and small crabs and whether different size classes display different rates of mortality. Currently, only two species of *Hematodinium* have been described based on the morphology of life history stages only encountered within the crab host. DNA sequencing indicates that two species or clades exist in the Northern Hemisphere (Small et al. 2007, Jensen et al. 2010), but recent discussions at a *Hematodinium* workshop (http://www.lobsterscience.ca/bcdworkshop/) suggest that ecotypes of the parasite may exist and these ecotypes could display some degree of host specificity. Finally, the potential influence of vessel traffic in the spread of the parasite cannot be determined.

The longest continuous *Hematodinium* disease-monitoring program is occurring in the eastern Bering Sea. That trawl-based monitoring program has evolved from disease monitoring based on microscopic examination of blood smears to the development and field implementa-

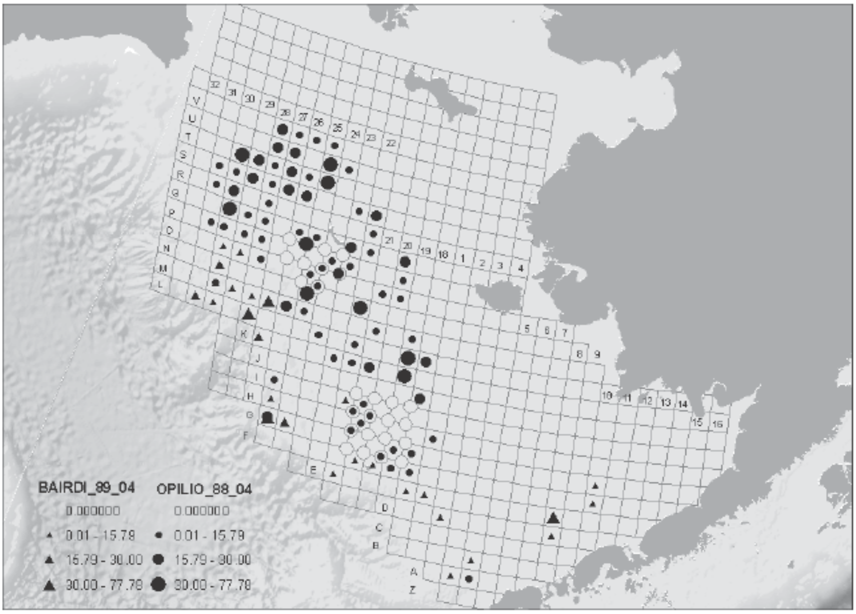

Figure 8. **Map depicting the prevalence and distribution of disease in Tanner crabs from the Bering Sea and in snow crabs from the Bering Sea, Norton Sound, and Chukchi Sea.**

tion of a PCR assay (Jensen et al. 2010). Hemolymph is extracted from randomly collected snow (*Chionoecetes opilio*), Tanner (*C. bairdi*), red king (*Paralithodes camtschaticus*), blue king (*P. platypus*), lyre (*Hyas* spp.), and hermit (*Pagurus* spp.) crabs captured during the annual fish and shellfish assessment survey. Sex, size, and shell condition are recorded for each sampled crab and the temperature and depth of each station is noted. The cumulative data reveal that in the eastern Bering Sea (1) the parasitic dinoflagellate is more prevalent in snow crab than in Tanner crab; (2) in recent years, *Hematodinium*-associated disease in Tanner crabs is primarily located on the outer shelf; (3) in snow crabs, the prevalence and distribution of disease increases with increase in latitude; (4) disease prevalence in snow crabs increases with increase in bottom sea temperature although the observation is not statistically significant, and no temperature trend is obvious for disease in Tanner crabs; and (5) depth prevalence profiles for snow and Tanner crabs are completely opposite—disease prevalences are greater at shallow depths in snow crab while in Tanner crabs, prevalences are greater at depth (Figs. 8-10).

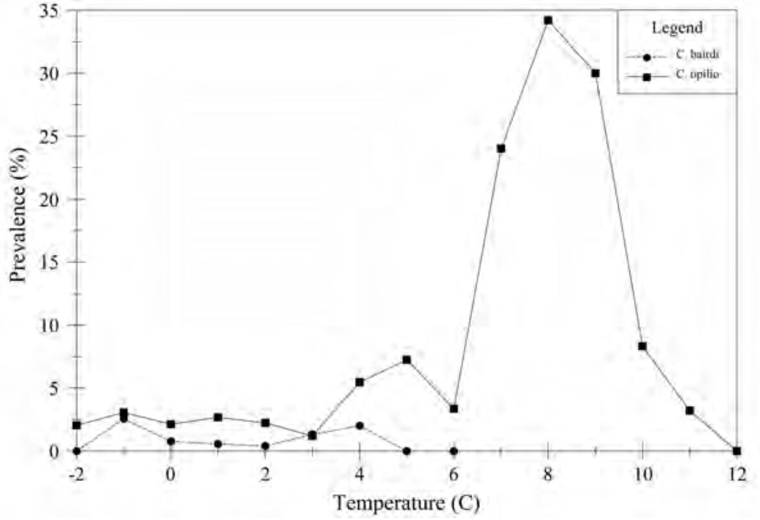

Figure 9. **Prevalence of disease plotted against temperature for both Tanner and snow crabs from the Bering Sea, Norton Sound, and Chukchi Sea.**

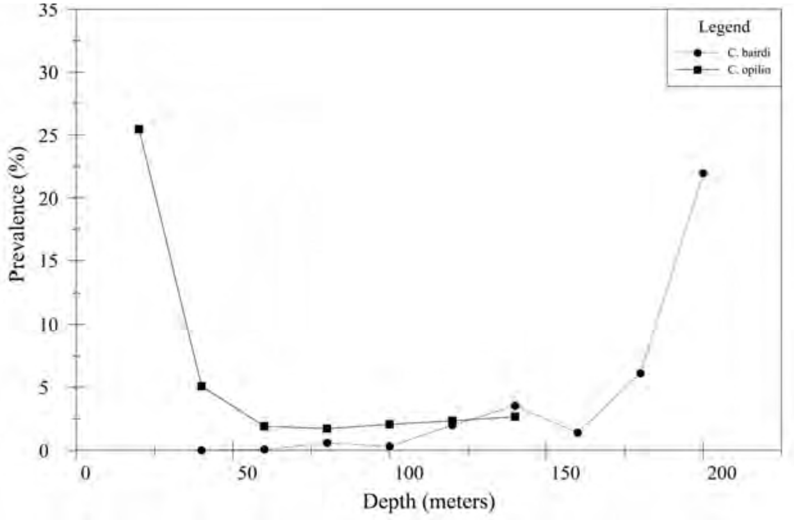

Figure 10. **Prevalence of disease plotted against depth for both Tanner and snow crabs from the Bering Sea, Norton Sound, and Chukchi Sea.**

The cumulative data from our summer surveys suggest that more than one ecotype may exist in the eastern Bering Sea. One ecotype appears to prefer deep, cooler water and while the other appears to prefer shallow, warmer water. Both ecotypes do not appear to co-exist at the same locations. Yet there are uncertainties. Because the eastern Bering Sea survey is conducted in the summer when water temperatures are at their highest, it is uncertain what occurs during the long cold months of the year. Snow and Tanner crabs overlap in distribution over much of the Bering Sea shelf, yet *Hematodinium* infections primarily occur in snow crabs rather than in Tanner crabs in this area. Additionally, although snow and Tanner crab hybrids have been encountered in the overlap area, not one hybrid has been identified or suspected of being *Hematodinium* positive.

Task 3. Create predictive models for future diseases that account for a changing climate, as well as for other influential factors

The current state of knowledge and development of predictive models for diseases other than those important to human health is not advanced. Lafferty (2009) notes that process-based models are dependent upon knowledge of the relationship between climate variables and vital rates, two variables that when considered in combination are not well known for many marine species. As a result, several monitoring programs rely on statistical models such as univariate or multiple logistic regression (Hosmer and Lemeshow 2000).

Logistic regression is typically applied to the eastern Bering Sea disease data. The results indicate the disease is associated with only size and shell condition; small recently molted crabs are more susceptible to infection than large old-shelled crabs. As a result, the depth and temperature tendencies as noted previously are not significant predictors of disease. Standardized monitoring programs are being implemented, but deficiencies still occur. For example, various methods are used to monitor the presence and distribution of the disease in targeted crustacean populations, each presenting different levels of detection accuracy (see Stentiford and Shields 2005). Several programs have adopted a molecular-based protocol, but field logistics often dictate a less technical and sensitive protocol. Small crabs (<70 mm carapace width) are poorly represented in pot-dependent data, as opposed to trawl-dependent collections, but disease prevalences from pot surveys are generally higher than those reported from trawl surveys (Pestal et al. 2003, Shields et al. 2007). Reconciliation of these differences has not been fully addressed. Monitoring programs may vary considerably with respect to duration and environmental data may not be routinely collected. Finally, the impact of population translocations is unknown. The geographic range of distribution of eastern Bering Sea snow crab has contracted to the north, in response to warming bottom temperatures (Orensanz et al. 2004). It is uncertain how the observed population shift may change the prevalence and distribution profile of *Hematodinium* infections in Bering Sea snow crab populations, and whether similar changes may be observed in other crustacean-*Hematodinium* associations.

Task 4. Recognize and address the contribution of human behavior to global climate change and its further effects on infectious disease emergence

Both the Gulf of Alaska and the Bering Sea have experienced remarkable changes over the past 30 years (NRC 1996, Spies 2007). Natural environmental fluctuations and human activities are at the root of these sweeping changes for both ecosystems. In the case of *Hematodinium*-associated disease in the North Pacific, Jensen et al. (2010) noted a lack of variability of ITS1 (internal transcribed spacer 1) in *Hematodinium* species from North Pacific hosts, and suggested that a possible explanation is the recent introduction of *Hematodinium* to this area. How the parasite may have been initially introduced and its subsequent spread to other areas of the North Pacific is unknown and requires additional research. As is the situation with many invasive species, it is possible that human activities such as fishing, transport of goods (including live marine organisms) and services, and tourism to name a few may have played and continues to play a role (see Molnar et al. 2008 for more detailed pathways) in the spread of *Hematodinium* species. In particular, it is likely that transport of live brood stock contributed to the introduction of *Hematodinium* species into aquaculture facilities in China (Li et al. 2008, Xu et al. 2010). The latest examples emphasize the need for reporting and continued monitoring of *Hematodinium*-associated diseases.

Summary

A number of factors confound efforts to develop correlations between marine diseases and climate change. For *Hematodinium*-associated diseases, the presumptive evidence suggests a correlation with climate change. However, each geographical region in which the disease is encountered presents a slightly different image. In various regions and to various degrees, temperature, salinity, and currents appear to affect disease occurrence. Even though only a few species of *Hematodinium* have been described, these differences may reflect the existence of several ecotypes. Still unexplained is the rapid expansion of *Hematodinium* species throughout the Northern Hemisphere since 1985. The Southern Hemisphere is also experiencing a general warming trend, but a review of the published literature indicates that *Hematodinium*-associated diseases are rarely encountered or absent altogether in indigenous crustacean populations, even though the parasitic dinoflagellate is known to occur in at least four species of Australian crabs. In general, it is not possible to properly address the four tasks; this is not surprising given many human diseases are influenced by multiple factors and not solely by climate. However, this review does emphasize the need for consistent or standardized data collection and vigilance in marine disease research.

References

Austin, H.M. 2002. Decadal oscillations and regime shifts: A characterization of the Chesapeake Bay marine climate. Am. Fish. Soc. Symp. 32:155-170.

Bednarski, J., C.E. Siddon, G.H. Bishop, J.F. Morado, and P. Jensen. 2010. Overview of bitter crab disease in Tanner crabs, *Chionoecetes bairdi*, in southeast Alaska. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and management of exploited crab populations under climate change. Alaska Sea Grant College Program, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.07

Briggs, R.P., and M. McAliskey. 2002. The prevalence of *Hematodinium* in *Nephrops norvegicus* from the western Irish Sea. J. Mar. Biol. Assoc. UK 82:427-433. doi:10.1017/S0025315402005684

Brown, B. 1997. Coral bleaching: Causes and consequences. Proceedings of the 8th International Coral Reef Symposium 1:65-74.

Chatton, É., and R. Poisson. 1931. Sur l'existence dans le sang des crabes. De Péridiniens parasites: *Hematodinium perezi* n.g., n.sp. (Syndinidae). CR Soc. Biol. 105:553-557. (In French.)

Colbourne, E., J. Craig, C. Fitzpatrick, D. Senciall, P. Stead, and W. Bailey. 2008. An assessment of the physical oceanographic environment on the Newfoundland and Labrador Shelf during 2007. Department of Fisheries and Oceans CSAS Doc. 2008/020. 16 pp. http://www.dfo-mpo.gc.ca/csas/

Dawe, E.G. 2002. Trends in prevalence of bitter crab disease caused by *Hematodinium* sp. in snow crab (*Chionoecetes opilio*) throughout the Newfoundland and Labrador continental shelf. In: A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley, and D. Woodby (eds.), Crabs in cold water regions: Biology, management, and economics. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 385-399.

Dawe, E.G., D.R. Mullowney, E.B. Colbourne, G. Han, J.F. Morado, and R. Cawthorn. 2010. Relationship of oceanographic variability with distribution and prevalence of bitter crab syndrome in snow crab (*Chionoecetes opilio*) on the Newfoundland-Labrador shelf. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and management of exploited crab populations under climate change. Alaska Sea Grant College Program, University of Alaska Fairbanks. (This volume.)

De'ath, G., J.M. Lough, and K.E. Fabricius. 2009. Declining coral calcification on the Great Barrier Reef. Science 323:116-119. doi:10.1126/science.1165283

de la Rocque, S., S. Morand, and G. Hendrickx (eds.), 2008. Climate change: Impact on the epidemiology and control of animal diseases. OIE Scientific and Technical Review 27/2. Office International des Épizooties, Paris. 287 pp.

Eigemann, F., A. Burmeister, and A. Skovgaard. 2008. Latent infections with *Hematodinium* sp. (Alveolata, Syndinea) in decapod crustaceans from Danish and Greenlandic waters. M.S. thesis, University of Copenhagen. 31 pp.

Epstein, P.R., B. Sherman, E. Spanger-Siegfried, A. Langston, S. Prasad, and B. McKay. 1998. Marine ecosystems: Emerging diseases as indicators of change. Center for Health and the Global Environment, Boston. 85 pp.

Fagan, B. 2000. The Little Ice Age: How climate made history 1300-1850. Basic Books, New York. 246 pp.

Gallien, L. 1940. Sur la presence dans le sang de *Platyonchus latipes* Penn., d'un péridinien parasite *Hematodinium perezi* Chatton et Poisson. Bull. Biol. 72:261-267. (In French.)

Greer, L., J.E. Jackson, H.A. Curran, T. Guilderson, and L. Teneva. 2009. How vulnerable is *Acropora cervicornis* to environmental change? Lessons from the early to middle Holocene. Geology 37:263-266. doi:10.1130/G25479A.1

Haines, A., R.S. Kovats, D. Campbell-Lendrum, and C. Corvalan. 2006. Climate change and human health: Impacts, vulnerability and mitigation. Lancet 367:2101-2109. doi:10.1016/S0140-6736(06)68933-2

Harvell, C.D., C.E. Mitchell, J.R. Ward, S. Altizer, A.P. Dobson, R.S. Osterfeld, and M.D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. Science 296:2158-2162. doi:10.1126/science.1063699

Harvell, C.D., K. Kim, J.M. Burkholder, R.R. Colwell, P.R. Epstein, D.J. Grimes, E.E. Hofmann, E.K. Lipp, A.D.M. Osterhaus, R.M. Overstreet, J.W. Porter, G.W. Smith, and G.R. Vasta. 1999. Emerging marine diseases: Climate links and anthropogenic factors. Science 285:1505-1510. doi:10.1126/science.285.5433.1505

Harvell, D., R. Aronson, N. Baron, J. Connell, A. Dobson, S. Ellner, L. Gerber, K. Kim, A. Kuris, H. McCallum, K. Lafferty, B. McKay, J. Porter, M. Pascual, G. Smith, K. Sutherland, and J. Ward. 2004. The rising tide of ocean diseases: Unsolved problems and research priorities. Front. Ecol. Environ. 2:375-382. doi:10.1890/1540-9295(2004)002[0375:TRTOOD]2.0.CO;2

Holland, D.M., R.H. Thomas, B. De Young, M.H. Ribergaard, and B. Lyberth. 2008. Acceleration of Jakobshavn Isbrae triggered by warm subsurface ocean waters. Nature Geoscience 1:659-664. doi:10.1038/ngeo316

Hosmer, D.W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley & Sons, Inc. New York. 375 pp. doi:10.1002/0471722146

IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: The physical science basis. In: S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller (eds.), Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge. 996 pp.

Jensen, P.C., K. Califf, V. Lowe, L Hauser, and J.F. Morado. 2010. Molecular detection of *Hematodinium* sp. in northeast Pacific *Chionoecetes* spp. and evidence of two Northern Hemisphere *Hematodinium* species. Dis. Aquat. Org. 89:155-166.

Jónsson, J. 1994. Fisheries of Iceland, 1600-1900. In: J. Jakobsson, O. Asthorsson, R.J.H. Beverton, B. Björnsson, N. Daan, K.T. Frank, J. Meincke, B. Rothschild, S. Sundby, and S. Tilseth (eds.), Cod and climate change, Reykjavik, 23-27 August 1993. ICES Mar. Sci. Symp. 198:3-16.

Kim, K., A.P. Dobson, F.M.D. Gulland, and D.C. Harvell. 2005. Diseases and the conservation of marine biodiversity. In: E.A. Norse and L.B. Crowder (eds.), Marine conservation biology: The science of maintaining the sea's biodiversity. Island Press, Washington, D.C., pp. 149-168.

Kushmaro, A., Y. Loya, M. Fine, and E. Rosenberg. 1996. Bacterial infection and coral bleaching. Nature 380:396. doi:10.1038/380396a0

Lafferty, K.D. 2009. The ecology of climate change and infectious disease. Ecology 90:888-900. doi:10.1890/08-0079.1

Lafferty, K.D., J.W. Porter, and S.E. Ford. 2004. Are diseases increasing in the ocean? Ann. Rev. Ecol. Evol. Syst. 35:31-54. doi:10.1146/annurev.ecolsys.35.021103.105704

Lamb, H.H. 1979. Climatic variation and changes in the wind and ocean circulation: The Little Ice Age in the northeast Atlantic. Quat. Res. 11:1-20. doi:10.1016/0033-5894(79)90067-X

Li, Y.Y., X.A. Xia, Q.Y. Wu, W.H. Liu, and Y.S. Lin. 2008. Infection with *Hematodinium* sp. in mud crabs *Scylla serrata* cultured in low salinity water in southern China. Dis. Aquat. Org. 82:145-150. doi:10.3354/dao01988

MacPerson, D.W., and B.D. Gushulak. 2008. Influences of migration and population mobility. In: D.A. Relman, M.A. Hamburg, E.R. Choffnes, and A. Mack. Global climate change and extreme weather events: Understanding the contributions to infectious disease emergence. National Academies Press, Washington, D.C., pp. 222-230.

Messick, G.A. 1994. *Hematodinium perezi* infections in adult and juvenile blue crabs *Callinectes sapidus* from coastal bays of Maryland and Virginia, USA. Dis. Aquat. Org. 19:77-82. doi:10.3354/dao019077

Messick, G.A., S.J. Jordan, and W.F. Van Heukelem. 1999. Salinity and temperature effects on *Hematodinium* sp. in the blue crab *Callinectes sapidus*. J. Shellfish Res. 18:657-662.

Meyers, T.R., T.M. Koeneman, C. Botelho, and S. Short. 1987. Bitter crab disease: A fatal dinoflagellate infection and marketing problem for Alaskan Tanner crabs, *Chionoecetes bairdi*. Dis. Aquat. Org. 3:195-216. doi:10.3354/dao003195

Meyers, T.R., J.F. Morado, A.K. Sparks, G.H. Bishop, T. Pearson, D. Urban, and D. Jackson. 1996. The distribution of bitter crab syndrome in Tanner crabs (*Chionoecetes bairdi*, *C. opilio*) from the Gulf of Alaska and the Bering Sea. Dis. Aquat. Org. 26:221-227. doi:10.3354/dao026221

Molnar, J.L., R.L. Gamboa, C. Revenga, and M.D. Spalding. 2008. Assessing the global threat of invasive species to marine biodiversity. Front. Ecol. Environ. 6:485-492. doi:10.1890/070064

Newman, M.W., and C.A. Johnson. 1975. A disease of blue crabs (*Callinectes sapidus*) caused by the parasitic dinoflagellate, *Hematodinium* sp. J. Parasitol. 63:554-557. doi:10.2307/3279346

NRC (National Research Council). 1996. The Bering Sea ecosystem. National Academy Press, Washington DC. 307 pp.

NRC (National Research Council). 2008. Ecological impacts of climate change. National Academies Press, Washington, D.C. 57 pp.

Orensanz, J., B. Ernst, D.A. Armstrong, P. Stabeno, and P. Livingston. 2004. Contraction of the geographical range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: An environmental rachet? CalCOFI Rep. 45:65-79.

Pestal, G.P., D.M. Taylor, J.M. Hoenig, J.D. Shields, and R. Pickavance. 2003. Monitoring the prevalence of the parasitic dinoflagellate *Hematodinium* sp. in snow crabs *Chionoecetes opilio* from Conception Bay, Newfoundland. Dis. Aquat. Org. 53:67-75. doi:10.3354/dao053067

Relman, D.A., M.A. Hamburg, E.R. Choffnes, and A. Mack. 2008. Global climate change and extreme weather events: Understanding the contributions to infectious disease emergence. National Academies Press, Washington, D.C. 279 pp.

Ryazanova, T.V. 2008. Bitter crab syndrome in two species of king crabs from the Sea of Okhotsk. Russ. J. Mar. Biol. 34:411-414. doi:10.1134/S1063074008060102

Shields, J.D., D.M. Taylor, P.G. O'Keefe, E. Colbourne, and E. Hynick. 2007. Epidemiological determinants in outbreaks of bitter crab disease (*Hematodinium* sp.) in snow crabs *Chionoecetes opilio* from Conception Bay, Newfoundland, Canada. Dis. Aquat. Org. 77:61-72. doi:10.3354/dao01825

Small, H.J., J.D. Shields, J.A. Moss, and K.S. Reece. 2007. Conservation in the first internal transcribed spacer region (ITS1) in *Hematodinium* species infecting crustacean hosts found in the UK and Newfoundland. Dis. Aquat. Org. 75:251-258. doi:10.3354/dao075251

Spies, R.B. 2007. Long-term ecological change in the northern Gulf of Alaska. Elsevier BV, Amsterdam. 589 pp.

Stentiford, G.D., and J.D. Shields. 2005. A review of the parasitic dinoflagellates *Hematodinium* and *Hematodinium*-like infections in marine crustaceans. Dis. Aquat. Org. 66:47-70. doi:10.3354/dao066047

Taylor, D.M., and R.A. Kahn. 1995. Observations on the occurrence of *Hematodinium* sp. (Dinoflagellata: Syndinidae), the causative agent of bitter crab disease in Newfoundland snow crab (*Chionoecetes opilio*). J. Invertebr. Pathol. 65:283-288. doi:10.1006/jipa.1995.1043

Thomas, R.H., W. Abdalati, E. Frederick, W. Krabill, S. Manizade, and K. Steffen. 2003. Investigation of surface melting and dynamic thinning on Jakobshavn Isbræ. J. Glaciol. 49:231-239.

Ward, J.R., and K.D. Lafferty. 2004. The elusive baseline of marine disease: Are diseases in ocean ecosystems increasing? PloS Biol. 2:542-547. doi:10.1371/journal.pbio.0020120

WHO. 2003. Climate change and human health: Risks and responses. World Health Organization, Geneva. 333 pp. Accessed July 2010: http://whqlibdoc.who.int/publications/2003/9241590815.pdf.

Williams, E.H., and L. Bunkley-Williams. 1990. The worldwide coral reef bleaching cycle and related sources of mortality. Atoll Res. Bull. 335. 71 pp.

Xu, W., J. Xie, H. Shi, and C. Li. 2010. *Hematodinium* infections in cultured ridgetail white prawns, *Exopalaemon carinicauda*, in eastern China. Aquaculture 300(1-4):25-31. doi:10.1016/j.aquaculture.2009.12.024

Dawe, E.G., D.R. Mullowney, E.B. Colbourne, G. Han, J.F. Morado, and R. Cawthorn. 2010. Relationship of Oceanographic Variability with Distribution and Prevalence of Bitter Crab Syndrome in Snow Crab (*Chionoecetes opilio*) on the Newfoundland-Labrador Shelf. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.06

Relationship of Oceanographic Variability with Distribution and Prevalence of Bitter Crab Syndrome in Snow Crab (*Chionoecetes opilio*) on the Newfoundland-Labrador Shelf

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Abstract

Bitter crab syndrome (BCS), is a disease caused by parasitic dinoflagellates of the genus *Hematodinium,* and occurs in several crab species of the genus *Chionoecetes* in the North Pacific and North Atlantic oceans. Infections in snow crab (*Chionoecetes opilio*) in the Northwest Atlantic have been common in the most northern Canadian fishing area on the Newfoundland-Labrador continental shelf but unknown or recent in other fishery areas in the Gulf of St. Lawrence and on the eastern Scotian Shelf. In this study we show that spatial variation in the distribution and prevalence of BCS in Newfoundland-Labrador snow crab is associated with variation in temperature and salinity. These associations reflect peak prevalence in small crabs that are distributed on hard substrates in shallow waters at low temperatures and salinities. We conclude that ocean circulation features, together with host population dynamics, are largely responsible for regulating the distribution of BCS within snow crab on the Newfoundland-Labrador shelf. Annual variations in distribution and prevalence were not a function of temperature variation, but were more likely affected by host population parameters. Broad scale distribution of BCS, within Canadian Atlantic snow crab, may be directly limited by low salinity. The implications of our results with respect to ocean climate change and distribution of *Hematodinium* spp. are also discussed.

Introduction

Bitter crab syndrome (BCS) or bitter crab disease (BCD) is a condition common to a variety of crustaceans, caused by infection with hemoparasitic dinoflagellates of the genus *Hematodinium* (reviewed by Stentiford and Shields 2005). The parasite destroys hemocytes via an unknown mechanism and negatively affects host physiology, creating an increased metabolic load on the host. This syndrome is fatal to its crustacean host and, in many species, results in an unpalatable taste that renders infected animals unmarketable. The global spatial distribution and number of species found to be infected has increased considerably in recent years (Morado et al. 2010). BCS occurs in crabs of the genus *Chionoecetes* in both the north Pacific (*C. opilio* and *C. bairdi*) and north Atlantic (*C. opilio*) (Eaton et al. 1991; Love et al. 1993; Meyers et al. 1987, 1990; Dawe 2002; Morado et al. 2000, 2010). In Atlantic Canadian snow crab (*C. opilio*) it has been limited to the eastern Newfoundland and Labrador continental shelf (Fig. 1). It has been virtually absent from snow crabs on the southern Grand Bank and off the south and west coasts of Newfoundland. It is unknown in snow crabs in the Gulf of St. Lawrence and, until 2008, on the eastern Scotian Shelf (Morado et al. 2010).

The Canadian Atlantic snow crab resource supports the world's largest snow crab fishery, with the largest component prosecuted at Newfoundland and Labrador. The Newfoundland fishery landed about 53,000 t in 2008, with an export value of about 300 million dollars (Canada DFO, unpublished data). BCS represents an important but unquantified source of mortality to Newfoundland snow crab and any expansion of BCS would impose an increased loss, throughout the Canadian Atlantic fishery. Quantification of mortality due to BCS would provide valuable information for the improved assessment and management of the resource. Elucidation of factors that regulate distribution and prevalence of BCS would allow prediction and mitigation of future effects, especially under the scenario of a changing climate.

BCS was visually detected in Newfoundland snow crab in 1990 and verified microscopically in 1992 (Taylor and Khan 1995). The spatial

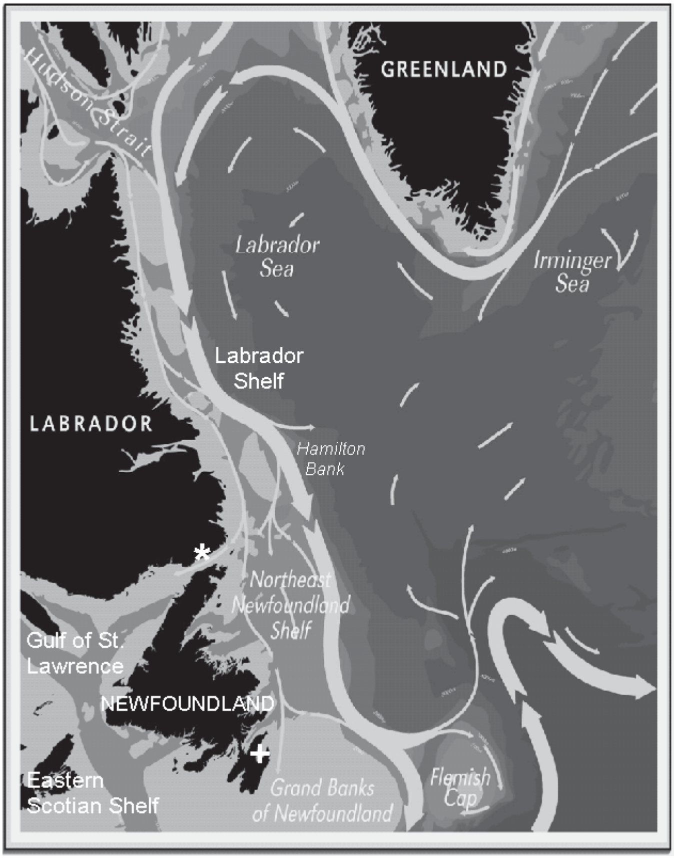

Figure 1. Location map showing the Newfoundland and Labrador shelf in relation to the Labrador Current and other place names mentioned in the text. + indicates the location of Conception Bay; * indicates the location of the Strait of Belle Isle.

distribution and prevalence of BCS in Newfoundland and Labrador snow crab have been monitored annually since 1995 from annual trawl surveys conducted along the eastern shelf in the fall (Dawe 2002, Dawe et al. 2009). BCS has also been monitored based on localized annual fall trap surveys in Conception Bay (Fig. 1) (Pestal et al. 2003; Shields et al. 2005, 2007). Those localized studies concluded that BCS prevalence is directly related to bottom temperature (Shields et al. 2007).

BCS has been found predominately in recently molted (new-shelled) snow crabs, and chronic cases can be recognized, in the fall, based on external signs that include abnormal pink or orange coloration of the dorsal carapace and joints of the walking legs, as well as an opaque white "cooked" appearance of the ventral carapace (Dawe 2002; Shields et al. 2005, 2007). Often, there are white opaque streaks along the translucent midventral merus leg section. Internally, opaque hemolymph is evident (Meyers et al. 1990, Dawe 2002). Our annual monitoring, and other studies to date, have been based on visual identification of such chronic cases. Comparison of diagnosis by visual examination with diagnosis by microscopic examination of blood smears (J.F. Morado, unpublished data) confirmed that all crabs identified visually as BCS+ were, in fact, infected with *Hematodinium* sp. However, that comparison also showed that the visual method for identifying chronic cases underestimates true prevalence. Our study, like others (e.g., Shields et al. 2005, 2007), assumes that trends based on observed chronic cases reflect trends in true distribution and prevalence.

In this paper we describe interannual variability in the spatial distribution and prevalence of BCS in snow crab on the eastern Newfoundland and Labrador continental shelf based on a 14-year survey time series. We investigate the relationships of distribution and prevalence with near-bottom temperature and salinity, and apply a particle drift model to examine the possible role of ocean circulation in regulating spatial distribution. We discuss factors that may play a role in regulating the distribution of BCS in our study area and in the entire Atlantic Canadian snow crab population. We also consider the implications of ocean climate change with respect to future changes in spatial distribution and prevalence of BCS.

Methods

Sampling

Snow crab samples were acquired and examined during 1995-2008 fall multispecies stratified random bottom trawl surveys, which extended from the Grand Bank northward throughout the northeast Newfoundland and southern Labrador continental shelf (Figs. 1-2). Spatial stratification of this area, for purposes of survey set allocation, is partially based on NAFO (Northwest Atlantic Fisheries Organization) Divisions. While these divisions hold no biological significance with respect to snow crab (Fig. 2), they do represent a convenient basis for facilitating spatial comparisons. The surveys utilized the Campelen 1800 survey trawl, a shrimp trawl with mesh size of 44-80 mm, and a nylon codend liner of 12.7 mm mesh. The trawl has a wingspread of about 16 m and a footrope equipped with rock-hopper gear. It was fished in standard tows of 15 min duration, at a speed of 3.0 knots, over a distance of 0.75 nm.

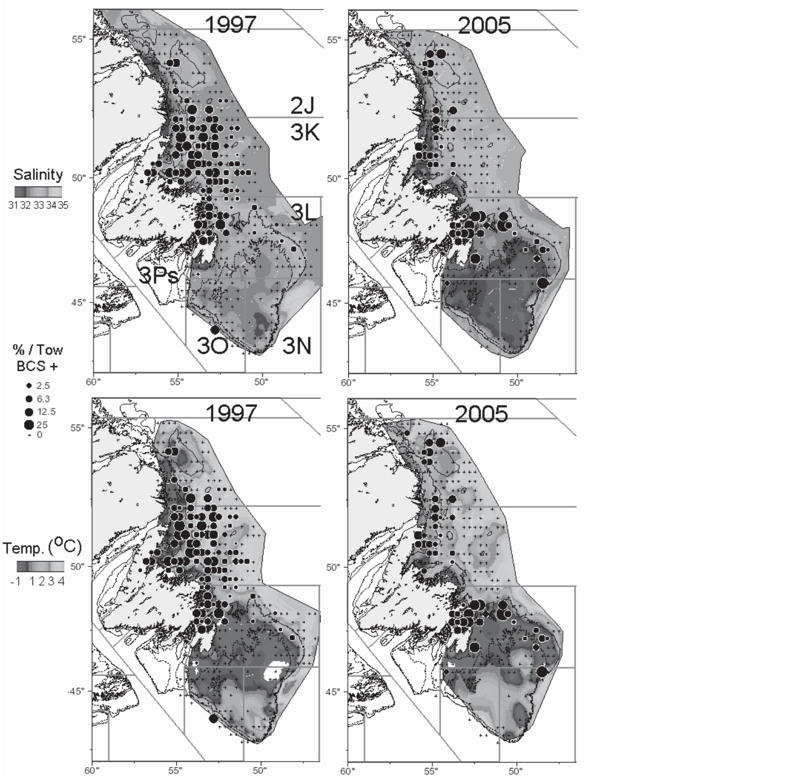

Figure 2. Distribution and prevalence of BCS+ (bitter crab syndrome) crabs during fall 1997 (left) and 2005 (right) trawl surveys in relation to near-bottom temperature (below) and salinity (above). + denotes sets that caught crabs but none were infected. Sets that caught no crabs are not shown. Salinity in ppt.

Snow crab catches were sorted by sex and either fully sampled or, in the case of very large catches, subsampled. In total, 186,834 crabs were captured in the surveys (Table 1). Crabs sampled were measured in carapace width (CW, mm), and maturity status was assigned to females (immature versus mature). All crabs were assigned one of three shell condition categories based on the relative extent of carapace fouling, which approximately reflects time elapsed since molting: (1) new-shelled—these crabs had last molted in spring of the current year; carapaces are clean, white ventrally, and iridescent; (2) intermediate-shelled—these crabs had last molted in spring of the previous year, carapaces are yellowed ventrally, not iridescent, and chelae bear ventral

Table 1. **Trawl catches by year, division, sex, and bitter crab syndrome.**

	2J				3K				3L				
	male		female		male		female		male		female		
	bcs -	bcs +	bcs -	bcs +	bcs -	bcs +	bcs -	bcs +	bcs -	bcs +	bcs -	bcs +	Total
1995	743	1	250	3	5534	169	3893	197	8848	429	5738	407	25,470
1996	1107	8	390	4	6817	100	3915	67	10021	11	3669	17	25,020
1997	1678	14	551	19	4766	198	1848	127	6888	103	2651	98	17,264
1998	2403	8	757	1	4143	123	946	29	4461	16	779	4	11,268
1999	1096	35	497	18	1170	3	208	0	2645	1	926	6	5,509
2000	1772	10	1231	10	7642	107	4968	63	2337	15	672	21	17,076
2001	3896	15	3590	8	5998	70	4600	33	5673	72	3603	42	23,703
2002	1111	32	768	34	4395	82	2247	104	5072	23	3322	28	16,108
2003	1092	9	786	6	2325	20	985	3	3356	41	1922	34	9,487
2004	1249	4	316	4	2773	67	1459	47	1489	53	939	77	7,228
2005	728	5	158	4	1340	10	745	4	2638	94	997	91	6,087
2006	886	3	206	0	4891	84	1809	65	2386	36	1187	31	10,698
2007	1005	0	377	1	1867	23	362	11	1546	3	285	0	4,475
2008	1246	9	719	13	2620	54	1139	14	2343	7	523	1	7,442
Total	20,011	152	10,597	125	56,280	1,112	29,125	764	59,705	904	27,213	857	186,834

scratches; (3) old-shelled—these crabs last molted at least two years ago, carapaces are heavily fouled dorsally and brown ventrally, and very old-shelled crabs have soft carapaces due to decalcification and decay in some leg joints.

Occurrence of advanced stages of BCS was noted based on macroscopic examination. In cases of unclear external characteristics, crabs were dissected and classified based on observation of the hemolymph. Observation of cloudy or milky hemolymph was taken as support for classification of such specimens as infected. Specimens displaying clear external characteristics of BCD were randomly selected and dissected to examine the hemolymph and to validate the macroscopic observations. All those specimens displayed milky hemolymph, supporting their categorization as infected.

Data on near-bottom temperature and salinity were also acquired from each survey set from a trawl-mounted conductivity, temperature, and depth (CTD) system.

Treatment and analysis of data

The spatial distribution of BCS-infected crabs (both sexes combined) was initially mapped, by year, in relation to near-bottom temperature and salinity. Before further investigating the possible relationship of spatial distribution and prevalence with oceanographic properties, it was necessary to establish the portion of the population susceptible to infection. Accordingly, we summarized BCS prevalence in relation to host shell condition to confirm, as previously found (Dawe 2002), that this syndrome is virtually exclusive to new-shelled crabs. All subsequent summaries and analyses were conducted on new-shelled crabs only. Prevalence of BCS was calculated as the percentage of new-shelled crabs caught that were infected (i.e., BCS+).

We described the relationship of BCS distribution and prevalence with oceanographic properties by partitioning prevalence into 1°C temperature bins and 0.5 ppt salinity bins by sex and division. Only data from sets that captured new-shelled crabs were included in this summary. The relationship of BCS distribution and prevalence with temperature and salinity was further investigated by describing temperature-salinity relationships by division for all new-shelled crabs caught versus those that were infected. A nonparametric categorical data analysis (CATMOD, SAS Institute 1985) was applied to determine the significance of relationships of prevalence with area (division), host sex, temperature, and salinity. Significance was assessed based on the conventional 0.05 probability level.

Further elaboration of the effects of temperature on distribution and prevalence required accounting for possible confounding effects of host distribution and demography. Accordingly, we examined, for males only, the size-specific relationship of BCS prevalence with bottom temperature and depth. The analysis was limited to males due to the greater size range and broader distribution of males than females (Dawe and Colbourne 2002). Size was summarized, for each division, by 3 mm CW groups and compared with prevalence as well as mean depth and bottom temperature for those sets where members of each group were caught. To investigate the possible effect of temperature on annual variability in distribution and prevalence we first compared annual trends, by sex, among NAFO divisions. We then applied simple linear regression to model the relationship of temperature with prevalence for each division by sex.

A particle drift model was applied to investigate the possible role of ocean currents in determining the distribution of BCS. The ocean circulation was obtained from a three-dimensional finite-element circulation model (Han et al. 2008) for the Newfoundland and Labrador shelf and slope. The model produced climatologically monthly mean circulation fields, which were validated against a number of observational data sets. The drift model considers effects of temporal variability and spatial structure of the circulation (Han and Kulka 2009). In addition, the effects of unaccounted horizontal motions were estimated assuming a random walk process where additional displacements were calculated using externally specified eddy diffusivity (150 m^2 per s) in the horizontal directions. The vertical movement was not considered.

Results

Spatial distribution and prevalence of infected crabs

The spatial distribution of BCS in snow crab varied considerably among years, as illustrated by the distributions in 1997 and 2005 (Fig. 2), but there were some consistencies. BCS was commonly encountered from the southern Labrador shelf (Div. 2J) south to the northern Grand Bank (Div. 3L). Sets of highest prevalence (12.6-25%) extended from coastal bays offshore to the middle shelf. BCS has been quite uncommon on the southern Grand Bank (Div. 3NO), where it was detected at 9 stations in total during 5 of the 14 survey years.

Most of the crabs caught in our surveys were new-shelled crabs (about 80%, Fig. 3) and most crabs found to be infected were new-shelled (>90%, Fig. 3). Overall prevalence of infection was low (<3%) but varied with sex and shell condition, being highest in new-shelled and female crabs.

Prevalence varied considerably over the time series for each of the three divisions where it was regularly encountered (Fig. 4). Prevalence (in new-shelled crabs) was consistently lower than 10% and usually lower than 6%. The two southern areas (Div. 3KL) trended together initially (during 1995-2001), but otherwise there was little similarity among areas.

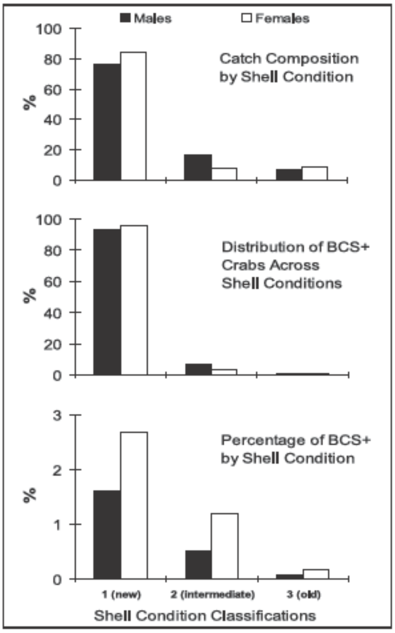

Figure 3. **Percentage distribution by sex across shell condition categories for all snow crabs caught in 1995-2008 surveys (above), and for BCS+ (bitter crab syndrome) snow crabs (middle). Also shown is the percentage infected by sex and shell condition (below).**

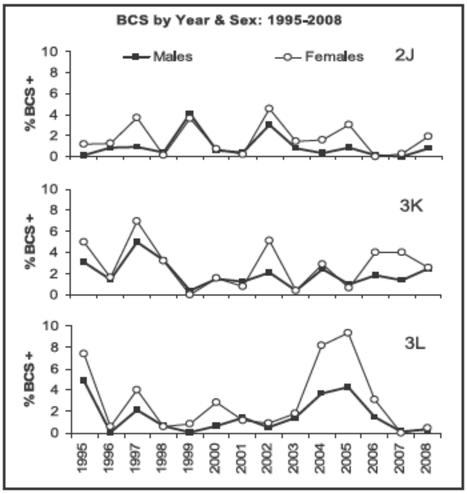

Figure 4. **Annual variation by sex and division in the prevalence of BCS (bitter crab syndrome) within new-shelled crabs.**

Relationship of distribution and prevalence with oceanographic properties

The spatial distribution of infected crabs differed among years as illustrated by contrasting 1997 and 2005 (Fig. 2). These examples include the year (1997) of highest prevalence in the central area (Div. 3K, Fig. 4) and the year (2005) of highest prevalence at the southern extreme of BCS distribution (Div. 3L, Fig. 4). Prevalence was relatively high in both of those years at the northern extreme (Div. 2J, Fig. 4). Overall, prevalence was more variable in the extreme areas (Div. 2J and 3L) than in central Div. 3K (Figs. 2 and 4). As illustrated in both years (Fig. 2), infected crabs were caught primarily on an offshore bank (Hamilton Bank, Fig. 1) at intermediate temperatures and salinities in Div. 2J, whereas they were caught across the northern Grand Bank (Div. 3L) at much lower temperatures and salinities (Fig. 2). In both Div. 3K and 3L, infected crabs were caught primarily on the inner to mid shelf, including coastal bays, whereas they were virtually absent along the outer shelf slope at maximum temperatures and salinities in all three divisions. The distribution of infected crabs in Div. 3K (Fig. 2) was more limited to the inner shelf in years of low prevalence (e.g., 2005) than in years of high prevalence (e.g., 1997).

Examination of the relationship of prevalence with temperature and salinity for all years combined (Fig. 5) showed that relationships differed among the three divisions. Generally however, across all areas, prevalence was highest at intermediate temperatures (1-2°C) and salinities (33-34.5 ppt). The southernmost area (Div. 3L) was exceptional in showing high prevalence at lowest temperatures (<0°C). The salinity of peak prevalence varied among divisions and was lowest (freshest) in Div. 3L. Overall, the relationship of prevalence with salinity was stronger than with temperature: prevalence decreased sharply below 33 ppt and was also relatively low at maximum salinities (34.5-35.0 ppt) in all divisions.

A categorical data analysis showed that the relationship of each of division, sex, temperature, and salinity with BCS prevalence was very highly significant (p <0.0001, Table 2). The analysis indicated that

Table 2. Results of maximum likelihood analysis of variance analysis of the effects of division, sex, temperature, and salinity on prevalence of bitter crab syndrome in new-shelled crabs.

Source	DF	Chi-square	*P* > chi square
Intercept	1	957.98	<0.0001
Division	2	184.17	<0.0001
Sex	1	151.40	<0.0001
Temperature	6	376.23	<0.0001
Salinity	7	279.22	<0.0001

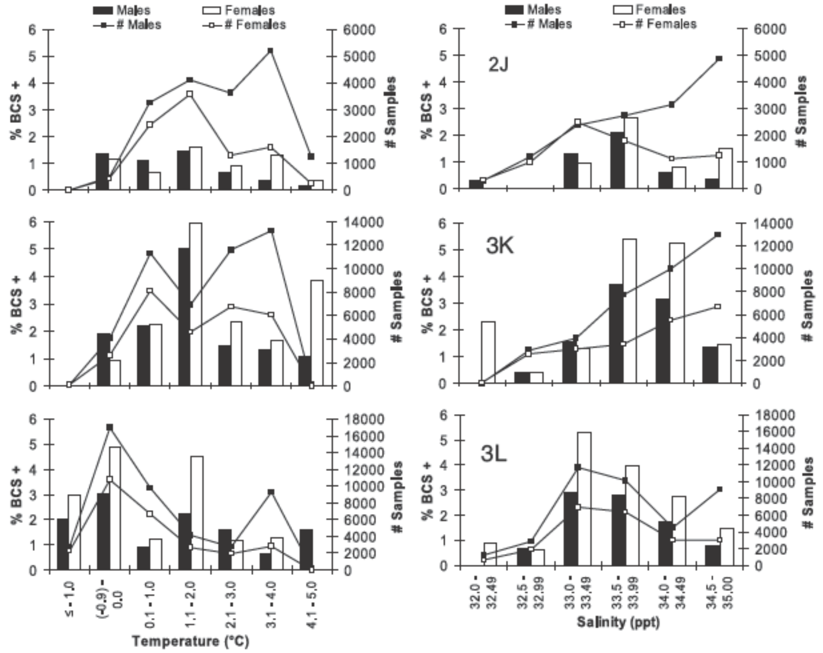

Figure 5. Relationship of BCS (bitter crab syndrome) prevalence in new-shelled crabs with near-bottom temperature (left) and salinity (right) by sex and division. Lines represent number of new-shelled crabs examined by sex.

prevalence was more closely related to temperature and salinity than it was to spatial effects (i.e., division).

The temperature-salinity (T-S) relationships for survey sets capturing new-shelled crabs (Fig. 6) differed among areas. All three areas included a common water mass, characterized by salinity increasing with temperature. The T-S relationship for this water mass was tighter in southernmost Div. 3L than in the more northern areas, where the salinity range was relatively broad at all ambient temperatures. This indicates less mixing in Div. 3L than in areas to the north. Div. 3L also includes a second shelf water mass, characterized by relatively low salinity and a strong annual cycle in temperature. This water mass represents fresh (<33 ppt) and seasonally warming water of the cold intermediate layer (CIL) that intersects the bottom on the shallow Grand Bank.

BCS-infected crabs were virtually absent from the low-salinity (<33 ppt) CIL water on the Grand Bank (Div. 3L, Figs. 2 and 6). Similarly, in the more northern areas, infected crabs were rarely encountered in

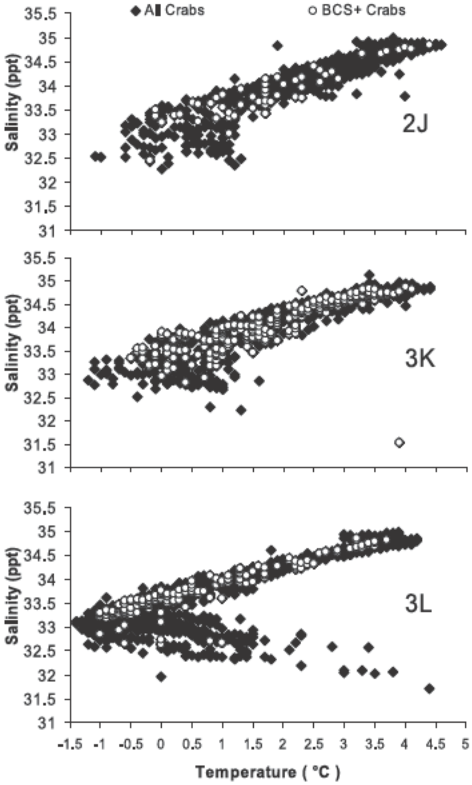

Figure 6. Temperature-salinity relationships for all survey sets that caught new-shelled crabs (sexes pooled) and for those that caught any BCS+ (bitter crab syndrome) crabs.

the more limited waters of lowest salinity (<33 ppt), extending along the coast (Figs. 2 and 6). Infected crabs were also relatively uncommon within the warmest and most saline waters of the mixed water mass, especially in Div. 2J (Fig. 6), where infected crabs were highly aggregated on Hamilton Bank (Figs. 1 and 2).

Oceanographic effects on annual variation in BCS distribution and prevalence

The relationships of prevalence with temperature and salinity were closely associated with host demographic characteristics, as we illustrate for males. When data were pooled across all years, it was apparent that BCS prevalence was highest in small males, with peak prevalence

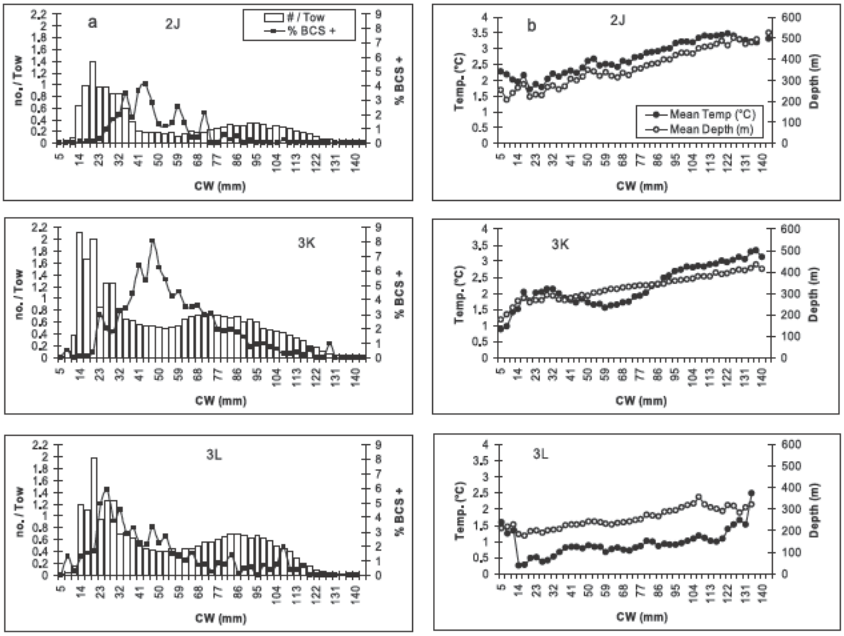

Figure 7. Division-specific relationships of new-shelled male snow crab size (carapace width) with survey catch rate and BCD (bitter crab disease) prevalence (a), and with mean bottom temperature and mean depth where new-shelled males were captured in those surveys (b).

occurring at sizes ranging 26-50 mm among the three divisions (Fig. 7a). Peak prevalence was higher in Div. 3K (8.1%) than in Div. 2J (4.2%) or Div. 3L (5.9%). These small crabs of peak prevalence were associated with shallow depths and near minimum temperatures in all divisions (Fig. 7b). Peak prevalence in Div. 2J and 3K occurred at similar sizes (44 and 50 mm CW respectively), depths (means of 298 and 287 respectively), and temperatures (means of 2.2 and 1.7°C respectively). In contrast, peak prevalence in Div. 3L occurred at much smaller size (26 mm CW), lesser depth (mean of 188 m), and lower temperature (mean of 0.4°C) than in the more northern divisions (Fig. 7).

Our regression analysis of yearly prevalence on bottom temperature showed that annual variation in prevalence was not related to temperature variation (Fig. 8). Both positive and negative associations were evident that were consistently very weak, as reflected in the goodness of fit criterion (r^2), which ranged from 0.002 to 0.18 for the divisional sex-specific comparisons.

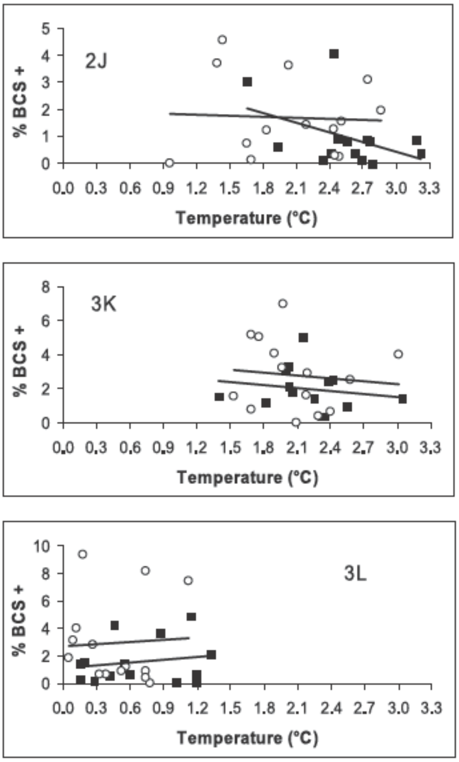

Figure 8. Linear regression models fitted to the data for BCD (bitter crab disease) prevalence in new-shelled crabs on ambient bottom temperature by division and sex. Open symbols represent females and closed symbols represent males.

Simulation of particle drift (Fig. 9) indicated that particles released on the shelf slope off southern Labrador (at either 100 m or 200 m) would be advected rapidly along the slope by the strong offshore branch of the Labrador Current (Fig. 1), and would be distributed along the warm saline northern and eastern slope of the Grand Bank after 180 days of release (Fig. 9). By contrast, particles released (at either depth) on the mid shelf off southern Labrador would be advected more slowly by relatively weak shelf currents including the inshore branch of the Labrador Current (Fig. 1) and would become dispersed throughout the northeast Newfoundland shelf (Div. 3K) within 30-50 days after release. Particles released (at 100 m) on the shallow inner shelf off southern Labrador would be rapidly advected southward to the inner shelf and

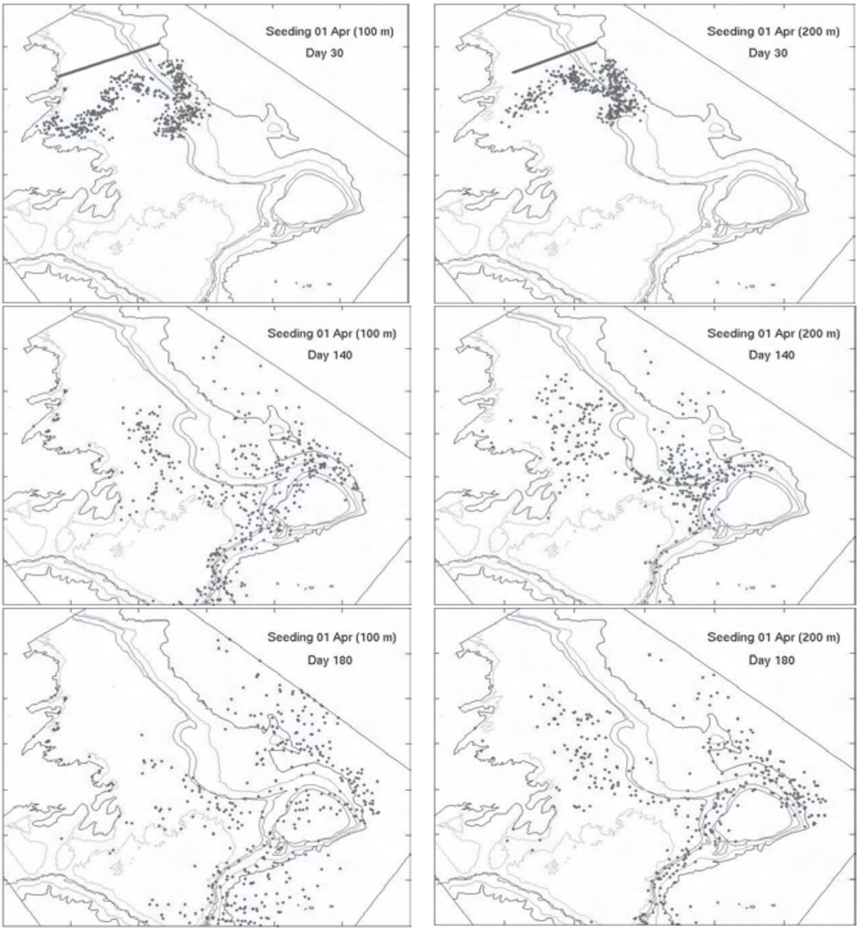

Figure 9. Simulation of drift of particles seeded along a transect extending across the southern Labrador shelf up to 180 days following release, for particles released at depths of 100 m (left) and 200 m (right). The seeding site is represented by the transect extending across the shelf in the top panels.

coast of Div. 3K within 30 days of release. Some particles, released on the mid to inner shelf, would be retained in Div. 3K, while most would continue to be advected southward. Within 140-180 days following release, these particles would become distributed across the northernmost portion of the Grand Bank (Fig. 9), due to the branching of the inshore component of the Labrador Current (Fig. 1). This distribution pattern is similar to that seen in infected crabs in Div. 3L (Fig. 2).

Discussion

Spatial distribution pattern

Our results showed that BCS-infected crabs were most commonly distributed from the southern Labrador shelf (Div. 2J) to the northern Grand Bank (Div. 3L). Survey catches of highest prevalence (maximum of 25%) occurred on Hamilton Bank in the northernmost area (Div. 2J) and extended from inshore bays to the middle shelf throughout the more southern portion of the distribution. This disagrees with Shields et al. (2005) who reported that BCS occurs predominately within the northern bays of Newfoundland. That conclusion, however, was based on a qualitative comparison of prevalence between trapped samples from a bay (Conception Bay, Fig. 1) and trawled samples from the shelf. A comparison of prevalence between those gear types from common surveys within Conception Bay has shown that prevalence of infection is higher in trapped samples than in trawled samples (Dawe et al. 2009), clearly indicating some sampling gear bias.

Relationship with oceanographic properties

We showed that BCS was most prevalent in Labrador slope water at intermediate temperatures and salinities. It was virtually absent from freshest water (<33 ppt) of coastal origin in northern areas or in the winter-chilled cold intermediate layer (<0°C) waters on the shallow Grand Bank in the most southern area. It was also uncommon in warmest (>3°C), most saline (>34 ppt) water of Labrador Sea origin along the shelf slope.

Highest prevalence at intermediate temperatures and salinities is closely associated with the demographic profile of infected crabs. We showed that prevalence (in males) was highest in small crabs distributed primarily on shallow-water hard substrates at near-minimal temperatures (Dawe and Colbourne 2002, Dawe et al. 2010). This is inconsistent with Shields et al. (2005) who concluded that prevalence increased with depth and was higher in areas with mud substrate than in areas with harder substrates. However, sampling in that study was targeted at the deep commercial fishing grounds of Conception Bay, characterized by a uniform soft mud substrate. Thus, sampling in that study was very limited at shallow depths with hard substrates, where small crabs are primarily distributed (Dawe et al. 2010). We did find some instances, such as Div. 3K in 1997, when prevalence was more broadly distributed across the entire size range than is typical (Dawe et al. 2009). This resulted in a distribution of infected crabs that extended farther offshore than usual, including deep, warm, saline areas with soft substrates, inhabited primarily by large males (Dawe and Colbourne 2002).

The low prevalence we found at lowest temperatures and salinities, most evident in Div. 3K, was related to the inverse relationship we found between prevalence and host size for males smaller than about 50 mm CW. We believe that this inverse relationship in smallest crabs may be an artifact of the visual method of detection. This is supported by microscopic examination of blood smears from Div. 3K trap surveys that showed maximum prevalence at the smallest sizes sampled, about 40 mm CW (Morado, unpubl. data). Crabs of this size and smaller molt more frequently than annually (Sainte-Marie et al. 1995, Hébert et al. 2002) and may incur a high size-related mortality due to the combined stresses of molting and BCS at infection intensities that are not visibly evident. This is consistent with our results that showed peak prevalence in Div. 3L males at much smaller sizes and lower temperatures than in the more northern areas. We interpret this as resulting from lower molting frequency of small crabs at lower temperatures in Div. 3L than in the more northern divisions. This implies that the overall relationship of temperature with true prevalence would be an inverse one.

An overall inverse relationship between prevalence and temperature, as we infer, would not be consistent with Shields et al. (2007) who concluded prevalence is directly related to temperature. That study concluded that increased prevalence in Conception Bay during 2003-2005 was related to an increase in temperature, which resulted in increased molting activity and subsequently an increased availability of suitable (new-shelled) hosts. However, our more extensive time series showed no such relationship between temperature and annual variability in prevalence. We believe the high prevalence in Conception Bay during 2003-2005 was due to a density-dependent effect rather than an effect of temperature. Density dependence would account for the observed increase in host size of peak prevalence in Conception Bay between the periods 1997-2002 and 2003-2005 (Shields et al. 2007). This likely reflects increased prevalence in one to several strong year classes that represent a recruitment pulse progressing through the host size range over several years. This is supported by the observed peak in Conception Bay trap survey catch rates of largest (legal-sized) new-shelled males in 2006, which was followed by a sharp decrease in both catch rate and BCS prevalence in 2007 (Dawe et al. 2009). Similarly, we found that high prevalence, in relatively small crabs on the northern Grand Bank (Div. 3L) during 2004-2005, was followed by increased abundance of (larger) pre-recruit males in 2007 and 2008 (Dawe et al. 2009). This pattern of increased prevalence in small crabs followed by progression throughout the host size range has also been observed in Div. 3K during 1995-1998 and 2004-2007 (Dawe et al. 2009). It is beyond the scope of this study to further elaborate density-dependent effects. However, we feel that any effect of temperature on annual prevalence level would likely be indirect and negative rather than positive, due to the inverse relationship of host size with both temperature and prevalence.

Effects of ocean circulation

Highest prevalence in small crabs, as we found, accounts for the spatial distribution pattern we observed. This pattern, as described above, agrees closely with the general distribution pattern of smallest male crabs, as depicted by Dawe and Colbourne (2002). We showed in particular that BCS distribution is limited to the inner portion of the central (Div. 3K) shelf, as are small crabs (Dawe and Colbourne 2002), in years like 2005 when it occurred mostly in small crabs (Dawe et al. 2009). In contrast, BCS distribution extends farther offshore to the middle shelf in years like 1997, when it was relatively prevalent in larger crabs (Dawe et al. 2009). This implies that advection is important in regulating the distribution of larval and settling crabs, as well as that of *Hematodinium* sp., resulting in highest prevalence in small (or smallest) crabs. Expansion of the spatial distribution of BCS within the snow crab host population is likely due to progression of BCS throughout the host's size range due to molting and ontogenetic migration (Dawe and Colbourne 2002) to deeper, warmer, and more saline areas.

The results of particle drift simulation support the proposed importance of circulation pattern in regulating the distribution of both larval crabs and *Hematodinium* sp. Low prevalence along the warm saline slope may be due to rapid advection and flushing of larvae and pathogen. By contrast, higher prevalence over the shelf and into bays may be due to slow flow and recirculation by the weak inshore branch of the Labrador Current that results in particle retention and increased opportunity for larval settlement as well as infection of potential hosts. This hypothesized role of retention by ocean currents is consistent with studies of BCS in southeast Alaska Tanner crabs, which suggested that high prevalence is related to retention within embayments and inlets (Myers et al. 1987, 1990). In our study this is strongly supported by the observed distribution of infected crabs on the southern Labrador shelf (Div. 2J). High BCS prevalence in that area has consistently been highly aggregated within a quasi-permanent recirculating gyre on Hamilton Bank. Also, the southern limit of BCS (with rare exceptions), across the broad northern slope of the Grand Bank coincides with the southern limit of the weaker inshore branch of the Labrador Current. In this area the inshore branch splits, with the nearshore southerly flowing component becoming topographically constrained and flowing swiftly through the Avalon Channel and around the southeastern extreme of the island. The easterly flowing component of the inshore branch merges with the faster-flowing offshore branch and continues along the deep eastern slope of the Grand Bank (Div. 3N) (Colbourne et al. 1997).

The virtual absence of infected crabs at salinities below 33 ppt in all areas, and especially within the cold intermediate layer on the Grand Bank, suggests that low salinity may limit the distribution of BCS. However, it is unclear whether this reflects a direct effect of salinity or an association of salinity with water mass circulation patterns. The consistent virtual absence of BCS in the cold intermediate layer across the northern Grand Bank, where circulation is not strong, implies a direct effect on *Hematodinium* survival or virulence. We recognize that the low prevalence we found at lowest salinities could be an artifact of failure to visually recognize BCS in smallest crabs at shallow depths and lowest salinities. However, we hypothesize that a limiting effect of low salinity may account for the absence of BCS within the snow crab resources of the Gulf of St. Lawrence. Low salinity waters along the Newfoundland coast and throughout the shallow Strait of Belle Isle (Fig. 1) may represent a barrier to transmission from the southern Labrador shelf into the Gulf. Furthermore, annual average salinities are generally <32.6 ppt at water depths <100 m throughout the Gulf (Petrie et al. 1996), where the snow crab fisheries are primarily prosecuted. A direct effect of salinity would be consistent with Messick et al. (1999) who found that intensity of infection in blue crabs (*Callinectes sapidus*) was limited by low temperature (<9°C) and salinity (<11 ppt). However, blue crabs in the coastal bays of Maryland live in much warmer and fresher waters than do snow crabs off Newfoundland and Labrador, and it is possible that different species of *Hematodinium* infect these hosts. The possible existence of several *Hematodinium* species with differing salinity tolerances is further supported by the recent occurrence of *Hematodinium* in a low salinity (<9 ppt) aquaculture facility in China (Li et al. 2008).

Implications of climate change

It is currently unknown how oceanographic properties, circulation pattern, and bathymetry may interact to maintain BCS in Atlantic Canadian snow crab practically limited to the eastern Newfoundland and Labrador shelf. While changes in flow of the inshore branch of the Labrador Current cannot be detected, it is known that volume transport of the stronger offshore branch has been increasing from the late 1990s to the early 2000s (Han et al. 2010). Under a scenario of future warming there would likely continue to be increasing volume transport of fresh water from the Arctic resulting in decreased shelf salinities. However, we feel that ocean circulation is not limiting further expansion of BCS distribution because snow crab throughout Atlantic Canadian waters are members of a single panmictic population (Puebla et al. 2008), with no barriers to larval (or any other particle) drift. Also, although *Hematodinium* sp. has been well established within Newfoundland snow crab for at least 14 years, it has only very recently been detected on the Scotian Shelf (Morado et al. 2010) and remains unknown in the Gulf of St. Lawrence, which receives inflow directly from the southern Labrador shelf through the Strait of Belle Isle. This absence from Gulf of St. Lawrence snow crab is not consistent with the recent rapid expansion of *Hematodinium* spp. worldwide throughout numerous crustacean host species (Morado et al. 2010).

We feel it is more likely that spatial differences in oceanographic properties result in reduced survival or virulence of *Hematodinium* in regions other than Newfoundland. Shields et al. (2007) speculated that increased warming would result in expansion of BCS to other areas, but this is not supported by our results that showed no direct relationship between temperature and prevalence. Furthermore, bottom temperatures along the Newfoundland shelf have remained above normal in recent years (Colbourne et al. 2009), while BCS prevalence has decreased (Dawe et al. 2009). A direct temperature effect on prevalence is also not consistent with higher ambient temperatures in Canadian snow crab fishery areas other than Newfoundland. We consider salinity to be a more likely property limiting expansion of BCS to other Atlantic Canadian snow crab fishing areas, for reasons described previously. This would be consistent with low ambient salinities in the Gulf of St. Lawrence, where BCS remains unknown.

Summary and conclusions

We acknowledge that variability in apparent prevalence may be affected by variability in biological processes such as host molt frequency and timing. However, our results lead to some general conclusions that are both plausible and well supported by trends. We conclude that the spatial distribution of BCS in snow crab on the eastern Newfoundland and Labrador shelf is largely regulated by ocean circulation. Weak flows and recirculation result in concentration of both *Hematodinium* sp. and settling crabs in shallow inshore areas and on offshore banks. We found that annual variation in prevalence was not directly related to ambient temperature and we feel that other factors likely interact to affect prevalence in any area, including host density-dependent factors. We hypothesize that salinity may affect expansion throughout the western Atlantic snow crab population, with low salinity directly limiting *Hematodinium* survival or virulence. Further studies will be required to investigate possible direct effects of salinity, including experiments on pathogen virulence and host susceptibility throughout the ambient salinity range. If salinity does reduce infection probability, it still remains unknown whether future changes in salinity might be so substantial as to affect the distribution and prevalence of BCS in the western Atlantic snow crab population.

References

Colbourne, E., B. De Young, S. Narayanan, and J. Helbig. 1997. A comparison of hydrography and circulation on the Newfoundland shelf during 1990-1993 to the long-term mean. Can. J. Fish. Aquat. Sci. 54(Suppl. 1):68-80. doi:10.1139/cjfas-54-S1-68

Colbourne, E., J. Craig, C. Fitzpatrick, D. Senciall, P. Stead, and W. Bailey. 2009. An assessment of the physical oceanographic environment on the Newfoundland and Labrador shelf during 2008. Canadian Science Advisory Secretariat Science Advisory Report 2009/032. 20 pp. Accessed July 2010: http://www.dfo-mpo.gc.ca/csas/Csas/status/2007/SAR-AS2007_008_E.pdf.

Dawe, E.G. 2002. Trends in prevalence of bitter crab disease caused by *Hematodinium* sp. in snow crab (*Chionoecetes opilio*) throughout the Newfoundland and Labrador continental shelf. In: A.J. Paul, E.G., Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley, and D. Woodby (eds.), Crabs in cold water regions: Biology, management, and economics. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 385-400.

Dawe, E.G., and E.B. Colbourne. 2002. Distribution and demography of snow crab (*Chionoecetes opilio*) on the Newfoundland and Labrador shelf. In: A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley, and D. Woodby (eds.), Crabs in cold water regions: Biology, management, and economics. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Dawe, E.G., S.J. Walsh, and E.M. Hynick. 2010. Capture efficiency of a multi-species survey trawl for snow crab (*Chionoecetes opilio*) in the Newfoundland region. Fish. Res. 101:70-79. doi:10.1016/j.fishres.2009.09.008

Dawe, E. et al. 2009. An assessment of Newfoundland and Labrador snow crab (*Chionoecetes opilio*) in 2007. Canadian Science Advisory Secretariat Science Advisory Document 2009/057. 160 pp.

Eaton, W.D., D.C. Love, C. Botelho, T.R. Meyers, K. Imamura, and T.M. Koeneman. 1991. Preliminary results on seasonality and life cycle of the parasitic dinoflagellate causing bitter crab disease in Alaskan Tanner crabs (*Chionoecetes bairdi*). J. Invertebr. Pathol. 57:426-434. doi:10.1016/0022-2011(91)90147-I

Han, G., and D. Kulka. 2008. Dispersion of eggs, larvae and pelagic juveniles of white hake (*Urophycis tenuis*) in relation to ocean currents of the Grand Bank: A modelling approach. J. Northwest Atl. Fish. Sci. 41:183-196. doi:10.2960/J.v41.m627

Han, G., K. Ohashi, N. Chen, and P.G. Myers, and J. Fisher. 2010. Decline and partial rebound of the Labrador Current 1993-2004: Monitoring ocean currents from altimetric and CTD data. J. Geophys. Res. 115, C12012. doi:10.1029/2009JC006091

Han G., Z. Lu, Z. Wang, J. Helbig, N. Chen, and B. deYoung. 2008. Seasonal variability of the Labrador Current and shelf circulation off Newfoundland. J. Geophys. Res. 113, C10013. doi:10.1029/2007JC004376

Hébert, M., G. Benhalima, G. Miron, and M. Moriyasu. 2002. Moulting and growth of male snow crab, *Chionoecetes opilio* (O. Fabricius, 1788) (Decapoda, Majidae), in the southern Gulf of St. Lawrence. Crustaceana 75(5):671-702. doi:10.1163/156854002760202679

Li, Y.Y., X.A. Xia, Q.Y. Wu, W.H. Liu, and Y.S. Lin. 2008. Infection with *Hematodinium* sp. in mud crabs *Scylla serrata* cultured in low salinity water in southern China. Dis. Aquat. Org. 82:145-150. doi:10.3354/dao01988

Love, D.C., S.D. Rice, D.A. Moles, and W.D. Eaton. 1993. Seasonal prevalence and intensity of bitter crab dinoflagellate infection and host mortality in Alaskan Tanner crabs *Chionoecetes bairdi* from Auke Bay, Alaska, USA. Dis. Aquat. Org. 15:1-7. doi:10.3354/dao015001

Messick, G.A., S.J. Jordan, and W.F. van Heukelem. 1999. Salinity and temperature effects on *Hematodinium* sp. in the blue crab *Callinectes sapidus*. J. Shellfish Res. 18:657-662.

Meyers, T.R., T.M. Koeneman, C. Botelho, and S. Short. 1987. Bitter crab disease: A fatal dinoflagellate infection and marketing problem for Alaskan Tanner crabs *Chionoecetes bairdi*. Dis. Aquat. Org. 3:195-216. doi:10.3354/dao003195

Meyers, T.R., C. Botelho, T.M. Koeneman, S. Short, and K. Imamura. 1990. Distribution of bitter crab dinoflagellate syndrome in southeast Alaskan Tanner crabs *Chionoecetes bairdi*. Dis. Aquat. Org. 9:37-43. doi:10.3354/dao009037

Morado, J.F., T.R. Meyers, and R.S. Otto. 2000. Distribution and prevalence of bitter crab syndrome in snow (*Chionoecetes opilio*) and Tanner (*Chionoecetes bairdi*) crabs of the Bering Sea. J. Shellfish Res. 19:646-647.

Morado, J.F., E.G. Dawe, D.R. Mullowney, C. Shavey, V. Lowe, R.J. Cawthorn, A. Burmeister, B. Zisserson, and E. Colbourne. 2010. Climate change and the worldwide emergence of *Hematodinium*-associated disease: Is there evidence for a relationship? In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and management of exploited crab populations under climate change. Alaska Sea Grant College Program, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.08

Pestal, G.P., D.M. Taylor, J.M. Hoenig, J.D. Shields, and R. Pickavance. 2003. Monitoring the prevalence of the parasitic dinoflagellate *Hematodinium* sp. in snow crabs *Chionoecetes opilio* from Conception Bay, Newfoundland. Dis. Aquat. Org. 53:67-75. doi:10.3354/dao053067

Petrie, B., K. Drinkwater, A. Sandström, R. Pettipas, D. Gregory, D. Gilbert, and P. Sekhon. 1996. Temperature, salinity and sigma-t atlas for the Gulf of St. Lawrence. Can. Tech. Rep. Hydrogr. Ocean Sci. 178. 256 pp.

Puebla, O., J.-M. Sévigny, B. Sainte-Marie, J.-C. Brêthes, A. Burmeister, E.G. Dawe, and M. Moriyasu. 2008. Population genetic structure of the snow crab (*Chionoecetes opilio*) at the northwest Atlantic scale. Can. J. Fish. Aquat. Sci. 65:425-436. doi:10.1139/F07-163

Sainte-Marie, B., S. Raymond, and J.-C. Brêthes. 1995. Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura, Majidae). Can. J. Fish. Aquat. Sci. 52:903-924. doi:10.1139/f95-091

SAS Institute Inc. 1985. SAS user's guide: Statistics, v. 5 edn. SAS Institute Inc., Cary. 957 pp.

Shields, J.D., D.M. Taylor, P.G. O'Keefe, E. Colbourne, and E. Hynick. 2007. Epidemiological determinants in outbreaks of bitter crab disease (*Hematodinium* sp.) in snow crabs *Chionoecetes opilio* from Conception Bay, Newfoundland, Canada. Dis. Aquat. Org. 77:61-72. doi:10.3354/dao01825

Shields, J.D., D.M. Taylor, S.G. Sutton, P.G. O'Keefe, D. Ings, and A. Pardy. 2005. Epizootiology of bitter crab disease (*Hematodinium* sp.) in snow crabs, *Chionoecetes opilio* from Newfoundland, Canada. Dis. Aquat. Org. 64:253-264. doi:10.3354/dao064253

Stentiford, G.D., and J.D. Shields. 2005. A review of the parasitic dinoflagellates *Hematodinium* and *Hematodinium*-like infections in marine crustaceans. Dis. Aquat. Org. 66:47-70. doi:10.3354/dao066047

Taylor, D.M., and R.A. Khan. 1995. Observations on the occurrence of *Hematodinium* sp. (Dinoflagellata: Syndinidae), the causative agent of bitter crab disease in Newfoundland and Labrador snow crab (*Chionoecetes opilio*). J. Invertebr. Pathol. 65:283-288. doi:10.1006/jipa.1995.1043

Bednarski, J., C.E. Siddon, G.H. Bishop, and J.F. Morado. 2010. Overview of Bitter Crab Disease in Tanner Crabs, *Chionoecetes bairdi*, in Southeast Alaska from 2001 to 2008. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.07

Overview of Bitter Crab Disease in Tanner Crab, *Chionoecetes bairdi*, in Southeast Alaska from 2001 to 2008

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Abstract

We present visual prevalence of infection and distribution trends in Tanner crab, *Chionoecetes bairdi,* infected with the dinoflagellate *Hematodinium* spp., the causative agent of bitter crab disease (BCD), in southeast Alaska from 2001 to 2008. Analysis of visual detection of BCD from annual research surveys showed that trends of prevalence among survey areas were inconsistent. In some locations a significant decrease in visually infected crab occurred over time, whereas BCD increased or remained stable in other areas. In addition, BCD generally declined slightly with depth. The prevalence of BCD was greater in recently molted crab, as determined by shell condition, and increased as shell size increased in new shell males. Although we cannot yet explain the variability in BCD, the dramatic differences in BCD prevalence over small spatial scales in southeast Alaska will foster a better understanding of BCD, especially as more detailed environmental data are obtained.

Introduction

A species of the parasitic dinoflagellate *Hematodinium* is the causative agent of a disease named bitter crab disease (BCD) in Tanner crab, *Chionoecetes bairdi,* in the North Pacific (Jensen et al. 2010). It is possible that infection occurs during the molt (January-May), and laboratory studies suggest the gestation period in the host crab is about 18 months. Visual signs of BCD are not obvious until the following winter when, in the late stages of the disease, infected crab exhibit exaggerated coloration of the carapace giving the appearance of a "cooked" crab, as well as white opaque hemolymph (Meyers and Burton 2009).

BCD was officially diagnosed in southeast Alaska Tanner crab in 1985, but it was likely present prior to this date (Meyers et al. 1987). Local studies on BCD have found that the intensity of the disease is greatest in August and September (Love et al. 1993) with widespread distribution of prevalence exceeding 90% infection in some areas of Lynn Canal (Meyers et al. 1990) and is nearly always fatal (Love et al. 1993).

Twenty years after its discovery, the distribution of BCD has increased and much is still unknown about the parasite's life history. *Hematodinium* spp. occur worldwide affecting over 30 species of crustaceans. Stentiford and Shields (2005) believe that *Hematodinium* spp. infections are one of the most economically significant diseases of Crustacea. During the 2008-09 commercial Tanner crab season in southeast Alaska, 9% of the commercial catch, or over 53,000 lbs, was discarded as BCD crabs by processors—an economic value of about $91,000 ex-vessel (ADFG unpubl. data).

The purpose of this paper is to provide an updated assessment of the visual prevalence and distribution of Tanner crabs infected by the dinoflagellate *Hematodinium* sp., in southeast Alaska. This region provides a unique opportunity to compare among many localized stocks that may help to more clearly identify the relationship between host and parasite. Our overall goal was to compare the trends of this lethal disease among several local crab populations. Specifically, we examined how BCD prevalence varied among areas as a function of crab biomass, depth, geographic location, and by sex, shell condition, and size.

Materials and methods

The Alaska Department of Fish and Game (ADFG) has conducted annual fall Tanner crab stock assessment pot surveys (TCS), during which crabs have been visually examined for the presence/absence of bitter crab disease (BCD) since 2001. Tanner crabs are also visually examined during annual summer red king crab assessment surveys (RKCS).

Visual detection of BCD based on the opaque ivory coloration of the shell (Jadamec et al. 1999) was validated through collection and analysis of hemolymph samples, either via the examination of blood smears, or more recently a DNA-based protocol (Jensen et al. 2010). The PCR (DNA polymerase chain reaction) analysis confirmed that 100% of the crabs visually detected as BCD positive were infected by the parasitic

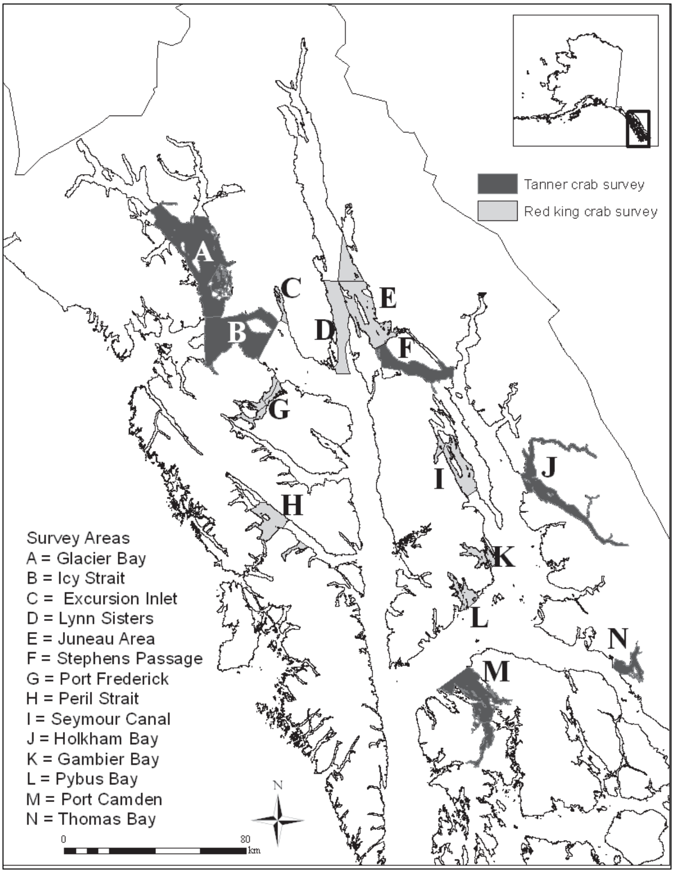

Figure 1. Southeast Alaska crab survey areas. Letters denote survey areas. The gray areas are red king crab and the black areas are Tanner crab survey areas.

dinoflagellate, although visual detection of BCD in the same population underestimated prevalence by 47% when compared to conventional PCR detection (Pam Jensen, NOAA, Seattle, 2009, pers. comm.).

Crabs from each pot were counted and classified into size/sex categories by quantifying carapace width, sex, shell condition, and clutch fullness of all mature females (Jadamec et al. 1999).

Survey data

Pot surveys were conducted in 14 geographically separate areas, throughout southeast Alaska (Fig. 1). Six areas are surveyed in the fall to explicitly target Tanner crab, and nine areas are designed to target red king crab in the summer, but have Tanner crab as a significant bycatch. The complex geography of southeast Alaska provides a unique ecosystem consisting of many small areas of suitable Tanner crab habitat adjacent to steep, deepwater habitats, which effectively isolate adult populations. Therefore, Tanner crabs from each of the survey areas are considered to be separate local stocks. Coincidentally, two of the areas (Stephens Passage and Holkham Bay) are sampled on both surveys. Although they are not identical, there is broad overlap between the fall and summer surveys in these two areas, which served as useful seasonal links between the two surveys. Surveyed areas correspond with commercial fishing grounds that account for 71% of the total Tanner crab harvest (1980-2000 average). Survey methods for both the TCS and the RKCS are similar. Each area is divided into one to five strata based on the historical density of the target species. Surveys are conducted in a random stratified sampling design with the number of pots (the sampling unit) allocated as a function of historical crab density. Each survey pot weighs approximately 159 kg and has two base rings, the bottom one with a diameter of 2.3 m. The sloping pot "sides" are 94 cm long, with a 12.7 cm shoulder at the top—the pot is 76 to 81 mm high. Crabs enter the pots through a 32.4 cm deep rigid plastic tunnel with entrance diameter of 70 cm, and exit diameter of 50 cm. The mesh is smaller than that of commercial pots; the body webbing is 9 cm and purse webbing 11 cm stretch mesh, and the four, 12 cm diameter escape rings are cable-tied shut, allowing the gear to retain prerecruit and female crabs. Details regarding TCS, RKCS, and pot location generation methods are documented elsewhere (Bednarski et al. 2008). Differences between the TCS and RKCS methods include different sampling dates and bait. The TCS is conducted in the fall (October), whereas the RKCS is conducted in the summer (June-July). The TCS uses an additional half of a round pink salmon as hanging bait.

Data analysis

We compared trends in the prevalence of BCD as a continuous variable of the proportion of bitter crab per pot. The data were transformed as the arcsine of the square-root of the proportion to reduce the heterogeneity of variances. Prevalence of bitter crab was also analyzed as a categorical variable by presence/absence. Because the survey data do not provide a relative index of abundance for juvenile males and females (Bednarski et al. 2008), trends in prevalence of BCD will mainly be described for mature crab.

To examine the yearly trends of prevalence of BCD among areas, an analysis of covariance (ANCOVA) was performed. There was a significant interaction between year and area (F ratio = 4.13, $p \leq 0.001$) for the full model. After removing Gambier Bay and Seymour Canal from the model, there was no significant interaction between year and area (*F* ratio = 1.58, $p = 0.10$). The reduced model (excluding Gambier Bay and Seymour Canal) was used to compare yearly trends of prevalence of BCD among areas. The mean BCD prevalence among areas (excluding Gambier Bay and Seymour Canal) was compared using the Tukey-Kramer HSD test. To examine the interaction between year and prevalence of BCD for Gambier Bay and Seymour Canal linear regression was performed for each area.

To examine the effect of host density on BCD prevalence, we looked at the correlation between mature male biomass (≥109 mm carapace width, all shell conditions), a well established data series calculated by CSA (catch-survey analysis) (Zheng et al. 2006, Siddon et al. 2009), and BCD prevalence in mature males (≥109 mm carapace width, all shell conditions). The CSA biomass estimate was used (rather than total crab CPUE, catch per unit effort) because the surveys generally target mature male crab and the catchability of the other size/sex classes is generally thought to be lower. Thus we felt that the CSA biomass estimate was a more reliable and consistent metric of host density.

To examine the difference between depth and prevalence of BCD among areas, an analysis of covariance (ANCOVA) was performed. There was a significant interaction between depth and area (*F* ratio = 8.21, $p = <0.001$) for the full model. After removing Holkham Bay and Port Frederick from the model there was no significant interaction between depth and area (*F* ratio = 1.70, $p = 0.07$). The reduced model was then used to examine the relationship between depth and prevalence of BCD among areas. Since depth was found to be a significant effect (*F* ratio = 34.57, $p < 0.001$), linear regression was used to examine the relationship between depth and prevalence of BCD for each area.

To examine if the prevalence of BCD varied by survey area, dummy variables based on latitudinal and longitudinal location were separately assigned to each survey area. Linear regression was then performed separately for prevalence of BCD by latitude and longitude.

Differences in BCD prevalence between male and female crabs were examined using chi-square analysis. To compare size distribution in relation to BCD prevalence within an area, new shell males and mature females were each grouped into 5 mm carapace width intervals (Fig. 2). Prevalence of BCD, as a continuous variable of the proportion of bitter crab per size group, was then calculated and transformed as the arcsine of the square-root of the proportion to reduce the heterogeneity of variances. Each area was standardized by sex for a sample size of at least 10 per size group. Linear regression was used for each sex to compare the difference between size and prevalence of BCD. To examine the reproductive success of new shell females, logistic regression with an odds ratio was used. All analyses were performed using JMP statistical software Version 6 (SAS Institute 2005).

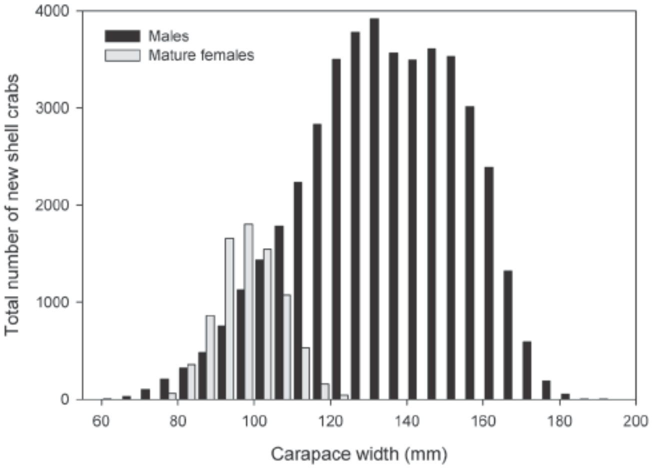

Figure 2. Size composition of new shell male and mature female Tanner crabs caught, 2001-2008. Mean carapace width (CW) for males 134 mm (1.06 SE) and mean CW for females 97 mm (0.70 SE).

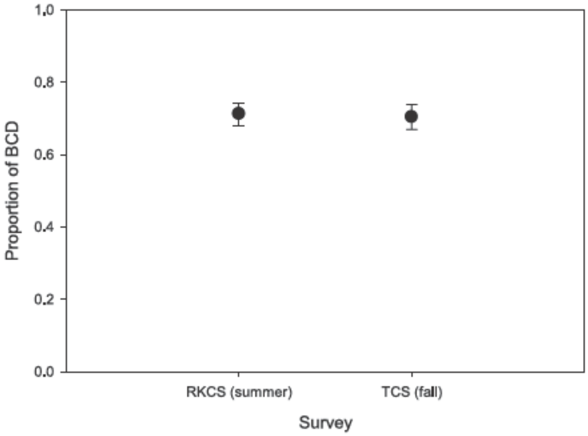

Figure 3. For Stephens Passage, mean proportion (arcsin√ transformed; ±SE) bitter crab disease prevalence in Tanner crab for TCS (Tanner crab survey) and RKCS (red king crab survey), 2001-2008.

Caveats of data

We could not examine seasonal patterns of BCD prevalence because of the confounding effect of survey area and season. However, Stephens Passage and Holkham Bay are each surveyed twice a year (in TCS and RKCS), and although the literature has noted a significant difference in BCD prevalence between seasons (Stentiford and Shields 2005), results of a one-way ANOVA found no difference between BCD prevalence in the TCS (2001-2008 fall) and RKCS (2001-2008 summer) data for Stephens Passage (F ratio = 0.02, $p = 0.88$; Fig. 3). For this reason, TCS and RKCS data were combined for Stephens Passage. However, RKCS data were excluded from Holkham Bay analysis because results of a one-way ANOVA found a significant difference between proportion of BCD prevalence in the TCS (2001-2008 fall) and RKCS (2001-2008 summer) data (F ratio = 8.1, $p = 0.001$). These data suggest a seasonal relationship at one site, but not at another, which provides more evidence that seasonal comparisons would be inappropriate for this data set.

Table 1. Mean comparisons among areas without declining prevalence, Tukey-Kramer HSD. Mean is the arc-sin of the square root of the proportion of bitter crab disease prevalence. Areas not connected by the same letter are significantly different.

Area	Sample size	Levels of prevalence						Mean prevalence
Port Frederick	304	A						0.69
Stephens Passage	450		B					0.49
Juneau area	374		B	C				0.43
Holkham Bay	255			C	D			0.34
Lynn Sisters	166				D	E		0.29
Excursion Inlet	279					E		0.23
Thomas Bay	350					E		0.23
Peril Strait	270					E		0.23
Pybus Bay	189						F	0.11
Glacier Bay	258						F	0.08
Icy Strait	211						F	0.04
Port Camden	75						F	0.001

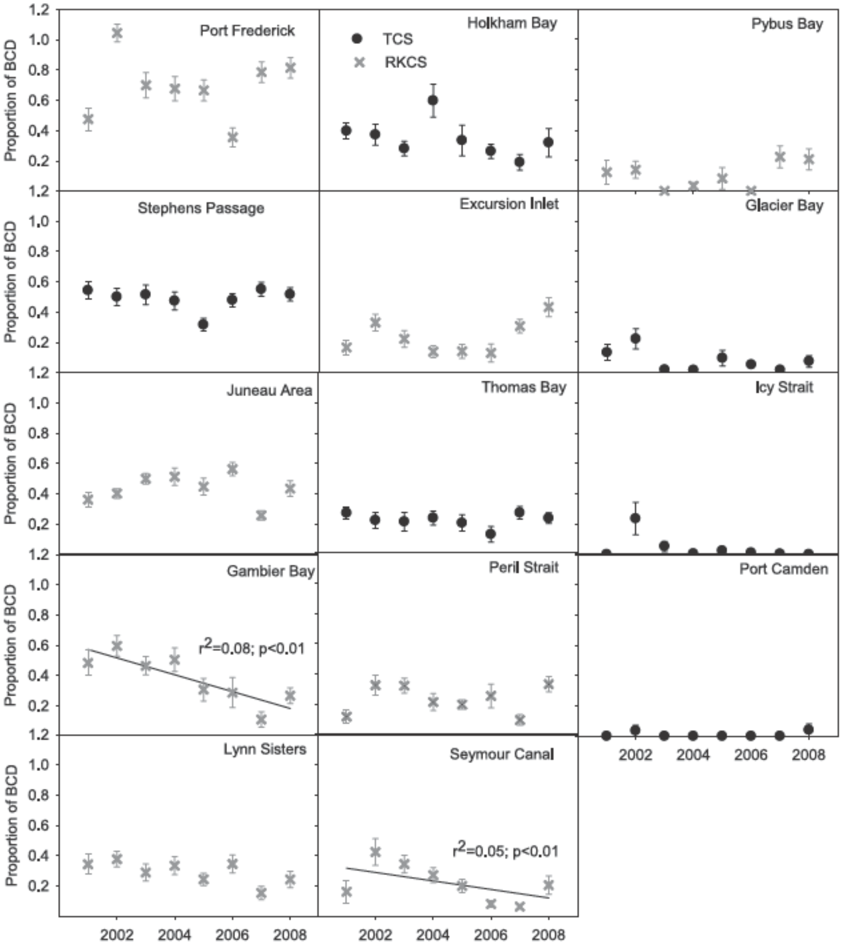

Figure 4. **For each survey area, the mean portion (arcsin√ transformed; ±SE) of bitter crab disease prevalence in Tanner crab by year, 2001-2008. Arranged by highest prevalence starting with top left corner, top to bottom. The graphs with the x's indicate red king crab survey areas (RKCS) and graphs with black dots indicate Tanner crab survey areas (TCS). Results from linear regression analysis displayed are areas excluded from the full ANCOVA model.**

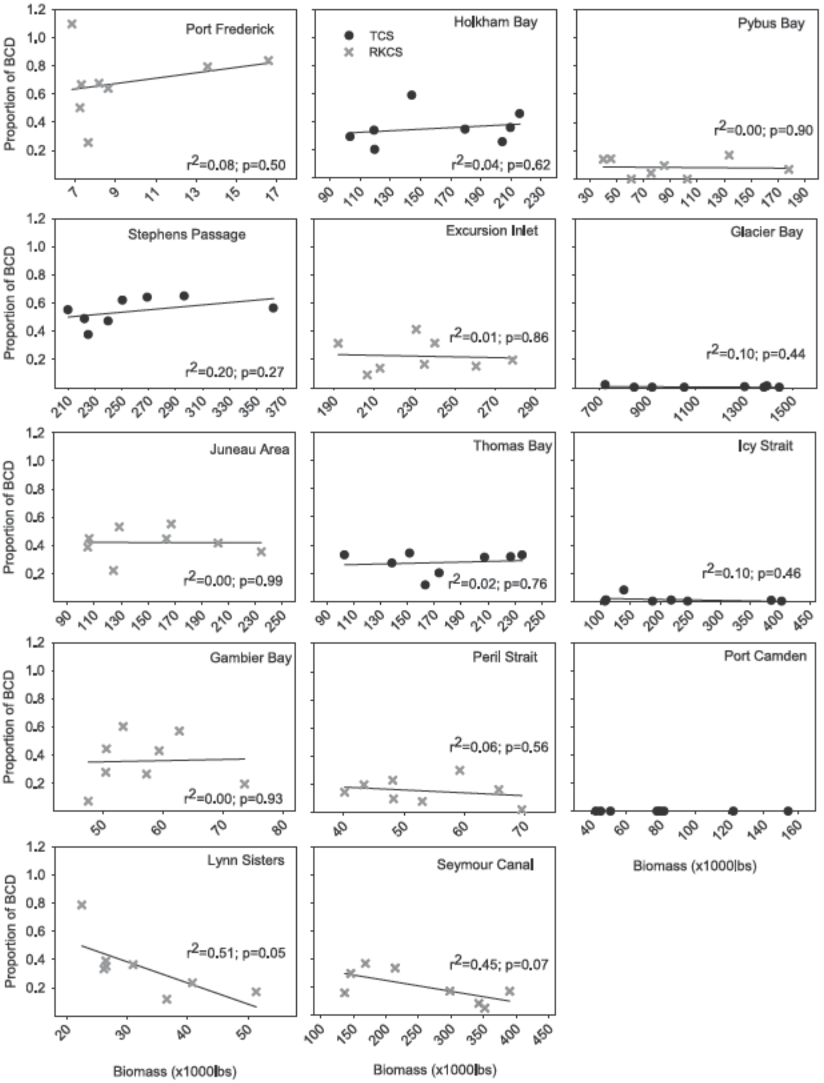

Figure 5. For each survey area, results of linear regression analysis, male Tanner crab (≥109 mm carapace width) proportion (arcsin√ transformed) of bitter crab disease prevalence by mature male biomass, 2001-2008.

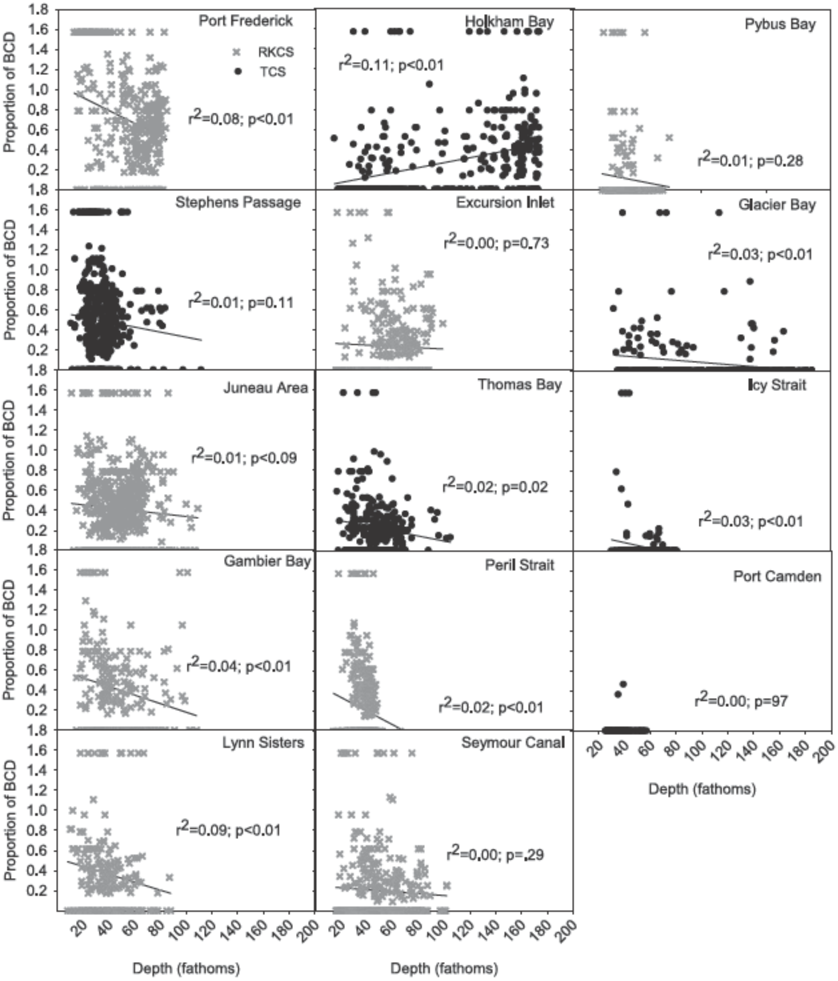

Figure 6. For each survey area, results of the linear regression, proportion (arcsin√ transformed) of bitter crab disease prevalence by depth (fathom), 2001-2008. Arranged by highest prevalence starting with top left corner, top to bottom. The graphs with gray x's are red king crab survey areas (RKCS) and graphs with black dots are Tanner crab survey areas (TCS).

Results

Temporal and spatial distribution of disease

Bitter crab disease (BCD) was found in all areas, but with dramatically different levels of infection (F ratio = 88.39, $p < 0.001$; Table 1; Fig. 4). In Gambier Bay and Seymour Canal, the proportional pot prevalence of bitter crab has been declining annually (Fig. 4). The remaining 12 survey areas show a relatively consistent prevalence for eight years (2001-2008; F ratio = 0.87, $p = 0.35$). Port Frederick, Stephens Passage, and Juneau area have the highest mean proportion of BCD prevalence (Table 1). In general, BCD levels are not related to abundance (as indexed by mature male biomass; Fig. 5). Many of the areas have similar levels of BCD prevalence; however, there is no pattern of BCD prevalence in relation to geographic position (latitude, $R^2 = 0.00$, $p = 0.54$; or longitude $R^2 = 0.00$, $p = 0.09$).

Overall, depth is a significant factor of prevalence of BCD for each area in the reduced model (F ratio = 34.57, $p < 0.001$), but does not explain much of the variability of BCD prevalence (all r^2 values <0.12; Fig. 6). Some contrasting patterns with depth were observed; infection declined with increasing depth in eight areas, whereas it increased with depth in Holkham Bay (Fig. 6). The increase with depth observed in Holkham Bay is possibly related to the larger depth range; the mean pot depth is 170 fathoms, whereas the mean depth for the other areas combined is 84 fathoms (SE = 0.62). This suggests that shallow and deep water habitats could be more stressful, leading to higher incidence of BCD.

Biological prevalence of disease

Males (10.5% prevalence rate) are proportionally more frequently infected with BCD than females (4.8% prevalence rate; $\chi^2 = 1{,}277$, $n = 117{,}451$, $p < 0.001$; Table 2). Independent of sex, most of the infected crabs are new shell (96%; $\chi^2 = 10{,}254$, $n = 117{,}451$, $p < 0.001$; Table 2), as 15% of all new shell crabs captured in the pot survey were infected with BCD. The proportion of BCD prevalence by size group of new shell males increased

Table 2. Sample sizes and percent prevalence of bitter crab disease in Tanner crab by sex and shell condition.

	Shell condition	Caught	BCD	%BCD
Female	New	11,060	2,155	19.5
	Old	34,496	38	0.1
Male	New	47,083	7,062	15.0
	Old	24,812	499	2.0
Total		117,451	9,754	8.3

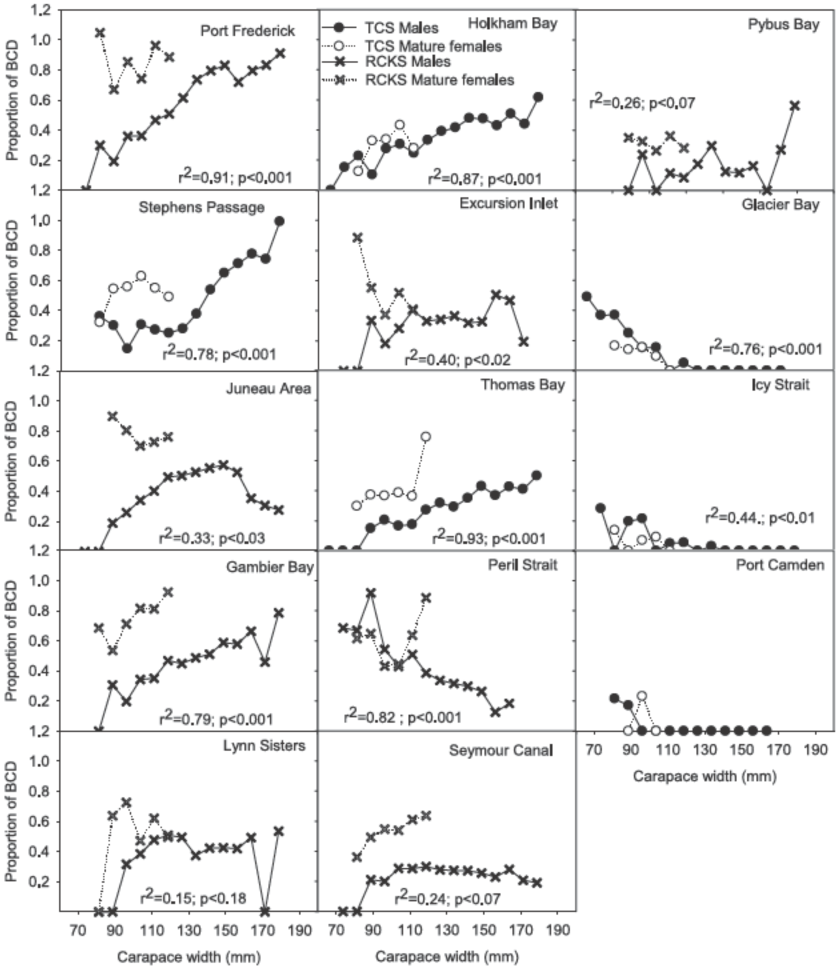

Figure 7. For each survey area, proportion of new shell male and mature female Tanner crabs with bitter crab disease (BCD) (arcsin√ transformed) in 5 mm intervals of carapace width (2001-2008). The graphs with x's indicate red king crab survey areas (RKCS) and the graphs with black circles indicate Tanner crab survey areas (TCS). Results of the linear regression analysis of proportion of BCD by carapace width for males are shown. Each area was standardized for a sample size of at least 10 per size group. Graphs are arranged by highest prevalence starting with top left corner, top to bottom.

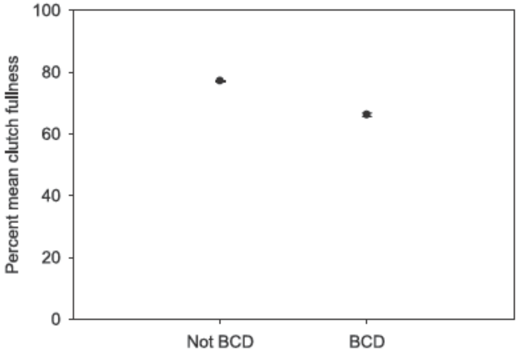

Figure 8. Mean (±SE) clutch fullness between healthy and bitter crab disease–infected females.

with size for nine areas (Excursion Inlet, Gambier Bay, Holkham Bay, Juneau area, Pybus Bay, Port Frederick, Seymour Canal, Stephens Passage, and Thomas Bay) and decreased with size for three areas (Glacier Bay, Icy Strait, and Peril Strait) (Fig. 7). Also, the proportion of BCD prevalence by size group of new shell mature females increased with size in two areas—Gambier Bay ($r^2 = 0.77$, $p < 0.001$) and Seymour Canal ($r^2 = 0.85$, $p < 0.001$; Fig. 7)—and the reproductive success of new shell females infected with BCD is reduced by 11% as indicated by visual examination of clutch fullness ($\chi^2 = 430.6$, $p < 0.001$) (Fig 8).

Discussion

BCD prevalence in southeast Alaska Tanner crab is localized, with few apparent temporal or spatial patterns; most areas have had relatively consistent levels of infection over eight years (detected visually), but a few areas had declining prevalence of BCD. The decreasing trends are not likely related to biases in catchability of pot gear because changes in BCD prevalence were not explained by annual mature male abundance. If catchability had been a factor; we should have observed an inverse trend in the prevalence of diseased crabs with mature male abundance. This is based on the concept that as abundance increases, unhealthy crabs would be outcompeted by healthy crabs entering and guarding the pot and when abundance was low there would be less competition. However, this pattern of inverse trend in prevalence was observed for only one area (Lynn Sisters), which suggests that catchability had little influence on the BCD prevalence patterns that we observed.

It is also unlikely that catchability affected the size-specific patterns of BCD prevalence that we observed. Although some gear comparison studies have found differences in catch rates of diseased crabs between pot and trawl gear, the differences are likely related to the smaller size retention of trawl surveys. *Hematodinium* sp. infected velvet swimmer crabs, *Necora puber*, from France, were captured in trawls more frequently than in traps, especially in later stages of the disease (Wilhelm and Mialhe 1996) and in Newfoundland, the prevalence of infected snow crabs, *Chionoecetes opilio,* was greater in trawls than in traps (Pestal et al. 2003, Shields et al. 2005). If the difference in prevalence by gear type is confounded by size selectivity, as trawl samples retain smaller crabs that are generally documented to have a greater prevalence of BCD (Pestal et al. 2003, Shields et al. 2005), then greater rates of prevalence would occur in trawl samples (Shields et al. 2005, Stentiford and Shields 2005). However, if comparison studies between trawl and pot gear adjusted the trawl data by size groups to match pot survey size groups the outcome might be different. For example, in a two-year study of infected snow crab in Newfoundland, Mullowney and Dawe (unpubl. data) compared crab size classes between gear types. The prevalence of BCD in adolescent males was greater in traps than in trawls and there was a prominent mode between 70 and 83 mm in traps, but in larger crabs (>83 mm), there was little difference in BCD prevalence by gear type. Therefore, it is possible that the BCD prevalence within the sizes selected by pot gear types is representative.

The prevalence of BCD in male Tanner crab increased with size in the majority of survey areas, and in mature females prevalence increased with size in two areas. Previous investigators found no differences in BCD prevalence with size and sex in southeast Alaska Tanner crab, but the documented prevalence rates were extremely high (>90%; Meyers et al. 1987). Increasing BCD prevalence with crab size is also contrary to the findings of other investigators (Stentiford and Shields 2005, Morado et al. 2010). The actual mode of disease transmission has not been documented, but one hypothesis is that juveniles might be more vulnerable to infection because they molt more frequently and it is possible that infection occurs at the time of molt (Meyers et al. 1990, Messick 1994). Adult crabs do not molt as frequently, but their cumulative exposure to the parasite is longer, creating more chance exposures via wounds, appendage loss, or shell erosion. For example, cumulative exposure is seen in Pacific herring, *Clupea pallasii*, with the protozoan parasite *Ichthyophonus hoferi* in Puget Sound, where the prevalence increased through age from 12% among juveniles to over 58% among the oldest adults, age 6 and up (Hershberger et al. 2002). Because BCD is well-established in southeast Alaska, the increase in prevalence with size could be related to cumulative exposure, especially given the fjord and embayment habitat where the free-living stage of the parasite is entrained because of a lack of tidal flushing in many areas. However, the role of oceanographic conditions in southeast Alaska is still unclear and is in contrast to observations from Newfoundland (Dawe et al. 2010, Morado et al. 2010). These observations of contrasting patterns of prevalence by size would provide good study areas on disease behavior and life history strategies.

BCD prevalence varied by depth in several areas; generally as depth increased, BCD prevalence decreased, but the opposite trend was observed in Holkham Bay. It is possible that depth is related to the bottom substrate and BCD infected crabs are more likely to be found in mud substrates, but this needs to be examined in southeast Alaska. Shields et al. (2005) found the odds of sampling a BCD positive crab on mud substrate was twice that of other substrates, and that substrate was significantly associated with depth.

This study suggests that the general trends of BCD prevalence could not be applied to all surveyed areas, which likely reflects the ecological and oceanographic complexity of southeast Alaska. In addition, because the study was dependent upon visual diagnosis, it is unclear how the patterns of BCD may change with the implementation of a more sensitive DNA-based assay.

Acknowledgments

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References

Bednarski, J., G. Bishop, and C. Siddon. 2008. Tanner crab pot survey methods for southeast Alaska. Alaska Department of Fish and Game, Commercial Fisheries Division, Regional Information Report No. 1J08-02, Juneau.

Dawe, E.G., D.R. Mullowney, E.B. Colbourne, G. Han, J.F. Morado, and R. Cawthorn. 2010. Relationship of oceanographic variability with distribution of bitter crab syndrome in snow crab (*Chionoecetes opilio*) on the Newfoundland-Labrador shelf. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and management of exploited crab populations under climate change. Alaska Sea Grant College Program, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.06

Hershberger, P.K, K. Stick, B. Bui, C. Carroll, B. Fall, C. Mork, J.A. Perry, E. Sweeny, J. Wittouck, and J. Winton. 2002. Incidence of *Ichthyophonus hoferi* in Puget Sound fishes and its increase with age of Pacific herring. J. Aquat. Anim. Health 14:50-56. doi:10.1577/1548-8667(2002)014<0050:IOIHIP>2.0.CO;2

Jadamec, L.S., W.E. Donaldson, and P. Cullenberg. 1999. Biological field techniques for *Chionoecetes* crabs. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Jensen, P.C., K. Califf, V. Lowe, L. Hauser, and J.F. Morado. 2010. Molecular detection of *Hematodinium* sp. in northeast Pacific *Chionoecetes* spp. and evidence of two Northern Hemisphere *Hematodinium* species. Dis. Aquat. Org. 89:155-166.

Love, D.C., S.D. Rice, D.A. Moles, and W.D. Eaton. 1993. Seasonal prevalence and intensity of bitter crab dinoflagellate infection and host mortality in Alaskan Tanner crabs *Chionoecetes bairdi* from Auke Bay, Alaska, USA. Dis. Aquat. Org. 15:1-7. doi:10.3354/dao015001

Messick, G.A. 1994. *Hematodinium perezi* infections in adult and juvenile blue crabs *Callinectes sapidus* from coastal bays of Maryland and Virginia, USA. Dis. Aquat. Org. 19(1):77-82. http://dx.doi.org/10.3354/dao019077

Meyers, T.M., C.A. Botelho, T.M. Koeneman, S. Short, and K.K. Imamura. 1990. Distribution of bitter crab dinoflagellate syndrome in southeast Alaskan Tanner crabs, *Chionoecetes bairdi*. Dis. Aquat. Org. 9:37-43. doi:10.3354/dao009037

Meyers, T.R., and T. Burton. 2009. Diseases of wild and cultured shellfish in Alaska. Alaska Department of Fish and Game, Fish Pathology Laboratories, Anchorage.

Meyers, T.R., T.M. Koeneman, C. Botelho, and S. Short. 1987. Bitter crab disease: A fatal dinoflagellate infection and marketing problem for Alaskan Tanner crabs *Chionoecetes bairdi*. Dis. Aquat. Org. 3(3):195-216. doi:10.3354/dao003195

Morado, J.F., E.G. Dawe, D. Mullowney, C.A. Shavey, V.C. Lowe, R.J. Cawthorn, A.-D. Burmeister, B. Zisserson, and E. Colbourne, 2010. Climate change and the worldwide emergence of *Hematodinium*-associated disease: Is there evidence for a relationship? In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and management of exploited crab populations under climate change. Alaska Sea Grant College Program, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.08

Pestal, G.P., D.M. Taylor, J.M. Hoenig, J.D. Shields, and R. Pickavance. 2003. Monitoring the prevalence of the parasitic dinoflagellate *Hematodinium* sp. in snow crabs *Chionoecetes opilio* from Conception Bay, Newfoundland. Dis. Aquat. Org. 67:67-75. doi:10.3354/dao053067

SAS Institute. 2005. JMP Version 6. SAS Institute Inc., Cary.

Shields, J.D., D.M. Taylor, P.G. O'Keefe, E. Colbourne, and E. Hynick. 2005. Epidemiology of bitter crab disease (*Hematodinium* sp.) in snow crabs *Chionoecetes opilio* from Newfoundland, Canada. Dis. Aquat. Org. 64:253-264. doi:10.3354/dao064253

Siddon, C., J. Bednarski, and G.H. Bishop. 2009. Southeast Alaska Tanner crab 2006 stock assessment and recommendations for the 2007 commercial fishery. Alaska Department of Fish and Game, Commercial Fisheries Division, Fishery Data Series No. 9-18, Anchorage.

Stentiford, G.D., and J.D. Shields. 2005. A review of the parasitic dinoflagellates *Hematodinium* species and *Hematodinium*-like infections in marine crustaceans. Dis. Aquat. Org. 66(1):47-70. doi:10.3354/dao066047

Wilhelm, G., and E. Mialhe. 1996. Dinoflagellate infection associated with the decline of *Necora puber* crab populations in France. Dis. Aquat. Org. 26(3):213-219. doi:10.3354/dao026213

Zheng, J., J.M. Rumble, and G.H. Bishop. 2006. Estimating southeast Alaska Tanner crab abundance using pot survey and commercial catch data. Alaska Fisheries Research Bulletin 12(2):196-211.

Sainte-Marie, B., H. Dionne, and M.-C. Alarie. 2010. Temperature and Age Dependent Fertile Period in Female Snow Crab (*Chionoecetes opilio*) at the Maturity Molt. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.01

Temperature and Age Dependent Fertile Period in Female Snow Crab (*Chionoecetes opilio*) at the Maturity Molt

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Abstract

Female snow crabs usually copulate and spawn for the first time shortly after their terminal molt to maturity. Laboratory experiments were conducted to determine (1) the duration of the female fertile period and whether it is temperature-dependent, (2) whether resorption or extrusion is used to cope with unfertilized eggs, and (3) if the amount of inseminated sperm and egg fertilization rate are dependent on the delay between molting and copulation. Experiments revealed that the degree of female molting synchronicity increased with temperature (0.5 vs. 3.7°C). Extrusion of unfertilized eggs was the most common outcome of failure to be inseminated. The time from molting to extrusion of unfertilized eggs (waiting time) was negatively related to female relative age at molting, positively related to female postmolt size, and declined with increasing temperature. Males passed less sperm to late than to early molters, but the amount of sperm increased with mating delay. Among females that were inseminated up to 60 d postmolt, fertilization rates <95% were observed only in a few late molters or late maters. Molting synchronicity and duration of fertile period (= waiting time) are two key factors influencing female mating success that may be modified by short-term changes in temperature, which may become more frequent and intense events under climate change.

Introduction

The operational sex ratio (OSR) is the relative abundance of sexually active males to receptive females at a given site and time (Emlen and Oring 1977). The OSR is a determinant of the direction and intensity of sexual competition and an important factor in mating success. Male-only or male-biased removals that characterize many crab and lobster fisheries skew the OSR to females, possibly reducing mate encounter rates, the proportion of females that are mated, and the amount of sperm that females receive (Smith and Jamieson 1991, Kruse 1993, Jivoff 2003). The problem may be particularly acute in lobster, anomurans, and some brachyuran species in which females cannot constitute sperm reserves for future reproductive events, because they lack the specialized structures (spermathecae, seminal receptacles) to do so, or shed these structures and their contents at molting (Sainte-Marie 2007). However, even in brachyuran species in which females can retain sperm through molting (e.g., Nagao and Munehara 2007) or are capable of long-term sperm storage after a terminal maturity molt, such as the snow crab *Chionoecetes opilio* (Brachyura, Majoidea), the OSR during the female's first mating season may be critical for immediate and sustained reproductive output (Sainte-Marie et al. 2008). Changes in the degree of synchronicity and duration of female sexual receptivity can modify OSR in favor or disfavor of females. For example, in a competitive environment a female is more likely to mate if she is not receptive at the same time as other females and/or if she remains receptive for a longer period than other females (Brockerhoff and McLay 2005).

Delayed mating may be costly to females when oocyte maturity and onset of female receptivity coincide. In many invertebrates, oocyte quality degrades as mating and fertilization are delayed, resulting in fitness losses from reduced fertilization rate or spontaneous embryo developmental arrest and death after fertilization (Williams and Bentley 2002, Moore et al. 2007). The incidence of females with fewer or no fertilized eggs increased with mating delay in one brachyuran (Paul and Adams 1984) and one anomuran (Sato et al. 2005). However, because sperm transfer was not assessed in these studies, it is not clear whether the reduction or lack of fertilization success was due to males allocating insufficient amounts of sperm to late mating females or to female infertility. Ultimately, when a virgin female crustacean does not encounter a mate, her full clutch of unfertilized oocytes may be extruded (McMullen and Yoshihara 1971, Paul and Adams 1984), resorbed without damage to the ovary (Hornung and Warburg 1994), or become necrotic and cause ovary damage (McMullen 1969, MacDiarmid and Butler 1999). These events terminate the female's fertile period, although in the snow crab the female may still remain receptive to mating for some time after extruding unfertilized or fertilized eggs (Urbani et al. 1998; BSM, pers.

obs.). For snow crab, the concept of a "fertile period" is more relevant in the context of this study than that of a "receptive period."

In eastern Canada, the terminal molt to maturity and first breeding season of female snow crab occur from January through March (Alunno-Bruscia and Sainte-Marie 1998, Moriyasu and Lanteigne 1998). When mates are not limiting in quantity or quality, females usually copulate and extrude fertilized eggs within 24 hours of molting to maturity (Sainte-Marie and Lovrich 1994). When mates are lacking, female snow crab may eventually extrude unfertilized oocytes or presumably resorb the oocytes, although the relative frequency of these behaviors and the delay for them to occur are not well documented. The primary goals of this study were to assess the duration of the fertile period in female snow crab at first breeding season and the costs of delayed mating. Initial experiments revealed strong year effects on the synchronicity and duration of the female fertile period that were thought to be related to differences in water temperature. Therefore, these initial experiments were followed up by controlled experiments to test this possibility. It is already known that small differences in temperature can modify other key aspects of reproduction in the stenothermic snow crab. For example, warming reduces egg incubation time from 2 years to 1 year (Moriyasu and Lanteigne 1998, Webb et al. 2007), and thus females are more frequently available for mating and the operational sex ratio becomes more skewed to females (Sainte-Marie et al. 2008). Knowledge of how temperature modifies reproduction is key to understanding the potential impacts of climate change on snow crab populations.

Material and methods

Experimental protocol

Three experiments were conducted. The initial 2005 and 2006 experiments aimed to measure the effects of delayed mating on female sperm accumulation and fertilization success, and they differed in the range of imposed mating delays (see below). The controlled 2007 experiment was staged to test for short-term temperature effects on synchronicity and duration of fertile period and on the fate of oocytes in unmated females.

Snow crab were collected with a ≈3 m wide beam trawl from 18 to 22 October 2004 and from 23 to 27 October 2005 off the south shore of the St. Lawrence Estuary (around 48°32N by 68°27W to 48°35N by 68°28W) in eastern Canada, and from 23 to 30 October 2006 off the north shore of the St. Lawrence Estuary (around 48°47N by 68°53W). Sampling depths ranged from 25 to 120 m and trawl sets lasted 10 min at a mean speed of 2-2.5 knots. Intact crabs were selected on board according to the following criteria: pubescent (i.e., last stage before terminal maturity molt) and >40 mm carapace width (CW) for females, and adult (i.e., terminally molted) and >70 mm CW for males. Criteria for distinguishing pubescent females and adult males are described in Sainte-Marie et al. (2008). Selected crabs were held in onboard tanks and then transferred from dock to holding facilities at Institut Maurice-Lamontagne (IML). There, crabs were kept separately by sex in 1,300 or 2,000 L communal tanks supplied with temperature-controlled seawater drawn from the St. Lawrence Estuary until they were used in experiments starting in January of the year following collection. Temperature and salinity were recorded usually on a daily basis during weekdays, and before experiments their mean and standard error were 2.0-2.1 ± 0.2°C and 28.0 ± 0.1‰ (both sexes) in 2004 ($n = 59$ in all cases); 2.0 ± 0.1°C for females, 3.1 ± 0.3°C for males, and 27.4 ± 0.2‰ (both sexes) in 2005 ($n = 52$ in all cases); 3.0 ± 0.1°C and 26.7 ± 0.2‰ for females in 2006 ($n = 59$ in all cases). Temperature and salinity remained well within the range of natural conditions experienced by snow crab in the St. Lawrence marine system (–1.8 to 4.5°C, 25 to 34‰). Photoperiod was modulated to reflect the natural light cycle. Crabs were fed twice weekly with excess thawed shrimp (*Pandalus borealis*) and capelin (*Mallotus villosus*).

The 2005 and 2006 experiments were initiated at the beginning of January when the supply of seawater to the female communal holding tank was shifted to a continuous flow of fresh, ambient temperature seawater from the St. Lawrence Estuary. A string of 40 or 60 L kreisel tanks and five 50 L aquaria for mating trials were also independently supplied with a continuous flow of the same seawater. Terminally molted females were collected daily from the communal holding tank, and molting date and exuviae CW were recorded. The exuviae was tagged, dried, and conserved for the purpose of identifying individual females (Gosselin et al. 2007) when multiple molts occurred on the same day. The female was then transferred to the first tank in the string of kreisel tanks. Three days postmolt, the female was marked with a small numbered tag (glue-on shellfish tags, type FPN, Hallprint) fixed to the dorsum with polyacrylamide glue, measured in CW, and moved to the next kreisel tank in the string so as to maintain low female densities in each tank. Subsequently, females were moved one kreisel tank forward every 3 days until up to 50 d had elapsed since molting in 2005 or up to 80 d in 2006. Females were checked daily for the presence of extruded eggs. Each molted female was scheduled for a mating trial at 3, 5, 7, 10, 14, or 20 d postmolt in 2005 and at 10, 14, 20, 30, 45, or 60 d postmolt in 2006. In a few cases the date of the actual mating trial departed from schedule by up to 2 days because of weekend leaves. Due to constraints on the total duration of the experiment, early molting females were in general scheduled later than late molting females, especially in 2006 due to longer postmolt delays for mating trials. On the day of the mating trial, the female was moved for 24 h into one of the five 50 L aquaria if she had not already extruded unfertilized eggs. These aquaria each contained one acclimated adult male of 81-95 mm CW. After 24 h, the female was removed, examined to see if she was berried and returned to the appropriate kreisel tank. Subsequently, we checked females daily for the presence of extruded eggs. A total of 58 females in 2005 and 70 in 2006 followed this protocol. The experiments ran until 18 April in 2005 (90 d from day of first molt) and until to 28 April in 2006 (109 d from day of first molt).

In 2005 and 2006, females were killed 20 d after extruding eggs or at the end of the experiment when they did not. When a female had been subjected to a mating trial and had extruded eggs after, 10-100 eggs were sampled from her clutch and examined fresh under a microscope to determine if they were cleaved. The clutch was removed by severing the pleopod endopods at their base and preserved in 100% ethanol; the two spermathecae were dissected out and preserved in 4% formalin in seawater. Subsequently, the clutch was blotted and weighed to the nearest 0.1 mg on a Mettler AE240 balance and the content of the right spermatheca was extracted and similarly weighed for determining spermathecal load (SL, see methods in Sainte-Marie and Lovrich 1994). Females that never extruded eggs were killed and dissected to determine ovary condition: color, relative size, firmness, and presence of residual oocytes or necrosis were noted.

The 2007 experiment was conducted in two strings of three 240 L flow-through, insulated tanks. The two strings of tanks were connected to two temperature-controlled head tanks of 710 L each, one at 0°C and one at 4°C, and water from each tank was mixed by computer-monitored valves in proportions aimed at producing target temperatures of 0.5°C in one string and 3.5°C in the other string. The flow of incoming fresh seawater through the experimental tanks was set to about 4 L per minute. Starting on 22 January, equal numbers of pubescent females were transferred to the first tank of the 0.5 and 3.5°C treatments, respectively. Tanks were checked daily for dead or molted females; in the latter case, the exuviae and live molted female were identified and measured following the procedure in the 2005 and 2006 experiments. Due to premolt mortality, the number of molted females was 54 in the 0.5°C treatment and 48 in the 3.5°C treatment. Molted females were transferred from the first to the second tank in the string and checked daily for the presence of eggs beneath the abdomen. When egg extrusion occurred, the date was noted and the female was transferred to the third tank in the string. The experiment was terminated on 2 May 2007 and all molted females that had not yet extruded eggs were killed and then preserved by injection/immersion in 4% formalin in seawater. These females were subsequently dissected to determine ovary condition as above.

Data analysis

Female relative molt increment was calculated as the difference between postmolt CW and premolt CW, divided by premolt CW, and multiplied by 100. The relative age of a female at molting was measured as the difference in days between her date of molt and the date of the first molt in each of the 2005 and 2006 experiments, or the date of the first day of the 2007 experiment. "Waiting time" is equivalent in many cases to the fertile period and it was defined as the number of days elapsed between female molt and extrusion of unfertilized eggs when the female was not inseminated.

Mean values are reported with their standard error (SE). We used Student's *t*-test or the Mann-Whitney test to compare means or medians between two samples, or the Kruskal-Wallis test when there were more than two samples. The chi-square (χ^2) test with Yates's correction was used to test whether the expression of certain female behaviors was independent of a fixed (treatment) or random (year) factor. Least squares linear regression was used to describe the relationship between female waiting time and relative age at molting. General linear models were used to model spermathecal load and clutch wet weight in the 2005 and 2006 experiments. In the case of SL, the categorical factor was year (experiment) and the quantitative factors (covariates) were relative age at molting and actual mating delay. Female postmolt CW was not included as a covariate because sperm allocation is known to be independent of female (and male) size in the snow crab (Sainte-Marie and Lovrich 1994, Sainte-Marie et al. 2008). In the case of clutch wet weight, categorical factors were year (experiment) and female mated status (subjected to mating trial, or not) and quantitative factors (covariates) were female postmolt CW, female relative age at molting, and time elapsed between female molt and spawning. Model fit was evaluated by examining residuals and in the case of clutch wet weight, the fit was improved by log-transformation of the dependent variable and female postmolt CW. Finally, we used a general linear model to evaluate the effects of categorical (experiment, treatment) and quantitative (covariates: relative age at molting and postmolt CW) factors affecting female waiting time. Type III sums of squares were used. Analyses were performed in Systat 10 (SPSS Inc., Chicago).

Results

Effects of delayed mating

The mean temperature was colder (Mann-Whitney test, $U = 856$, $P < 0.001$) and the mean salinity higher (Mann-Whitney test, $U = 5058$, $P < 0.001$) during the 2005 experiment (0.26 ± 0.09°C, 28.5 ± 0.1‰; $n = 83$) than during the 2006 experiment (1.54 ± 0.06°C, 27.3 ± 0.4‰; $n = 84$). Females began to molt later and subsequently molted less synchronously in the colder 2005 experiment (first molt on 18 January, 39 days between date of occurrence of 25th and 75th percentile of cumulative

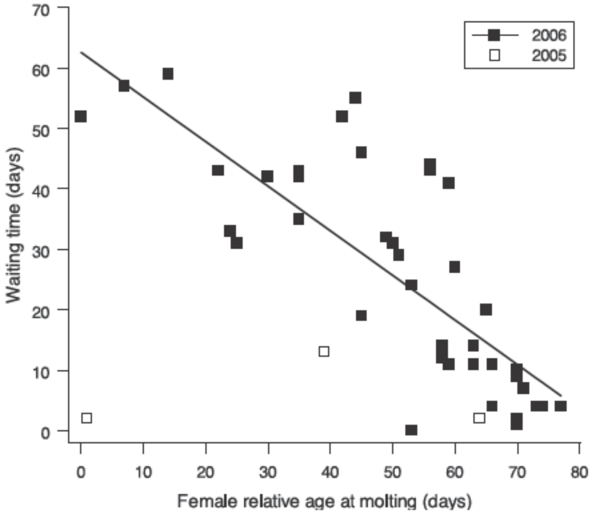

Figure 1. Relationship between female waiting time (i.e., difference between date of terminal molt and date of extrusion of unfertilized eggs) and relative age at molting (i.e., difference between date of female molt and date of first molt in the experiment) for snow crab females that extruded eggs before their scheduled mating attempt in the 2005 and 2006 experiments. Regression statistics for 2006 data: $y = 63.94 - 0.74x$, $r^2 = 0.607$, $F = 58.74$, $P < 0.001$.

molts from start of experiment) than in the warmer 2006 experiment (9 January, 24 d). However, mean CW and relative molt increment of pubescent females were the same in 2005 (49.6 ± 0.5 mm, 15.1%; $n = 58$) and 2006 (50.0 ± 0.4 mm, 15.0%; $n = 70$).

Table 1 summarizes the salient effects of mating delay on female behavior and reproductive outcome in the 2005 and 2006 experiments. Actual mating delays were grouped into treatments of 3-7, 10-14, 20-30, 45, and 60 d. As a result of scheduling early molting females for late mating trials and vice versa, the average relative age at molting decreased with increasing mating delay in 2005 and 2006 (Table 1; Kruskal-Wallis in each year, $P < 0.002$) and was always much greater for the same mating delay group in 2006 compared to 2005 (Table 1; Mann-Whitney for each group, $P < 0.001$).

Few females extruded a clutch of unfertilized eggs before their mating trial in 2005 (5.2% of 58), but many did so in 2006 (57.1% of 70). Analysis of pooled data for common mating delay treatments (10-14 and 20-30 d) revealed a significant difference between the two experiments in the relative frequency of females that spawned before their mating

Table 1. Behavior and outcome of delayed mating for virgin female snow crab in 2005 and 2006 experiments. Mating delay is the number of days elapsed between female terminal molt and mating trial. Mean relative age at molting is calculated from the difference between the date of molting of individual females and the date of first molt in the experiment.

Year 2005	16 (100.0%)	19 (100.0%)	16 (88.9%)	–	–	d. Number (percent) of inseminated females with >95% eggs fertilized
	16 (100.0%)	19 (95.0%)	18 (94.7%)	–	–	c. Number (percent) of paired females that were inseminated
	1 (5.9%)	0 (0.0%)	2 (9.5%)	–	–	b. Number (percent) of initial females that extruded eggs before mating trial
	17 (50.5 d)	20 (45.9 d)	21 (29.2 d)	–	–	a. Female initial number and (mean relative age in days at molting)
Mating delay (d)	3-7	10-14	20-30	45	60	Female behavior and outcome
Year 2006	–	18 (76.9 d)	22 (61.1 d)	15 (41.8 d)	15 (34.9 d)	a. Female initial number and (mean relative age in days at molting)
	–	7 (38.9%)	11 (50.0%)	9 (60.0%)	13 (86.7%)	b. Number (percent) of initial females that extruded eggs before mating trial
	–	7[a] (70.0%)	10 (90.9%)	5 (83.3%)	2 (100.0%)	c. Number (percent) of paired females that were inseminated
	–	5 (71.4%)	9 (90.0%)	4 (80.0%)	1 (50.0%)	d. Number (percent) of inseminated females with >95% eggs fertilized

[a] One female died during the mating trial and was excluded from analyses.

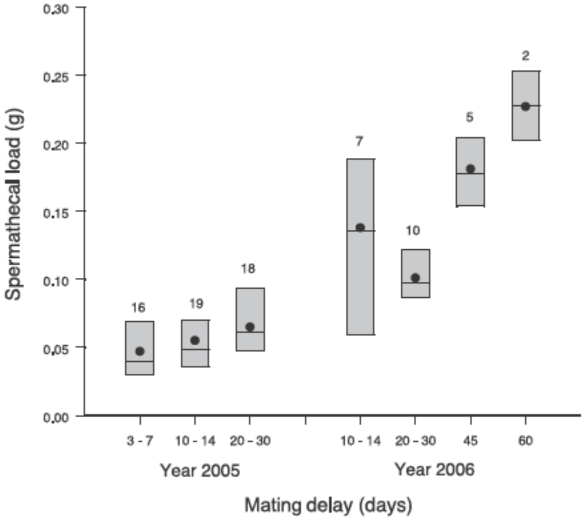

Figure 2. Spermathecal load (SL) of female snow crab after pairing for 24 h with one adult male snow crab at a scheduled mating delay (i.e., number of days elapsed after terminal molt) in the 2005 and 2006 experiments. Boxplots show median and lower and upper quartiles of SL and the full black circles represent mean SL. Sample size appears above the boxplots.

trial (4.9% in 2005 vs. 45.0% in 2006: $\chi^2 = 15.44$, $P < 0.001$). In 2006, the waiting time was inversely related to the relative age of molted females (Fig. 1). Moreover, the proportion of females that spawned before the mating trial was directly related to mating delay (Table 1; Spearman rank correlation, $r_s = 1.0$, $P < 0.001$).

Males engaged in precopulatory guarding in all mating trials. The proportion of females inseminated during the mating trials was independent of mating delay (Table 1) and was high overall (96.4% of 55 females in 2005, 82.8% of 29 females in 2006). There was no significant difference between the two experiments in the proportion of trialed females that were inseminated based on pooled data from the common 10-14 and 20-30 d mating delay treatments (94.9% in 2005 vs. 81.0% in 2006: $\chi^2 = 1.60$, $P = 0.206$). With only one exception, females that were not inseminated during the mating trial were third or last quartile molters. Excluding non-inseminated females, spermathecal load tended to increase with mating delay in both experiments and was higher overall in 2006 compared to 2005 (Fig. 2). A general linear model (adjusted $R^2 = 0.566$, $P < 0.001$) with SL as the dependent variable revealed a strong year effect ($F_{1,73} = 43.03$, $P < 0.001$), a weak positive effect of actual mating delay (coefficient 9.05×10^{-4}, $F_{1,73} = 4.56$, $P = 0.036$), and a weak negative effect of female relative age at molting (coefficient -4.73×10^{-4}, $F_{1,73} = 4.04$, $P = 0.048$) on sperm accumulation by females. Female postmolt CW and the interaction of year and actual mating delay were not significant sources of variability ($P > 0.1$) if added to the model.

Clutch wet weight did not vary between females that spawned unfertilized eggs before their mating trial and those that spawned after their mating trial. A general linear model revealed a strong year effect ($F_{1,113} = 30.65$, $P < 0.001$), no effect of female mated status ($F_{1,113} = 1.33$, $P = 0.252$), a strong positive effect of ln postmolt CW ($F_{1,113} = 113.09$, $P < 0.001$), a negative effect of number of days elapsed between molting and spawning ($F_{1,113} = 8.72$, $P = 0.004$) and no effect of female relative age at molting ($F_{1,113} = 2.38$, $P = 0.126$) on ln clutch wet weight. The model with only significant factors (adjusted $R^2 = 0.604$, $P < 0.001$) resulted in coefficients of 2.919 for ln postmolt CW ($F_{1,115} = 112.12$, $P < 0.001$) and of -5.22×10^{-3} for number of days elapsed between molting and spawning ($F_{1,115} = 20.86$, $P < 0.001$).

The proportion of inseminated females that extruded a clutch with >95% eggs fertilized was high overall (96.2% of 53 females in 2005 and 79.2% of 24 females in 2006) and there was no clear pattern in the proportion of successful females as a function of mating delay (Table 1). The two experiments did not differ in the proportion of inseminated females that extruded a well-fertilized clutch based on the common 10-14 and 20-30 d mating delay treatments (94.6% in 2005 vs. 82.4% in 2006: $\chi^2 = 0.88$, $P = 0.349$). With only one exception, egg samples with >5% unfertilized eggs came either from fourth quartile molters that were mated 10-30 days postmolt or from females that were subjected to a long mating delay (45-60 d postmolt).

Five females that were subjected to a mating trial did not extrude eggs before the end of the experiment (Table 2). Ovaries appeared to be normal (i.e., large orange ovaries with discrete, detachable oocytes) in three of these females, but in one female the ovaries were liquefied and in another they were completely necrotic (i.e., melanized and hard).

Molting schedule and waiting time in relation to temperature

The two treatments in the 2007 experiment remained close to target temperatures of 0.5°C (realized: 0.45 ± 0.02°C; $n = 155$, one measurement per tank per day) and 3.5°C (3.67 ± 0.01°C; $n = 157$) and had an identical salinity of 28.8 ± 0.1‰. Pubescent females measured 50.4 ± 0.3 mm CW ($n = 102$) and the relative molt increment did not differ between treatments (t-test, $t = 1.451$, $P = 0.150$) and averaged 16.4%. The molting rate was faster in the warm (50% of molts at day 28) than in the cold (50% of molts at day 38) treatment (Fig. 3; Mann-Whitney test, $U =$

Table 2. Characteristics of female snow crab that did not extrude eggs after mating in the 2005 and 2006 experiments. Molt, mating trial, and death are all expressed as number of days elapsed since start of experiment. Ovary condition was determined at the end of the experiment.

Year	Molt (d)	Mating trial (d)	SL (g)	Death (d)	Ovary condition
2005	16	47 (D_{30})	0	90	Normal
2005	59	73 (D_{14})	0	90	Normal
2006	77	87 (D_{10})	0	109	Normal
2006	80	90 (D_{10})	0.19	109	Liquefied
2006	87	97 (D_{10})	0.26	109	Necrotic

Postmolt day scheduled for the mating trial appears in parentheses (Dx).
SL = spermathecal load.

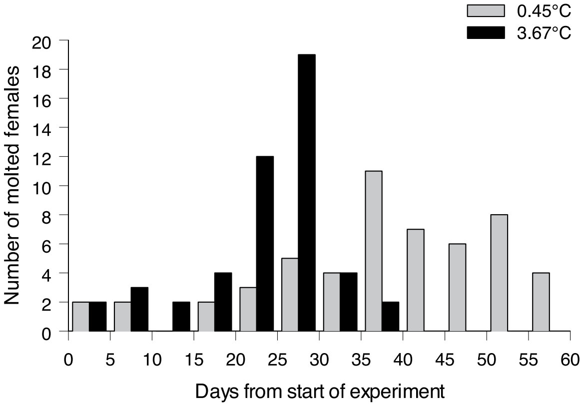

Figure 3. Temporal distribution of the terminal molt of female snow crab at a mean temperature of 0.45 or 3.67°C in the 2007 experiment. Females were held communally before the onset of the experiment.

2130, $P < 0.001$). Moreover, females molted more synchronously in the warm (9 days between occurrence of 25th and 75th percentile of cumulative molts) than in the cold (17 d) treatment (Fig. 3). This assessment of the temperature effect is conservative because all females had molted before the end of the experiment in the warm treatment but not in the cold treatment.

A majority of the females extruded eggs before the end of the 2007 experiment. However, that proportion was significantly different (χ^2 =

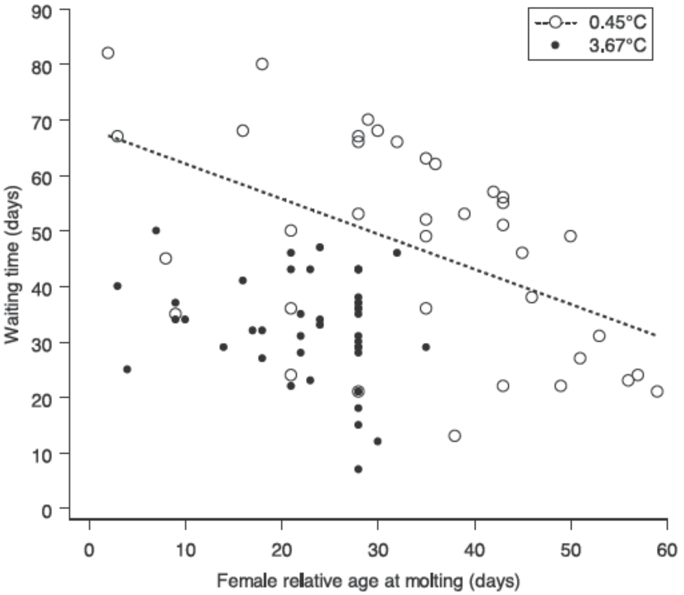

Figure 4. Relationship between female waiting time (i.e., difference between date of terminal molt and date of extrusion of unfertilized eggs) and relative age at molting (i.e., difference between date of female molt and first day of experiment) for unmated snow crab females in the 2007 experiment. Regression statistics for 0.45°C treatment: $y = 68.44 - 0.63x$, $r^2 = 0.253$, $F = 12.17$, $P = 0.001$.

8.89, $P = 0.003$) and higher in the warm (93.6% of 47 females) than in the cold (70.4% of 54 females) treatment. Waiting time approximated a normal distribution with a median value of 33.5 days in the warm treatment, whereas the distribution was scattered with a median value of 49.5 days in the cold treatment (Figs. 4 and 5). Since many more females had not extruded eggs in the cold ($n = 16$) compared to the warm ($n = 3$) treatment when the experiment was terminated, it is likely that the real median waiting time is underestimated to a greater degree in the cold than in the warm treatment.

Females that had not extruded eggs by the end of the 2007 experiment were a median 70 d from molting in the warm treatment compared to 52.5 days in the cold treatment (Fig. 5). The ovaries of females that had not extruded eggs before the end of the experiment were examined and all appeared to be normal, suggesting they might have extruded eggs had the experiment been continued.

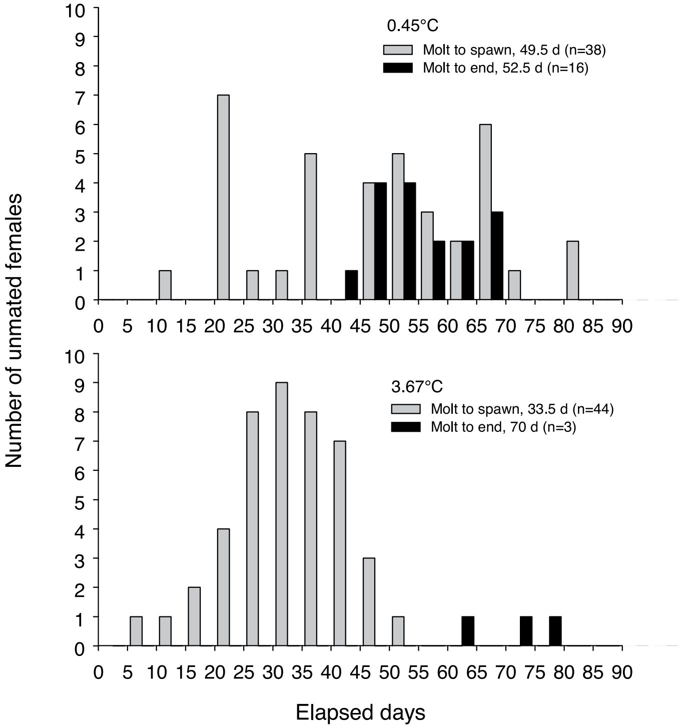

Figure 5. Number of days elapsed between terminal molt and extrusion of unfertilized eggs (molt to spawn = waiting time) or end of the experiment (molt to end) for unmated female snow crab at a mean temperature of 0.45 and 3.67°C in the 2007 experiment. Median values and sample size are shown.

Female waiting time was inversely related to relative age at molting in the cold treatment (Fig. 4), but the negative trend in the warm treatment was not significant (Pearson correlation, $r = -0.21$, $P = 0.176$) possibly due to synchronous molting and lack of females of relatively old molting age (i.e., > 35 d, see Fig. 5). A general linear model with waiting time for the 2007 treatments and the 2006 experiment (adjusted $R^2 = 0.522$, $P < 0.001$) revealed a significant effect of experiment/treatment ($F_{2,117} = 28.79$, $P < 0.001$), a negative effect of female relative age at molting (coefficient −0.643, $F_{1,117} = 28.79$, $P < 0.001$), and a positive effect of female postmolt CW (coefficient 0.844, $F_{1,117} = 7.99$, $P = 0.005$). The estimated average difference in waiting time between the smallest (51.6 mm CW) and largest (70.3 mm CW) postmolt female in our experiments was 15.8 days, all other things being equal. Waiting time adjusted to average female relative age at molting and to average postmolt CW declined significantly ($P < 0.001$ for all pairwise comparisons) from 45.7 ± 2.0 d ($n = 38$) in the 0.45°C treatment of 2007, to 37.0 ± 2.3 d ($n = 40$) in the 2006 experiment (1.54°C), and finally to 24.0 ± 2.1 d ($n = 44$) in the 3.67°C treatment of 2007. This suggests a negative effect of increasing temperature on the duration of female fertile period.

Discussion

Virgin, mature female snow crab rarely attempt to resorb a full complement of oöctyes when left unmated. Instead, unfertilized eggs are extruded and attach to the pleopods, as also occurs in *C. bairdi* (Paul and Adams 1984). Depending on temperature, unfertilized snow crab eggs may retain a normal appearance for up to 2-4 months and be held for as long as 8-10 months before they are lost (Elner and Beninger 1995, Sainte-Marie and Carrière 1995). A plausible explanation for why unmated females extrude unfertilized eggs, which entails considerable loss of energy (e.g., Hornung and Warburg 1994) unless females eventually ingest their eggs, is that oosorption is not a viable option as suggested in this study by one female with extensive and probably irreversible ovary necrosis (also see MacDiarmid and Butler 1999).

Individual female snow crab showed considerable variability in their propensity to wait for a mate before giving up their clutch, as seen in other invertebrates (Moore et al. 2007). Part of this variability in snow crab can be explained by female relative age at molting, with late molters giving up within days of molting compared to weeks or months for early molters, and by female body size with larger females waiting longer than smaller females. For logistic reasons, we did not distribute females evenly among mating delay treatments in the 2005 and 2006 experiments: early molting females were preferentially scheduled for long mating delays and late molting females were preferentially scheduled for short mating delays. This bias was greater in the 2006 experiment than in the 2005 experiment and it contributed substantially to the year effects perceived in female behavior and reproductive outcome.

Our experiments indicate that virgin female snow crab may pair sexually, be inseminated, and produce a clutch of well fertilized eggs for up to 60 d after their terminal molt. This observation considerably extends the maximum duration of receptivity/fertility in *Chionoecetes*, which was reported to be 30 d in *C. bairdi* (Paul and Adams 1984). In several brachyuran crabs, female receptivity is constrained by the time during which the gonopore operculae remain mobile and allow insertion of male gonopods for sperm transfer (e.g., Brockerhoff and McLay 2005). However, in *C. bairdi* and *C. opilio* the operculae are permanently mobile after the terminal molt (Paul and Adams 1984; BSM pers. observ.) and snow crab females are attractive for a long time because they passively exude a metabolic byproduct of chitin synthesis that excites mating behavior in males (Bouchard et al. 1996, Bublitz et al. 2008). As a caveat on our determination of the fertile period, we note that we did not assess whether delayed mating could have negative effects in the longer term, e.g., developmental arrest and embryo death.

Excluding cases where the female was not inseminated, incomplete or failed fertilization occurred in females that molted or mated late. In these cases, the likely reason for reduced fertility is oocyte overmaturation (Fissore et al. 2002, Moore et al. 2007), as concluded for an anomuran crab (Sato et al. 2005). This explanation probably also accounts for why late molting females were inclined to extrude a full complement of unfertilized eggs sooner than early molting females. It may also be the reason that males discriminated against some late molters by not inseminating them (assuming the female was receptive to mating) or by providing them with less sperm than early molters. Somewhat paradoxically, females mating late after their molt accumulated more sperm than females mating soon after their molt. Snow crab females can have multiple mates during their first breeding season (Urbani et al. 1998, Sainte-Marie et al. 2008). If a late molting female is less likely to re-mate prior to extruding eggs because she cannot wait, it may be advantageous for the male to be more generous because the chances are good that his sperm will be used once or more during the female's lifetime. All of the foregoing implies that males are capable of assessing female reproductive condition quite finely.

Strong year effects were apparent both in spermathecal load and in clutch wet weight. Differences in SL between females in the 2006 and 2007 experiments could reflect interannual differences in the level of male sperm reserves. Rondeau and Sainte-Marie (2001) reported such differences and found that males with smaller sperm reserves allocated less sperm than similarly sized males with larger reserves. Differences in clutch wet weight between females in 2006 and 2007 may reflect variation in nutritional status of females by year or collection site that impact on ovary development as reported for snow and other crabs (e.g., Dugan et al. 1994, Dutil et al. 2009).

Temperature clearly modified two key aspects of female reproduction: warming advanced and synchronized female terminal molting and reduced their waiting period. These effects occurred with a temperature shift of 0.7-2.5°C relative to holding conditions in the controlled 2007 experiment. A rapid shift in temperature of this magnitude may occur and last for several days or weeks on snow crab grounds in the St. Lawrence Estuary and Gulf of St. Lawrence when winter warming or early ice break occur, and when upwelling events occur. Although the impacts of sudden changes in temperature on molting and reproductive behavior of female crabs have apparently received little or no attention to date, the effects observed in this study are consistent with a delayed maturity molt and slower ovary development rate (and, on the present authors' presumption, slower oocyte overmaturation as well) at colder than at warmer temperatures in other crustaceans (e.g., Mocquard et al. 1989, Tarling and Cuzin-Roudy 2003). Greater molting synchrony and a shorter waiting (i.e., fertile) time will both deflate the operational sex ratio (OSR) (e.g., Brockerhoff and McLay 2005). Consequently, males may mate at a faster rate and allocate less guarding time and sperm to individual females (Rondeau and Sainte-Marie 2001). With less time to recharge between matings, male sperm reserves may become depleted. This may be especially true in species where large (dominant) males are preferred by females and targeted by fishing (Kendall and Wolcott 1999, Jivoff 2003, Sato and Goshima 2007). As a result of a deflated OSR, females may have reduced mate encounter rates, fewer opportunities for mate choice, accumulate less sperm, and be more vulnerable to sperm limitation (Kendall and Wolcott 1999, Rondeau and Sainte-Marie 2001, Jivoff 2003, Sato and Goshima 2007).

This study has emphasized the effects of short-term changes in temperature, related for example to extreme meteorological events, on molting pattern and reproductive behavior when females reach their ultimate life history phase (adulthood). The frequency and duration of extreme events and of atypical seasons may increase with climate change (Fischlin et al. 2007). Moreover, climate change may also modify the thermal history of female snow crabs over the 5.5-7.5 year span from settlement to adulthood (Alunno-Bruscia and Sainte-Marie 1998). This can have profound effects: for example, a warmer thermal history may cause females to become larger (i.e., potentially more fecund) at adulthood (Orensanz et al. 2007, Sainte-Marie et al. 2008). How short-term temperature forcing interacts with the longer thermal history of females remains to be investigated. Nonetheless, it is clear that climate change has the potential to modify many key aspects of the snow crab mating system at various time scales.

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References

Alunno-Bruscia, M., and B. Sainte-Marie. 1998. Abdomen allometry, ovary development, and growth of female snow crab, *Chionoecetes opilio*, in the northwest Gulf of Saint Lawrence. Can. J. Fish. Aquat. Sci. 55:459-477. doi:10.1139/cjfas-55-2-459

Bouchard, S., B. Sainte-Marie, and J.N. McNeil. 1996. Indirect evidence indicates female semiochemicals release male precopulatory behaviour in the snow crab, *Chionoecetes opilio* (Brachyura: Majidae). Chemoecology 7:39-44. doi:10.1007/BF01240636

Brockerhoff, A.M., and C.L. McLay. 2005. Factors influencing the onset and duration of receptivity of female purple rock crabs, *Hemigrapsus sexdentatus* (H. Milne Edwards, 1837) (Brachyura: Grapsidae). J. Exp. Mar. Biol. Ecol. 314:123-135. doi:10.1016/j.jembe.2004.08.018

Bublitz, R., B. Sainte-Marie, C. Newcomb-Hodgetts, N. Fletcher, M. Smith, and J. Hardege. 2008. Interspecific activity of the sex pheromone of the European shore crab (*Carcinus maenas*). Behaviour 145 (part 10, Suppl. SI):1465-1478.

Dugan, J.E., D.M. Hubbard, and A.M. Wenner. 1994. Geographic variation in life-history of the sand crab, *Emerita analoga* (Stimpson) on the California coast: Relationships to environmental variables. J. Exp. Mar. Biol. Ecol. 181:255-278. doi:10.1016/0022-0981(94)90132-5

Dutil, J.-D., R. Larocque, S. Valois, E. Mayrand, and B. Sainte-Marie. 2009. Spatial, annual and seasonal patterns in the condition and muscle size of snow crab. Mar. Biol. 156:1903-1916. doi:10.1007/s00227-009-1223-0

Elner, R.W., and P.G. Beninger. 1995. Multiple reproductive strategies in snow crab, *Chionoecetes opilio*: Physiological pathways and behavioral plasticity. J. Exp. Mar. Biol. Ecol. 193:93-112. doi:10.1016/0022-0981(95)00112-3

Emlen, S.T., and L.W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223. doi:10.1126/science.327542

Fischlin, A., G.F. Midgley, J.T. Price, R. Leemans, B. Gopal, C. Turley, M.D.A. Rounsevell, O.P. Dube, J. Tarazona, and A.A. Velichko. 2007. Ecosystems, their properties, goods, and services. In: M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden, and C.E. Hanson (eds.), Climate change 2007: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 211-272.

Fissore, R.A., M. Kurokawa, J. Knott, M. Zhang, and J. Smyth. 2002. Mechanisms underlying oocyte activation and postovulatory ageing. Reproduction 124:745-754. doi:10.1530/rep.0.1240745

Gosselin, T., B. Sainte-Marie, and J.-M. Sévigny. 2007. Individual identification of decapod crustaceans II: Natural and genetic markers in snow crab (*Chionoecetes opilio*). J. Crust. Biol. 27:399-403. doi:10.1651/S-2771.1

Hornung, E., and M.R. Warburg. 1994. Oosorption and oocyte loss in a terrestrial isopod under stressful conditions. Tissue Cell 26:277-284. doi:10.1016/0040-8166(94)90102-3

Jivoff, P.R. 2003. A review of male mating success in the blue crab, *Callinectes sapidus*, in reference to the potential for fisheries-induced sperm limitation. Bull. Mar. Sci. 72:273-286.

Kendall, M.S., and T.G. Wolcott. 1999. The influence of male mating history on male-male competition and female choice in mating associations in the blue crab, *Callinectes sapidus* (Rathbun). J. Exp. Mar. Biol. Ecol. 239:23-32. doi:10.1016/S0022-0981(99)00022-2

Kruse, G.H. 1993. Biological perspectives on crab management in Alaska. In: G.H. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn (eds.), Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 355-384.

MacDiarmid, A.B., and M.J. Butler. 1999. Sperm economy and limitation in spiny lobsters. Behav. Ecol. Sociobiol. 46:14-24. doi:10.1007/s002650050587

McMullen, J.C. 1969. Effects of delayed mating on the reproduction of king crab, *Paralithodes camtschatica*. J. Fish. Res. Board Can. 26:2737-2740.

McMullen, J.C., and H.T. Yoshihara. 1971. Deposition of mature eggs in unmated king crabs, *Paralithodes camtschatica* (Tilesius). Tr. Am. Fish. Soc. 3:583-584. doi:10.1577/1548-8659(1971)100<583:DOMEIU>2.0.CO;2

Mocquard, J.P., P. Juchault, and C. Souty-Grosset. 1989. The role of environmental factors (temperature and photoperiod) in the reproduction of terrestrial isopod *Armadillidium vulgare* (Latreille, 1804). Monit. Zool. Ital. (N.S.) Monogr. 4:305-331.

Moore, P.J., W.E. Harris, and A.J. Moore. 2007. The cost of keeping eggs fresh: Quantitative genetic variation in females that mate late relative sexual maturation. Am. Nat. 169:311-322. doi:10.1086/510687

Moriyasu, M., and C. Lanteigne. 1998. Embryo development and reproductive cycle in the snow crab, *Chionoecetes opilio* (Crustacea: Majidae), in the southern Gulf of St. Lawrence, Canada. Can. J. Zool. 76:2040-2048. doi:10.1139/cjz-76-11-2040

Nagao, J., and H. Munehara. 2007. Characteristics of broods fertilized with fresh or stored sperm in the helmut crab *Telmessus cheiragonus*. J. Crust. Biol. 27:565-569. doi:10.1651/S-2703.1

Orensanz, J.M., B. Ernst, and D. Armstrong. 2007. Variation of female size and stage at maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering Sea. J. Crust. Biol. 27:576-591. doi:10.1651/S-2790.1

Paul, A.J., and A.E. Adams. 1984. Breeding and fertile period for female *Chionoecetes bairdi* (Decapoda, Majidae). J. Crust. Biol. 4:589-594. doi:10.2307/1548073

Rondeau, A., and B. Sainte-Marie. 2001. Variable mate-guarding time and sperm allocation by male snow crabs (*Chionoecetes opilio*) in response to sexual competition, and their impact on the mating success of females. Biol. Bull. 201:204-217. doi:10.2307/1543335

Sainte-Marie, B. 2007. Sperm demand and allocation in decapod crustaceans. In: J.E. Duffy and M. Thiel (eds.), Evolutionary ecology of social and sexual systems: Crustaceans as model systems. Oxford University Press, New York, pp. 191-210. doi:10.1093/acprof:oso/9780195179927.003.0009

Sainte-Marie, B., and C. Carrière. 1995. Fertilization of the second clutch of eggs of snow crab, *Chionoecetes opilio*, from females mated once or twice after their molt to maturity. Fish. Bull. U.S. 93:759-764.

Sainte-Marie, B., and G.A. Lovrich. 1994. Delivery and storage of sperm at first mating of female *Chionoecetes opilio* (Brachyura, Majidae) in relation to size and morphometric maturity of male parent. J. Crust. Biol. 14:508-521. doi:10.2307/1548997

Sainte-Marie, B., T. Gosselin, J.-M. Sévigny, and N. Urbani. 2008. The snow crab mating system: Opportunity for natural and unnatural selection in a changing environment. Bull. Mar. Sci. 83:131-161.

Sato, T., and S. Goshima. 2007. Female choice in response to risk of sperm limitation by the stone crab, *Hapalogaster dentata*. Anim. Behav. 73:331-338.

Sato, T., M. Ashidate, and S. Goshima. 2005. Negative effects of delayed mating on the reproductive success of female spiny king crab, *Paralithodes brevipes*. J. Crust. Biol. 25:105-109. doi:10.1016/j.anbehav.2006.05.016

Smith, B.D., and G.S. Jamieson. 1991. Possible consequences of intensive fishing for males on the mating opportunities of Dungeness crabs. Tr. Am. Fish. Soc. 120:650-653. doi:10.1577/1548-8659(1991)120<0650:NPCOIF>2.3.CO;2

Tarling, G.A., and J. Cuzin-Roudy. 2003. Synchronization in the molting and spawning activity of northern krill (*Meganyctiphanes norvegica*) and its effect on recruitment. Limnol. Oceanogr. 48:2020-2033.

Urbani, N., B. Sainte-Marie, J.-M. Sévigny, D. Zadworny, and U. Kuhnlein. 1998. Sperm competition and paternity assurance during the first breeding period of female snow crab *Chionoecetes opilio* (Brachyura: Majidae). Can. J. Fish. Aquat. Sci. 55:1104-1113. doi:10.1139/cjfas-55-5-1104

Webb, J.B., G.L. Eckert, T.C. Shirley, and S.L. Tamone. 2007. Development and hatching in *Chionoecetes opilio* (snow crab) with variation in incubation temperature. Biol. Bull. 213:67-75. doi:10.2307/25066619

Williams, M.E., and M.G. Bentley. 2002. Fertilization success in marine invertebrates: The influence of gamete age. Biol. Bull. 202:34-42. doi:10.2307/1543220

Slater, L.M., K.A. MacTavish, and D. Pengilly. 2010. Preliminary Analysis of Spermathecal Load of Primiparous Snow Crab (*Chionoecetes opilio*) from the Eastern Bering Sea, 2005-2008. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.10

Preliminary Analysis of Spermathecal Load of Primiparous Snow Crab (*Chionoecetes opilio*) from the Eastern Bering Sea, 2005-2008

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Abstract

Male snow crab (*Chionoecetes opilio*) are harvested commercially in the eastern Bering Sea. Female snow crab possess sperm storage organs and can store sperm for successive clutch fertilization, a feature that could buffer the stock from recruitment overfishing by the males-only fishery. To better understand factors affecting reproductive potential of eastern Bering Sea snow crab, sperm reserves were assessed for primiparous crab in 2005, 2007, and 2008 through measurements of spermathecal load (SL). Area of collection and female size had significant effects on SL, and interactions existed between SL, area of collection, female size, and year. Patterns of female sperm reserves in the eastern Bering Sea underscore the importance of understanding the effects of spatial processes on the eastern Bering Sea snow crab stock.

Introduction

The eastern Bering Sea snow crab (*Chionoecetes opilio*) stock supports an important commercial fishery in which only males above a minimum size are harvested. The minimum legal size is 79 mm carapace width (CW); however, the effective minimum size based on industry preference is 102 mm CW (Bowers et al. 2008). The stock's biomass of mature males and females declined abruptly prior to the 2000 fishery and annual

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harvests fell from a range of 66-329 million pounds during 1990-1999 to a range of 24-57 million pounds during 2000-2008 (Turnock and Rugolo 2008).

Female snow crab possess sperm storage organs (spermathecae) and can store sperm for fertilization of successive clutches (Sainte-Marie and Carrière 1995). This storage capacity, coupled with male polygyny and female polyandry, could provide a safeguard for snow crab stocks from recruitment overfishing by a males-only fishery (Orensanz et al. 2005). However, a study on snow crab in the Gulf of St. Lawrence demonstrated that females do not always acquire sufficient sperm stores from their first mating season to fully fertilize successive clutches (Sainte-Marie et al. 2002). A previous study of primiparous (mature females carrying their first clutch) snow crab in the eastern Bering Sea revealed relatively low sperm reserves, with lowest levels in the northern sampling area (Rugolo et al. 2005). Although sperm reserves of primiparous snow crab can vary due to naturally occurring spatial or temporal variation in sex ratio (Sainte-Marie et al. 2002), consideration must also be given to the possibility that removal of large males by the commercial fishery could contribute to sperm limitation and reduced productivity in the eastern Bering Sea stock.

In response to the reported low levels of sperm reserves in primiparous snow crab (Rugolo et al. 2005) and to fishery conservation concerns arising from the decline of the eastern Bering Sea snow crab stock in the late 1990s, the Alaska Department of Fish and Game (ADF&G) initiated a program in 2005 to monitor the sperm reserves of snow crab in the eastern Bering Sea. The objective of the monitoring program is to determine if large-scale interannual variability in sperm reserves occurs in the eastern Bering Sea, as has been documented in the northwest Atlantic Ocean (Sainte-Marie et al. 2002). The long-term goals of the program are to better understand the factors that determine the productivity of the stock and to provide data for stock assessment. Here we present preliminary results from this monitoring program on spermathecal load (SL) of primiparous snow crab. We are currently restricting our analysis to primiparous crab to avoid the confounding effects for multiparous crab (mature females carrying their second or subsequent clutch) of senescence and possible participation in multiple mating seasons. Though both SL and sperm cell counts are being collected as measures of sperm reserves, at this time we present only SL due to incomplete processing of samples preserved for sperm cell counts. Previous studies have shown a high correlation of SL with sperm cell counts for primiparous females (Rondeau and Sainte-Marie 2001, Sainte-Marie et al. 2002) and presentation of SL allows for comparison with results from a previous study of snow crab in the eastern Bering Sea (Rugolo et al. 2005).

Methods

We collected primiparous snow crab from the eastern Bering Sea in 2005, 2007, and 2008 (Fig. 1). Mature snow crab were identified as primiparous by the clean, new-shell condition of the exoskeleton (NMFS shell condition code 2 as described in Chilton et al. 2008) and presumably include only females carrying their first clutch since their molt to maturity, though some samples may be in their second year of a biennial spawning cycle. Crab were collected opportunistically from the National Marine Fisheries Service (NMFS) Resource Assessment and Conservation Engineering Division eastern Bering Sea trawl survey in all years and from the ADF&G Pribilof District king crab survey in 2008. On the NMFS survey, an 83-112 eastern otter trawl was used to target crabs and groundfish (see Chilton et al. 2008 for methods), and on the ADF&G survey, 7 foot × 7 foot × 2.8 foot crab pots were used to target crab (see Gish 2006 for methods). Our objective was to transport live primiparous snow crab to the lab to allow for examination of egg viability and collection of additional information for a concurrent study; therefore only crab that appeared fit and vigorous were collected. In 2005 crab were collected from the northern edge of surveyed stations, and in 2007 and 2008 samples were collected from a broader spatial area (Fig. 1).

Crab retained for this study were tagged for individual identification and ability to associate samples with collection location. Samples were placed in nylon onion bags and held in the vessels' circulating seawater hold. Upon return to port, crab were transferred to insulated ice chests and covered in seawater-soaked burlap bags and ice packs and transported to Kodiak. In the lab, samples were sorted and live crab were held in flow-through seawater tanks chilled to ~3°C and fed a mixture of herring and squid twice a week. Crab that died throughout the study were either processed shortly after dying or frozen for later processing. All samples were processed within six months of collection.

During processing, CW was measured to the nearest 0.1 mm and each of the paired spermatheca were extracted and preserved. Additionally, if the clutch appeared undisturbed, clutch fullness was scored according to NMFS survey protocols (see Chilton et al. 2008) and, if the crab was processed unfrozen, a subsample of eggs was examined under a dissecting microscope for the presence of dead or unusual eggs. Spermathecae were stored in 4 or 10% buffered formalin for at least a week, after which the epithelial wall and cuticle were removed and SL was determined as the wet weight of the spermathecal contents measured to the nearest 0.0001 g. We measured SL from the right spermatheca from samples collected in 2005 and from the left spermatheca from samples collected in 2007 and 2008. Previous research has shown SL is generally equally distributed between the right and left spermathecae (Sainte-Marie and Lovrich 1994, Sainte-Marie et al. 2002, Duluc et al. 2005).

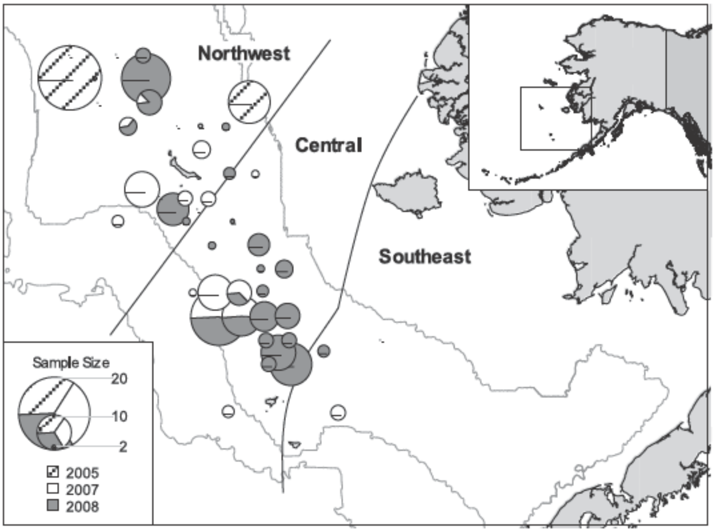

Figure 1. **Map of study area in the eastern Bering Sea (study area outlined in inset map) and sample size of primiparous snow crab processed for spermathecal load by year. Spatial areas (northwest, central, and southeast) used for analysis are shown as well as bathymetric contours of the shelf at 50, 100, and 200 m depth.**

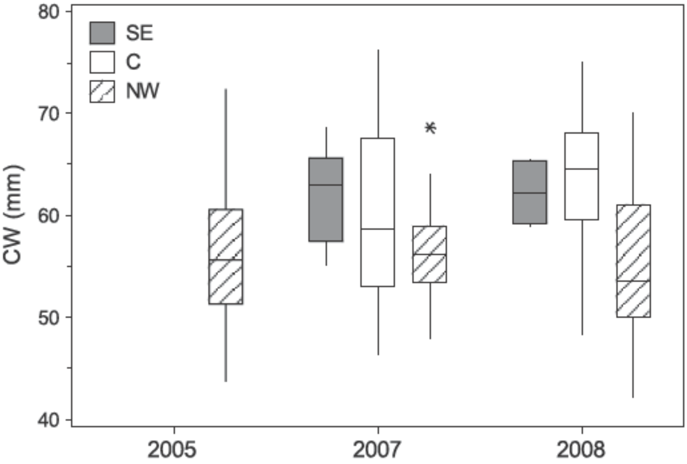

Figure 2. **Size (CW: carapace width) of primiparous snow crab collected from the eastern Bering Sea by year and area of collection (SE: southeast; C: central; NW: northwest) reveals variations by spatial area and smallest sizes in the NW area. Boxplots show medians, quartiles, ranges, and an outlier (asterisk).**

Trends in SL associated with year, area of collection, and female size (CW) were examined. We used the three spatial areas defined by Ernst et al. (2008) from general descriptions of the eastern Bering Sea (Schumacher and Stabeno 1998) modified to reflect ontogenetic migration patterns of mature female snow crab between 1978 and 2003 (Fig. 3 in Ernst et al. 2008) to analyze our data based on area of collection: southeast (SE), central (C), and northwest (NW) (Fig. 1). Due to the positively skewed distribution of SL, the data were $\log_{10}$ transformed to meet assumptions of normality and homogeneity of variance. An analysis of covariance (ANCOVA) was used to test if year, area of collection, and female size (CW) had an effect on $\log_{10}$ SL in 2007 and 2008. Year and area of collection were treated as categorical predictor variables, CW was treated as a continuous predictor variable, and all possible interactions among predictor variables were considered. Data from 2005 were not included in this analysis because crabs were not collected from all areas in that year.

Results

Measurements of SL and CW were obtained from 309 primiparous snow crab collected from the SE, C, and NW areas during 2005, 2007, and 2008 (Table 1). The size of females ranged from 42.2 to 76.3 mm CW and averaged 59.4 mm CW (SD = 7.0). Female size varied by area of collection, with those from the NW area tending to be smaller than those collected from the C and SE areas (Fig. 2). Crab examined for clutch fullness predominantly had clutches between ¾ full (264 of 299) and full (30 of 299). Crab examined for egg viability predominantly had healthy, normally developing clutches without any visible dead or unfertilized eggs (156 of 174).

Primiparous snow crab in this study had SL that ranged from 0.001 to 0.180 g and averaged 0.042 g (SD = 0.036). The mean SL varied by area of collection, with SL tending to be lowest in the NW area (mean = 0.030 g, SD = 0.027), intermediate in the C area (mean = 0.052 g, SD = 0.40), and highest in the SE area (mean = 0.091 g, SD =

Table 1. Number of primiparous snow crab processed for this study by year and area of collection (SE: southeast; C: central; NW: northwest).

	Area of collection		
Year	SE	C	NW
2005	0	0	56
2007	6	41	53
2008	4	102	47

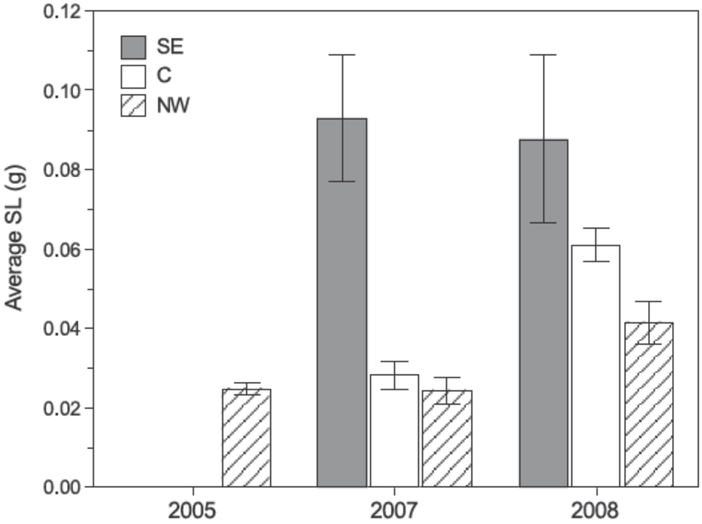

Figure 3. **Mean spermathecal load (SL) of primiparous snow crab collected from the eastern Bering Sea by year and area of collection (SE: southeast; C: central; NW: northwest) reveals variations between spatial areas and between years within each spatial area. Error bars display +1 standard error of the mean.**

0.038). The mean SL also varied by year within each area of collection (Fig. 3). The annual mean SL was similar between 2005 and 2007 in the NW area, increased between 2007 and 2008 in the NW and C areas, and decreased slightly between 2007 and 2008 in the SE area.

ANCOVA results (Table 2) revealed that area of collection and CW had significant effects on $\log_{10}$ SL; however, year did not. A significant effect due to the interaction between year and area of collection was detected, as indicated by the different trends described above between the C and NW areas and the SE area. The interaction between year and CW did not have a significant effect on $\log_{10}$ SL. However, a significant effect due to the interaction between spatial area and CW existed. This interaction was further examined, and a positive relationship between $\log_{10}$ SL and CW was detected in all areas; regression analysis revealed this relationship to be significant in the C area ($r^2 = 0.16$, $P < 0.001$) and the NW area ($r^2 = 0.13$, $P < 0.001$), but not in the SE area ($r^2 = 0.14$, $P = 0.296$, Fig. 4). Finally, a significant effect on $\log_{10}$ SL due to the interaction among year, area of collection, and CW was detected (Table 2).

Table 2. Analysis of covariance of $\log_{10}$ spermathecal load for eastern Bering Sea primiparous snow crab in 2007 and 2008, treating year and area of collection (area; see Fig. 1) as categorical predictor variables and female size (CW: carapace width) as a continuous predictor variable.

Variable	df	*F*	*P*
Year	1, 241	0.0182	0.893
Area	2, 241	7.3112	<0.001
CW	1, 241	7.0215	0.009
Year × area	2, 241	3.5303	0.031
Year × CW	1, 241	0.0013	0.971
Area × CW	2, 241	7.2787	<0.001
Year × area × CW	2, 241	3.3799	0.036

Note: df, degrees of freedom; F, F statistic; *P*, probability level

Discussion

Our results revealed significant size-dependent and spatial variations in sperm reserves of primiparous snow crab in the eastern Bering Sea. The positive association of SL with female size (CW) is similar to results for other snow crab stocks (Sainte-Marie et al. 2002). Spatial patterns in our study were confounded by the trend of decreasing size at maturity with latitude in the eastern Bering Sea (Zheng et al. 2001, Orensanz et al. 2007), as evidenced in our samples (Fig. 2). However, spatial variation in CW does not entirely explain the spatial variation observed in SL. Primiparous snow crab collected in the SE area had higher average SL values at size than those collected in the C area and those collected in the C area had higher average SL values at size than those collected from the NW area (Fig. 4). Additionally, SL varied between 2007 and 2008, but inter-annual variation was dependent on area of collection (Table 2, Fig. 3) . The low SL levels in our study relative to those reported for other snow crab stocks (see below) indicate it is unlikely that female sperm storage capacity is responsible for the relationship of increasing SL with female size. Alternate mechanisms for this relationship include male selectivity and preference for larger females (MacDiarmid and Butler 1999, Wedell et al. 2002) or spatial variability in male availability and reproductive fitness.

A comparison of our results to a previous study of primiparous snow crab in the eastern Bering Sea (Rugolo et al. 2005) reveals greater mean SL in our study in the NW area than from the same area in 2002 (mean = 0.016 g, N = 85) and 2003 (mean = 0.015 g, N = 77). However, within the C area, the mean SL from our study was lower in 2007

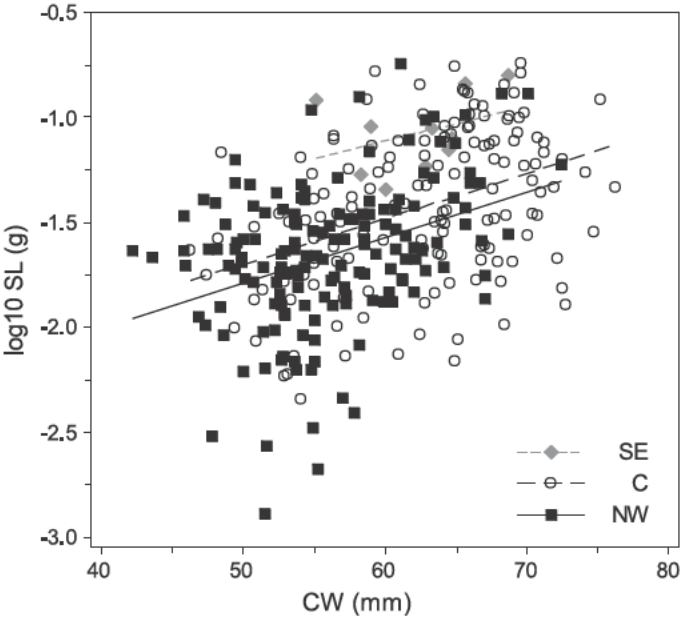

Figure 4. Log_{10} spermathecal load (SL) of primiparous snow crab for all years by area of collection (SE: southeast; C: central; NW: northwest) reveals positive correlations with female size (CW: carapace width). Regressions are significant for the C and NW areas ($P <$ 0.001).

(mean = 0.028 g) but similar in 2008 (mean = 0.061 g) to the mean SL reported from the same area in 2002 (mean = 0.050 g, N = 6 and mean = 0.045 g, N = 85) and 2003 (mean = 0.041 g, N = 85 and mean = 0.070 g, N = 88).

Sperm reserves in our study were generally low in comparison with other snow crab stocks. Sainte-Marie and Sainte-Marie (1998) defined levels of SL observed in snow crab from the northwest Atlantic Ocean as low (0.001-0.1 g), moderate (0.2-0.5 g), or large (1.0-1.8 g). According to their criteria, all crab in our study had low SL values except six crab with moderate SL values. These exceptions included one collected from the SE area in 2007 (SL = 0.157 g) and five collected from the C and NW areas in 2008 (SL range = 0.161-0.180 g). A comparison of the annual mean SL from each area of our study to annual mean SL of primiparous snow crab observed through a recruitment pulse in Baie Sainte-Marguerite showed that only the highest values from our study (those from the SE area and the C area in 2008) were within the range they observed

(0.031 to 0.130 g SL, after adjustment to a constant female size over an observed size range of 36 to 69 mm CW) (Sainte-Marie et al. 2002).

A temporal cycle of SL may exist in the eastern Bering Sea, similar to the cycle reported for primiparous snow crab in the northwest Atlantic Ocean (Sainte-Marie et al. 2002, 2008), and the sperm reserves from our study may correspond to a low period. However, it is important to note that the significant effect on $\log_{10}$ SL due to the interaction of year and spatial area in our study suggests the timing, period, and amplitude of such a cycle may vary spatially within the eastern Bering Sea. While sperm reserves were relatively low in our study, observations of egg viability indicate the majority of crab received sufficient sperm stores during mating to fully fertilize their first clutch of ontogeny.

The spatial variation we observed in SL of primiparous snow crab further confirms the importance of considering spatially dependent processes in understanding eastern Bering Sea snow crab stock dynamics (Parada et al. 2010). A sampling design representative of snow crab distribution in the eastern Bering Sea will be employed for our future collection of data on snow crab sperm reserves. Further analysis of sperm reserves, including variation with life history by comparison between the primiparous and multiparous components of the snow crab stock and a more detailed look at sperm reserves through analysis of sperm cell counts, will be conducted and may provide additional insights into the patterns and relationships presented here. We anticipate that continued monitoring and analysis will help determine whether sperm reserves can be a valuable predictor of male availability and reproductive fitness in the eastern Bering Sea snow crab stock.

Acknowledgments

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References

Bowers, F.R., M. Schwenzfeier, K. Milani, K. Herring, M. Salmon, E. Russ, J. Shaishnikoff, R. Burt, and H. Barnhart. 2008. Annual management report for the commercial and subsistence shellfish fisheries of the Aleutian Islands, Bering Sea and the Westward Region's Shellfish Observer Program, 2007/08. Alaska Department of Fish and Game, Fishery Management Report 08-73, Anchorage. 255 pp.

Chilton, E.A., C.E. Armistead, and R.J. Foy. 2008. The 2008 eastern Bering Sea continental shelf bottom trawl survey: Results for commercial crab species. NOAA Tech. Memo. NMFS-AFSC-187. 88 pp.

Duluc, C., B. Sainte-Marie, and J-C. Brêthes. 2005. Value of indicators for assessing recent mating in brachyuran crabs. J. Mar. Biol. Assoc. U.K. 85:129-135.

Ernst, B., J.M. Orensanz, and D.A. Armstrong. 2008. Patterns of potential mating opportunities in snow crab (*Chionoecetes opilio*) from the eastern Bering Sea, Chapter 4. In: D.A. Armstrong, J. Burgos, B. Ernst, and J.M. Orensanz. Female effective reproductive output of the snow crab stock in the eastern Bering Sea. NPRB (North Pacific Research Board) Final Report, pp. 125-159.

Gish, R.K. 2006. The 2005 Pribilof District king crab survey. Alaska Department of Fish and Game, Fishery Management Report 06-60, Anchorage. 49 pp.

MacDiarmid, A.B., and M.J. Butler. 1999. Sperm economy and limitation in spiny lobsters. Behav. Ecol. Sociobiol. 46:14-24.

Orensanz, J.M., B. Ernst, D.A. Armstrong, and A.M. Parma. 2005. Detecting early warning signs of recruitment overfishing in male-only crab fisheries: An example from the snow crab fishery. In: G.H. Kruse, V.F. Gallucci, D.E. Hay, R.I. Perry, R.M. Peterman, T.C. Shirley, P.D. Spencer, B. Wilson, and D. Woodby (eds.), Fisheries assessment and management in data-limited situations. Alaska Sea Grant, University of Alaska Fairbanks, pp. 267-287.

Orensanz, J.M., B. Ernst, and D.A. Armstrong. 2007. Variation of female size and stage at maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering Sea. J. Crust. Biol. 27:576-591.

Parada, C., D.A. Armstrong, B. Ernst, S. Hinckley, and J.M. Orensanz. 2010. Spatial dynamics of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea—putting together the pieces of the puzzle. Bull. Mar. Sci. 86(2):413-437.

Rondeau, A., and B. Sainte-Marie. 2001. Variable mate-guarding time and sperm allocation by male snow crabs (*Chionoecetes opilio*) in response to sexual competition, and their impact on the mating success of females. Biol. Bull. 201:204-217.

Rugolo, L., D. Pengilly, R. MacIntosh, and K. Gravel. 2005. Reproductive potential and life history of snow crabs in the eastern Bering Sea. In: D. Pengilly. Bering Sea snow crab fishery restoration research final comprehensive performance report. Alaska Department of Fish and Game, NOAA Cooperative Agreement NA17FW1274, pp. 57-324.

Sainte-Marie, B., and C. Carrière. 1995. Fertilization of the second clutch of eggs of snow crab, *Chionoecetes opilio*, from females mated once or twice after their molt to maturity. Fish. Bull. 93:759-764.

Sainte-Marie, B., and G.A. Lovrich. 1994. Delivery and storage of sperm at first mating of female *Chionoecetes opilio* (Brachyura: Majidae) in relation to size and morphometric maturity of male parent. J. Crust. Biol. 14:508-521.

Sainte-Marie, G., and B. Sainte-Marie. 1998. Morphology of the spermatheca, oviduct, intermediate chamber, and vagina of the adult snow crab (*Chionoecetes opilio*). Can. J. Zool. 76:1589-1604.

Sainte-Marie, B., J.-M. Sévigny, and M. Carpentier. 2002. Interannual variability of sperm reserves and fecundity of primiparous females of the snow crab (*Chionoecetes opilio*) in relation to sex ratio. Can. J. Fish. Aquat. Sci. 59:1932-1940.

Sainte-Marie, B., T. Gosselin, J.-M. Sévigny, and N. Urbani. 2008. The snow crab mating system: Opportunity for natural and unnatural selection in a changing environment. Bull. Mar. Sci. 83(1):131-161.

Schumacher, J.D., and P.J. Stabeno. 1998. Continental shelf of the Bering Sea. In: A.R. Robinson and K.H. Brink (eds.). The sea. John Wiley & Sons, New Jersey, pp. 789-822.

Turnock, B.J., and L.J. Rugolo. 2008. Stock assessment of eastern Bering Sea snow crab. In: Stock assessment and fishery evaluation report for the king and Tanner crab fisheries of the Bering Sea and Aleutian Islands regions. North Pacific Fishery Management Council, Anchorage. 76 pp.

Wedell, N., M.J.G. Gage, and G.A. Parker. 2002. Sperm competition, male prudence and sperm-limited females. Trends Ecol. Evol. 17:313-320.

Zheng, J., G.H. Kruse, and D.R. Ackley. 2001. Spatial distribution and recruitment patterns of snow crabs in the eastern Bering Sea. In: G.H. Kruse, N. Bez, A. Booth, M.W. Dorn, S. Hills, R.N. Lipcius, D. Pelletier, C. Roy, S.J. Smith, and D. Witherell (eds.), Spatial processes and management of marine populations. Alaska Sea Grant, University of Alaska Fairbanks, pp. 233-255.

Chilton, E.A., R.J. Foy, and C.E. Armistead. 2010. Temperature Effects on Assessment of Red King Crab in Bristol Bay, Alaska. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.05

Temperature Effects on Assessment of Red King Crab in Bristol Bay, Alaska

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Abstract

Bottom trawl surveys are conducted annually by the National Marine Fisheries Service in the eastern Bering Sea. One goal of the survey is to estimate the abundance of mature red king crab (*Paralithodes camtschaticus*) in Bristol Bay, Alaska. We hypothesize that not all mature red king crab females are mated at the time of the survey due to mismatched spatial overlap of males and females. Stock assessment models account for this by estimating the female contribution as the number of newly molted, ovigerous females with uneyed embryos from the survey. In years with colder than average water temperatures, embryo development and the molt-mate cycle are delayed. This delay likely impacts the migration of mature female red king crab to mating areas and their ability to extrude uneyed embryos, thereby affecting survey abundance estimates. The ratio of females with eyed embryos to females with uneyed embryos in cold years is higher at the start of the survey compared to warm years. The higher ratio of eyed to uneyed embryos in cold years is a result of the extended embryo development due to the colder water temperatures, and affects the distribution of mature females as well as their availability the bottom trawl survey.

Introduction

The biology, abundance, and distribution of red king crab (*Paralithodes camtschaticus,* RKC) in Bristol Bay on the eastern Bering Sea shelf are assessed annually during bottom trawl surveys conducted by the National Marine Fisheries Service. Due to consistent survey timing, temporal and spatial climate variability in the region likely affects the uncertainty in the estimation of the abundance and distribution of RKC. Specifically, temperature affects variability in growth (Stevens 1990), embryo development, and larval hatching (Shirley et al. 1990, Stevens and Swiney 2007), fishery catches (Mueter et al. 1995), and recruitment indices (Zheng and Kruse 2000, 2006) of RKC. Loher and Armstrong (2005) concluded that ovigerous female RKC shifted to the central shelf of Bristol Bay in the early 1980s coincident with warmer winters and earlier seasonal warming of bottom water temperatures. More recently, from 2003 to 2008, winters in the eastern Bering Sea have been relatively colder, which results in an increase of ice coverage (mid March), as well as colder bottom water temperatures in the spring and summer seasons evidenced by a persistent subsurface cold pool (<2°C) in Bristol Bay (Napp 2009). It is not known how these temperature changes and subsequent effects on crab biology, abundance, and distribution impact the annual assessment of RKC in the eastern Bering Sea.

Water temperature in the eastern Bering Sea is a function of decadal variability in the strength of the Aleutian Low Pressure System in winter: colder water temperatures and higher ice coverage in the spring are associated with a weak Aleutian Low and warmer water temperatures and lower ice coverage associated with a strong Aleutian Low (Zheng and Kruse 2006). The extent of sea ice coverage is variable and related to the location of the Aleutian Low, which typically produces northeast winds in the winter that freeze the seawater and push the ice southwestward (Stabeno et al. 2001). The Ice Retreat Index, defined by Overland et al. (2008) as sea ice coverage after March 15 at 56-58°N, 163-165°W, increased in 2006-2008 compared to the previous five years, reflecting the recent trends in colder water temperatures and high ice coverage. As a response to changing water temperatures, the ecosystem in the Bering Sea is shifting northward (Overland and Stabeno 2004).

Recent cooler water temperatures have impacted the reproductive cycle of RKC in Bristol Bay as well as the distribution of mature male and female RKC (Chilton et al. 2010), which in turn may affect the sampling availability of those crab for abundance estimation. Red king crab reproduce annually with females molting to a soft-shelled state prior to mating with a hard-shell male (Powell and Nickerson 1965). Female RKC extrude a clutch of fertilized eggs (uneyed embryos) roughly 24 days later in the abdomen where the eyed embryos are brooded for nearly a full year until hatching (Stevens and Swiney 2007). Timing of the female molting and mating cycle in Bristol Bay RKC is variable, occurring from the end of January to the end of June (Otto et al. 1990). Primiparous females, brooding their first egg clutch, migrate to nearshore waters and commence molting and mating earlier in the year than multiparous females which are brooding their second or subsequent egg clutch. Larval development is prolonged in primiparous females, which results in a relatively synchronous hatch date with multiparous females the following year (Stevens and Swiney 2007).

Over the last two decades, the annual eastern Bering Sea bottom trawl survey has begun sampling in Bristol Bay at the end of May or in early June (hereafter referred to as May), with the start date dependent on charter vessel availability. The start date may vary within a three-week period each year. The intent is to sample the RKC population after the molt-mate cycle when mature female RKC have completed the annual molting phase required prior to mating with mature males (Otto 1986). After the molt-mate cycle, mature females carrying newly extruded, uneyed embryos migrate onto the shelf from nearshore coastal waters. There are limited data available on migration patterns associated with RKC reproduction in the eastern Bering Sea. Based on in situ observations of RKC mating in Gulf of Alaska waters near Kodiak Island, the majority of the molt-mate cycle is assumed to take place in nearshore, shallow waters (Powell and Nickerson 1965).

The objectives of this paper are to (1) identify temperature variability within the past decade, (2) assess effects of this variability on the reproductive status of mature female RKC, and (3) assess the effects of this variability on the abundance and distribution of mature female RKC.

Materials and methods

Data collection

The eastern Bering Sea bottom trawl survey has been conducted annually since 1975 by chartering two commercial fishing vessels (Chilton et al. 2009). Both vessels begin the standard survey in Bristol Bay in late May and move west toward the shelf break, sampling alternate columns of the survey grid to complete the standard survey by late July (Fig. 1). This study focused on a core set of 46 stations within the 136 Bristol Bay survey stations, which encompass the majority of the red king crab distribution between 1999 and 2008 (Fig. 1).

Each station consisted of one tow within a 20 × 20 nautical mile (nmi) cell of the survey grid using a standard 83-112 Eastern otter trawl with a 25.3 m headrope and a 34.1 m footrope. Each tow was approximately 0.5 hours in duration and 2.8 km in length at a speed of 1.54 m per second. Net mensuration equipment was used to monitor the net's fishing performance during each tow, and a bottom contact sensor (inclinometer) was attached to the center of the footrope to measure bottom contact of the net at 1-second intervals. The bottom contact of the footrope and GPS data were used to calculate distance fished and fishing power was assumed to be equal between the vessels (Chilton et al. 2009). Water column temperatures were collected at 6-second intervals throughout the duration of each tow using a Seabird SBE-39

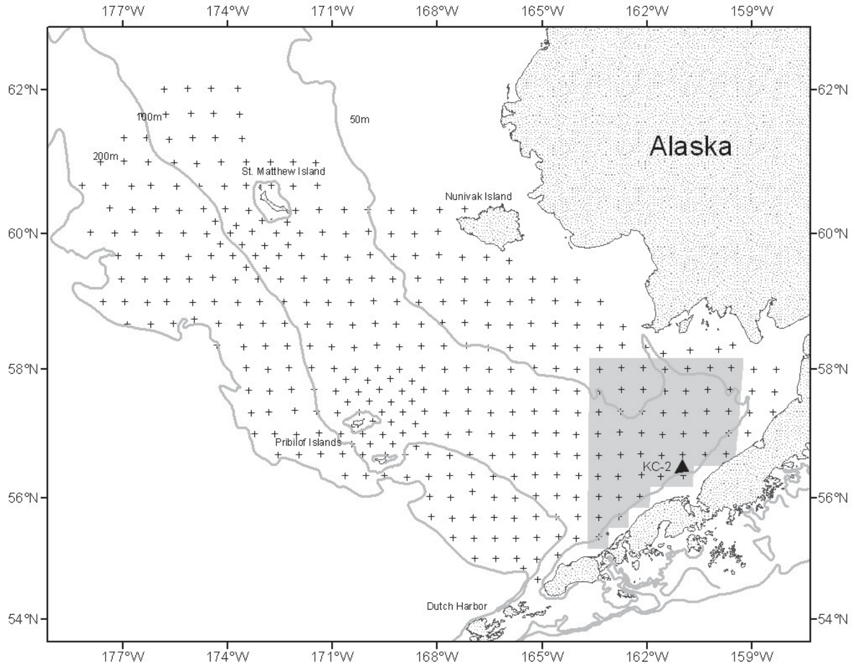

Figure 1. Station map of the National Marine Fisheries Service annual bottom trawl survey in the eastern Bering Sea. The area highlighted in gray encompasses the stations used in this study and the triangle identifies the location of the KC-2 mooring.

bathythermograph continuous data recorder (Sea-Bird Electronics Inc., Bellevue) attached to the headrope of the net.

All crab were removed from the catch, sorted by species and sex, and a total catch weight and count was obtained for each species. Individual carapace lengths (CL) were measured (± 1 mm) to provide a size-frequency distribution for each sample. All female crab abdomens were evaluated based on the size of the egg clutch (0 = immature, 1 = mature female no eggs, 2 = trace to ⅛, 3 = ¼, 4 = ½, 5 = ¾, 6 = full), the condition of the egg clutch (0 = no eggs, 1 = uneyed, 2 = eyed, 3 = dead, 4 = empty egg cases), and the color of the eggs (0 = no eggs, 2 = purple, 3 = brown, 4 = orange, 5 = purple-brown, 6 = pink).

When the molt-mate cycle was delayed in May and less than 80% of the mature female RKC (≥89 mm CL; Otto et al. 1990) were carrying clutches of uneyed embryos, a subset of survey stations within Bristol Bay were resurveyed in July. The purpose of the resurvey is to assess the number of females that have completed the molt-mate cycle, indicated by the newly extruded, uneyed embryos. The stations selected for resampling were based on that year's center of female RKC distribution in May, as well as historical knowledge of female distribution based on previous surveys in Bristol Bay (Chilton et al. 2009).

Data analysis

Egg condition codes were used to assess the stage in the molt-mate cycle of mature females during the survey. The presence of eyed embryos, empty egg cases, or no eggs in mature sized females indicated that the female had not yet extruded a new clutch of uneyed embryos, whereas mature females brooding uneyed embryos indicated completion of the molt-mate cycle. The ratio of females with eyed embryos to females with uneyed embryos was derived as a measurement of the molt-mate cycle progression during the survey. To address the effects of temperature variability on the molt-mate cycle over 1999 to 2008, the ratio of eyed to uneyed embryos in mature females was compared to average bottom temperatures and the spatial variability of embryo development was described with respect to average water temperatures within the core study area. A two-sample *t*-test, assuming unequal variance, was used to test for significant differences between water temperatures collected in May and July of cold years.

To investigate the relationship between RKC abundance estimates and water temperature over the last decade, changes in the spatial distribution of mature female densities in relation to mean bottom temperatures were described. In cold years, abundance estimates of mature females were compared between May and July to assess seasonal changes in distribution.

Mature female crab density (number per nmi^2) was estimated at each station by calculating the area swept by the trawl (nmi^2) as the product of the distance traveled while the net had bottom contact and an effective width of 15.2 m. Distance traveled by the trawl was determined from ship positions recorded using GPS equipment at the beginning and end of each tow, whereas effective width was recorded by trawl mensuration gear.

Total mature female crab abundance was estimated as the product of the average crab density at each station multiplied by the total area of the stations sampled (Table 1). Total area was calculated using an area of 401 nmi^2 for each 20 × 20 nmi cell due to a spherical projection of the station grid surface in an area as large as the eastern Bering Sea. Abundance estimates were reported as averages with 95% confidence intervals (1.96 SE).

Table 1. Details and total area swept abundance estimates for mature female red king crab in Bristol Bay from stations sampled in May and July in cold years (1999, 2000, 2006, 2007, and 2008). Station locations are outlined in black in Fig. 4.

Sampling dates	Station count	Total area (nmi²)	Mature female abundance (millions)	Abundance 95% CI (millions)	Mean bottom temperature (°C)
May 23-30, 1999	31	12,431	11.40	4.9	0.1
July14-20, 1999	31	12,431	14.99	6.74	2.5
May 24–Jun 1, 2000	23	9,223	11.39	5.70	1.7
July19-23, 2000	23	9,223	19.34	8.12	4.6
June 3-8, 2006	30	12,030	22.25	7.34	2.3
July 19-24, 2006	30	12,030	32.39	9.72	4.2
June 12-18, 2007	32	12,832	26.67	8.54	1.8
July 23-29, 2007	32	12,832	37.07	15.20	3.4
June 5-12, 2008	32	12,832	25.22	10.84	1.4
July 20-25, 2008	32	12,832	36.48	25.17	3.6

Results

Mean bottom temperatures in Bristol Bay in May fluctuated over 1999 to 2008, ranging from –0.7°C in 1999 to 6.3°C in 2005. For the purpose of this analysis, the five years with the highest average bottom temperatures in May were defined as warm years, ranging from 3.4 to 4.3°C in 2001 to 2005. Mean bottom temperatures in May of the cold years of 1999, 2000, 2006, 2007, and 2008 ranged from 0.1 to 2.2°C (Table 2).

Stations sampled in May of the cold years had high numbers of mature female RKC brooding eyed embryos fertilized the previous season due to delayed development and hatching of the embryo in cold water. These high numbers resulted in a higher ratio of eyed to uneyed embryos in May for all five cold years compared to the warm years. The eyed to uneyed embryo ratio in cold years ranged from 6.54 to 0.45, whereas the ratio in warm years ranged from 0.06 to 0.01 (Table 2). High ratios are indicative of a low percentage of mature females completing the molt-mate cycle in May, with only 13% to 67% of mature females brooding uneyed embryos in cold years compared to 94% to 99% in warm years. The low percentages of females with uneyed embryos in May required resampling in July to assess the reproductive stage of

Table 2. Mean bottom water temperatures measured during the National Marine Fisheries Service annual bottom trawl survey in the eastern Bering Sea, with the warm years highlighted in gray. Sample months correspond with sampling dates in Table 1. An asterisk (*) indicates a statistically significant difference between monthly mean bottom temperature for May and July for that year (two sample *t*-test, alpha = 0.05).

Sample month	Mean bottom temperature (°C)	Standard deviation (°C) (n = Stations)	Two sample *t*-test values		Eyed to uneyed embryo ratio
May 1999	0.1	0.8 (41)	$t = -11.9$	$p < 0.001$	6.54
July 1999	2.5*	0.8 (31)			0.02
May 2000	1.7	0.5 (49)	$t = -9.2$	$p < 0.001$	1.45
July 2000	4.6*	1.6 (23)			0.01
June 2001	3.5	0.3 (40)			0.01
June 2002	3.4	0.6 (52)			0.06
June 2003	4.2	0.4 (51)			0.01
June 2004	3.9	0.5 (61)			0.03
June 2005	4.3	0.5 (49)			0.01
June 2006	2.2	0.7 (69)	$t = -12.5$	$p < 0.001$	0.59
July 2006	4.2*	0.8 (30)			0.01
June 2007	1.8	0.9 (68)	$t = -7.4$	$p < 0.001$	0.86
July 2007	3.4*	1.0 (32)			0.01
June 2008	1.4	0.7 (76)	$t = -9.5$	$p < 0.001$	0.45
July 2008	3.6*	1.1 (32)			0.00

mature female RKC. Thirty-one stations were resampled in 1999, 23 in 2000, 31 in 2006, and 32 in 2007 and 2008 (Table 1).

In all five cold years, bottom water temperatures increased significantly from 0.1-1.4°C in May to 2.5-4.6°C in July (Table 2). Due to the increase in bottom water temperatures at the resampled stations, the eyed to uneyed embryo ratio in mature females decreased in July and ranged from 0.02 in 1999 to 0.00 in 2008.

In cold years when the ratio of eyed to uneyed embryos for mature females was higher, females with eyed embryos were distributed at warmer stations depending on the location of the cold pool and suggests that crab were avoiding cold water (Fig. 2). Based on the high eyed to uneyed ratios, the temperatures at these stations (2.0-4.0°C) were not warm enough to advance the molt-mate cycle as in the defined warm years.

In May of the warm years, the RKC mature female density was higher in the center of Bristol Bay and distributed in temperatures rang-

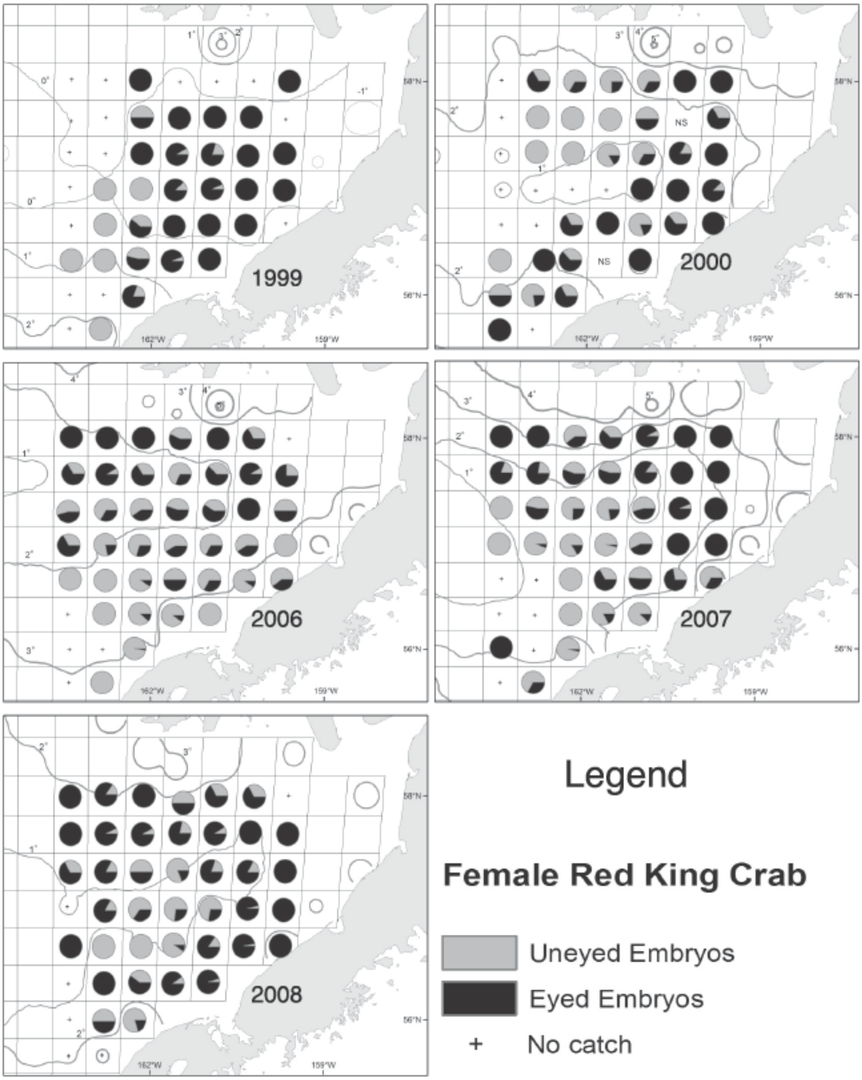

Figure 2. **Proportion of mature female red king crab with uneyed or eyed embryos encountered on the National Marine Fisheries Service annual bottom trawl survey in Bristol Bay, in May of the cold years (1999, 2000, 2006, 2007, and 2008). Contours define mean bottom water temperatures, with <2°C depicting the cold pool. NS = station not sampled in 2000.**

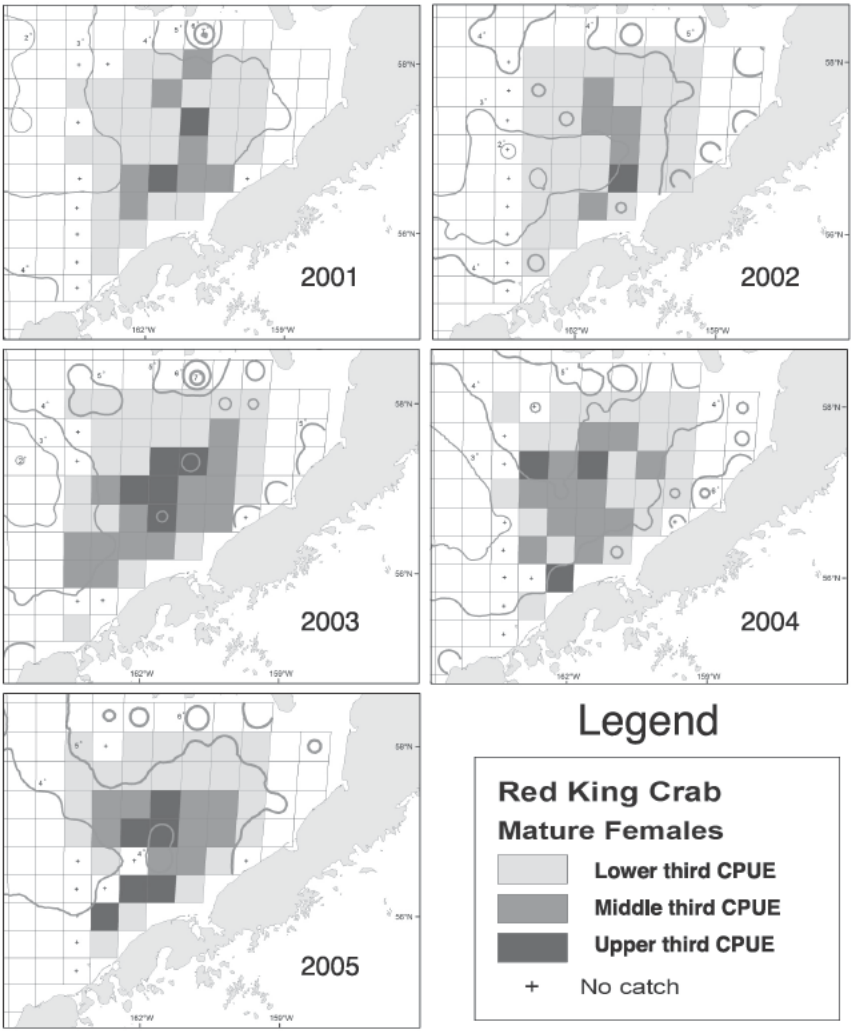

Figure 3. Distribution of mature female red king crab CPUE with respect to bottom water temperatures collected on the National Marine Fisheries Service annual bottom trawl survey in Bristol Bay, in May of warm years (2001-2005). Contours define mean bottom water temperatures, with <2ºC depicting the cold pool.

ing from 3.0 to 4.0°C on the shelf (Fig. 3). When the cold pool (<2.0°C) extended onto the Bristol Bay shelf in May of the cold years, particularly in 2000 and 2006, mature females were also distributed in bottom temperatures of 3.0-4.0°C and were much closer to shore. When the cold pool was prevalent throughout the whole Bristol Bay area in May, such as 1999, 2007, and 2008, higher densities of mature females were distributed in nearshore areas, but mature females were also distributed in water temperatures of 1.0°C and less (Fig. 4). This suggests that in the coldest of years, mature female crab may be forced into colder waters than the preferred 3.0-4.0°C range.

The abundance estimates of mature female RKC in cold years were affected by the movement of crab noted above, and increased between May and July in all five cold years. The total abundance estimate for mature females in May ranged from 11.39 ± 5.70 million crab to 26.67 ± 8.54 million crab among all cold years. The total abundance estimate for mature females in July ranged from 14.99 ± 6.74 million crab to 37.07 ± 15.20 million crab among all cold years. The increase in abundance between May and July in any particular year ranged from 3.59 million crab to 11.26 million crab (Fig. 5, Table 1).

Discussion

Over the last decade, bottom water temperatures in the eastern Bering Sea have been influenced by the extent of the ice coverage and resulting cold pool. In addition to the point estimates of bottom temperature observed during this study, average daily bottom temperatures collected at NOAA's Pacific Marine Environmental Laboratory KC-2 mooring anchored at 65 m in Bristol Bay (Fig. 1; 56.498°N, 160.999°W) recorded later seasonal warming between May and July during the last decade (Fig. 6). Additionally, winter temperatures were colder and the ice coverage in the eastern Bering Sea was extended in these years (Overland et al. 2008). This temperature variability, potentially caused by regional climate variability, has profound effects on the life history of RKC.

Historically, low catches of RKC in the eastern Bering Sea are strongly correlated with colder sea surface temperatures 10 years prior to the fishery (Mueter et al. 1995), although Zheng and Kruse (2000, 2006) found that warmer water temperatures resulted in a decreased recruitment of juvenile RKC. The results reported in our study show that both seasonal and interannual changes in the distribution of mature female RKC are associated with spring bottom water temperatures and specifically, the location of the eastern Bering Sea cold pool.

Controlled laboratory studies of RKC have linked warmer water temperatures to a decrease in development time of RKC embryos, while colder temperatures delay embryo development and larval hatching (Shirley et al. 1990, Stevens and Swiney 2007). Larval survival is affected

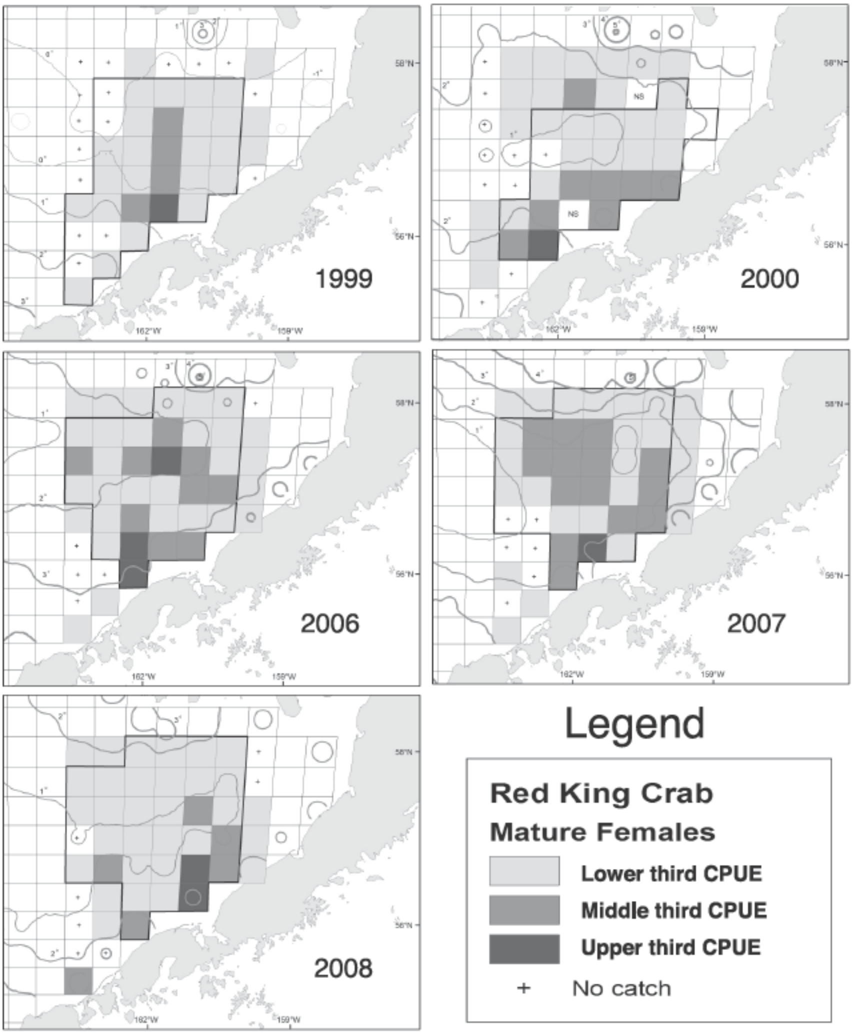

Figure 4. Distribution of mature female red king crab CPUE with respect to bottom water temperatures collected on the National Marine Fisheries Service annual bottom trawl survey in Bristol Bay, in May of cold years (1999, 2000, 2006, 2007, and 2008). Contours define mean bottom water temperatures, with <2°C depicting the cold pool. NS = station not sampled in 2000. The black outline in each year represents stations resampled in July.

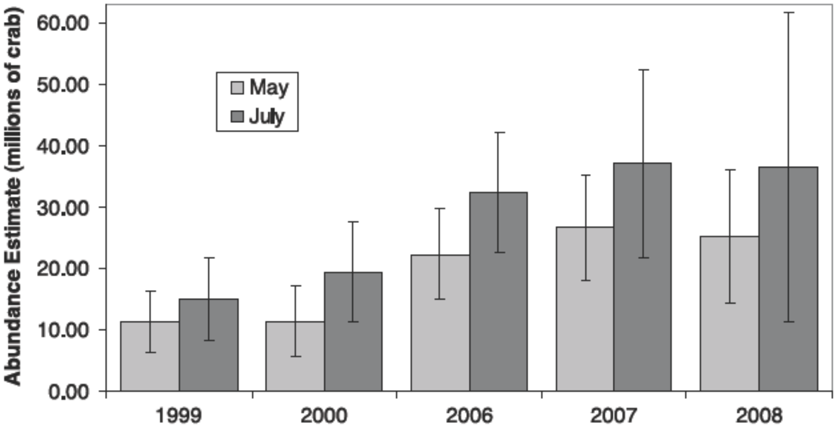

Figure 5. Area-swept abundance estimates (± 95% confidence intervals) of mature female red king crab collected during the National Marine Fisheries Service annual bottom trawl survey in Bristol Bay.

by this delay when hatching occurs in low density prey fields, such as after the spring phytoplankton bloom (Paul and Paul 1980, Shirley and Shirley 1989). We found that the higher ratio of eyed to uneyed embryos in May of the cold years is a result of the extended embryo development and larval hatching period and reflects the impact of colder temperatures on the seasonal timing of mature female RKC migrating from the Bristol Bay shelf to nearshore shallow waters to complete the molt-mate cycle with males. Larval hatching from these females may be occurring in less than optimal water temperatures for growth, feeding, and recruitment.

Spatial and temporal variability in bottom temperature has been associated with the migration of ovigerous RKC females to water temperatures optimal for embryo development and successful larval hatching (Stone et al. 1992). Specifically, seasonal migration patterns of RKC in the Gulf of Alaska have been related to feeding and reproduction (Stone et al. 1992), with female RKC seasonally migrating offshore to deeper water for feeding and onshore for the molt-mate cycle with males. Tagged RKC females in the eastern Gulf of Alaska were tracked over a period of 12 months following their seasonal migration patterns from waters deeper than 50 m in late summer and fall to depths less than 27 m in the winter, followed by the final inshore shallow water migration for molting and mating with hard shell males in April and May (Stone et al. 1993). In the eastern Bering Sea, information on the seasonal migration patterns of RKC associated with their molt-mate cycle is not well described (Dew 2008). Based on our study, we suggest that temperature

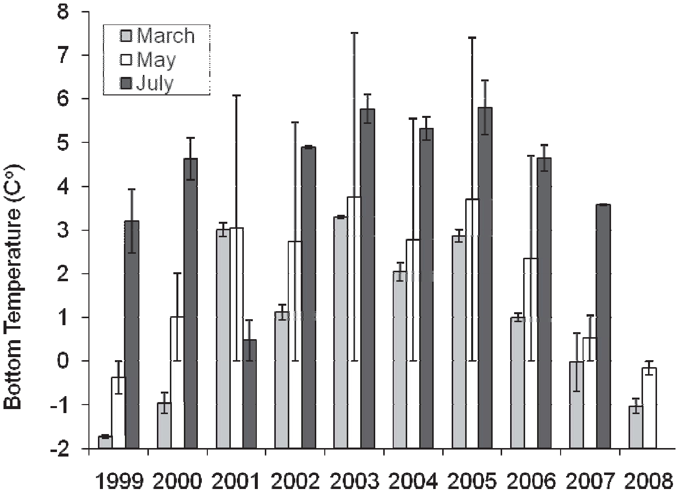

Figure 6. Monthly mean bottom water temperatures (± SD) at buoy KC-2A in Bristol Bay during March, May, and July 1999-2008.

effects on the molt-mate cycle must be considered in addition to the annual migration patterns occurring between nearshore mating locations to summer feeding and overwintering back on the shelf.

It has been previously shown that interannual variability in RKC distribution is associated with bottom temperatures and may have implications for population assessment (Loher and Armstrong 2005). In the late 1970s, mature female RKC were localized along the eastern edge of Bristol Bay when a cold pool of <1°C water extended onto the eastern Bering Sea shelf. By the mid 1980s, the bottom temperatures on the shelf increased and mature female RKC shifted to the central area of Bristol Bay. In our study, the addition of a later sampling period in July showed seasonal movements of females, further highlighting the importance of temperature variability in the eastern Bering Sea not only on reproductive timing but also on migration patterns and locations of RKC mating along the eastern edge of Bristol Bay.

In cold years, the temperature-delayed molt-mate cycle of RKC in Bristol Bay impacts the distribution of mature females and their availability to our assessment survey. The increase in abundance estimates of mature females from May to July in all five cold years is positively associated with warming bottom temperatures as the females move back onto the Bristol Bay shelf in July. This increase in abundance, coupled with the decrease in the ratio of eyed to uneyed embryos in July, is a reflection of the migration pattern commencing after completion of the molt-mate cycle. Dew (2008) suggested delaying the start date of the eastern Bering Sea bottom trawl survey in cold years as a method of improving estimates of red king crab females that have completed the molt-mate cycle.

Sampling in both May and July of a warm year would provide an excellent opportunity to test the relationship between water temperatures and the distribution of females completing the molt-mate cycle for further investigation into the seasonal migration patterns of female RKC. Future research focusing on the relationship between bottom temperatures and the distribution of male RKC is needed to understand the spatial overlap between mature male and female RKC, as well as the mating potential of RKC in cold years. This is essential information for population dynamics and management of this commercially important species.

References

Chilton, E.A., C.E. Armistead, and R.J. Foy. 2009. The 2009 eastern Bering Sea continental shelf bottom trawl survey: Results for commercial crab species. NOAA Tech. Memo. NMFS AFSC 1769. 88 pp.

Chilton, E.A., C.E. Armistead, and R.J. Foy. 2010. The 2010 eastern Bering Sea continental shelf bottom trawl survey: Results for commercial crab species. NOAA Tech. Memo. NMFS AFSC 1989. 144 pp.

Dew, C.B. 2008. Red king crab mating success, sex ratio, spatial distribution, and abundance estimates as artifacts of survey timing in Bristol Bay, Alaska. N. Am. J. Fish. Manage. 28:1618-1637.

Loher, T., and D.A. Armstrong. 2005. Historical changes in the abundance and distribution of ovigerous red king crabs (*Paralithodes camtschaticus*) in Bristol Bay (Alaska), and potential relationship with bottom temperature. Fish. Oceanogr. 14:292-306.

Mueter, F.J., B.L. Norcross, and T.C. Royer. 1995. Do cyclic temperatures cause cyclic fisheries? In: R.J. Beamish (ed.), Climate change and northern fish populations conference. Can. Spec. Publ. Fish. Aquat. Sci. 121:119-129.

Napp, J. 2009. The Bering Sea: Current status and recent events. North Pacific Marine Science Organization (PICES) Press 17:40-43.

Otto, R.S. 1986. Management and Assessment of eastern Bering Sea king crab stocks. In: G.S. Jamieson and N. Bourne (eds.), North Pacific workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92:83-106.

Otto, R.S., R.A. MacIntosh, and P.A. Cummiskey. 1990. Fecundity and other reproductive parameters of female red king crab (*Paralithodes camtschaticus*) in Bristol Bay and Norton Sound, Alaska. In: Proceedings of the International Symposium on King and Tanner Crabs. Alaska Sea Grant, University of Alaska Fairbanks, pp. 65-90.

Overland, J.E., and P.J. Stabeno. 2004. Is the climate of the Bering Sea warming and affecting the ecosystem? EOS 85:309-316.

Overland, J., M. Wang, C. Ladd, P. Stabeno, N. Bond, and S. Salo. 2008. Eastern Bering Sea Climate FOCI. In: J. Bolt (ed.), North Pacific groundfish stock assessment and fishery evaluation reports for 2009: Appendix C, Ecosystem considerations for 2009. North Pacific Fishery Management Council, Anchorage, pp. 43-50.

Paul, A.J., and J.M. Paul. 1980. The effect of early starvation on late feeding success of king crab zoeae. J. Exp. Mar. Bio. Ecol. 44:247-251.

Powell, G.C., and R.B. Nickerson. 1965. Reproduction of king crabs, *Paralithodes camtschaticus* (Tilesius). J. Fish. Res. Board Can. 22:101-111.

Shirley, S.M, and T.C. Shirley. 1989. Interannual variability in density, timing and survival of Alaskan red king crab *Paralithodes camtschaticus* larvae. Mar. Ecol. Prog. Ser. 54:51-59.

Shirley, T.C., S.M. Shirley, and S. Korn. 1990. Incubation period, molting and growth of female red king crabs: Effects of temperature. In: Proceedings of the International Symposium on King and Tanner Crabs. Alaska Sea Grant, University of Alaska Fairbanks, pp. 51-63.

Stabeno, P.J., N.A. Bond, N.B. Kachel, S.A. Salo, and J.D. Schumacher. 2001. On the temporal variability of the physical environment over the southeastern Bering Sea. Fish. Oceanogr. 10:81-98.

Stevens, B.G. 1990. Temperature dependent growth of juvenile red king crab (*Paralithodes camtschaticus)* and its effects on size-at-age and subsequent recruitment in the eastern Bering Sea. Can. J. Fish. Aquat. Sci. 47:1307-1317.

Stevens, B.G., and K.M. Swiney. 2007. Hatch timing, incubation period, and reproductive cycle for captive primiparous and multiparous red king crab, *Paralithodes camtschaticus*. J. Crust. Biol. 27:37-48.

Stone, R.P., C.E. O'Clair, and T.C. Shirley. 1992. Seasonal migration and distribution of female red king crabs in a southeast Alaskan estuary. J. Crust. Biol. 12:546-560.

Stone, R.P., C.E. O'Clair, and T.C. Shirley. 1993. Aggregation behavior of female red king crab, *Paralithodes camtschaticus,* in Auke Bay, Alaska. Can. J. Fish. Aquat. Sci. 50:750-758.

Zheng, J., and G.H. Kruse. 2000. Recruitment patterns of Alaskan crabs in relation to decadal shifts in climate and physical oceanography. ICES J. Mar. Sci. 57:438-451.

Zheng, J., and G.H. Kruse. 2006. Recruitment variation of eastern Being Sea crabs: Climate-forcing or top-down effects? Prog. Oceanogr. 68:184-204.

Swiney, K.M., J.B. Webb, G.H. Bishop, and G.L. Eckert. 2010. Temporal and Spatial Variability of Alaska Red King Crab Fecundity, and Accuracy of Clutch Fullness Indices in Estimating Fecundity. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.11

Temporal and Spatial Variability of Alaska Red King Crab Fecundity, and Accuracy of Clutch Fullness Indices in Estimating Fecundity

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Abstract

Stock assessment and management of the Alaska red king crab, *Paralithodes camtschaticus*, will be improved by incorporating information on egg production in the development of biological reference points; therefore, an understanding of spatial and temporal variability in fecundity is needed. Here we compare summer fecundity estimates in red king crab, taking into account differences in female size, from three time periods in Bristol Bay, Alaska (1980s, 2007, 2008) and from four areas in southeastern Alaska in 2008. Fecundity of likely primiparous (<105 mm CL) Bristol Bay females was significantly greater in 2007 followed by the 1980s and 2008. Among likely multiparous females (≥105 mm CL), fecundity was greater in 2007 and 2008 (which did not differ) than in the 1980s. Fecundity of crabs in southeastern Alaska did not vary significantly among areas sampled. Red king crabs in Bristol Bay were more fecund than crabs in southeastern Alaska. The temporal and spatial variability in fecundity observed in this study should be considered in development of biological reference points and fishery stock assessments. A second objective of this study was to assess the current methods for estimating egg production on crab abundance and distribution surveys and by observers onboard commercial vessels. We compared quantitative measures of fecundity with clutch fullness indices (CFI), which score egg clutches by a visual estimate of egg clutch size relative to abdomen size in either 10% or 25% fullness increments. Significant differences in fecundity were not detected between consecutive CFI scores, suggesting that current CFI methods are not exact estimators of fecundity. More precise and easily executed methods to estimate egg production are needed.

Introduction

A priority for fishery managers is to develop biological reference points based on monitored characteristics of a population, such as reproductive potential, that reflect population status (Smith and Sainte-Marie 2004). Stock assessment and management of Alaska red king crab, *Paralithodes camtschaticus,* including the stocks in Bristol Bay and southeastern Alaska, do not directly incorporate egg production. The harvest strategy employed by the Alaska Department of Fish and Game (ADFG) for Bristol Bay red king crabs uses a length-based population model for stock assessment that defines male reproductive potential as mature male abundance grouped into 5 mm carapace length (CL) size bins multiplied by the maximum number of females with which a male in a particular size bin can mate (Zheng et al. 1995). Female spawning abundance, which is a proxy for female reproductive potential, is set equal to male reproductive potential or mature female abundance, whichever is less (Zheng et al. 1995). A review of Bering Sea and Aleutian Islands red king crab stock assessment by scientists from the Center for Independent Experts (CIE) determined that this method is inadequate because it does not incorporate egg production (Bell 2006, Caputi 2006, Cordue 2006). In southeastern Alaska, ADFG uses a 3-stage catch-survey analysis (Collie and DeLong 1998, Clark et al. 2003) to estimate mature and legal male population size. Catch per unit effort (CPUE) of two female size classes and an index of egg production (proportion of females with less than 25% clutch fullness), along with CPUE for four recruit classes of red king crab males, are compared with baseline levels to determine stock status, which is used to assign a tiered harvest rate (0, 5, 10, 15, or 20% of mature males or a maximum of 50% of legal males) to each survey area. An independent review of southeastern Alaska red king crab stock assessment recommended further research on female egg production in order to preserve reproductive potential and ensure sustainable management of red king crab fisheries (Quinn et al. 2006). Including indices of egg production in development of biological reference points will improve the stock assessment and management of these stocks.

An understanding of the red king crab mating system is necessary when considering fecundity, the number of embryos a female is brooding, in the development of biological reference points. Timing of red king crab mating is variable and can occur from the end of January through the end of June (Otto et al. 1990, Stone et al. 1993, Stevens and Swiney 2007a). Mating occurs between larger hard-shelled males and smaller soft-shelled females. Typically, within two days after molting and mating, eggs are extruded from the ovaries onto the abdomen and adhere to setae on the pleopods (Stevens and Swiney 2007a). Fertilization is external and fertilized embryos are brooded approximately 10 to 12 months until hatching (Powell and Nickerson 1965, Powell et al. 1973, Stevens and Swiney 2007a). Variability in the timing of molting, mating, brooding duration, hatch timing (Powell et al. 1973, Otto et al. 1990, Stevens and Swiney 2007a), egg loss (Matsuura and Takeshita 1985), and growth (Powell et al. 1973, Stevens and Swiney 2007b) have been reported between primiparous (brooding first clutch) and multiparous (brooding second or subsequent egg clutch) females and among size classes for red king crab. Fecundity increases with female size (Otto et al. 1990), but variability in fecundity of primiparous and multiparous females is unknown.

Fecundity was estimated for Alaska red king crab populations in Bristol Bay, Kodiak Island waters, Norton Sound, and Kachemak Bay in the 1960s-1980s, and differences in fecundity were reported between and within areas (Haynes 1968, Otto et al. 1990, Johnson et al. 2001). Spatial and temporal variability in fecundity is difficult to determine from these studies because they were limited in the size ranges of females and years sampled. It is important to routinely estimate fecundity of fished crustacean stocks, as temporal changes in fecundity have been observed that can have implications in management of the species (DeMartini et al. 2003). An improved understanding of temporal and spatial variability in fecundity and more recent quantitative estimates of fecundity are needed to develop an index of red king crab egg production.

Survey biologists and fishery observers onboard commercial vessels assess egg production by estimation of clutch fullness index (CFI), which scores egg clutches in fullness increments. For management of the Bristol Bay red king crab stock, CFI data are not directly incorporated into fishery management models, but the data are reported annually in stock assessments (Zheng and Siddeek 2009). CFIs may be used as a tool to estimate fecundity; however, the validity of this approach should be further evaluated. For example, fecundity of Kodiak red king crab generally increased with increasing CFI scores, but observer agreement in assigning CFIs was "less than moderate" (Johnson et al. 2001).

Prior to our study, the most recent Bristol Bay red king crab fecundity estimates were from the 1980s, and fecundity estimates had not been previously reported for red king crabs from southeastern Alaska. Furthermore, current CFI methods have not been examined to determine if CFIs can be used as a tool to estimate red king crab fecundity. Our objectives were to (1) better understand spatial and temporal variability in Alaska red king crab fecundity by comparing summer fecundity estimates from three periods in Bristol Bay, Alaska (1980s, 2007, and 2008) and from four areas in southeastern Alaska in 2008, and (2) assess the reliability of different CFI scoring methods in estimating fecundity by comparing fecundity estimates with CFIs for crabs collected during National Marine Fisheries Service (NMFS) and ADFG crab abundance and distribution surveys, and by observers onboard commercial vessels during the Bristol Bay red king crab fishery.

Materials and methods

Data collection

For temporal comparisons of fecundity, egg clutches of ovigerous red king crab females were collected in Bristol Bay, Alaska (Fig. 1), during the 1980s, 2007, and 2008 NMFS Alaska Fisheries Science Center eastern Bering Sea bottom trawl surveys conducted from June through July. Collections are referred to as follows: BB80s (Bristol Bay summer 1982, 1983, 1985), BB07 (Bristol Bay summer 2007), and BB08 (Bristol Bay summer 2008). Historical Bristol Bay 1982, 1983, and 1985 data presented in Otto et al. (1990) were used for this analysis. The three years of 1980s data were pooled because the samples were collected under a multiyear framework in which only full clutches were collected, and sampling continued until 10 clutches had been collected in 5 mm CL size groups of ovigerous females ranging from 80 and 135 mm CL. Clutches were preserved at sea in 10% buffered formalin and later processed in the laboratory. Refer to Otto et al. (1990) for full sampling protocols. For BB07, ovigerous females were sampled from 10 mm size bins between 90 and 140 mm CL and clutches were preserved at sea in 10% buffered formalin. BB08 ovigerous females were sampled from 10 mm size bins between 80 and 150+ mm CL and samples were frozen at sea. For the BB07 and BB08 collections, ovigerous females were haphazardly collected until 20 clutches per size bin were attained regardless of clutch size. Upon collection, CL measured to the nearest 1.0 mm, shell condition, and CFI were recorded (Donaldson and Byersdorfer 2005); samples were later processed in the laboratory. Additionally, egg clutches were collected by shellfish fishery observers during the 2007 commercial Bristol Bay red king crab fishery (hereafter referred to as OBS07) using the same protocols as the BB08 samples.

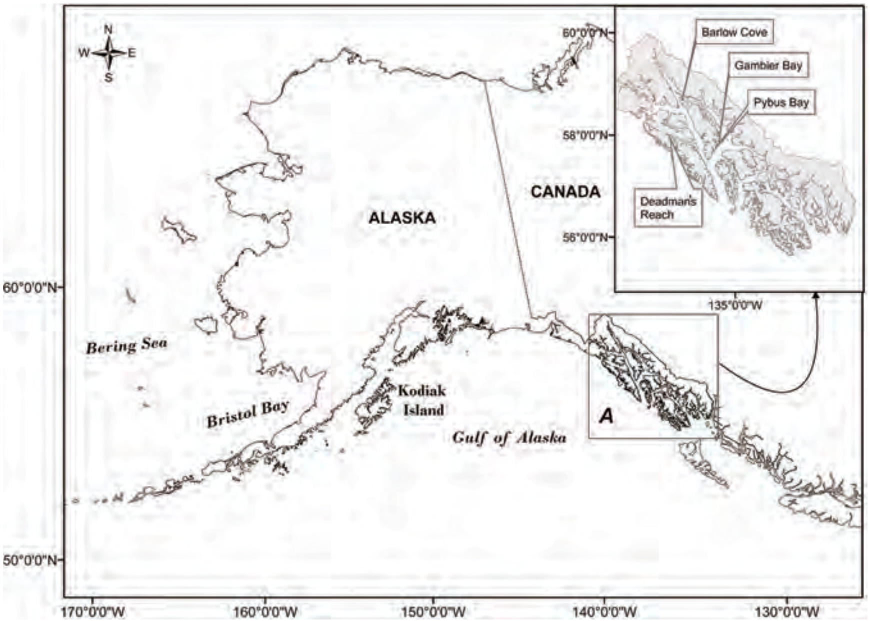

Figure 1. **Samples were collected from Bristol Bay, Alaska, and (A) areas within southeastern Alaska.**

In southeastern Alaska in 2008 (hereafter referred to as SEAK08), sampling goals for female red king crabs were to collect females with a representative size-frequency distribution and a range of clutch fullness values for spatial comparisons. Females were haphazardly collected from pot survey catches in June and July 2008 during the ADFG southeastern Alaska red king crab pot survey from four discrete survey areas in the northeastern Gulf of Alaska: Barlow Cove, Gambier Bay, Pybus Bay, and Deadman's Reach (Fig. 1). The goal was to sample eight females per 15 mm size bin between 105 and 150 mm CL and four females each <105 mm CL and >150 mm CL, as females in these size ranges were relatively uncommon in pot survey catches. Half of the females in each size bin were targeted to have CFI ≤70% and >70%. Upon collection, carapace length, shell condition, and CFI were recorded. Egg clutches were collected and put in individual cheesecloth bags with ties that retained all of the eggs and maintained immersed in circulating seawater at ambient temperature aboard the survey vessel and in the laboratory. All egg clutches were processed in the laboratory within three weeks of collection.

Fecundity

Samples for temporal and spatial fecundity analyses were collected at the same time of year, shortly after egg extrusion, to minimize the potential effects of egg loss on fecundity estimates. Fecundity was estimated using dry weight methods. BB80s samples were processed by stripping embryos off of the pleopods and air drying the clutch until a constant weight was achieved. Two subsamples of approximately 250 embryos were randomly selected, weighed, and counted after the eggs were dried (Otto et al. 1990). BB07, BB08, SEAK08, and OBS07 were processed using slightly different methods, in which the subsamples were randomly selected and counted before the embryos were dried at 60°C until a constant weight was achieved. For all samples, fecundity was estimated by dividing the total weight of embryos by the average of the two estimates of individual embryo weight that were obtained from the subsamples (Otto et al. 1990).

To separate multiparous and primiparous females in Bristol Bay, we conducted separate analyses for females greater and less than 105 mm CL, based on size-at-maturity in Bristol Bay and growth estimates (Otto et al. 1990, Stevens and Swiney 2007b); however, it is possible that this division does not completely separate primiparous and multiparous females. Unless mated in a controlled environment, it is impossible to distinguish primiparous and multiparous females, because female red king crabs molt shortly before mating and have indeterminate growth. Few ovigerous females less than 104 mm CL were collected in the southeastern Alaska samples so only likely multiparous females are included in analyses.

Clutch fullness indices

Biologists on NMFS Alaska Fisheries Science Center eastern Bering Sea bottom trawl surveys and ADFG southeastern Alaska red king crab stock assessment surveys, and shellfish fishery observers onboard commercial vessels, assess red king crab egg production by estimating clutch fullness indices (CFI). CFIs score egg clutches by a visual estimate of egg clutch size relative to abdomen size, and scoring methods vary by agency. NMFS scores clutches as immature, mature with no embryos, trace to 12.5% full, and in 25% intervals from 25% to 100% full. Shellfish fishery observers score clutches as no embryos, trace to 12.5% full, and in 25% intervals from 25% to 100% full. ADFG in southeastern Alaska scores clutches in intervals of 10% from 0% to 100% full. BB07/BB08, SEAK08, and OBS07 fecundity estimates were compared with CFI data collected for the egg clutches during the surveys to assess the precision of CFI in estimating fecundity. The different methods for assessing CFI were examined separately to determine if methodology affected the precision of CFI in estimating fecundity. Bristol Bay 2007 and 2008 data were combined since the same CFI methods were used for both data sets. ADFG southeastern Alaska CFIs were placed into low (40-70% full) and high (80-100% full) bins.

Statistical analysis

To make comparisons across areas, years, and CFI we examined the relationship between fecundity and CL using ANCOVA and multiple linear regressions. The Shapiro-Wilk *W* test for normality and Levene's test for homogeneity of variance were used to determine if data met assumptions of ANCOVA and multiple linear regression. Some data did not pass these tests and natural log transformation of data did not change the significance of results, so only untransformed data were analyzed. Examination of residual plots suggest that these data did not grossly violate assumptions and ANCOVA, and multiple linear regressions are reasonably robust to minor departures from these assumptions (Hassard 1991). Equality of slopes from the regression lines was tested and when slopes were homogeneous ANCOVA was used. When the slopes differed, multiple linear regressions were used for comparisons among groups. For ANCOVA analysis, year, area, and CFI were grouping independent variables, CL was the covariate, and fecundity was the response variable. When significant differences were detected, Tukey LSD post-hoc tests with a Bonferroni correction were used for multiple comparisons among areas or years. Full model multiple linear regressions were used with CL and area or CFI as independent variables, fecundity as the dependent variable and the interaction term of CL × area or CL × CFI included. If significant differences were not detected between groups they were dropped from the model. Due to differences in upper size limits sampled in the Bristol Bay collections, only females 105-145 mm CL were used in the temporal analysis. Statistical analyses were conducted in SPSS 11.5.1 (SPSS Inc., Chicago).

Results

Fecundity of Alaska red king crabs increased significantly ($p < 0.001$) with increasing female size in all years and areas studied; however, size alone does not explain all of the variability in the linear regressions with R^2 values ranging from 0.29 to 0.79 (Figs. 2, 3, 4). Variation in fecundity estimates among females of similar size was observed. For example, mean fecundity estimates of 100,878 to 161,857 and 148,192 to 286,540, were observed for BB07 females of 100 and 130 mm CL respectively (Fig. 2). In Barlow Cove, fecundity estimates of females 130 mm CL range from 161,127 to 213,323 (Fig. 3).

Temporal differences in fecundity were detected between likely primiparous (ANCOVA, $F_{2,157} = 22.912$, $p < 0.001$; Fig. 2a) and likely multiparous (ANCOVA $F_{2,214} = 8.083$, $p < 0.001$; Fig. 2b) Bristol Bay red

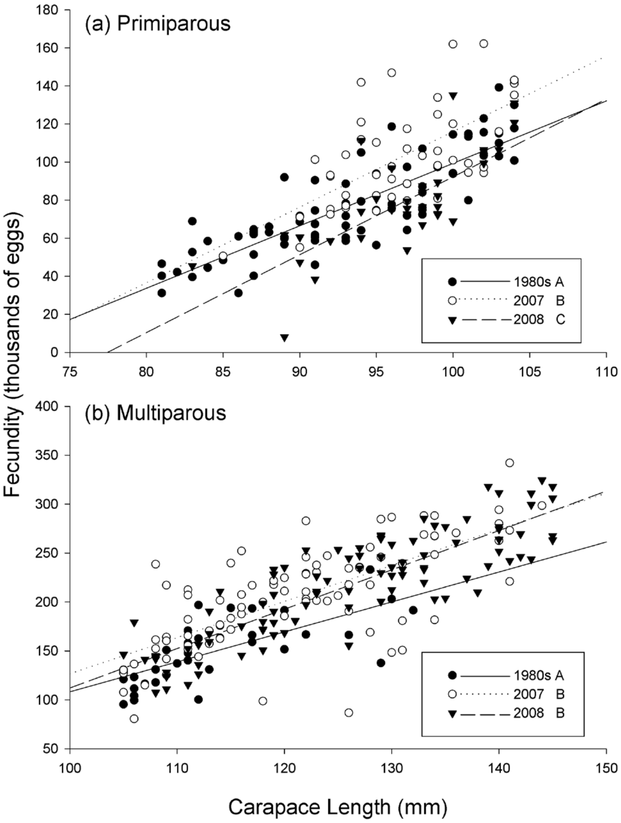

Figure 2. Fecundity with regression lines of Bristol Bay red king crabs: (a) primiparous 1980s = 1982, 1983, 1985 summer collections (R^2 = 0.73, n = 76), 2007 = summer 2007 collections (R^2 = 0.43, n = 48), 2008 = summer 2008 collections (R^2 = 0.56, n = 37); and (b) multiparous 1980s (R^2 = 0.49, n = 34), 2007 (R^2 = 0.51, n = 87), 2008 (R^2= 0.75, n = 97). Years marked with different letters denote significant differences (Tukey HSD, p < 0.05).

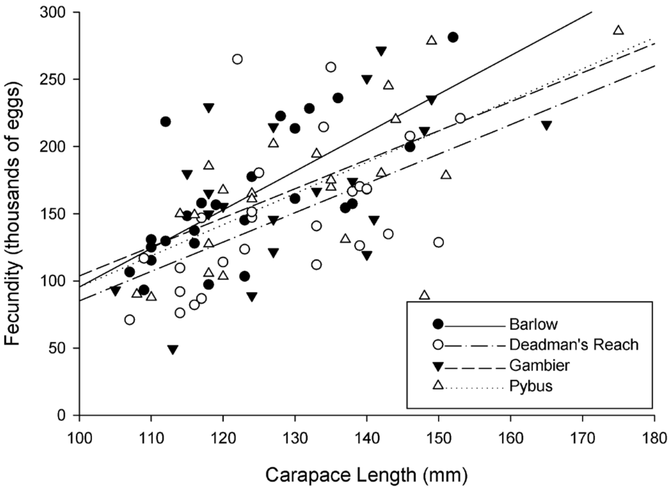

Figure 3. Fecundity with regression lines of 2008 southeastern Alaska red king crabs from Barlow Cove (R^2 = 0.51, n = 25); Deadman's Reach (R^2 = 0.29, n = 27); Gambier Bay (R^2 = 0.30, n = 20); and Pybus Bay (R^2 = 0.46, n = 23). No significant differences were detected between areas (ANCOVA, p = 0.158).

Table 1. Multiple linear regression of NMFS clutch fullness index (CFI) groups and fecundity.

Model	Coefficient	Standard error	*t*-ratio	*P*
Comparison of CFI 50%, 75%, and 100%. CFI 100% base[a]				
Constant	–30,7830.48	12,814.00	–24.02	<0.001
CL	4,192.18	107.92	38.85	<0.001
CFI	90,805.45	40,309.03	2.25	0.025
CL × CFI	–967.46	354.49	–2.73	0.007
Comparison of CFI 50% and 100%. CFI 50% base				
Constant	–21,7025.03	41,088.86	–5.28	<0.001
CL	3,224.72	363.03	8.88	<0.001
CFI	–85,862.51	44,028.77	–1.95	0.053
CL × CFI	913.65	386.56	2.36	0.019

[a] No significant difference detected between CFI 75% and 100%, so CFI 75% was dropped from model.

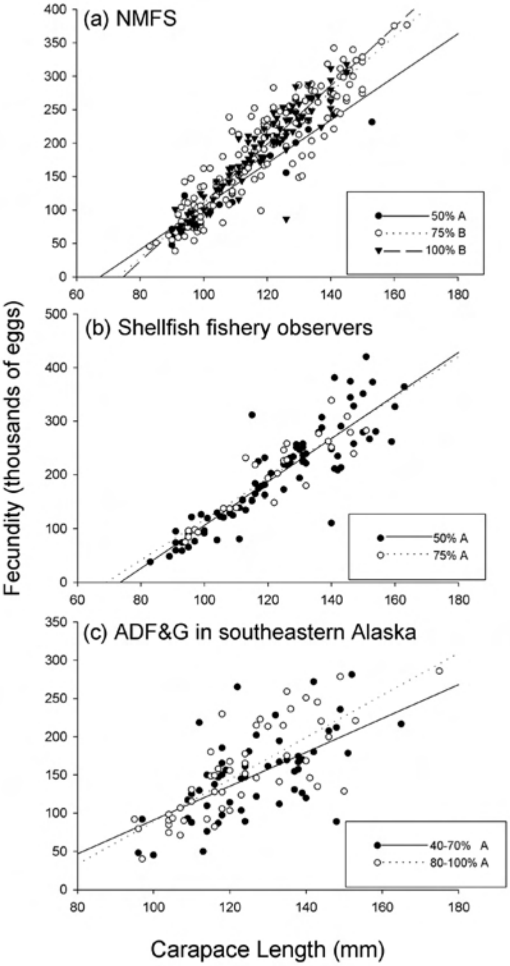

Figure 4. Fecundity with regression lines of multiparous 2008 Bristol Bay and southeastern Alaska red king crabs. Bristol Bay = 2008 summer collections (R^2 = 0.79, n = 110), southeastern Alaska = 2008 summer collections (R^2 = 0.36, n = 95). Bristol Bay females were significantly more fecund that southeastern Alaska females (multiple linear regression, p = 0.001).

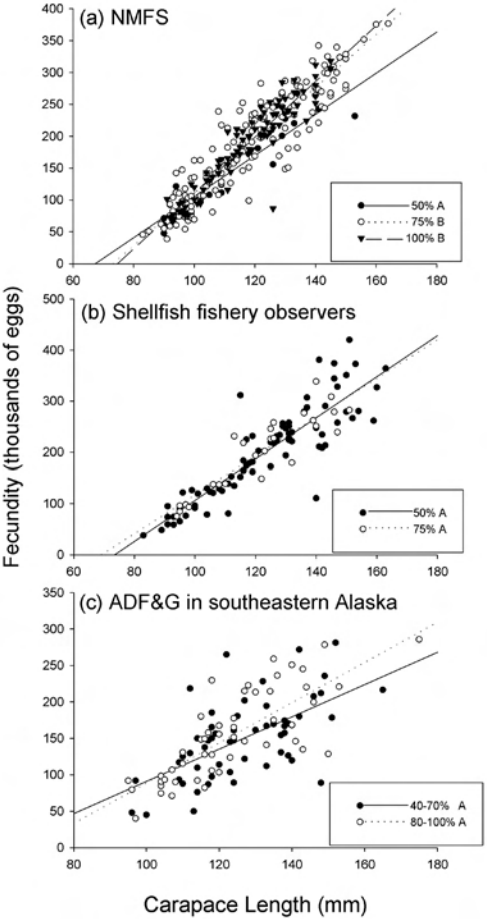

Figure 5. Fecundity with regression lines for (a) NMFS, 50% full ($R^2 = 0.87$, n = 22), 75% full ($R^2 = 0.85$, n = 166), 100% full ($R^2 = 0.87$, n = 89); (b) shellfish fishery observers, 50% full ($R^2 = 0.78$, n = 79), 75% full ($R^2 = 0.81$, n = 26); and (c) ADFG in southeastern Alaska 40-70% full ($R^2 = 0.37$, n = 55), 80-100% full ($R^2 = 0.60$, n = 51) clutch fullness indices. CFI marked with different letters denote significant differences (multiple linear regressions and ANCOVA, $p < 0.05$).

king crabs. Among likely primiparous crabs, females sampled in 2007 were most fecund (ANCOVA adjusted mean 97,645, SE = 2,435.00) followed by females sampled in 1980s (ANCOVA adjusted mean 84,040, SE = 1,953.20) and 2008 (ANCOVA adjusted mean 73,298, SE = 2,756.21) (Tukey HSD, $p \leq 0.006$, Fig. 2a). Fecundity of likely multiparous Bristol Bay red king crabs was significantly greater in 2007 (ANCOVA adjusted mean 20,9607, SE = 3,400.45) and 2008 (ANCOVA adjusted mean 20,3298, SE = 3,320.18) (which did not differ), than in the 1980s (ANCOVA adjusted mean 18,3240, SE = 5,690.47) (Tukey HSD, $p < 0.05$, Fig. 2b).

Fecundity of crabs in southeastern Alaska in summer 2008 did not vary significantly among areas sampled (ANCOVA $F_{3,90} = 1.775$, $p = 0.158$; Fig. 3), therefore southeastern Alaska samples were pooled to make regional comparisons of 2008 fecundity between Bristol Bay and southeastern Alaska. Red king crabs in Bristol Bay were significantly more fecund than crabs in southeastern Alaska (multiple linear regression, $t = 3.29$, $p = 0.001$) and the interaction of size and location was significant (multiple linear regression, $t = -4.71$, $p < 0.001$, Fig. 4).

In comparisons of fecundity among CFI categories, CFI was not a reliable predictor of fecundity. For pooled BB07 and BB08 data, the fecundities of egg clutches classified as NMFS 50%, 75%, and 100% CFI categories were not significantly different from each other, except egg clutches classified as 100% CFI were more fecund than crabs assigned a 50% CFI (Table 1, Fig. 5a). Likewise significant differences in fecundity were not detected between shellfish fishery observer 50% and 75% CFI (ANCOVA $F_{1,102} = 0.323$, $p = 0.571$) or ADFG in southeastern Alaska low (40-70%) and high (80-100%) CFI categories (ANCOVA $F_{1,103} = 1.930$, $p = 0.168$, Fig. 5).

Discussion

We observed temporal and spatial variability in Alaska red king crab fecundity in this study. Likely multiparous Bristol Bay females were less fecund in the 1980s than in 2007 or 2008 (Fig. 2b) and females had lower fecundity in southeastern Alaska relative to Bristol Bay (Fig. 4); however, fecundity did not differ among areas within southeastern Alaska (Fig. 3). These observed differences in fecundity are not unprecedented, as differences in fecundity have been reported for red king crab (Sato 1958, Otto et al. 1990, Sherbakova et al. 2008) and other decapod species (Thomas 1964, Jewett 1981, Brante et al. 2003, Bas et al. 2007), but explanations for the observed differences are rarely presented. Nonetheless four mechanisms that may affect fecundity and reproductive success of decapod crustaceans have been suggested. Fecundity may be regulated by density-dependent factors in which high population density yields a smaller size at maturity resulting in lower population fecundity (Chittleborough 1976, Sampedro et al. 1997, DeMartini et al. 2003). Second, reduction of reproductive success due to sperm limitation has been hypothesized for lithodid species including the spiny king crab, *Paralithodes brevipes* (Sato et al. 2005, 2006, 2007) and *Hapalogaster dentate* (Sato and Goshima 2006). Third, egg loss was observed throughout the incubation period for red king crab with higher egg loss rates earlier versus later during brooding (Matsuura and Takeshita 1985). Common sources of egg loss are brooding of unfertilized eggs, abrasion, disease, and egg predators. Egg loss has been reported for some Alaska red king crab populations due to heavy mortality attributed to brood predators (Kuris et al. 1991); however, egg clutches examined in this study did not appear to have been preyed upon by egg predators. Fourth, latitude and environment, including water temperature and food availability/quality, have been shown to influence gamete development, reproductive cycles, and size at maturity among many crab species (Chittleborough 1976, Sastry 1983, Shields 1991) which may result in variability of fecundity under different conditions.

In this study, we examined fecundity of likely primiparous (<105 mm CL) and likely multiparous (≥105 mm CL) crabs separately. Our intent was to exclude primiparous females from the group of large sized crabs at the cost of potentially having a combination of primiparous and multiparous females in the group of small sized crabs. No differences were detected between fecundity of likely multiparous BB07 and BB08 females; however, significant differences were detected between these years among likely primiparous females (Fig. 2). These results suggest that smaller females may have more variable fecundity than larger females. Alternately, shifts in the number of females maturing and extruding eggs or size at maturity, which are known to be variable in Bristol Bay (Otto et al. 1990), may have altered the ratio of primiparous to multiparous females between 2007 and 2008. If primiparous red king crabs are less fecund than equal-sized multiparous females, then the decrease in fecundity between 2007 and 2008 may have been due to an increased proportion of primiparous females sampled in 2008. These uncertainties illustrate the difficulties in discerning potential differences in fecundity between primiparous and multiparous female red king crab.

Within Bristol Bay, likely multiparous females were less fecund in the 1980s than in 2007 or 2008 (Fig. 2b). The BB80s collections occurred during a time of decline in the stock beginning in 1980 and resulting in a fishery closure in 1983 (Bowers et al. 2008). Bristol Bay abundance estimates in 1979 were 76.945 million mature males and 154.290 million mature females compared to only 8.850 million mature males and 11.937 million mature females in 1985 (Zheng and Siddeek 2009). In comparison, stock abundance was higher in 2007 and 2008 with an estimated 22.235 and 25.933 million mature males and 62.816 and 58.303 million mature females respectively (Zheng and Siddeek 2009). The stock decline in the 1980s may have affected reproductive success. In 1982, it is estimated that 44% of females greater than 99 mm CL did not extrude eggs; in contrast, from 1975 through 1981 at the most 18% of females greater than 99 mm CL did not extrude eggs in a given year (Otto et al. 1990). Otto et al. (1990) reported that clutch sizes of females that did extrude eggs in 1982 did not appear to differ from other years they examined except in 1984 when an unusually high proportion of partial clutches was observed. Bristol Bay red king crabs in the early 1980s may have shown signs of decreased reproductive success; however, it is difficult to attribute the lower fecundity observed in this study during the BB80s to this phenomenon as only females with full clutches were sampled.

We observed variation in fecundity of similar sized females collected from the same location at the same time (Figs. 2, 3). Differences in fecundity may be attributed to some females being primiparous and others multiparous; however, this does not explain the differences observed among larger females. Females may have developed their gonads in different environmental conditions such as water temperature and/or were exposed to food of variable quantity and quality which effected fecundity. Genetic information on Alaska red king crab stock structure is lacking, therefore it is not known if Bristol Bay red king crab are a single population. It is possible that differences in fecundity observed may be the result of sampling different populations. Alternately, fecundity may naturally vary between similar sized females from the same population exposed to similar environmental conditions.

Our data suggest that current CFI methods of NMFS, ADFG in southeastern Alaska, and ADFG Shellfish Observer Program, may be useful to distinguish large differences in fecundity (e.g., >50% for NMFS) but are not accurate estimators of fecundity. The lack of significant differences among CFI scores may be attributed to inconsistencies in observer scoring, resulting in significant overlap in fecundity between different CFIs. Similar issues are encountered for estimating egg production of eastern Bering Sea snow crab, *Chionoecetes opilio,* for monitoring and management (Orensanz et al. 2003). Orensanz et al. (2003) concluded that estimating fecundity is costly and time consuming, and that CFI methods used for snow crab are subjective. They concluded that clutch volume may be a better indicator of individual female egg production because it is easily measured and correlates well with fecundity and clutch weight estimates.

Development of more precise measures of egg production will improve Alaska red king crab stock assessment and management if biological reference points based upon egg production are implemented. The utility of using clutch volume as an indicator of individual egg production rather than estimating fecundity for Bristol Bay red king crab is currently being examined (Katherine Swiney, NMFS, Kodiak). Clutch volumes for red king crab are being determined in the laboratory from egg clutches collected and frozen at sea. Eggs are stripped off of the pleopods and put into a graduated cylinder with a known volume of water. After the eggs are added the volume is noted and the initial volume of water is subtracted to derive the volume of eggs. Preliminary data suggest that clutch volumes are a better estimator of fecundity than CFI (NMFS, unpubl. data). Using clutch volumes to estimate fecundity is quicker than estimating fecundity with the dry weight methods used in this study; however, before we recommend using clutch volume to measure egg production, the method must be validated. For example, if individual females brood eggs of different sizes then the female brooding larger eggs may have a higher estimated fecundity due to an observed larger clutch volume than a female brooding the same amount of smaller eggs.

The incorporation of reproductive potential in the development of biological reference points is a pressing fishery management need for Alaska red king crab stocks. We found that red king crab fecundity is variable spatially, temporally, and by female size/reproductive status. Thus, variability in fecundity should be considered in development of egg production-based biological reference points, stock assessment, and management models. In addition, our data suggest that the CFI data collection protocols currently used by NMFS, shellfish fishery observers, and ADFG in southeastern Alaska may lack the precision necessary to accurately estimate fecundity. More precise and easily executed methods to estimate egg production are needed.

Acknowledgments

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References

Bas, C.C., E.D. Spivak, and K. Anger. 2007. Seasonal and interpopulational variability in fecundity, egg size, and elemental composition (CHN) of eggs and larvae in a grapsoid crab, *Chasmagnathus granulatus*. Helgol. Mar. Res. 61:225-237. doi:10.1007/s10152-007-0070-y

Bell, M.C. 2006. Review of Alaska crab overfishing definitions. University of Miami Independent System for Peer Reviews. 35 pp. Accessed Dec. 2010: http://www.fakr.noaa.gov/npfmc/analyses/KTCAM24/CIE_Overfishing406.pdf.

Bowers, F.R., M. Schwenzfeier, S. Coleman, B.J. Failor-Rounds, K. Milani, K. Herring, M. Salmon, and M. Albert. 2008. Annual management report for the commercial and subsistence shellfish fisheries of the Aleutian Islands, Bering Sea, and the westward region's shellfish observer program, 2006/07. Alaska Department of Fish and Game, Fishery Management Report 08-02. 190 pp.

Brante, A., M. Fernandez, L. Eckerle, F. Mark, H.O. Portner, and W. Arntz. 2003. Reproductive investment in the crab *Cancer setosus* along a latitudinal cline: Egg production, embryo losses and embryo ventilation. Mar. Ecol. Prog. Ser. 251:221-232. doi:10.3354/meps251221

Caputi, N. 2006. Alaskan crab overfishing definitions review. University of Miami Independent System for Peer Reviews. 22 pp. Accessed Dec. 2010: http://www.fakr.noaa.gov/npfmc/analyses/KTCAM24/CIE_Overfishing406.pdf.

Chittleborough, R.G. 1976. Breeding of *Panulirus longipes cygnus* George under natural and controlled conditions. Aust. J. Mar. Freshw. Res. 27:499-516. doi:10.1071/MF9760499

Clark, J.E., T. Koeneman, C.A. Botelho, S. Merkouris, and D. Woodby. 2003. Estimation of red king crab (*Paralithodes camtschaticus*) abundance and available harvest in Southeast Alaska for the 2001/2002 season using a pot survey. Alaska Department of Fish and Game, Regional Information Report 1J03-25. 75 pp.

Collie, J.S., and A.K. DeLong. 1998. Development of a three-stage catch-survey analysis. Report to the Alaska Department of Fish and Game. University of Rhode Island, Graduate School of Oceanography. 36 pp.

Cordue, P. 2006. Report on Bering Sea and Aleutian Islands crab stock overfishing definitions. University of Miami Independent System for Peer Reviews. 26 pp. Accessed Dec. 2010: http://www.fakr.noaa.gov/npfmc/analyses/KTCAM24/CIE_Overfishing406.pdf.

DeMartini, E.E., G.T. DiNardo, and H.A. Williams. 2003. Temporal changes in population density, fecundity, and egg size of the Hawaiian spiny lobster (*Panulirus marginatus*) at Necker Bank, Northwestern Hawaiian Islands. Fish. Bull.101:22-31.

Donaldson, W.E., and S.C. Byersdorfer. 2005. Biological field techniques for lithodid crabs. Alaska Sea Grant College Program, University of Alaska Fairbanks. 76 pp.

Hassard, T.H. 1991. Understanding biostatistics. Mosby Year Book, Inc., St. Louis. 292 pp.

Haynes, E.B. 1968. Relation of fecundity and egg length to carapace length in the king crab, *Paralithodes camtschatica*. Proc. Nat. Shellfish. Assoc. 58:60-62.

Jewett, S.C. 1981. Variations in some reproductive aspects of female snow crabs *Chionoecetes opilio*. J. Shellfish Res. 1:85-99.

Johnson, B.A., S.F. Blau, and R.E. Baglin. 2001. Fecundity of red king crabs (*Paralithodes camtschaticus*) off Kodiak Island, Alaska, and an initial look at observer agreement of clutch fullness. In: A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley, and D. Woodby (eds.), Crabs in cold water regions: Biology, management and economics. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 305-321.

Kuris, A.M., S.F. Blau, A.J. Paul, J.D. Shields, and D.E. Wickham. 1991. Infestation by brood symbionts and their impact on egg mortality of the red king crab, *Paralithodes camtschatica*, in Alaska: Geographic and temporal variation. Can. J. Fish. Aquat. Sci. 48:559-568. doi:10.1139/f91-071

Matsuura, S., and K. Takeshita. 1985. Development and decrease in number of eggs attached to pleopods of laboratory-reared king crabs, *Paralithodes camtschatica* (Tilesius). In: Proceedings of the International King Crab Symposium. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 155-165.

Orensanz, J.M., B. Ernst, D.A. Armstrong, and A.M. Parma. 2003. Detecting early warnings of recruitment overfishing in male-only crab fisheries: An example from the snow crab fishery. In: G.H. Kruse, V.F. Gallucci, D.E. Hay, R.I. Perry, R.M. Peterman, T.C. Shirley, P.D. Spencer, B. Wilson, D. Woodby (eds.), Fisheries assessment and management in data-limited situations. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 267-287.

Otto, R.S., R.A. MacIntosh, and P.A. Cummiskey. 1990. Fecundity and other reproductive parameters of female red king crab (*Paralithodes camtschatica*) in Bristol Bay and Norton Sound, Alaska. In: Proceedings of the International Symposium on King and Tanner Crabs. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 65-90.

Powell, G.C., and R.B. Nickerson. 1965. Reproduction of king crabs, *Paralithodes camtschatica* (Tilesius). J. Fish. Res. Board Can. 22:101-111.

Powell, G.C., B. Shafford, and M. Jones. 1973. Reproductive biology of young adult king crabs *Paralithodes camtschatica* (Tilesius) at Kodiak, Alaska. Proc. Nat. Shellfish. Assoc. 63:77-87.

Quinn, T.J. II, T.C. Shirley, and T.M. Koeneman. 2006. Southeast Alaska red king crab stock assessment review. Alaska Department of Fish and Game, Special Publication 06-12. 46 pp.

Sampedro, M.P., L. Fernandez, J. Freire, and E. Gonzalez-Gurriaran. 1997. Fecundity and reproductive output of *Pisidia longicornis* (Decapoda, Anomura) in the Ria de Arousa (Galicia, NW Spain). Crustaceana 70:95-110. doi:10.1163/156854097X00384

Sastry, A.N. 1983. Ecological aspects of reproduction. In: F.J. Vernbert and W.B. Vernberg (eds.), The biology of Crustacea, vol. 8. Environmental adaptations. Academic Press, New York, pp. 179-270.

Sato, S. 1958. Studies on larval development and fishery biology of king crab, *Paralithodes camtschatica* (Tilesius). Bull. Hokkaido Reg. Fish. Res. Lab. 99 pp.

Sato, T., and S. Goshima. 2006. Impacts of male-only fishing and sperm limitation in manipulated populations of an unfished crab, *Hapalogaster dentata*. Mar. Ecol. Prog. Ser. 313:193-204. doi:10.3354/meps313193

Sato, T., M. Ashidate, T. Jinbo, and S. Goshima. 2006. Variation of sperm allocation with male size and recovery rate of sperm numbers in spiny king crab *Paralithodes brevipes*. Mar. Ecol. Prog. Ser. 312:189-199. doi:10.3354/meps312189

Sato, T., M. Ashidate, T. Jinbo, and S. Goshima. 2007. Does male-only fishing influence reproductive success of the female spiny king crab, *Paralithodes brevipes*. Can. J. Fish. Aquat. Sci. 64:735-742. doi:10.1139/F07-044

Sato, T., M. Ashidate, S. Wada, and S. Goshima. 2005. Effects of male mating frequency and male size on ejaculate size and reproductive success of female spiny king crab *Paralithodes brevipes*. Mar. Ecol. Prog. Ser. 296:251-262. doi:10.3354/meps296251

Sherbakova, N.V., E.N. Drobyazin, and O.M. Korn. 2008. Peculiarities of reproductive biology and larval development of the red king crab *Paralithodes camtschaticus* in Peter the Great Bay, Sea of Japan. Russ. J. Mar. Biol. 34:374-383. doi:10.1134/S1063074008060059

Shields, J.D. 1991. The reproductive ecology and fecundity of *Cancer* crabs. In. A. Wenner and A. Kuris (eds.), Crustacean issue 7: Crustacean egg production. A.A. Balkema, Rotterdam, pp. 193-213.

Smith, S.J., and B. Sainte-Marie. 2004. Biological reference points for invertebrate fisheries: Introduction. Can. J. Fish. Aquat. Sci. 61:1303-1306. doi:10.1139/f04-135

Stevens, B.G., and K.M. Swiney. 2007a. Hatch timing, incubation period, and reproductive cycle for captive primiparous and multiparous red king crab, *Paralithodes camtschaticus*. J. Crust. Biol. 27:37-48. doi:10.1651/S-2663.1

Stevens, B.G., and K.M. Swiney. 2007b. Growth of female red king crabs *Paralithodes camtschaticus* from Kodiak, Alaska, during pubertal, primiparous, and multiparous molts. Alaska Fish. Res. Bull. 2:270-277.

Stone, R.P., C.E. O'Clair, and T.C. Shirley. 1993. Aggregating behavior of ovigerous female red king crab, *Paralithodes camtschaticus,* in Auke Bay, Alaska. Can. J. Fish. Aquat. Sci. 50:750-758. doi:10.1139/f93-086

Thomas, H.J. 1964. The spawning and fecundity of the Norway lobsters (*Nephrops norvegicus* L.) around the Scottish coast. J. Cons. Int. Explor. Mer 29:221-229.

Zheng, J., and M.S.M. Siddeek. 2009. Bristol Bay red king crab stock assessment in spring 2009. In: North Pacific Fishery Management Council (ed.), Stock assessment and fishery evaluation report for the king and Tanner crab fisheries of the Bering Sea and Aleutian Islands regions. North Pacific Fishery Management Council 2009 BSAI SAFE report, pp. 1-106.

Zheng, J., M.C. Murphy, and G.H. Kruse. 1995. A length-based population model and stock-recruitment relationships for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. Can. J. Fish. Aquat. Sci. 52:1229-1246.

Siddon, C.E. and J.A. Bednarski. 2010. Variation in Size at Maturity of Tanner Crab in Southeastern Alaska, U.S.A. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.13

Variation in Size at Maturity of Tanner Crab in Southeastern Alaska, U.S.A.

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Abstract

Predicting climate change effects on commercially important species is an increasingly important issue for fisheries scientists. It requires understanding how climate change will affect oceanographic conditions and how this will influence population dynamics of target species. Utilizing natural experiments where oceanographic conditions change over small spatial scales is one way to examine the role of climate change. We examine the variability of the size at maturity for Tanner crab (*Chionoecetes bairdi*) in the fjord system of southeastern Alaska. Variation in size at maturity for male and female crabs was examined among six survey areas and compared with changes in latitude, depth, temperature, temperature fluctuations, and fishing pressure.

The size at maturity varied significantly among areas for both male and female Tanner crabs, but they were not correlated. Male size at maturity averaged 117 mm carapace width (CW) and ranged from 108 mm in Glacier Bay to 135 mm in Stephens Passage. Female size at maturity averaged 89 mm CW, with a minimum in Glacier Bay (85 mm) and a maximum in Port Camden (95 mm). Average water temperatures ranged from 5.5°C in Holkham Bay to 7.7°C in Port Camden. Temperature fluctuations varied substantially, with almost no change in water temperatures in Holkham Bay and Port Camden, and temperature drops of 1°C in 1 hour in Icy Strait. No environmental or fishing pressure variables explained variations in size at maturity; this suggests other biological factors may play a greater role in determining size at maturity for Tanner crab in southeastern Alaska.

Introduction

One of the most difficult tasks for fisheries biologists today is predicting the influence of global climate change on commercially important species. This requires knowledge of how climate change will affect oceanographic conditions and a mechanistic understanding of how these changes translate into modifying population dynamics. Many studies have shown the importance of increases in water temperature on growth rates (e.g., Brander 1995, Calcagno et al. 2005), size at maturity (e.g., Dhillon and Fox 2004), and fecundity (e.g., Pörtner et al. 2001). In addition to increases in seawater temperatures, changes in current patterns, salinity, and increased variability of environmental factors have been predicted, yet there is little experimental evidence on how increased variability (e.g., temperature fluctuations) may affect population dynamics (but see Sanford 2001). Fishing pressure can also affect population parameters through increased mortality and by changes in size at maturity (Reznick et al. 1997, Conover and Munch 2002, Sainte-Marie et al. 2008). Understanding the potential interaction between climate change and fishing pressure will be necessary for the long-term sustainability of many commercial species.

Size at maturity has a strong tie to population dynamics, as it can influence reproductive output through the combination of fecundity and number of lifetime reproductive cycles. In general, fecundity increases with body size and does so for Tanner crabs (*Chionoecetes bairdi*; Webb 2009). Also, if size is related to age in Tanner crab then crabs that mature at an earlier age have an increased probability of reproducing more times (i.e., seasons) before senescence. Therefore crabs that mature at a smaller size (younger age) may have greater lifetime fitness, even though their fecundity in a given year would be smaller compared to larger (older) crabs. However, this assumes that crabs have similar overall life expectancies regardless of the size (age) in which they mature.

Size at maturity in Tanner and snow crabs has been shown to vary in the Bering Sea and is correlated with latitude, longitude, depth, temperature, and year (Somerton 1981, Otto and Pengilly 2002, Orensanz et al. 2007, Zheng 2008). However, no clear picture has emerged regarding the cause(s) of this variability, although Orensanz et al. (2007) strongly emphasize temperature as the causative factor. Tanner crabs in southeastern Alaska provide another opportunity to examine the importance of oceanographic variability and fishing on population parameters on population structure, specifically size at maturity. Tanner crab populations in southeastern Alaska span 4 degrees of latitude and have spatially distinct benthic populations with differences in oceanographic conditions in this fjord-dominated system. Freshwater input, current patterns, and water temperature all vary over relatively small spatial scales. Male Tanner crabs have also been commercially harvested in southeastern Alaska since 1968, with large fluctuations in yearly harvest and consistently high exploitation rates (Clark et al. 2001). The male-only fishery also allows us to examine difference between the combination of environmental and fishing effects (males) and environmental effects only (females).

Here we address the importance of oceanographic conditions and fishing pressure on the size at maturity of Tanner crabs in southeastern Alaska. Specifically, we examined how size at maturity varied as a function of geographic location, bottom temperature, temperature fluctuations, and fishing pressure for both male and female crabs.

Materials and methods

All data were collected during the Alaska Department of Fish and Game Tanner crab surveys in southeastern Alaska from 1997 to 2008 (Fig. 1). The survey consists of a stratified random pot survey in 2-6 areas (areas added throughout the time series) conducted in October of each year. Approximately 40-60 pots were set within each area (proportional to area size). In addition to the typical data collected (carapace width, sex, shell condition, etc.) maximum height of the right chela of male crabs was measured to the nearest millimeter using vernier calipers. Further survey details have been documented elsewhere (Bednarski et al. 2008).

Size at maturity

Differences in size at maturity among locations were analyzed with a generalized linear model approach using a binomial distribution and a Logit link function. Main effects for the model were carapace width, location, and their interaction. The response variable was maturity (mature/immature) as determined through the program MATURE (see below). Post hoc contrast analyses were conducted to test specific differences among locations. In addition, size at 50% maturity (L50) for both male and female crabs was estimated using logistic regression for each location. Data from all years were pooled (for each location) to look at broad scale differences, and due to sample size limitations in some location/year combinations.

Although we recognize that mean mature size can be a more appropriate metric for females (Somerton 1981, Zheng 2008), preliminary analyses showed a very strong correlation between the mean mature and the L50 carapace widths in l0 locations throughout southeastern Alaska ($p < 0.0001$, $r^2 = 0.94$, n = 10). Thus, for consistency of methods and the ability to directly compare male and female results we feel using L50 for females is warranted. Interestingly, a similar relationship between mean mature and L50 was found for male crabs ($p = 0.01$, $r^2 = 0.83$, n = 6).

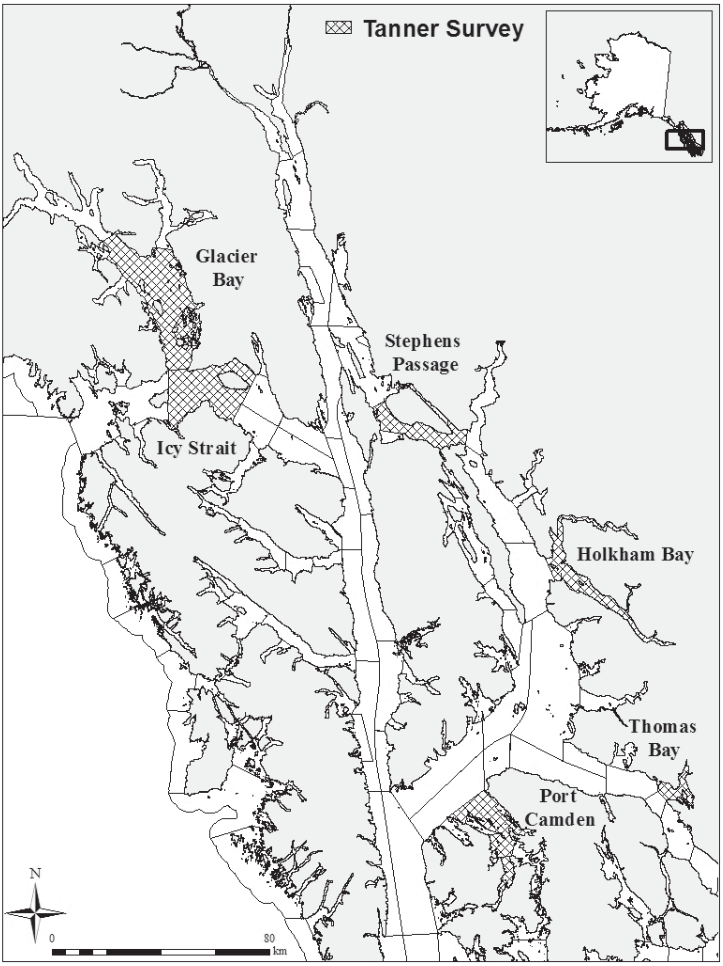

Figure 1. Southeast Alaska annual Tanner crab stock assessment survey areas, Alaska Department of Fish and Game.

A random subsample of male crabs was taken from the pooled data to remove any effect of recruitment pulses on size at maturity estimates and to foster comparisons across areas. Fifteen crabs were randomly selected from each of the eight size categories: ≤100, 101-110, 111-120, 121-130, 131-140, 141-150, 151-160, >160 mm carapace width. Total sample size equaled 120 for each area. All analyses were done using JMP® statistical software version 7.0.1 (SAS Institute 2007).

Maturity for both male and female Tanner crabs was determined morphometrically. Although the change from morphometrically immature to morphometrically mature is well described (e.g., Somerton 1981, Tamone et al. 2007, Zheng 2008) as a change in the allometric relationship between carapace width and chela height, these changes are visually subtle and hard to distinguish in the field. Therefore males were separated using the MATURE software (Somerton 1981), which iteratively fits two regression lines to log-transformed carapace width and chela heights and then assigns a maturity status (mature/immature) to each data point (see Zheng 2008 for a detailed description of the MATURE software).

Mature and immature female Tanner crabs are easily separated due to an abrupt morphological change where the abdominal flap increases in size disproportionately to the carapace width at the maturity molt (Hartnoll 1978), and they were determined visually in the field.

Temperature

Bottom temperature was collected on a majority of pots set within each area from 2006 to 2009. Tidbit temperature loggers were attached to the pots and recorded temperature every hour (~17-24 measurements). Average temperature of each logger was used to calculate mean bottom temperature of a given survey area for each year. In addition, temperature fluctuations (*TF*) were calculated as the mean of the standard deviation of each logger for each year:

$$TF = \frac{\sum_{i=1}^{n} SD_i}{n},$$

where SD_i is the standard deviation of temperature logger *i*, and *n* is the number of temperature loggers deployed within a given survey area.

Correlation analyses

Potential explanations of the variability in size at maturity among areas (for both males and females), were examined with correlation analyses. We explored the possible relation of size at maturity to center of latitude, mean depth, average water temperature, and mean temperature fluctuations as reported in Table 1. In addition, the possible relation of size at maturity to commercial fishing pressure: average commercial harvest (1985-2004, see Table 1) and harvest density (average catch/fished area) were examined.

Results

The relationship between log-transformed carapace width and chela height showed a very clear distinction between morphometrically mature and immature Tanner crabs (Fig. 2).

Table 1. Latitude, depth, bottom temperatures, temperature fluctuations, and average commercial harvest for each survey area. Latitude was visually estimated as the center of each survey area using ArcGIS software.

Survey area	Latitude (center)	Mean depth ±SD (m)	2006-2009 mean temperature ±SD (C)	2006-2009 mean temperature fluctuations ±SD (C)	Harvest (lbs) 1985-2004
Glacier Bay	58.65	185 ± 62	6.16 ± 0.34	0.19 ± 0.05	150,538
Icy Strait	58.33	113 ± 15	6.17 ± 0.07	0.26 ± 0.07	145,824
Stephens Passage	58.23	57 ± 16	6.23 ± 0.44	0.16 ± 0.05	140,266
Holkham Bay	57.75	232 ± 90	5.52 ± 0.20	0.07 ± 0.05	172,306
Thomas Bay	57.02	91 ± 27	6.69 ± 0.15	0.17 ± 0.12	56,645
Port Camden	56.85	68 ± 16	7.77 ± 0.08	0.08 ± 0.05	83,188

Table 2. Generalized linear model results for testing the effects of carapace width, survey location, and their interaction on the maturity of male and female Tanner crab.

Sex	Effect	df	$\chi 2$	*p*
Male	Location	5	55.96	<0.0001
	Carapace width	1	327.51	<0.0001
	L × C	5	3.28	0.66
Female	Location	5	212.86	<0.0001
	Carapace width	1	1195.18	<0.0001
	L × C	5	41.57	<0.0001

Morphometric maturity varied significantly as a function of carapace width and location for both males and females (Table 2, Fig. 3). Size at maturity for males was smallest in Glacier Bay (107.9 mm); intermediate for Icy Strait, Holkham Bay, Port Camden, and Thomas Bay; and largest for Stephens Passage (135.1 mm). The overall mean size at maturity for the six areas was 117.2 mm. This constitutes a 27% increase in size at maturity between Glacier Bay and Stephens Passage and a difference of approximately 12% in these two areas from the mean size at maturity.

The size at maturity for females was smallest in Glacier Bay (84.7 mm) and Icy Strait (84.2 mm) and largest for Stephens Passage (93.3 mm) and Port Camden (95.3 mm). This constitutes a 10% increase in size at maturity between Icy Strait and Stephens Passage. Although size at maturity was smaller in Glacier Bay and larger in

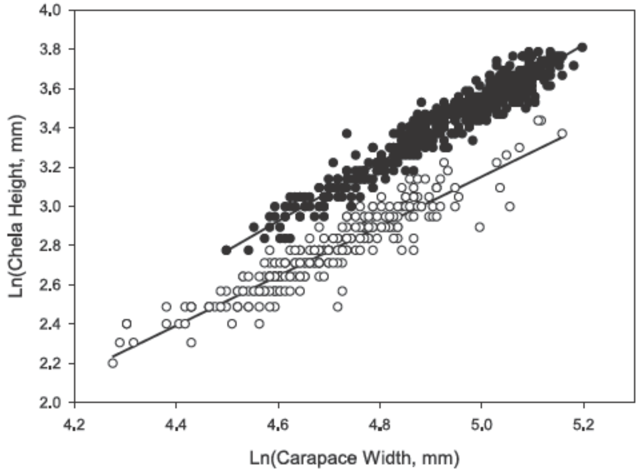

Figure 2. Log-transformed relationships between carapace width and chela height for immature (open circles) and mature (closed circles) male Tanner crab. The two regression lines were estimated using the MATURE program.

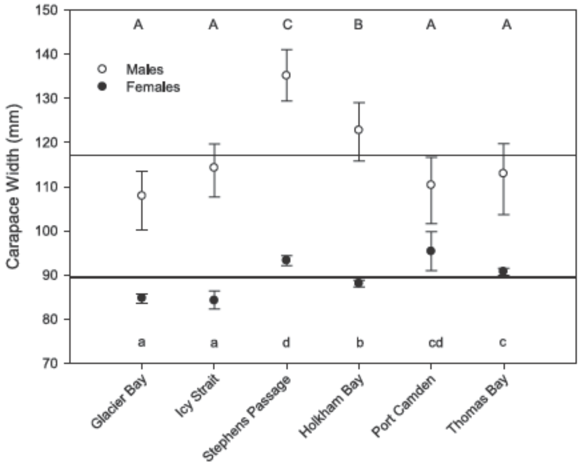

Figure 3. Mean (± 95% confidence interval) size at 50% maturity for male (open circles) and female (closed circles) Tanner crab for six survey areas in southeastern Alaska. Reference lines indicate overall means for males (top) and females (bottom). Significant differences among areas (from generalized linear model post-hoc contrasts; see methods) are represented by different letters; capital letters indicate males and lower case letters are females.

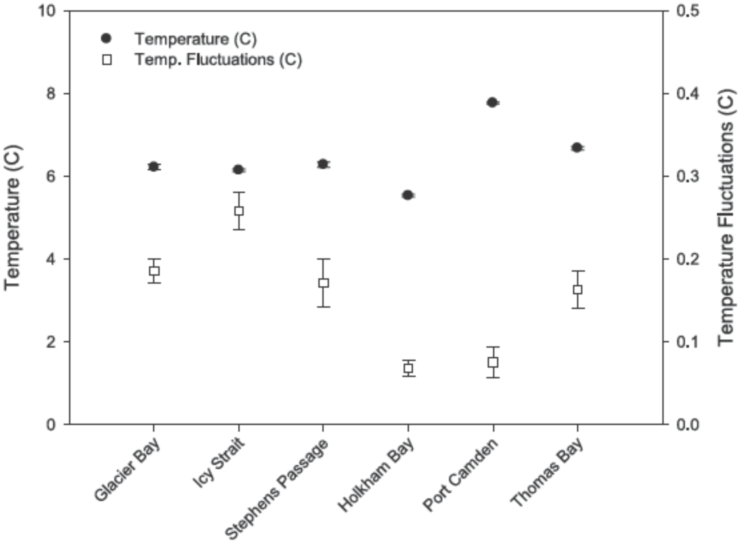

Figure 4. Mean (± SD) temperature (closed circles) and temperature fluctuations (open circles) for each of the six survey areas.

Stephens Passage for both males and females, the variation in size at maturity was not correlated with sex ($p = 0.36$, $r^2 = 0.21$, n = 6).

Average bottom temperature ranged from 5.52ºC ± 0.20 (SD) at Holkham Bay to 7.77ºC ± 0.08 at Port Camden (Fig. 4) over four years. Interestingly, the three areas with large glacial input (Glacier Bay, Stephens Passage, and Holkham Bay) were the coldest and only varied in average bottom temperature by 0.17ºC. There was no relationship between temperature and latitude or temperature and depth (p values > 0.09). Temperatures fluctuated markedly in some areas and minimally in others (Figs. 4, 5). Temperature fluctuations were most dramatic at Icy Strait and Glacier Bay and were tidally driven (Fig. 5). These fluctuations occurred across the depth distribution of pots (data not shown).

Latitude, depth, temperature, temperature fluctuations, or any metric of fishing pressure, did not help explain the large variations in size at maturity for male or female Tanner crabs (all p values > 0.21).

Discussion

Size at maturity for Tanner crabs showed dramatic differences over relatively small spatial scales and between sexes (Fig. 3). Size at maturity changed 18 mm for males and 10 mm for females over ~160 km between Glacier Bay and Stephens Passage. However, the changes in size at

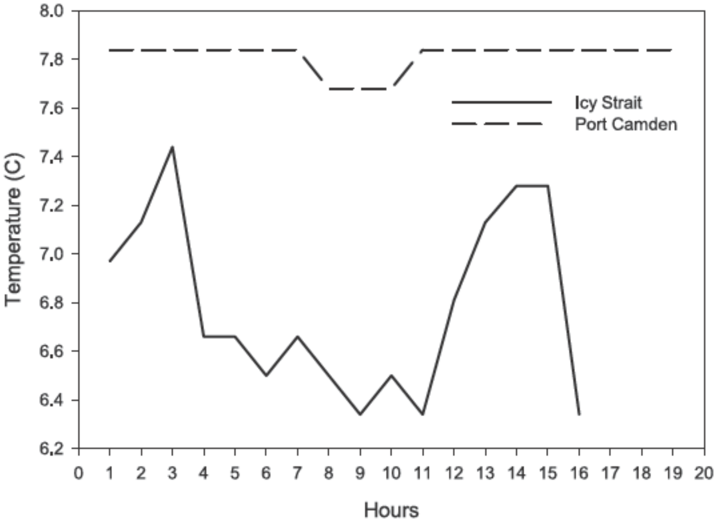

Figure 5. Temperature fluctuations of representative temperature loggers from Port Camden (dashed line) and Icy Strait (solid line). Depths were 66 m for Port Camden and 64 m for Icy Strait.

maturity between the sexes were not consistent among areas. These results suggest that different mechanisms are responsible for the variation in size at maturity between males and females. This is reasonable since the fishery for Tanner crabs is a male-only fishery, and there is some evidence that female Tanner crabs move less than mature male crab (J.K. Neilsen, University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, pers. comm.), which may increase the potential influence of small-scale environmental changes on females.

Changes in size at maturity are fairly well documented over relatively large spatial scales and often correlate with latitude, longitude, and/or bottom temperatures (Somerton 1981, Otto and Pengilly 2002, Orensanz et al. 2007, Zheng 2008). However, our data suggest that smaller-scale factors may play as important a role in determining the size at maturity of Tanner crab. In southeastern Alaska significant changes occurred in less than 0.4 degrees of latitude (45 km), whereas similar changes in the Bering Sea occurred over 2 or more degrees of latitude (e.g., Orensanz et al. 2007). Although southeastern Alaska is a fjord-dominated system, it provides evidence that latitude, depth, and temperature used to predict size at maturity in the Bering Sea are not the proximate cause.

Although latitude, longitude, and depth are generally proxies for some biological factor, temperature can have a direct or indirect influence on life history traits through physiological constraints or biotic interactions. Temperature can directly influence consumption and growth rates (e.g., Kondzela and Shirley 1993) and size at maturity (Dhillon and Fox 2004). Interestingly, the Dhillon and Fox (2004) study showed that medaka (*Oryzias latipes*) fed adequate diets grew faster and matured earlier (and at a larger size) than those fed a limiting diet. This suggests that food availability may be a major component contributing to the variation in size at maturity in Tanner crab. If so, then temperature may be important indirectly through modifying prey abundance or interaction strengths (consumption rates).

The concept that male size at maturity would be influenced by strong fishing pressure is strongly supported by experimental manipulations (e.g., Reznick et al. 1997, Conover and Munch 2002) and the intensity of fishing pressure on male Tanner crabs in southeastern Alaska. Harvest rates of Tanner crab have been estimated to average 60% over the past decade (Zheng et al. 2007) and high harvest rates have been a concern of regional biologists for nearly two decades (Clark et al. 2001). However, fishing pressure is a relatively new selective force and determining an appropriate predictor of fishing pressure is difficult. We examined an average harvest over 20 years and a corresponding harvest density as a proxy for relatively long-term population sizes and harvest rates. However, both predictors may not accurately reflect the appropriate selective force either due to being a poor estimate and/or being measured at an incorrect temporal scale. Biomass estimates for the past 20 years were not available, so commercial harvest data were used. Although harvest data generally can scale with population sizes, changes in effort, gear efficiency, weather, and economic incentives can all serve to disrupt any relationship between harvest and population size. It is even more difficult to assess the utility of harvest density since it incorporates all the issues of commercial harvest along with an area estimate of viable crab habitat. Though our estimates are reasonable for some areas with distinct boundaries (e.g., Thomas Bay), others are significantly larger (e.g., Glacier Bay; Nielson et al. 2007), while others may be significantly smaller due to non-suitable crab habitat within a given survey area.

The large variation in the sizes at maturity for Tanner crab poses an interesting problem, in that no environmental or fishing pressure predictor could help explain the variability in southeastern Alaska. These results suggest that we either sampled a nonrepresentative portion of the crab populations, or more likely, that Tanner crabs are being influenced by other biological/environmental factors. The likelihood of a sample bias is relatively small. Data for male size at maturity were pooled over years then randomly subsampled across the size range of carapace widths. These methods should act to minimize any chances of year-to-year variability due to density dependent issues, and minimize the influence of strong recruitment pulses (and thus oversampling a given size class). In addition, we must be somewhat cautious in concluding there is no relationship between temperature and size at maturity.

The relative scarcity of temperature data (4 years) compared to size at maturity data (12 years) may have reduced the ability to detect a relationship. As more temperature data are collected, this relationship can be re-evaluated with fully overlapping data to increase statistical power.

Changing oceanographic conditions due to climate change is of growing concern due to the unknown effects it will have on commercially important species. Predicting these changes requires a mechanistic understanding of how oceanographic conditions are going to change and how they influence population dynamics. Our data suggest that size at maturity has no strong direct relationship with differences in temperature or temperature fluctuations and therefore may be relatively insensitive to small climate changes.

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References

Bednarski, J., G. Bishop, and C. Siddon. 2008. Tanner crab pot survey methods for southeast Alaska. Alaska Department of Fish and Game, RIR 1J08-02.

Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES J. Mar. Sci. 52(1):1-10. doi:10.1016/1054-3139(95)80010-7

Calcagno, J.A., G.A. Lovrich, S. Thatje, U. Nettelmann, and K. Anger. 2005. First year growth in the lithodids *Lithodes santolla* and *Paralomis granulosa* reared at different temperatures. J. Sea Res. 54:221-230. doi:10.1016/j.seares.2005.04.004

Clark, J.E., K.K. Imamura, and T.M. Koeneman. 2001. The 1997 and 1998 southeast Alaska Tanner crab stock assessment surveys. Alaska Department of Fish and Game, RIR 1J01-06.

Conover, D.O., and S.B. Munch. 2002 Sustaining fisheries yields over evolutionary time scales. Science 297:94-96. doi:10.1126/science.1074085

Dhillon, R.S., and M.G. Fox. 2004. Growth-independent effects of temperature on age and size at maturity in Japanese medaka (*Oryzias latipes*). Copeia 1:37-45. doi:10.1643/CI-02-098R1

Hartnoll, R.G. 1978. The determination of relative growth in Crustacea. Crustaceana 34:281-293. doi:10.1163/156854078X00844

Kondzela, C.M., and T.C. Shirley. 1993. Survival, feeding, and growth of juvenile Dungeness crabs from southeastern Alaska reared at different temperatures. J. Crust. Biol. 13(1):25-35. doi:10.2307/1549120

Nielson, J.K., S.J. Taggart, T.C. Shirley, and J. Mondragon. 2007. Spatial distribution of juvenile and adult female Tanner crabs (*Chionoecetes bairdi*) in a glacial fjord ecosystem: Implications for recruitment processes. ICES J. Mar. Sci. 64(7):1772-1784. doi:10.1093/icesjms/fsm158

Orensanz, J.M., B. Ernst, and D.A. Armstrong. 2007. Variation of female size and stage at maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering Sea. J. Crust. Biol. 27(4):576-591. doi:10.1651/S-2790.1

Otto, R.S., and D. Pengilly. 2002. Spatiotemporal trends in Tanner crab (*Chionoecetes bairdi*) size at maturity. In: A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley, and D. Woodby (eds.), Crabs in cold water regions: Biology, management, and economics. Alaska Sea Grant, University of Alaska Fairbanks, pp. 339-350.

Pörtner, H.O., et al. 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: Developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). Cont. Shelf Res. 21(18-19):1975-1997. doi:10.1016/S0278-4343(01)00038-3

Reznick, D.N., F.H. Shaw, H.F. Rodd, and R.G. Shaw. 1997 Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275:1934-1937. doi:10.1126/science.275.5308.1934

Sainte-Marie, B., T. Gosselin, J.-M. Sévigny, and N. Urbani. 2008. The snow crab mating system: Opportunity for natural and unnatural selection in a changing environment. Bull. Mar. Sci. 83(1):131-161.

Sanford, E. 2001. The feeding, growth, and energetics of two rocky intertidal predators (*Pisaster ochraceus* and *Nucella canaliculata*) under water temperatures simulating episodic upwelling. J. Exp. Mar. Biol. Ecol. 273(2):199-218. doi:10.1016/S0022-0981(02)00164-8

SAS Institute. 2007. JMP Version 7.0.1. SAS Institute, Cary, North Carolina.

Somerton, D.A. 1981. Regional variation in the size and maturity of two species of Tanner crab (*Chionoecetes bairdi* and *C. opilio*) in the eastern Bering Sea, and its use in defining management subareas. Can. J. Fish. Aquat. Sci. 38:163-174. doi:10.1139/f81-022

Tamone, S.L, S.J. Taggart, A.G. Andrews, J. Mondragon, and J.K. Nielsen. 2007. The relationship between circulating ecdysteroids and chela allometry in male Tanner crabs: Evidence for a terminal molt in the genus *Chionoecetes*. J. Crust. Biol. 27(4):635-642. doi:10.1651/S-2802.1

Webb, J.B. 2009. Reproductive success of multiparous female Tanner crab (*Chionoecetes bairdi*) fertilizing eggs with or without recent access to males. J. Northw. Atl. Fish. Sci. 41:163-172. doi:10.2960/J.v41.m611

Zheng. J. 2008. Temporal changes in size at maturity and their implications for fisheries management for eastern Bering Sea Tanner crab. J. Northw. Atl. Fish. Sci. 41:137-149. doi:10.2960/J.v41.m623

Zheng, J., J.M. Rumble, and G.H. Bishop. 2007. Estimating southeast Alaska Tanner crab abundance using pot survey and commercial catch data. Alaska Fish. Res. Bull. 12(2):227-242.

Webb, J. and J. Bednarski. 2010. Variability in Reproductive Potential among Exploited Stocks of Tanner Crab (*Chionoecetes bairdi*) in Southeastern Alaska. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.12

Variability in Reproductive Potential among Exploited Stocks of Tanner Crab (*Chionoecetes bairdi*) in Southeastern Alaska

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Abstract

For many exploited crab stocks, management has been challenged by uncertainty in estimation of abundance, effective spawning biomass, and stock-recruit relationships. Crab fishery management strategies strive to optimize trade-offs between yield and variability in yield by harvesting males only above a minimum size limit, typically set at one molt larger than size of 50% male maturity. However, there is limited understanding of the implications of this harvest strategy for mating frequency and female reproductive potential (e.g., sperm limitation). To evaluate reproductive potential of female Tanner crab (*Chionoecetes bairdi*), we characterized egg viability, spermathecal load, and sperm cell counts in six spatially discrete locations in southeastern Alaska. All females carried viable egg clutches with low incidence ($\bar{x}$< 1%) of nonviable eggs. Mean spermathecal load was significantly lower in primiparous compared to multiparous females in four of five locations compared, but sperm cell counts were similar between primiparous and multiparous females in all locations. Mean sperm cell counts were significantly higher when fresh ejaculate was present versus when it was absent for both primiparous (454% higher) and multiparous females (320% higher). The proportion of primiparous and multiparous females with fresh ejaculate was correlated with mean sperm cell counts by location and may be a useful index of variability in female sperm cell counts among stocks. Evidence of sperm limitation was not observed in this study, but mean sperm cell counts of primiparous females by location were negatively correlated with exploitation rate index suggesting

that male-only harvest may decrease levels of stored sperm available for fertilization of a subsequent clutch.

Introduction

Management of many decapod crustacean fisheries is complicated by lack of precise aging techniques, high recruitment variability, and uncertainty in stock-recruit relationships, all of which can result in difficulty in estimation of stock productivity and sustainable harvest levels. In response to this uncertainty, conservation and monitoring of population reproductive potential have been recommended (Kruse 1993, Smith and Sainte-Marie 2004) and adopted as a primary management objective for crab stocks in Alaska (NPFMC 1998, Woodby et al. 2005).

A management concern for exploited crab stocks is that size- and sex-selective exploitation or natural variability in sex ratio may result in decreased population egg production due to sperm limitation (Orensanz et al. 1998). Specifically, female-skewed sex ratios associated with large male-only harvest or natural variability could result in insufficient availability of males with the characteristics necessary to fully inseminate and maximize the viable egg production of all mature females (Smith and Jamieson 1991, Hines et al. 2003, Ashidate et al. 2007). Recent contributions have improved understanding of crab life history, reproductive biology, and mating systems (e.g., Sato et al. 2005, Sainte-Marie et al. 2008) and the robustness of biological indicators of recent mating for females has been evaluated for at least one species (Duluc et al. 2005). However, progress has been limited in integrating this knowledge into development of indices of female mating success and sperm reserves at the appropriate spatial and temporal scales for management.

Evaluation of multiple factors including fecundity, egg viability, and sperm reserves is likely to be necessary for characterization of variability in reproductive potential. For Tanner *(Chionoecetes bairdi)* and snow *(C. opilio)* crabs, commercially valuable species in Alaska, reductions in viable egg production due to sperm limitation are likely to be a threshold response (Paul and Adams 1984, Sainte-Marie and Lovrich 1994, Sainte-Marie et al. 2002), and may be observed as occurrences of barren mature females, females with clutches of mixed viable and nonviable eggs, females with egg cases prior to the usual period of larval release, or reduced fecundity if nonviable eggs are lost during brooding (Paul 1984, Sainte-Marie and Carrière 1995). For Tanner and snow crabs, species that store sperm across annual reproductive cycles, monitoring of egg viability and fecundity could provide information on spatiotemporal variability in viable egg production. Estimates of female sperm reserves could be used to assess mating frequency and the relative spatiotemporal vulnerability of crab stocks to sperm limitation.

The Tanner crab is a commercially valuable species in Alaska targeted by commercial fisheries from the eastern Bering Sea to southeastern Alaska. Statewide annual harvests peaked in the early 1980s at about 82,000 t before declining precipitously and continuing at low levels (~4,500 t) with intermittent or long-term closures in all management areas through the present (Woodby et al. 2005). Key features of Tanner crab reproductive biology include a terminal molt to maturity for both sexes and complex mating behaviors and dynamics. Female Tanner crab that complete the terminal molt to reproductive maturity, after which copulation and extrusion of the first egg clutch occurs, are termed primiparous (Paul and Adams 1984). Multiparous females, carrying a second or later clutch, may fertilize a clutch from fresh sperm obtained by mating in hard-shell condition after larval release or stored sperm from previous matings (Adams and Paul 1983). After mating a new clutch of eggs is extruded onto the female's abdomen and incubated for approximately twelve months until hatching (Donaldson and Adams 1989, Swiney 2008, Webb 2009).

A fishery for Tanner crab has occurred in southeastern Alaska, a complex network of fjords, islands, and connecting waterways, since the 1960s. Annual stock assessment surveys have been conducted in six spatially discrete locations in southeastern Alaska since 2001 (Bednarski et al. 2008). Legal and mature male biomasses are independently estimated annually for each location from a two-stage catch-survey analysis model (Zheng et al. 2006). Model estimates of male biomass and survey indices of the male:female sex ratio contrast among locations. These data provide a framework to assess functional relationships between these indices and direct measures of reproductive potential including the prevalence of indicators of recent mating, viable egg production, and sperm reserves. The objectives of this study were to assess the fecundity, egg viability, and sperm reserves among primiparous and multiparous female Tanner crab from the survey areas in southeastern Alaska, compare these measures with survey and model indices of sex ratio and exploitation rate, and evaluate indicators of recent mating as robust indicators of sperm reserves.

Materials and methods

Female Tanner crab were collected from six locations during the Alaska Department Fish and Game southeast Alaska Tanner crab pot survey in October 2007 (Fig. 1). Pot survey design and survey biological data collection protocols are detailed in Bednarski et al. (2008). Female Tanner crab were haphazardly collected from pot catches to meet sampling goals by shell condition (*n* = 15 females for each shell condition class) within each survey location. Females were classified by shell condition, which is an assessment of color and wear on the exoskeleton, as new

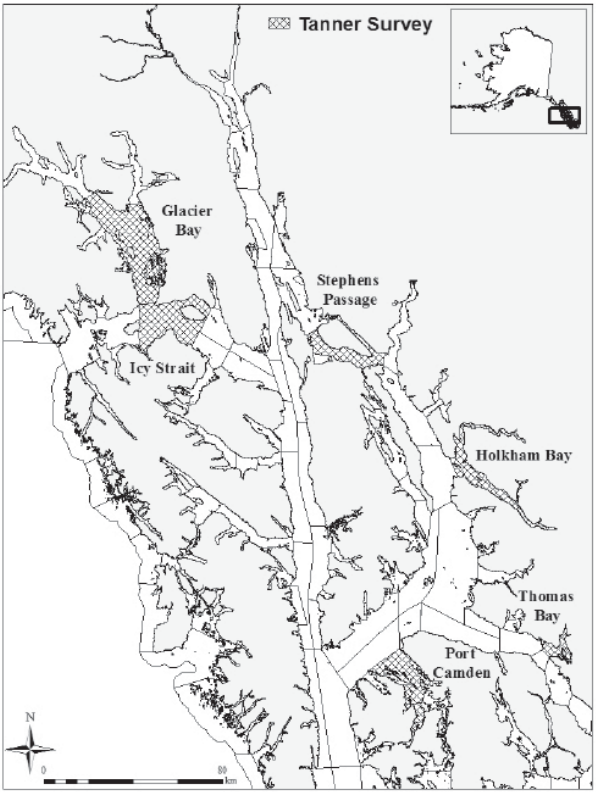

Figure 1. Areas (crosshatched) of southeastern Alaska surveyed annually during the Alaska Department of Fish and Game Tanner crab stock assessment pot survey.

shell (SC3), old shell (SC4), or very old shell (SC5) (Jadamec et al. 1999). For clarity, new shell, primiparous females with clean firm exoskeletons brooding their first egg clutch; multiparous females with exoskeletons of intermediate shell condition, likely brooding their second or third egg clutch; and multiparous females with darkened, highly worn exoskeletons, which are likely brooding their third or greater clutch of ontogeny, will be referred to as SC3, SC4, and SC5 respectively, throughout the manuscript. Sample sizes were limited in some locations by limited catches of females of certain shell conditions (Table 2). Upon collection females were individually marked with numbered plastic tags attached to the third left pereiopod using a plastic tie. In Holkham Bay, Thomas Bay, and Port Camden females were dissected aboard the vessel. The

Table 1. Categories of mature male and female Tanner crab by size, sex, and shell condition and metrics used to calculate indices of sex ratio among locations in southeastern Alaska.

Population segment	Metric	Shell condition	Carapace width (mm)
Primiparous female (PF)	Pot survey CPUE	3	n/a
Multiparous female (MF)	Pot survey CPUE	4	n/a
All mature male (AMM)	Pot survey CPUE	3-5	>109.3
New-shell legal male (NLM)	Pot survey CPUE	3	>137.9
Old-shell legal male (OLM)	Pot survey CPUE	4-5	>137.9
Legal male biomass (LMB)	Model biomass estimate	3-5	>137.9
Mature male biomass (MMB)	Model biomass estimate	3-5	>109.3

SC3 = individuals with with firm, clean exoskeletons.
SC4 = individuals with exoskeletons intermediate between SC3 and SC5.
SC5 = individuals with darkened, highly worn exoskeletons.

abdomen and egg clutch of each female was detached and preserved in 80% ethanol and the right spermathecae was removed without perforation and preserved in 10% formalin. In Stephens Passage, Icy Strait, and Glacier Bay females were frozen and processed for reproductive condition in the laboratory.

Indicators of mating and sperm reserves

Females were assessed at the time of dissection for indicators of mating including fresh grasping marks (Paul 1984) and the presence of fresh ejaculate at the open (ventral) end of the spermathecae (Duluc et al. 2005). Fresh grasping marks visible as areas of lighter coloration on the dorsal surface of the first three walking legs are due to abrasion of the exocuticle by the chelae of males as females are grasped during the mating period. Due to the soft condition of their exoskeleton during the molting/mating period, grasping marks are unlikely to be observed on the walking legs of pubescent/primiparous females.

For measurement of sperm reserves, the right spermatheca was removed from formalin at least seven days after preservation. The wall of the spermatheca was removed and the spermathecal load (SL), or weight of the spermathecal contents, was measured to the nearest 0.1 mg on a Mettler AE163 analytical microbalance. Estimated sperm cell counts were determined by homogenization and dilution of spermathecal contents followed by visual counts of sperm cells using replicate hemacytometers. The estimated number of sperm cells in the spermatheca was then calculated as the mean of four replicate counts

Table 2. Mean spermathecal load (SL) and sperm cell counts (SSC) of the right spermatheca and the proportion of females with fresh ejaculate (PFFE) and grasping marks (PFGM) for female Tanner crab by survey location and for all locations combined in southeastern Alaska in October 2007. Significant differences (Tukey HSD, $p < 0.05$) in spermathecal load and sperm cell counts by shell condition and location are indicated by dissimilar letters. Means for all locations combined are presented for comparison.

Location	SC	N	Mean of SL (g)	SE of SL	Mean of SCC	SE of SCC	PFFE	PFGM
Glacier Bay	3	21	0.049 f	0.017	1.64×10^7 bc	5.79×10^6	0.29	
	4	8	0.134 abcd	0.023	1.09×10^7 abc	4.54×10^6	0.67	0.00
Holkham Bay	3	12	0.043 def	0.010	3.05×10^7 a	7.90×10^6	0.92	
	4	9	0.277 a	0.025	2.61×10^7 abc	8.07×10^6	1.00	0.80
	5	6	0.180 ab	0.030	9.83×10^6 abc	5.52×10^6	0.33	0.20
Icy Strait	3	5	0.024 f	0.022	5.94×10^6 c	5.39×10^6	0.20	
	4	10	0.172 abc	0.031	2.52×10^7 abc	7.66×10^6	0.60	0.25
Port Camden	3	8	0.045 cdef	0.016	3.01×10^7 abc	1.55×10^7	0.88	
	4*	3	0.177	0.025	3.21×10^7	3.04×10^7	1.00	0.50
Stephens Passage	3	12	0.031 ef	0.013	1.36×10^7 abc	4.54×10^6	0.08	
	4	12	0.305 a	0.031	2.16×10^7 ab	4.46×10^6	0.50	0.50
	5*	1	0.309		3.05×10^7			
Thomas Bay	3	14	0.027 ef	0.005	2.01×10^7 abc	6.38×10^6	0.33	
	4	10	0.093 bcde	0.011	2.86×10^7 abc	1.18×10^7	0.80	1.00
	5	5	0.172 abc	0.026	1.96×10^7 abc	7.69E+10^6	0.60	0.67
All Locations	3	72	0.039	0.006	1.98×10^7	3.14×10^6	0.42	
	4	52	0.200	0.016	2.32×10^7	3.52×10^6	0.28	0.40
	5	12	0.187	0.021	1.56×10^7	7.69E+10^6	0.42	0.25

[*] Excluded from analysis due to limited sample size

SC3 = new-shell, primiparous females with clean firm exoskeletons brooding their first egg clutch.

SC4 = multiparous females with exoskeletons of intermediate shell condition, likely brooding their second or third egg clutch.

SC5 = multiparous females with darkened, highly worn exoskeletons, likely brooding their third or greater clutch.

multiplied by the dilution factor. All sperm cell counts were those of the right spermatheca only and total sperm counts per female would be approximately double assuming similarity of sperm cell counts between the paired spermathecae (Sainte-Marie and Lovrich 1994).

Indices of sex ratio and harvest rate

To evaluate variability in reproductive potential with indices of sex ratio among locations, mean pot catch-per-unit-effort (CPUE) was calculated for various combinations of female and male Tanner crab by size and shell condition from the survey conducted in October 2007 (Table 1). Survey sampling design, gear, and biological data collection protocols are detailed in Bednarski et al. (2008). Escape mechanisms are blocked on survey pots to increase retention rates for small crab; females at least one molt prior to the molt to maturity are commonly observed in survey sampling, indicating that pots retain female crab at or below the size-at-maturity (~80 mm CW, Hilsinger 1976). A second alternative index of sex ratio was also calculated by location as the ratio of estimates of legal and total mature male biomass from a catch-survey-analysis model (Zheng et al. 2006) to multiparous and primiparous female survey CPUE. To assess possible relationships between harvest and sperm reserves an index of exploitation rates by location was determined for each survey location from the model estimates of legal male biomass divided by the landed catch in number of individuals in the subsequent winter fishery (February 2007).

Egg viability and fecundity

To determine the proportion of viable eggs in a clutch, two subsamples of ~200 to 250 eggs were removed from the center and periphery of the dorsal surface of the egg clutch and individually classified as viable or nonviable based on structure and color. Eggs were primarily in the intermediate, yolk reduction stage of development allowing reasonable determination of viable versus nonviable eggs from ethanol preserved and frozen samples. For measurement of fecundity, the replicate subsamples examined for viability were counted and placed in pre-weighed drying pans. The remaining eggs in the clutch were then gently stripped from the pleopods using forceps and placed in a pre-weighed drying pan. Embryo subsamples and clutch were dried to constant weight in a 60°C oven for >48 h and weighed to the nearest 0.1 mg on a Mettler AE163 analytical microbalance. Fecundity was estimated by dividing the clutch dry weight by the mean of the weight of an individual embryo estimated from the two counted subsamples. Differences in preservation method were included as a factor in statistical analyses to account for possible differences in fecundity estimation with preservation method.

Statistical methods

Nested analysis of variance was used to evaluate differences in sperm reserves by shell condition among locations. Levene's test for homogeneity of variance, residual plots, Cook's distance, and the Shapiro-Wilk test for normality were used to assure that data met assumptions for analysis. Both spermathecal load and sperm cell count data met assumptions after Box-Cox transformation, and significant ($p < 0.05$) differences between groups were determined using a Tukey HSD post-hoc test. When influential outliers were detected, the model was refit exclud-

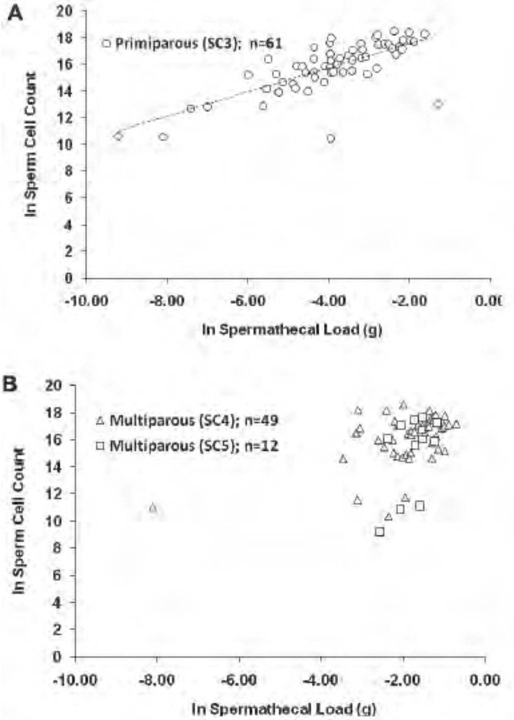

Figure 2. The spermathecal load/sperm cell count relationship of (A) primiparous (SC3) and (B) old shell multiparous (SC4) and very old shell multiparous (SC5) female Tanner crab from southeastern Alaska. Sperm cell counts increased significantly with spermathecal load for primiparous females (ln y = ln $0.92x + 19.47$, $R^2 = 0.67$, $F = 119.7$, d.f. = 70, $p < 0.0001$; but were not linearly related for multiparous (SC4 or SC5) females. Eleven SC3 females with spermathecal loads or sperm cell counts estimated to be zero were excluded from this analysis.

ing the outliers and differences between group means were examined for changes in significant differences. Differences in sperm cell counts and spermathecal load with the presence or absence of indicators of recent mating within shell condition groups were examined with Mann-Whitney/Wilcoxon rank sign tests. The Bonferroni adjustment was used to increase the threshold of significance (α) to control for Type I error due to multiple pair-wise comparisons. Relationships between sperm reserves, survey and model indices of sex ratio, and exploitation rate index were compared using Pearson correlation coefficients. Analysis of

Table 3. Sample size, mean sperm cell count, and mean spermathecal load of the right spermatheca by shell condition and indicators of recent mating for female Tanner crab collected in southeastern Alaska in October 2007. *P*-values are reported from Mann-Whitney rank-sign tests of significant differences in mean sperm cell count and mean spermathecal load between females with or without fresh ejaculate or grasping marks within each shell condition group. Statistical comparisons and standard errors are not presented for SC5 females without grasping marks due to low sample size.

			Sperm cell count		Spermathecal load	
Shell condition	Fresh ejaculate present	N	Mean ± SE	*p*	Mean ± SE	*p*
3	Yes	41	$3.65 \times 10^7 \pm 5.80 \times 10^6$	<0.0001*	0.063 ± 0.008	<0.0001*
	No	30	$7.99 \times 10^6 \pm 2.03 \times 10^6$		0.021 ± 0.007	
4	Yes	37	$2.87 \times 10^7 \pm 4.51 \times 10^6$	0.0086*	0.21 ± 0.017	0.2142
	No	15	$8.97 \times 10^6 \pm 2.56 \times 10^6$		0.17 ± 0.033	
5	Yes	5	$2.66 \times 10^7 \pm 6.58 \times 10^6$	0.0424	0.21 ± 0.027	0.4649
	No	5	$4.82 \times 10^6 \pm 2.56 \times 10^6$		0.15 ± 0.029	
Shell condition	Grasping marks present	N	Mean ± SE	*p*	Mean ± SE	*p*
4	Yes	31	$3.26 \times 10^7 \pm 6.81 \times 10^6$	0.0278*	0.20 ± 0.027	0.5569
	No	21	$1.69 \times 10^7 \pm 3.42 \times 10^6$		0.20 ± 0.019	
5	Yes	2	3.52×10^7		0.17	
	No	8	$1.70 \times 10^7 \pm 3.43 \times 10^6$		± 0.025	

*Significant differences in sperm cell counts and spermathecal load with presence/absence fresh ejaculate by shell condition were adjusted with Bonferroni correction for multiple comparisons ($p < 0.017$), $p < 0.05$ for sperm cell counts and spermathecal load with the presence/absence of grasping marks.

SC3 = new-shell, primiparous females with clean firm exoskeletons brooding their first egg clutch.

SC4 = multiparous females with exoskeletons of intermediate shell condition, likely brooding their second or third egg clutch.

SC5 = multiparous females with darkened, highly worn exoskeletons, likely brooding their third or greater clutch.

covariance was used to examine sources of variability in fecundity with main factors of carapace width, shell condition, mean embryo weight, clutch preservation method, and location. Nonsignificant terms ($p > 0.05$), which included location, preservation method, and an interaction term between these variables, were dropped from the model. Statistical analyses were conducted in JMP 8.02 (SAS Institute, Cary, NC).

Results

Sperm reserves by shell condition and location

The number of primiparous and multiparous female Tanner crab collected and processed for sperm reserves varied among survey locations

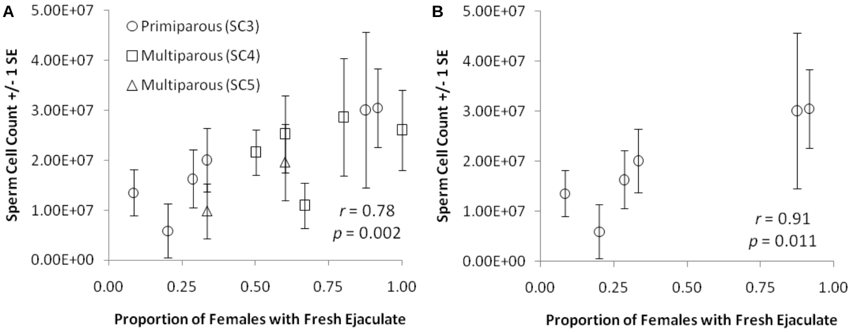

Figure 3. Mean sperm cell counts and proportion of females with fresh ejaculate (PFFE) by location and shell condition for female Tanner crab in southeastern Alaska. Significant correlations ($p < 0.05$) between sperm cell counts and PFFE were observed among (A) all shell condition and location groups and (B) primiparous females. Data are also presented in Table 4.

(Table 2). For females from all locations combined, a linear relationship was observed between sperm cell count and spermathecal load for SC3 females ($r^2 = 0.67$, $F = 119.7$, $p < 0.0001$, d.f. = 59), but not for SC4 or SC5 females (Fig. 2). Spermathecal load varied significantly ($R^2 = 0.63$, $F = 16.82$, d.f. = 131, $p < 0.0001$) among locations and shell condition groups. Spermathecal load was higher for SC4 and SC5 versus SC3 females in four of five locations and similar between SC4 and SC5 multiparous females in the locations in which SC5 females were sampled (Table 2). Within the SC3 (primiparous) shell condition category, females from Port Camden, Holkham Bay, Thomas Bay, and Stephens Passage had greater spermathecal load than those in Glacier Bay or Icy Strait. While for SC4 and SC5 (multiparous) categories, females in Thomas Bay had lower spermathecal load than those from the other locations (Table 2). Within location, with the exception of Thomas Bay, SC4 and SC5 females had significantly greater spermathecal load than SC3 females (Table 3). SC4 females from Port Camden were excluded from comparisons of sperm reserves by location and shell condition due to low sample sizes.

Sperm cell counts also varied significantly ($R^2 = 0.22$, $F = 2.82$, d.f. = 131, $p < 0.002$) among groups by shell condition and location, but few significant differences were observed relative to the number of groups compared and the model explained a low proportion of the overall variance observed. SC3 females in Holkham Bay had significantly greater sperm cell counts than those in Glacier Bay and Icy Strait, and SC4 females from Stephens Passage had greater sperm cell counts than SC3 females in Icy Strait (Table 2). Mean sperm cell counts were generally

Table 4. Pearson's correlation coefficient (r) and p-value of relationships among mean sperm cell count (SCC), mean spermathecal load (SL), and the proportion of females by area with fresh ejaculate (PFFE) or fresh grasping marks (PFGM) for primiparous (SC3) and old-shell multiparous (SC4) female Tanner crab in southeastern Alaska.

	All mature females (SC3-5)			
	Mean SL		Mean SCC	
	r	p-value	r	p-value
PFFE	0.32	0.28	0.78	0.002
PFGM (SC4-5)	−0.23	0.61	0.73	0.06
	Primiparous females (SC3)			
PFFE	0.57	0.22	0.91	0.011
	Multiparous females (SC4)			
PFFE	−0.04	0.93	0.36	0.54
PFGM	0.76	0.13	−0.26	0.67

Significant ($p < 0.05$) relationships are indicated by boxes and shown in Fig. 4.

similar among shell condition groups within a location, and no significant differences in sperm cell counts were observed among shell condition groups within locations (Table 2).

Indicators of recent mating

The presence of fresh ejaculate or a white deposit at the ventral, open end of the spermathecae for all females and fresh grasping marks on the anterior pairs of pereiopods for multiparous females have been proposed as indicators of recent mating and were associated with increased sperm reserves in this study. Considering females from all locations combined, spermathecal load was significantly higher ($Z = 5.02$, $p < 0.0001$) between SC3 females classified as having fresh ejaculate versus those without, but a similar result was not observed for SC4 ($Z = 1.23$, $p = 0.22$) or SC5 ($U = 0.46$, $p = 0.52$) females (Table 3). Estimated mean sperm cell counts were significantly higher for SC3 ($Z = 4.90$, $p < 0.0001$) and SC4 females ($Z = 2.61$, $p = 0.0086$) with versus without fresh ejaculate, but did not differ for SC5 ($U = 4.12$, d.f. = 1, $p = 0.042$) females (Table 3). For SC4 females the presence of fresh grasping marks was associated with significantly higher sperm cell counts ($Z = 2.19$, $p = 0.028$), while spermathecal load was similar between groups ($U = 0.57$, $p = 0.56$). Higher sperm cell counts with the presence of fresh ejaculate suggested that an increase in mean sperm cell count might be observed with an increased proportion of females with indicators of recent mating in each study location. This was confirmed as a significant positive

Table 5. Pearson's correlation coefficient (*r*) and *p*-value of relationships by area between female mean spermathecal load (SL in g) and mean sperm cell counts (SCC), survey/model indices sex ratio (defined in Table 1), and model estimates of exploitation index for Tanner crab in southeastern Alaska.

	Primiparous females (SC3)			
	Mean SL		Mean SCC	
	r	*p*-value	*r*	*p*-value
NLM CPUE/PF CPUE	−0.47	0.35	−0.50	0.31
OLM CPUE/PF CPUE	0.16	0.76	−0.34	0.51
OSM CPUE/PF CPUE	−0.73	0.10	−0.54	0.26
AMM CPUE/PF CPUE	−0.27	0.60	−0.40	0.43
LMB/PF CPUE	0.07	0.89	−0.37	0.46
MMB/PF CPUE	0.50	0.30	−0.24	0.63
Exploitation rate	**−0.90**	**0.01**	−0.75	0.08
	Multiparous females (SC4)			
NLM CPUE/MF CPUE	0.67	0.21	−0.05	0.21
OLM CPUE/MF CPUE	0.86	0.06	0.06	0.91
OSM CPUE/MF CPUE	0.10	0.81	0.71	0.18
AMM CPUE/MF CPUE	0.71	0.17	0.01	0.98
LMB/MF CPUE	0.86	0.06	−0.14	0.82
MMB/MF CPUE	0.48	0.40	−0.10	0.86
Exploitation rate	−0.34	0.57	0.53	0.34

Significant correlations ($p < 0.05$) are indicated in bold and boxed relationships are presented in Fig. 5.

correlation ($r = 0.91$, d.f. = 5, $p = 0.011$) observed between mean sperm cell counts for SC3 females by location and the proportion of SC3 females in each location classified as having fresh ejaculate (Table 4, Fig. 3). Similarly, a significant positive correlation ($r = 0.78$, d.f. = 12, $p = 0.002$) was observed between the mean sperm cell counts of females of all shell condition groups by location and the proportion of females with fresh ejaculate (Table 4, Fig. 3).

Indices of sex ratio and exploitation rate

Results of correlations between sperm reserves, sex ratio indices, and exploitation rate index by locations were mixed (Table 5). A significant negative correlation was observed between the mean spermathecal load of SC3 females and the index of exploitation rate by location (Table 5, Fig. 4). The strongest correlations observed for multiparous females were between model estimates and survey indices of male abundance to the survey index (CPUE) of SC4 and SC5 female abundance (Table 5,

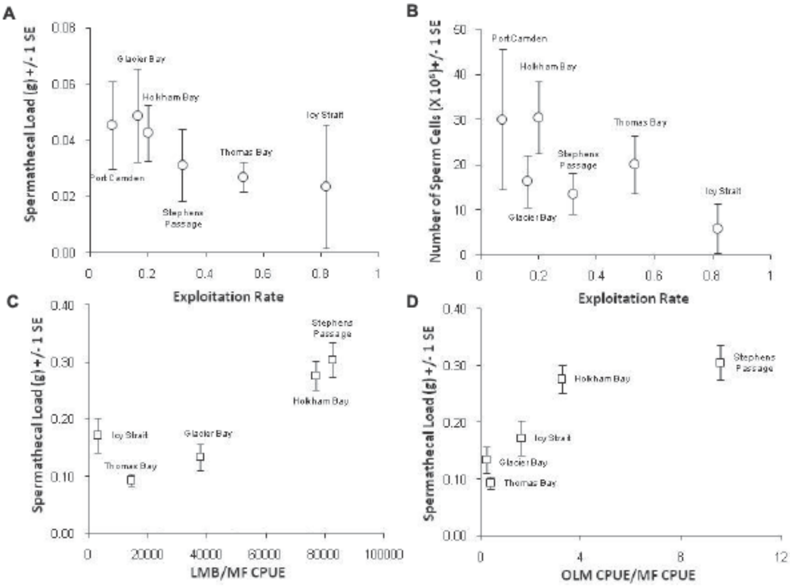

Figure 4. Pearson's correlation coefficient (*r*) and *p*-value of relationships between (A) mean spermathecal load of primiparous (SC3) females and index of exploitation rate by area (B) mean sperm cell counts of primiparous (SC3) females and index of exploitation rate by area (C) mean spermathecal load of multiparous (SC4) females and the ratio of model estimated legal-size male biomass (LMB) to the survey CPUE of multiparous females (MF CPUE) by area and (D) mean spermathecal load of multiparous (SC4) females and the ratio of survey CPUE of old-shell (SC4 and SC5), legal-size males (OLM) to the survey MF CPUE.

Fig. 4). This pattern may imply that the mean spermathecal load of multiparous females may increase with increased abundance of legal-sized males relative to SC4 and SC5 females among locations.

Fecundity and embryo viability

Female carapace width, shell condition, and mean embryo weight were significant predictors of variability in female fecundity (ANCOVA, Table 6), while preservation method and location were not. Nonsignificant effects were removed and the reduced model was used to estimate parameters. The reduced model fit the data well ($r^2 = 0.86$, $F = 193.2$, $p < 0.0001$) and significant differences were observed for each level of the shell condition factor. Adjusted mean fecundities estimated from ANCOVA indicated that SC4 females ($\bar{Y} = 190{,}373$) were 48% more fecund

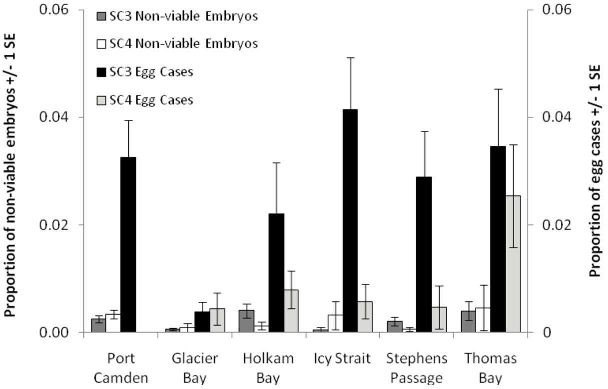

Figure 5. Proportion of egg cases to viable embryos, and nonviable to viable embryos, by area determined from counted subsamples (>400 embryos per female) for primiparous (SC3) and multiparous (SC4) female Tanner crab in southeastern Alaska.

than SC3 ($\overline{Y}$ = 116,021) females and the fecundity of SC5 ($\overline{Y}$ = 156,546) females was intermediate, 30% higher than SC3 females but 20% lower than SC4 females. For SC3 and SC4 females the mean proportion of nonviable embryos was less than 1.0% across locations (Fig. 5). A greater mean proportion of egg cases was observed in the egg clutches of SC4 versus SC3 females in all locations. The mean proportion of egg cases ranged from less than 0.5% for SC3 and SC4 females in Glacier Bay to a maximum of nearly 5.0% for SC3 females in Icy Strait (Fig. 5). No trends of or thresholds for reductions in fecundity were observed in comparisons of residuals of predicted fecundity (observed – predicted) with sperm cell counts, indicating that sperm limitation was unlikely in this study (Fig. 6).

Discussion

Characterization of the patterns of sperm reserves by location and between females of varied reproductive history (e.g., primiparous versus multiparous) may provide insight into variability in sperm reserves and, by extension, resilience against future sperm limitation. In this study we observed differences in spermathecal load but similar sperm cell counts between primiparous and multiparous females. This difference may have been due to the accumulation of seminal plasma, transferred with spermatophores during mating (Sainte-Marie et al. 2000), as the duration of an individual's reproductive history increased.

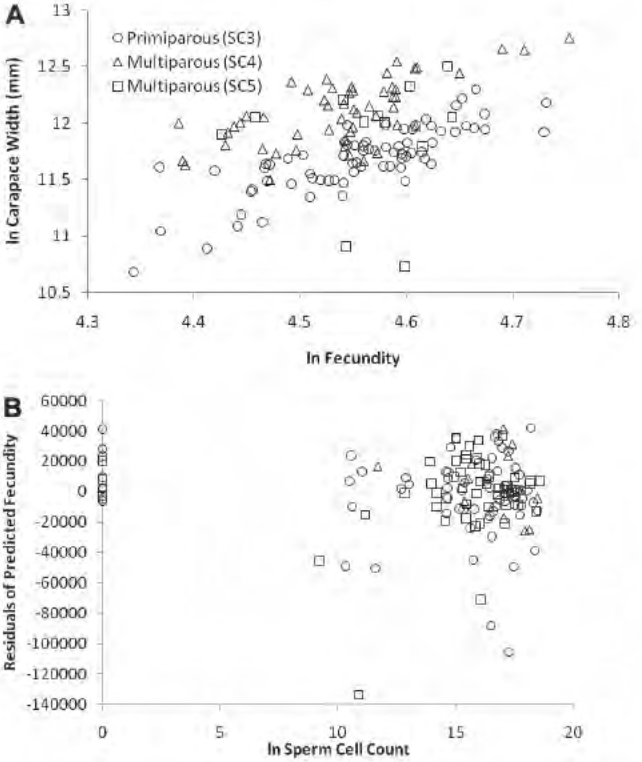

Figure 6. (A) Fecundity versus carapace width and (B) residuals of predicted fecundity (prediction equation in Table 5) versus sperm cell counts for primiparous (SC3), multiparous (SC4), and multiparous (SC5) female Tanner crab from southeastern Alaska.

Hypothetically, if females mated during consecutive annual mating periods but the rate of decrease in the number of sperm cells, due to expenditure for clutch fertilization or mortality, was greater than the rate of decrease of stored seminal plasma, then seminal plasma could accumulate without a concurrent increase in the number of stored sperm cells. In support of this hypothesis, a very similar pattern was observed for primiparous and multiparous female snow crab from Japan (Yamasaki et al. 1994, their groups A and B). Factors determining patterns of sperm cell counts and spermathecal load are likely to differ between primiparous and multiparous female Tanner crab. Primiparous females generally molt to maturity and mate in shallow water from January to May (Stevens et al. 1994), whereas multiparous

Table 6. Results and parameter estimates ± SE of reduced model ANCOVA ($Y = e^{a+b_1 \ln CW + b_2 SC + b_3 MEW}$) of the effect of carapace width (CW), shell condition (SC), and mean egg weight (MEW) of fecundity of female Tanner crab collected from northern and southern survey areas in southeastern Alaska in 2007. Factors and interaction terms (preservation method [PM] and location) that were not significant ($p < 0.05$) in the full model were removed and parameter estimates and fit statistics for significant factors are from the reduced model.

Source	d.f.	Sum of squares	*F*-ratio	*p*-value
		Reduced model		
ln CW	1	5.94	315.4	<0.0001
SC	2	7.45	138.0	<0.0001
MEW	1	2.59	198.0	<0.0001
Error	130	2.39		
		Factors removed from reduced model		
Location	5	0.02	0.28	0.92
PM	1	0.024	1.28	0.26
PM × MEW	1	0.054	2.89	0.091

Y	*a*	b_1	b_2	b_3	r^2	N
Fecundity	−0.07 ± 0.70	3.17 ± 0.22	SC3 0 SC4 0.48 ± 0.03* SC5 0.30 ± 0.05*	−13,600 ± 1,160	0.86	135

*($p < 0.05$), Tukey HSD.

SC3 = new-shell, primiparous females with clean firm exoskeletons brooding their first egg clutch.

SC4 = multiparous females with exoskeletons of intermediate shell condition, likely brooding their second or third egg clutch.

SC5 = multiparous females with darkened, highly worn exoskeletons, likely brooding their third or greater clutch.

females hatch their larvae and mate over several weeks in April and May (Stevens 2003, Webb 2009). The extended duration of the timing of the molt to maturity and sperm storage from a single mating period for primiparous females, versus a temporally compressed mating period and sperm storage reflecting integration of multiple annual reproductive cycles in multiparous females, could result in contrasting patterns of sperm reserves between these groups. Additional factors affecting the relationship between spermathecal load and sperm cell counts observed in female Tanner crab likely include variability in the reproductive potential of male mate(s), the number copulations within a mating season, the number of accrued mating seasons, and differences in the number of sperm required for clutch fertilization which vary with female fecundity (reviewed by Sainte-Marie et al. 2008). Our results indicated that female Tanner crab in southeastern Alaska were unlikely to accrue significantly greater sperm reserves in terms of number of sperm cells with increasing duration of reproductive history.

It is important to evaluate differences in sperm reserves between females of similar reproductive history among stocks to improve understanding of population processes associated with variability in sperm reserves and to identify stocks with potentially greater risk of sperm limitation. In this study, SC4 females in Holkham Bay and Stephens Passage had greater spermathecal load than those in Thomas Bay (Table 2). Assuming a similar number of reproductive cycles completed among SC4 females across locations; females in Holkham and Stephens may have, through ontogeny, experienced mating conditions (e.g., sex ratio) more favorable to acquisition of sperm reserves than those in Thomas Bay. Consistent with observations for SC4 females, SC3 females from Holkham Bay had greater mean sperm cell counts than females from Glacier Bay or Icy Strait (Table 2). These results suggest that females in Holkham Bay may be more likely to acquire greater sperm reserves perhaps due to greater availability of males during mating than other locations in southeastern Alaska.

Field studies of female Tanner crab sperm reserves in Alaska have only recently been undertaken and have differing results. Mean spermathecal loads of primiparous (SC3) females in this study (0.0385 g ± 0.0060) were lower than those observed for primiparous females (0.0895 g ± 0.013) from the southeastern Bering Sea. However, mean sperm cell counts were higher ($1.98 \times 10^7 \pm 3.14 \times 10^6$ vs. $5.54 \times 10^6 \pm 1.30 \times 10^6$) for females in this study versus Gravel and Pengilly (2007). Mean spermathecal loads and sperm cell counts of SC4 females in this study (0.20 ± 0.016 g, $2.32 \times 10^7 \pm 3.52 \times 10^6$) were lower than multiparous females from southeastern Alaska inferred to have recently mated (0.44 ± 0.026 g, $9.35 \times 10^7 \pm 7.83 \times 10^6$) in situ, but similar to those that fertilized a clutch with stored sperm without access to males (0.21 g ± 0.043 g, $2.00 \times 10^7 \pm 7.53 \times 10^6$) in the laboratory (Webb 2009).

Both grasping marks and the presence of fresh ejaculate in the spermathecae have been used for estimating variability in the frequency of recent mating for snow crab (Taylor 1996, Duluc et al. 2005). In this study the presence of a white layer of fresh ejaculate at the base of the right spermatheca indicated a highly significant increase (a factor of 2.96) in spermathecal load and sperm cell count (a factor of 4.54) for SC3 females and sperm cell counts for SC4 females (a factor of 3.20) (Table 3). The presence of fresh grasping marks was associated with an increase in sperm cell counts for SC4 females (a factor of 1.92). The larger relative difference in sperm cell counts based on fresh ejaculate versus fresh grasping marks is similar to the experimental findings of

Duluc et al. (2005) which identified fresh ejaculate as an improved indicator of recent mating. In this study all SC3 females carried clutches of fertilized eggs at the time of collection and had likely acquired adequate sperm reserves for clutch fertilization during mating at the molt to maturity. Thus, for SC3 females, the presence of fresh ejaculate was useful for classification of females with greater or lesser levels of sperm reserves stored from mating at the molt to maturity. The spermathecae of multiparous females with visible fresh ejaculate often contained one or more ejaculates darker in color (beige to black) located dorsally of the white ejaculate. If the entire deposit of fresh ejaculate was expended for clutch fertilization and the spermathecae contained only darker ejaculate, it is likely that the female would not be recognized as recently mated (Duluc et al. 2005). Thus, similar to primiparous females, the presence of fresh ejaculate in the spermathecae of multiparous females is indicative of females with sperm reserves acquired during recent mating in excess of that needed for clutch fertilization. The difference in mean spermathecal loads (0.04 g) and sperm cell counts (1.98×10^7) observed between multiparous females with or without ejaculate in this study was less than those (0.24 g, 7.35×10^7) observed between females that had fertilized a clutch with stored sperm or likely mated and extruded a clutch fertilized with sperm from recent mating (Webb 2009). Several factors may account for these differences, including the amount of sperm acquired at mating that might have been higher in Webb (2009) because those females were collected in an area closed to fishing. Females in the current study were also collected later in the reproductive cycle and spermathecal load may have decreased with increasing storage time (Sainte-Marie 1993).

The proportion of females with fresh ejaculate in the spermathecae varied among locations in this study. While females completing the molt to maturity are obligated to mate in order to produce a fertilized egg clutch and sperm reserves are a function of operational sex ratio (Sainte-Marie et al. 2002), specific factors determining the frequency of mating of multiparous females are not well understood (see Sainte-Marie et al. 2008). Based on mating indicators or measurement of sperm reserves, several studies in Alaska have implied that most (~90%) of multiparous female Tanner crabs mate on an annual basis (Paul 1984, Webb 2009). The proportion of females with ejaculate remaining from recent mating ranged from 0.50 to 1.00 and 0.08 to 0.92 for SC3 and SC4 females, respectively, among locations in this study (Table 2). This suggests to us that the proportion of multiparous females identifiable as mated on an annual basis may be more variable than previously recognized. In this study, increased proportions of females with fresh ejaculate were associated with increased mean sperm cell counts among locations for primiparous females and among location and shell condition groups for all females, and may be useful as an indicator of relative differences in sperm reserves among areas (Table 3, Fig. 5).

Comparison of quantitative indices of abundance or sex ratio from stock assessment surveys or models with empirical measures of variability in reproductive potential may assist fisheries managers in identifying levels of sex ratio or exploitation rate index which may result in female sperm reserves in excess of those needed for clutch fertilization. In this study decreasing sperm cell counts of SC3 females were associated with increasing exploitation rate index by location (Fig. 5); for multiparous females the strongest associations were observed between mean spermathecal loads and survey or model estimates of sex ratio of large males to multiparous females. Interpretation of the robustness of these relationships is limited by sample sizes in some locations and a need for additional data across years. However, it can be preliminarily concluded that increased exploitation rates may be inversely related to primiparous female sperm reserves and that differences in the amount of sperm accrued by multiparous females may vary as a function of the relative availability of legal-sized males during the mating season.

Defining sources of variability in female fecundity can provide understanding of how egg production may vary with biological characteristics or environmental factors. Previous studies have described seasonal variability in fecundity (Hilsinger 1976) and differences in the size-fecundity relationship between primiparous and multiparous female Tanner crab (Somerton and Meyers 1983). In addition to carapace width and shell condition, our results indicated that mean embryo weight is negatively associated with fecundity for Tanner crab in southeastern Alaska. Variability in mean embryo weight among female brachyuran crabs has been described as a maternal effect and may be associated with variability in embryo and larval quality (Gimenez and Anger 2003). A similar relationship was also observed for *Chionoecetes bairdi* in previous studies (Paul and Fuji 1989) and *C. opilio* from the Gulf of St. Lawrence, Canada (Sainte-Marie 1993). Similar to Somerton and Meyers' (1983) finding, lower fecundity, but of a greater magnitude (48% versus 30%), was observed between SC3 and SC4 females in this study. Differences in these estimates may be due to the separation of multiparous females into two shell condition classes in this study versus one in Somerton and Meyers (1983). In this study, fecundity of multiparous (SC5) females was intermediate between SC3 and SC4 females (Table 5), and pooling of SC4 and SC5 females would have reduced the magnitude of differences in the size-fecundity relationship between SC3 and SC4 females. The fecundities of female Tanner crab in this study were generally similar to those from the northern Gulf of Alaska (Hilsinger 1976), but detailed comparisons were not possible because Hilsinger (1976) did not separate size-fecundity relationships between primiparous and multiparous females.

It is unlikely that sperm limitation was a substantial limiting factor in female egg production in this study. Mean prevalence of nonviable embryos and egg cases was low in all areas (≤~ 5%). Qualitatively, greater prevalences were not associated with lower mean sperm reserves for SC3 females in areas such as Icy Strait and Stephens Passage (Table 2, Fig. 6). In support of this observation, both primiparous and multiparous females with zero sperm cells detected in the right spermatheca had fecundities either greater than or similar to those predicted by the ANCOVA model (Fig. 7).

Our results suggest that fishery managers wishing to evaluate appropriate harvest levels among exploited stocks should concurrently assess female sperm reserves and viable embryo production on spatiotemporal scales relevant to management, and compare trends with survey or model indices of the relative abundance of mature males and females. We observed that the sperm reserves of female Tanner crab in southeastern Alaska varied with reproductive ontogeny. For most individuals, both primiparous and multiparous, a high proportion of the sperm available for clutch fertilization was associated with recent mating, which was indicated by the presence of fresh, white, ejaculate in the spermatheca. The proportion of females with fresh ejaculate in the spermatheca by location was significantly correlated with variability in mean sperm cell counts and may be useful as an index of spatiotemporal variability in female sperm reserves. Further, decreased primiparous sperm reserves were significantly correlated with increased exploitation rate index. Differences in multiparous female spermathecal loads were associated with model- and survey-derived indices of sex ratio. If these relationships prove robust with additional years of data collection, it may be possible to define target or limit reference points for management based on functional relationships between these indices and female sperm reserves, which could result in low risk of decreased viable egg production due to sperm limitation for female Tanner crab.

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References

Adams, A.E., and A.J. Paul. 1983. Male parent size, sperm storage, and egg production in the crab *Chionoecetes bairdi* (Decapoda: Majidae). Int. J. Invert. Reprod. 6:183-187.

Ashidate, M.T. Sato, T. Jinbo, and S. Goshima. 2007. Does male-only fishing influence the reproductive success of the female spiny king crab, *Paralithodes brevipes*? Can. J. Fish. Aquat. Sci. 64:735-742. doi:10.1139/F07-044

Bednarski, J., G. Bishop, and C. Siddon. 2008. Tanner crab pot survey methods for southeast Alaska. Alaska Department of Fish and Game, Regional Information Report IJ08-02.

Donaldson, W.E., and A.E. Adams. 1989. Ethogram of behavior with emphasis on mating for the Tanner crab *Chionoecetes bairdi* Rathbun. J. Crustacean Biol. 9:37-53. doi:10.2307/1548445

Duluc, C., B. Sainte-Marie, and J.C. Brêthes. 2005. Value of indicators for assessing recent mating in brachyuran crabs. J. Mar. Biol. Assoc. U.K. 85:129-135. doi:10.1017/S0025315405010945h

Gimenez, L., and K. Anger. 2003. Larval performance in an estuarine crab, *Chasmagnathus granulata*, is a consequence of both larval and embryonic experience. Mar. Ecol. Prog. Ser. 249:251-264. doi:10.3354/meps249251

Gravel, K.A., and D. Pengilly. 2007. Investigations on reproductive potential of snow and Tanner crab females from the eastern Bering Sea in 2005. Alaska Department of Fish and Game, Fishery Data Series 07-23.

Hilsinger, J.R. 1976. Aspects of the reproductive biology of female snow crabs, *Chionoecetes bairdi*, from Prince William Sound and the adjacent Gulf of Alaska. Mar. Sci. Comm. 2:201-225.

Hines, A.H., P.R. Jivoff, P.J. Bushmann, J. Van Montfrans, S.A. Reed, D.L. Wolcott, and T.G. Wolcott. 2003. Evidence for sperm limitation in the blue crab, *Callinectes sapidus*. Bull. Mar. Sci. 72:287-310.

Jadamec, L.S., W.E. Donaldson, and P. Cullenberg. 1999. Biological field techniques for *Chionoecetes* crabs. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Kruse, G.H. 1993. Biological perspectives on crab management in Alaska. In*:* G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II (eds.), Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 355-384.

NPFMC. 1998. Summary of the fishery management plan for Bering Sea/Aleutian Islands king and Tanner crabs. North Pacific Fishery Management Council. Anchorage, Alaska. Accessed February 2010: http://www.fakr.noaa.gov/npfmc/fmp/crab/crabfmpsum.htm.

Orensanz, J.M., J. Armstrong, D. Armstrong, and R. Hilborn. 1998. Crustacean resources are vulnerable to serial depletion: The multifaceted decline of crab and shrimp fisheries in the greater Gulf of Alaska. Rev. Fish Biol. Fish. 8:117-176. doi:10.1023/A:1008891412756

Paul, A.J. 1984. Mating frequency and viability of stored sperm in the Tanner crab *Chionoecetes bairdi* (Decapoda, Majidae). J. Crustacean Biol. 4:375-381. doi:10.2307/1548037

Paul, A.J., and A.E. Adams. 1984. Breeding and fertile period for female *Chionoecetes bairdi* (Decapoda: Majidae). J. Crustacean Biol. 4:589-594. doi:10.2307/1548073

Paul, A.J., and A. Fuji. 1989. Bioenergetics of the Alaskan crab *Chionoecetes bairdi* (Decapoda: Majidae). J. Crustacean Biol. 9:25-36. doi:10.2307/1548444

Sainte-Marie, B. 1993. Reproductive cycle and fecundity of primiparous and multiparous female snow crab, *Chionoecetes opilio*, in the northwest Gulf of Sainte Lawrence. Can. J. Fish. Aquat. Sci. 50:2147-2156. doi:10.1139/f93-240

Sainte-Marie, B., and C. Carrière. 1995. Fertilization of the second clutch of eggs of snow crab, *Chionoecetes opilio*, from females mated once or twice after their molt to maturity. Fish. Bull. 93:759-764.

Sainte-Marie, B., and G.A. Lovrich. 1994. Delivery and storage of sperm at first mating of female *Chionoecetes opilio* (Brachyura: Majidae) in relation to size and morphometric maturity of male parent. J. Crustacean Biol. 14:508-521.

Sainte-Marie, G., B. Sainte-Marie, and J.-M. Sévigny. 2000. Ejaculate-storage patterns and the site of fertilization in female snow crabs (*Chionoecetes opilio*; Brachyura, Majidae). Can. J. Zool. 78:1902-1917.

Sainte-Marie, B., J-M. Sévigny, and M. Carpentier. 2002. Interannual variability of sperm reserves and fecundity of the snow crab (*Chionoecetes opilio*) in relation to sex ratio. Can. J. Fish. Aquat. Sci. 59:1932-1940.

Sainte-Marie, B., T. Gosselin, J-M. Sévigny, and N. Urbani. 2008. The snow crab mating system: Opportunity for natural and unnatural selection in a changing environment. Bull. Mar. Sci. 83(1):131-161.

Sato, T., M. Ashidate, S. Wada, and S. Goshima. 2005. Effects of male mating frequency and male size on ejaculate size and reproductive success of female spiny king crab *Paralithodes brevipes*. Mar. Ecol. Prog. Ser. 206:251-262. doi:10.3354/meps296251

Smith, B.D., and G.S. Jamieson. 1991. Possible consequences of intensive fishing for males on the mating opportunities of Dungeness crabs. Trans. Am. Fish. Soc. 120:650-653.

Smith, S.J., and B. Sainte-Marie. 2004. Biological reference points for invertebrate fisheries: Introduction. Can J. Fish. Aquat. Sci. 61:1303-1306. doi:10.1139/f04-135

Somerton, D.A., and W.S. Meyers. 1983. Fecundity differences between primiparous and multiparous female Alaskan Tanner crab (*Chionoecetes bairdi*). J. Crustacean Biol. 3:183-186. doi:10.2307/1548254

Stevens, B.G. 2003. Timing of aggregation and larval release by Tanner crabs, *Chionoecetes bairdi*, in relation to tidal current patterns. Fish. Res. 65:201-216. doi:10.1016/j.fishres.2003.09.015

Stevens, B.G., J.A. Haaga, and W.E. Donaldson. 1994. Aggregative mating of Tanner crabs, *Chionoecetes bairdi*. Can. J. Fish. Aquat. Sci. 51:1273-1280. doi:10.1139/f94-127

Swiney, K.M. 2008. Egg extrusion, embryo development, timing and duration of eclosion, and incubation period of primiparous and multiparous Tanner crabs (*Chionoecetes bairdi*). J. Crustacean Biol. 28:334-341. doi:10.1651/0278-0372(2008)028[0334:EEEDTA]2.0.CO;2

Taylor, D.M. 1996. Aspects of multiparous snow crab (*Chionoecetes opilio*) fecundity in insular Newfoundland waters. M.S. thesis, Memorial University of Newfoundland, Canada.

Webb, J. 2009. Reproductive success of multiparous female Tanner crab, *Chionoecetes bairdi*, fertilizing eggs with or without recent access to males. J. Northw. Atl. Fish. Sci. 41:163-172. doi:10.2960/J.v41.m611

Woodby, D., D. Carlile, S. Siddeek, F. Funk, J.H. Clark, and L. Hulbert. 2005. Commercial fisheries of Alaska. Alaska Department of Fish and Game, Special Publication 05-09.

Yamasaki, A., S. Fujita, K. Uchino, and T. Toshima. 1994. Research into the ecology of snow crabs in the waters off Kyoto Prefecture, IX. Numbers of sperm in the spermathecas of female snow crabs. Res. Rep. Kyoto Inst. Ocean Fish. Sci. 17:19-24. (Can. Transl. Fish. Aquat. Sci. 5663.)

Zheng, J., J.M. Rumble, and G.H. Bishop. 2006. Estimating southeast Alaska Tanner crab abundance using pot survey and commercial catch data. Alaska Fish. Res. Bull. 12:196-211.

Worton, C.L., D. Urban, K.M. Swiney, Z. Grauvogel, and S. Byersdorfer. 2010. Size at Physiological Maturity and Minimum Size at Functional Maturity for Male Dungeness Crabs in Alaska Waters. In: Biology and management of exploited crab populations under climate change (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.14

Size at Physiological Maturity and Minimum Size at Functional Maturity for Male Dungeness Crabs in Alaska Waters

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Abstract

Alaska Department of Fish and Game harvest regulations for Dungeness crab (*Cancer magister*) set size limits to ensure that males have an opportunity to mate at least once before recruiting to the fishery. In Alaska, the Dungeness crab size limit is based upon studies conducted in British Columbia in the 1960s and it is unknown whether the current commercial size limit of 165 mm carapace width (CW) is appropriate for stocks in Alaska. We determined the size at male physiological maturity and minimum size at functional maturity via field collections and noncompetitive laboratory mating studies using crabs collected from Kodiak Island, Alaska. Physiological maturity was determined by examining males for the presence of spermatophores in the vas deferens. Onset of physiological maturity was observed at 62 mm CW, 50% physiological maturity at 64.6 mm CW, and 100% maturity at 71 mm CW. Laboratory mating studies were conducted to examine male functional maturity, defined as the ability of a male and female to mate, resulting in extrusion of fertilized eggs. A polymerase chain reaction analysis was used to confirm that the putative father contributed to the fertilization of the eggs. Males were functionally mature at a minimum of 112 mm CW, smaller than previously reported. Until functional maturity can be defined in a competitive setting, a full functional maturity schedule is determined, and the importance of small males in the mating of larger females is examined, changing the size limit is not recommended.

Introduction

Commercial exploitation of Dungeness crabs (*Cancer magister*) has been occurring on the West Coast of the United States since the 1860s (Cleaver 1949, Miller 1976, Donaldson and Donaldson 1992) and in Alaska since 1913 (Hoopes 1973). The first harvest regulations were imposed in 1897 in California and restricted the possession and sale of female crabs in an attempt to preserve crab populations (Methot 1988). In 1903, the minimum size limit of male crabs was set at 152 mm carapace width (CW), including spines, and was influenced more by market demands than biological reasons (Poole and Gotshall 1965). California, Oregon, and Washington later adopted commercial fishery regulations barring the retention of male Dungeness crabs less than 159 mm CW since there was no market for crabs smaller than this (Cleaver 1949). Alaska adopted similar regulations for the management of Dungeness crab fisheries by allowing harvest of only male crabs 165 mm CW or larger; although no research on size of male maturity in Alaska was conducted to support that size limit.

In general, Alaska crab fishing regulations are based on the premise that allowing male crabs to mate once before becoming vulnerable to the commercial fishery will protect the reproductive potential of the crab stocks (Donaldson and Donaldson 1992, Paul 1992). However, economic and market considerations have also been important in setting the actual size limits (Donaldson and Donaldson 1992). The minimum size limits for commercial crab harvest are typically derived by adding the expected annual growth to the size at maturity (Somerton 1981) and have been used for many crab fisheries to protect the breeding stocks of crab populations (Donaldson and Donaldson 1992, Paul 1992). Brachyuran crabs exhibit wide variation in size at maturity between different geographic areas (Hines 1989); therefore the size at maturity estimates from British Columbia (Butler 1960) used to determine the legal size limits in Alaska may not be reflective of Alaska Dungeness crab populations. Male Dungeness crab sexual maturity is based on both physiological status (ability to produce spermatophores) and functional status (mating that results in the production of a fertilized brood). Alaska populations have not been examined for size at either physiological or functional maturity, and maturity data are limited throughout their range. In northern British Columbia, the smallest males examined, 109 mm CW, were physiologically mature (Butler 1960). Based upon collections of mating pairs and presence of "mating marks," Butler (1960) concluded that males were functionally mature at approximately 132 mm CW (Butler's carapace widths were converted to exclude the tenth anterolateral spine [Wainwright and Armstrong 1993]). Female size at sexual maturity in British Columbia and Washington was approximately 93-100 mm CW (Butler 1960, Orensanz and Gallucci 1988).

The size at maturity of female Dungeness crab is also important because it can determine the minimum size of successful mating for male crabs. Mating among Dungeness crabs occurs between recently molted soft-shelled females and considerably larger hard-shelled males (MacKay 1943, Butler 1960, Snow and Neilsen 1966). Prior to female ecdysis, a pre-mating embrace is formed, the female molts, and mating occurs (MacKay 1943, Butler 1960, Snow and Neilsen 1966).

After copulation, viable sperm can be stored in paired spermathecae for as long as 2.5 years (Hankin et al. 1989), as sperm can be retained across molts (Shirley and McNutt 1989). Eggs are fertilized as they pass the spermathecae during extrusion (Jensen et al. 1996), approximately 6 months after mating (Oh and Hankin 2004). Eggs are brooded externally until hatching by adhering to the setae on the pleopods (Jaffe et al. 1987). The first male to mate with a soft-shelled female places a sperm plug in the vagina, which prevents subsequent males from contributing sperm to the spermathecae during that reproductive season (Jensen et al. 1996). Sperm plugs remain for approximately 180 days post mating which extends beyond the reproductive season (Oh and Hankin 2004). However, the sperm plug does not prevent subsequent copulation. Sperm from any additional males enters the bursa, which is located distal to the spermathecae, and is thought not to contribute to fertilization (Jensen et al. 1996). In Dungeness crab fertilization, last male precedence (the last male to deposit sperm in the spermathecae) prevails. However, last male precedence can be disrupted when a female already has a large amount of stored sperm in her spermathecae and the volume of new incoming sperm to the spermathecae is large enough to displace the stored sperm (Pamela Jensen, Alaska Fisheries Science Center, Seattle, 2008, pers. comm.). Functional maturity not only depends on the ability of the male to mate with the female but also on the size and maturity stage of the female, mating timing, and the number and volume of sperm deposits. The complexity of the Dungeness mating process does not always ensure that the male that mates will sire a clutch of eggs.

Our study is an important step toward evaluating whether the current size limits for Dungeness crabs in Alaska allow males to mate at least once before recruiting to the fishery. We determined male size at physiological maturity and minimum size at functional maturity, and the potential limits of female maturity on functional maturity, by examining reproductive dynamics of Dungeness crabs via field collec-

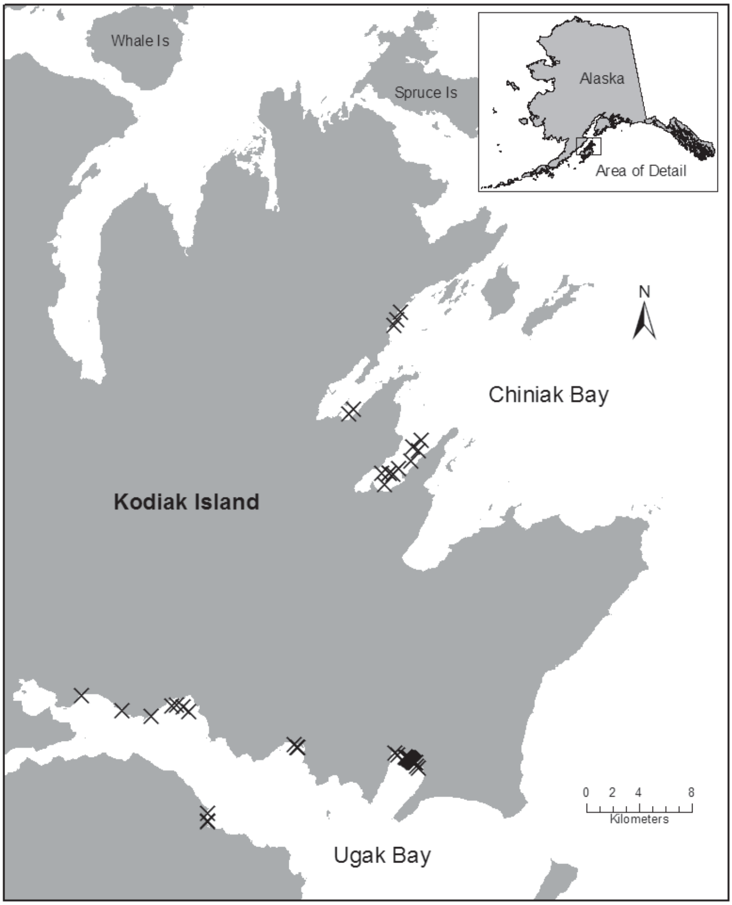

Figure 1. Collection sites of Dungeness crabs from Kodiak Island, Alaska, 2002-2004.

tions, conducting noncompetitive laboratory mating experiments, and performing genetic analysis of resulting broods to confirm successful mating. In addition, we document male growth based on historical tagging data from southeastern Alaska and Kodiak Island.

Materials and methods

Field collections

A total of 1,019 Dungeness crabs ranging from 38 to 190 mm CW were collected from locations within Chiniak and Ugak bays on the east side of Kodiak Island, Alaska, (Fig. 1) from 2002 to 2004, using modified pots and a small trawl net.

A 4.9 m long, small-mesh trawl net with a 4.7 m footrope, two 4.0 kg trawl doors, and net body and cod-end composed of 3.0 cm mesh web was towed in the head of the bays at depths ranging from 2.4 to 10.7 m. Seventy-five tows were made with the trawl net at depths 1-23 m and the majority of crabs were found at less than 5 m.

In September 2002, in order to collect mating pairs, five crab pots were modified to retain otherwise sublegal crabs by lining the pot perimeters, tops, and bottoms, and covering escape rings with 1.3 cm hardware cloth or 2.5 cm shrimp web. Seven pairs of crabs were observed in mating embraces in pots with male sizes ranging from 157 to 178 mm CW and females from 114 to 141 mm CW, female sizes ranged from 6.1 to 27.4% smaller than the males. The pots captured sublegal male crabs (<165 mm CW), but the size of the crabs was almost exclusively greater than 110 mm CW. Only 17 male crabs 82-104 mm CW were captured with the pots.

Of the crabs captured, 444 males and 276 females were transported live to the seawater laboratory of the Alaska Fisheries Science Center in Kodiak. Individual crab CWs were measured to the nearest 1.0 mm anterior to the tenth anterolateral spine and each crab was tagged with an individually numbered tag and a cable tie around a walking leg. Males and females were held in separate ambient sand-filtered flow-through seawater tanks (3.1°C to 12.4°C) and fed a mixed diet of fish and squid ad libitum twice a week.

Male physiological maturity

From late July through November 2002, the season during which the peak male gonad development has been shown to occur (Swiney and Shirley 2001), a total of 416 male Dungeness crabs of 40-105 mm CW were collected for spermatophore analysis. Once back in the laboratory, male crabs were dissected immediately and a portion of the vas deferens was removed. Smears of seminal fluid were made and examined microscopically for the presence of spermatophores; males whose vas deferentia contained spermatophores were considered physiologically mature.

Male size at 50% physiological maturity was estimated by the logistic equation

$$PROPx = 1/(1 + e^{ax+b}) \ ,$$

where $PROPx$ is the proportion of males that are mature males at CW x in mm and a and b are fitted parameters, based on nonlinear least squares regression (Minitab 2005). Size at 50% maturity was estimated as $-\hat{b}/\hat{a}$, where $\hat{a}$ and $\hat{b}$ are the least squares estimates of a and b. Standard error (SE) for the CW estimate is reported.

Male functional maturity

In 2003 and 2004, during the mating season (May-June), males 95-186 mm CW (which were expected to be physiologically mature based upon year one physiological data), and females 49-183 mm CW were collected for mating experiments. Only males that successfully mated with females resulting in the extrusion of fertilized eggs were considered to be functionally mature. Since the females have the ability to retain sperm across molts and may have mated prior to coming into the laboratory, genetic analysis was used to confirm that our putative male actually contributed to the fertilization of the eggs (see genetic methods section).

A total of 106 noncompetitive laboratory mating experiments were conducted between May 2003 and September 2004 to examine male functional maturity and female size at maturity (Table 1). To confirm the onset of female ecdysis, five males larger than 165 mm CW were placed in the female holding tank. After a male grasped a female in a premating embrace, the female was removed prior to molting and placed in an individual mating tank with a male. Males ranging in size from 92 mm to 162 mm CW were paired with females of premolt sizes from 69 mm to 121 mm CW; females ranged between 19% and 42% smaller than the males. Female postmolt sizes ranged from 84 mm to 135 mm CW, which reduced the female size to between 1-29% smaller than the male (Table 1). Each male was used once for the mating studies. We kept pairs in the tank for 3 weeks after the female molted to give the pair ample time to mate. We observed pairs once daily: occurrences of premating embraces, molting, mating, postmating embraces, and mortalities were recorded. A video camera was used to record three successful mating events.

Upon completion of the mating experiments, males were dissected, examined for the presence of spermatophores as described above, and a sample of leg muscle tissue was collected for genetic analysis. Females were measured, retagged, and held in a communal tank where they were examined twice a week to see if they had extruded eggs. During

Table 1. Summary of results for Dungeness mating experiments and genetic analysis of female and male tissues.

Male CW[a] (mm)	Female CW[a] (mm)		Molted twice[b]	Mating behavior[c]	Spermathecae[d]	Extruded eggs	Male allele present		Mixed paternity	
	Premolt	Postmolt					Eggs	Spermathecae	Eggs	Spermathecae
96	77	96	y	n	n/a	n/a	n/a	n/a	n/a	n
97	76	93	n	n	n/a	n/a	n/a	n/a	n/a	n/a
102	78	94	n	y	n/a	n/a	n/a	n/a	n/a	n/a
103	69	84	n	n	n/a	n/a	n/a	n/a	n/a	n/a
104	83	103	n	n	n/a	n/a	n/a	n/a	n/a	n/a
104	76	96	y	n	n/a	n/a	n/a	n/a	n/a	n/a
105	83	100	y	n	n	n/a	n/a	n	n/a	n
105	79	94	y	y	n	n/a	n/a	n/a	n/a	n/a
105	92	114	y	n	y	n/a	n/a	n/a	n/a	n/a
106	81	101	n	n	y	y	n/a	n/a	y	n
106	82	100	y	n	y	n/a	n/a	y	n/a	n
107	82	101	n	n	y	y	n/a	n/a	n	n
107	69	84	n	y	n/a	n/a	n/a	n/a	n/a	n/a
107	81	91	n	n	n	n/a	n/a	n/a	n/a	n/a
108	77	96	y	y	n/a	n/a	n/a	n/a	n/a	n/a
109	77	98	y	n	n/a	n/a	n/a	n/a	n/a	n/a
111	84	104	y	n	y	y	n/a	n/a	n	n
112	76	97	y	n	y	n/a	n/a	n/a	n/a	n
112	83	112	n	y	n	n/a	n/a	y	n/a	n
112	84	104	y	n	n	n/a	n/a	y	n/a	y
112	83	101	y	y	y	y	y	y	n	n
114	80	101	n	n	n/a	n/a	n/a	n/a	n/a	n/a
115	84	105	y	y	y	y	n/a	n/a	n	n
115	87	106	y	y	n/a	n/a	n/a	n/a	n/a	n/a
116	80	104	y	n	y	y	n/a	n/a	y	n
117	80	101	n	y	n/a	n/a	n/a	n/a	n/a	n/a
118	81	103	y	y	y	y	n/a	n/a	n	n
118	88	110	n	y	y	y	y'	y	y	n
118	83	103	n	n	y	n/a	n/a	n/a	n/a	n/a
118	89	110	y	n	n/a	n/a	n/a	n/a	n/a	n/a
119	82	113	n	y	y	n/a	n/a	n/a	n/a	n/a
120	94	116	n	y	y	n/a	n/a	y	n/a	y
120	82	110	y	y	y	y	y	y	n	n
120	83	102	n	y	n/a	n/a	n/a	n/a	n/a	n/a
120	86	106	y	n	n/a	n/a	n/a	n/a	n/a	n/a
121	79	97	y	n	n/a	n/a	n/a	n/a	n/a	n/a
123	91	112	n	y	y	y	y	y	n	y
123	91	112	y	y	n	y	y'	n	y	n
124	86	108	y	y	y	y	n/a	n/a	y	y
125	85	109	y	y	y	n/a	n/a	n/a	n/a	n/a

Table 1. (continued)

Male CW[a] (mm)	Female CW[a] (mm)		Molted twice[b]	Mating behavior[c]	Spermathecae[d]	Extruded eggs	Male allele present		Mixed paternity	
	Premolt	Postmolt					Eggs	Spermathecae	Eggs	Spermathecae
125	94	118	y	y	n/a	n/a	n/a	n/a	n/a	n/a
126	100	120	y	n	y	n/a	n/a	n	n/a	n
126	90	111	y	n	y	y	y	y	n	n
128	79	97	y	y	y	n/a	n/a	n/a	n/a	n/a
129	94	115	n	n	y	y	y'	n/a	n	n/a
129	97	121	n	y	y	y	y	y	n	n
130	86	109	y	y	y	y	n/a	n/a	n	n
130	86	108	n	y	y	n/a	n/a	y	n/a	y
130	88	111	y	n	y	n/a	n/a	n/a	n/a	n/a
130	85	103	n	n	n/a	n/a	n/a	n/a	n/a	n/a
131	99	121	n	y	y	y	y	y	n	n
132	86	108	y	y	y	y	n/a	n/a	y	n
132	90	108	y	n	y	y	y	y	y	n
132	85	103	n	y	n/a	n/a	n/a	n/a	n/a	n/a
132	91	111	y	y	n/a	n/a	n/a	n/a	n/a	n/a
133	94	114	n	y	y	n/a	n/a	y	n/a	n
133	82	101	n	y	y	y	n/a	n/a	n	y
133	83	103	n	y	n/a	n/a	n/a	n/a	n/a	n/a
134	87	109	y	y	y	y	n/a	n/a	y	n
134	90	110	y	n	y	n/a	n/a	y	n/a	n
134	95	111	n	n	y	y	y	y	n	n
134	98	120	n	y	y	y	y	y	y	n
134	90	113	y	y	y	y	y	y	n	n
134	95	117	y	y	y	y	y	y'	n	y
134	85	105	n	n	n/a	n/a	n/a	n/a	n/a	n/a
134	100	121	n	y	y	y	n/a	n/a	n/a	n/a
135	92	114	n	y	y	n/a	n/a	y	n/a	n
135	89	110	n	y	y	y	y	y'	n	y
135	92	114	n	y	y	y	n/a	n/a	n/a	n/a
136	-	118	n	y	y	n/a	n/a	y'	n/a	y
136	90	111	n	y	y	n/a	n/a	y	n/a	n
136	101	123	n	y	y	y	y	y	n	n
136	88	108	n	n	n/a	n/a	n/a	n/a	n/a	n/a
137	88	108	n	y	y	y	n/a	n/a	n	n
137	89	113	y	n	y	n/a	n/a	y	n/a	n
137	98	117	n	y	y	y	y	y	n	n
137	90	110	n	y	y	y	y	y	y	n
137	98	120	y	n	y	y	y	y	n	n
137	95	116	y	n	n/a	n/a	n/a	n/a	n/a	n/a

Table 1. (continued)

Male CW[a] (mm)	Female CW[a] (mm)		Molted twice[b]	Mating behavior[c]	Spermathecae[d]	Extruded eggs	Male allele present		Mixed paternity	
	Premolt	Postmolt					Eggs	Spermathecae	Eggs	Spermathecae
138	89	108	y	y	y	y	y	y	n	n
138	83	101	y	n	y	n/a	n/a	n/a	n/a	n/a
138	86	109	y	y	n/a	n/a	n/a	n/a	n/a	n/a
139	81	99	y	y	y	y	n/a	n/a	n	n
139	102	126	n	y	y	y	y	y	n	n
139	101	122	n	y	y	y	y'	y	y	n
139	101	121	n	y	y	y	y'	y	y	n
139	89	107	y	y	n/a	n/a	n/a	n/a	n/a	n/a
140	100	120	n	y	y	n/a	n/a	n	n/a	y
140	98	119	n	n	y	n/a	n/a	y	n/a	n
140	98	118	n	n	y	y	n/a	n/a	n/a	n/a
141	109	129	n	y	y	y	y'	y'	n	y
141	103	121	n	y	y	y	y	y	n	y
141	103	123	n	y	y	y	n/a	n/a	n/a	n/a
141	102	122	n	y	y	y	n/a	n/a	n/a	n/a
142	107	130	n	y	y	y	n/a	n/a	n/a	n/a
143	104	123	n	y	y	y	n/a	n/a	n/a	n/a
144	99	117	n	y	y	n/a	n/a	y	n/a	n
144	98	121	n	y	n/a	n/a	n/a	n/a	n/a	n/a
145	111	133	n	y	y	y	y	y	y	y
146	102	122	n	y	y	y	y	y	y	n
147	104	123	n	y	y	y	y	y	n	y
149	101	121	n	y	y	n/a	n/a	y	n/a	y
149	105	125	n	y	y	y	y	y	n	y
149	121	135	n	y	y	y	n/a	n/a	n/a	n/a
153	100	123	n	y	y	n/a	n/a	y	n/a	n
153	99	120	n	y	y	n/a	n/a	n/a	n/a	n/a
162	97	115	n	y	y	-	-	y	n	n

[a] CW = carapace width.

[b] Females that molted, potentially mated, and did not extrude eggs that mating season and molted the following year.

[c] Premolt embrace, postmolt embraces, and/or mating observed from once a day observations.

[d] Sperm present in spermathecae.

y' Four loci with alleles specifically from the putative father and therefore considered a likely parent.

n/a Not applicable. Tissue not sampled (male muscle, spermathecae and/or eggs).

the mating experiments conducted in 2003, females were sacrificed immediately after egg extrusion and 14 spermathecae, 13 egg clutches, and 27 leg muscle tissue samples were removed and preserved for genetic analysis. During the 2004 mating experiments, 49 females were held until the eggs were eyed and then sacrificed and processed as in 2003. Some females died after being paired with a male, before extruding an egg clutch. Ovary color was assessed for maturity stage (Wild 1983) and the spermathecae and leg muscle tissue were processed for genetic analysis to determine if mating occurred. All tissues collected for genetic analysis were preserved in 100% ethanol.

Genetic methods

Genetic analysis was conducted on sperm stored in the spermathecae and egg clutches to confirm if the male from the noncompetitive mating experiments mated and contributed spermatophores to the female. We used highly polymorphic genetic markers, microsatellites described by Jensen and Bentzen (2004) and Toonen et al. (2004), to detect male allele presence in the spermathecae contents and egg clutches from the laboratory mating experiments. Eight DNA samples were then used to test and optimize 23 primer pairs for polymerase chain reaction (PCR) amplification of the DNA.

The genotypes of the mating pairs were determined from leg muscle tissue. A total of 124 individual parents, 61 males and 63 females, were genotyped from leg tissues. Sperm samples from the spermathecae of 63 mated females were also genotyped. To harvest the remaining sperm stored by the fertilized females in their spermathecae, the lower genitalia was dissected to remove excess muscle and connective tissue to reveal the spermathecae. The vaginal tract was then opened, starting from the hole where the bursa was located and moving toward the spermathecae. The sperm was then flaked into a separate tube using forceps. To collect DNA from the offspring, eight replicates of approximately 50 to 100 eggs were taken from arbitrary locations in the egg clutch and placed in separate tubes. Appropriate sample size of eggs was determined by testing PCR product from extractions using 1, 2, 4, 6, 8, 10, 12, and approximately 50 eggs from one egg clutch. Initially in 2002, the genetic component was not part of this project so some males were not sampled for genetics analysis. But for crosses in which a putative father was available, that male's genotype was compared to the spermathecae and eggs for any mismatches.

PCR for both the parent and the offspring genotyping was carried in10 µl reaction volumes consisting of 10mM Tris-HCl, 50mM KCl, 0.2mM each dNTP, 20mM $MgCl_2$, and 0.5 units Applied Biosystems (AB) AmpliTaq® DNA polymerase using an ABI 9700 thermalcycler. Thermal cycling profiles were 95°C denaturation for 2 minutes followed by 30 cycles of 92°C denaturation for 30 seconds, annealing temperature

Table 2. Polymerase chain reaction (PCR) multiplexes and conditions used for microsatellite amplification.

Multiplex designation	Annealing temperature	Primers	Label	Primer concentration
Multiplex1	60°C	*Cma1* [a]	6FAM	0.25μM
		Cma2 [b]	VIC	0.25μM
		Cma3	NED	0.25μM
Multiplex2	60°C	*Cma5*	6FAM	0.25μM
		Cma6	VIC	0.25μM
		Cma12	NED	0.25μM
Multiplex3	58°C	*Cma17*	6FAM	0.25μM
		Cma18	VIC	0.25μM
		Cma43	NED	0.25μM
		Cma53	PET	0.25μM
Multiplex4	62°C	*Cma4* [b]	PET	0.25μM
		Cma9a [a]	VIC	0.25μM

[a] PCR products unscorable in several individuals, so no scores were included.
[b] Suspicious peaks led to dropping these loci from MPR and EPR calculations.

(Table 2) for 1 minute, 72°C extension for 1 minute, and completed with a 72°C final extension for 3 minutes. A 0.25μM concentration was used for all primers (Table 2). PCR products were size-fractionated using an ABI3730 DNA Analyzer with v2.0 collection software (AB). Samples were prepared for injection following instructions included with the GeneScan™ 500LIZ™ standard. Data were analyzed, using the local Southern sizing algorithm in the GeneMapper® software v3.7 (AB). Fragment sizes of 35, 250, and 340 were excluded from the size standard analysis algorithm. GENEPOP v3.4 (Raymond and Rousset 1997) was used to calculate allele frequencies and the inbreeding coefficient estimate (F_{IS}) for each locus and to test for departures from genotype frequencies expected under Hardy-Weinberg equilibrium.

Exclusion power (EPR) is a measure of utility of a marker or set of markers for excluding a random individual from a population as a parent, given the genotype of the other parent and the offspring. We calculated EPR for each locus using the formula given in DeNise et al. (2004) and Jamieson (1965). Match probability ratio (MPR), the probability of randomly drawing two individuals with identical genotypes from a population, was calculated for each locus as the squared frequency of the most common allele in order to provide the most conservative power estimate. The cumulative MPR was calculated as the sequential product of MPR for each added locus (DeNise et al. 2004).

We required at least four loci with alleles in the spermathecae and egg clutch specifically from the putative father to consider him the likely parent. For crosses for which no putative father was available, any spermathecae or egg genotypes exhibiting more than two non-maternal alleles were considered evidence for multiple paternities.

Historical growth per molt

Male growth per molt data are limited to tagging studies done from 1963 to 1969 in southeastern Alaska (Lehman and Osborn 1970) and near Kodiak, Alaska, from 1970 to 1974 and 1986 (Alaska Department of Fish and Game, Kodiak, unpubl. data) with premolt sizes ranging from 117 to 179 mm CW. For this reason we used southeastern Alaska (Lehman and Osborn 1970) and Kodiak data sets independently to calculate the number of molts functionally mature males would undergo before reaching legal size limit. A simple linear regression model was used to describe the dependence of the postmolt CW size on the premolt CW size for both data sets. The linear model

$$y = \beta_0 + \beta_1 x,$$

where x is the premolt CW, y is the postmolt CW, and β_0 and β_1 are parameters to be estimated, was fitted by least squares regression applied to each of the data sets. From this point forward in this article, the Kodiak data set will be refer to as Kodiak Alaska 1970s since the majority of the tagging was done from 1970 to 1974, except for 10 crabs that were tagged in 1986, and the southeastern Alaska data set will be referred to as Southeast Alaska 1960s.

Results

Male physiological maturity

Parameter estimates for the CW-maturity logistic equation were $\hat{a} = 0.554$ and $\hat{b} = -35.731$ ($P < 0.0001$). The smallest male observed to have spermatophores present was 62 mm CW, and the vas deferentia of all males ≥71 mm CW that were examined showed the presence of spermatophores. From the logistic regression parameter estimates, size at 50% physiological maturity was estimated to be 64.6 mm (SE of CW = 0.14 mm; Fig. 2).

Genetic results

Ten of the 12 microsatellite loci amplified consistently in the samples produced scorable peaks. Two of these loci (*Cma2* and *Cma4*) produced peaks that appeared irregular on closer inspection, and were scored differently in successive amplifications. They also exhibited an inherent nonspecific binding artifact that produced peaks in those loci that did

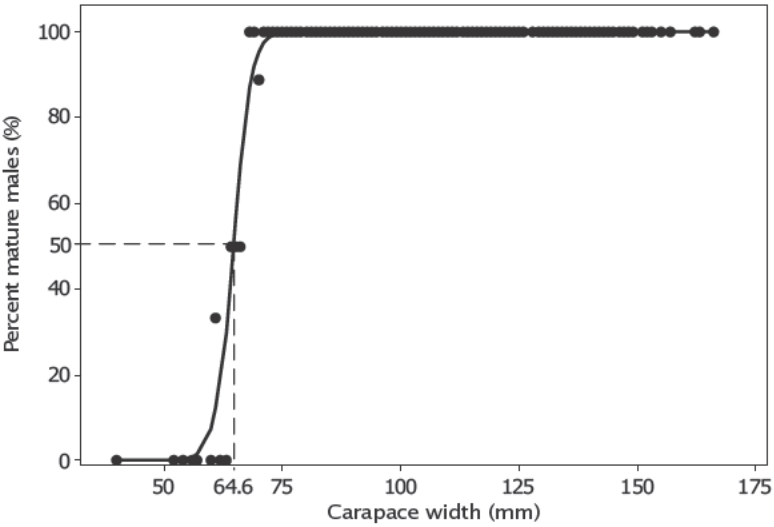

Figure 2. **Percentage of male Dungeness crabs that were physiologically mature based on the presence of spermatophores as a function of carapace width (mm) with logistic regression [*PROPx* = 1/(1+$e^{0.554x\text{-}35.731}$, $P < 0.0001$, $n = 363$] fit to the data (solid line) and the estimated size at which 50% of males are physiologically mature (dashed lines).**

Table 3. **Genotyping success rate for ten microsatellite loci in parental crab muscle tissue and in spermathecae and egg samples.**

	Parental	Offspring	
Locus	Muscle	Spermathecae	Egg
Cma5v1	100.0%	100.0%	79.8%
Cma6v1	100.0%	100.0%	78.9%
Cma53v1	99.1%	98.4%	90.1%
Cma17v1	99.1%	98.4%	83.4%
Cma18v1	99.1%	91.9%	77.4%
Cma43v1	98.2%	98.4%	88.0%
Cma12v1	98.2%	100.0%	84.0%
Cma3v1	98.2%	100.0%	68.7%
Cma2av1	98.2%	100.0%	62.0%
Cma4v1	91.9%	96.8%	69.9%

not originate from true alleles, so they were excluded from analysis. The remaining eight primer pairs yielded clean, easily scorable peaks in all samples examined, allowing adequate detection of the parental alleles and providing high statistical power to detect multiple paternity.

Genotyping success rates were high for muscle and spermathecae, but were lower for eggs (Table 3). No significant PCR product appeared until the 12-egg extraction, and the yield from the 12 eggs was too small to consistently detect multiple inheritances. Marker failure in the egg samples resulting in lower genotype success rates may be explained by the high levels of yolk in the uneyed eggs, which inhibits the PCR process (Pamela Jensen, Alaska Fisheries Science Center, Seattle, 2008, pers. comm.), and the low concentrations of DNA that occur in newly developed eggs.

The markers were highly variable within the parent collection, with individual loci exhibiting between 4 and 32 alleles (Table 4). One locus (*Cma12*) exhibited genotypic frequencies that departed significantly ($P < 0.0001$) from those expected under Hardy-Weinberg equilibrium. This appeared to be due to an excess of homozygotes ($F_{IS} = 0.150$), which in turn may be explained by the fact that many alleles at this locus were at the upper detectable size limit given the chemistry and hardware used.

Parentage analyses by exclusion performed using eight microsatellite loci resulted in an EPR of 99.8% and MPR of 0.0%, suggesting considerable statistical power for the detection of multiple paternity (Table 4).

Functional maturity

Premating embraces were observed in males ranging from 102 to 162 mm CW and often occurred within 10 minutes after being placed in the tank with the female. Only five pairs were observed mating; the smallest male in those five pairs was 102 mm CW. Postmating embraces were less common and only observed in 24 mating experiments. This is likely a reflection of limiting observations to one per day during only daylight hours.

As a result of the noncompetitive mating experiments, 50 egg clutches were extruded 85 to 498 days after the first molt, 18 females molting a second time before extruding an egg clutch (Table 1). A total of 29 egg clutches were genotyped for paternity analysis and all had alleles from the male parent (Table 1). Males that sired egg clutches ranged in size from 112 mm CW to 149 mm CW. The observed male minimum size at functionally maturity was 112 mm CW.

Macroscopic examination of spermathecae revealed the presence of stored sperm in all females from the mating experiments. Every male that successfully contributed alleles to the sperm stored in the spermathecae also sired a clutch of eggs (Table 1). Examination of males that contributed alleles to the sperm stored by the females showed that all males as small as 106 mm CW have the ability to mate with females;

Table 4. Numbers of alleles and frequencies of the most common alleles (*p*) of 10 microsatellite markers in a collection of Dungeness crab from Kodiak Island, Alaska. Match probability ratio (MPR) and exclusion power (EPR) based on these allele frequencies are listed for each individual marker and for the cumulative set of markers.

Locus	Number of alleles	*p*	MPR		EPR	
			Locus	Cumulative	Locus	Cumulative
Cma5	8	0.350	12.3%	12.3%	53.3%	53.3%
Cma6	7	0.680	46.2%	5.7%	26.8%	65.8%
Cma53	4	0.859	73.8%	4.2%	11.3%	69.7%
Cma17	16	0.194	3.8%	0.2%	76.5%	92.9%
Cma18	17	0.286	8.2%	0.0%	71.5%	98.0%
Cma43	13	0.319	10.2%	0.0%	65.8%	99.3%
Cma12	9	0.505	25.5%	0.0%	44.8%	99.6%
Cma3	10	0.382	14.6%	0.0%	57.6%	99.8%
Cma2[a]	32	0.113	1.3%	0.0%	88.4%	100.0%
Cma4[a]	19	0.287	8.2%	0.0%	67.2%	100.0%

[a] Loci not used in the parentage analyses.

however, it is unknown if those males would have sired egg clutches since the females died before they were able to extrude an egg clutch. Based on the condition of the female ovaries it was unlikely that 65% of these females would have extruded eggs in that reproductive season because their ovaries were immature.

Multiple paternity was detected in 10 clutches of eggs (34%) from females ranging in size from 101 to 133 mm postmolt CW and males ranging from 106 mm CW to 146 mm CW (Table 1). Multiple sperm contributions of males were detected in the stored sperm of 12 out of the 63 females sampled for spermathecae contents, but mixed paternity was detected in eggs of only five of those females. The design of this study dictated that females had the opportunity to mate with only one male in the laboratory. Therefore, the incidence of multiple paternity in this study was the result of the females mating in the wild prior to being brought into the laboratory.

Growth estimates

Fitted linear regression models for growth per molt estimates for Kodiak Alaska 1970 ($y = 0.889x + 42.670$, $r^2 = 0.52$, $P < 0.0001$, $n = 59$) and the Southeast Alaska 1965 ($y = 1.305x - 20.061$, $r^2 = 0.88$, $P < 0.0001$, $n = 362$) both showed a good linear relationship between premolt CW and postmolt CW (Fig. 3). Based upon observed minimum male size of func-

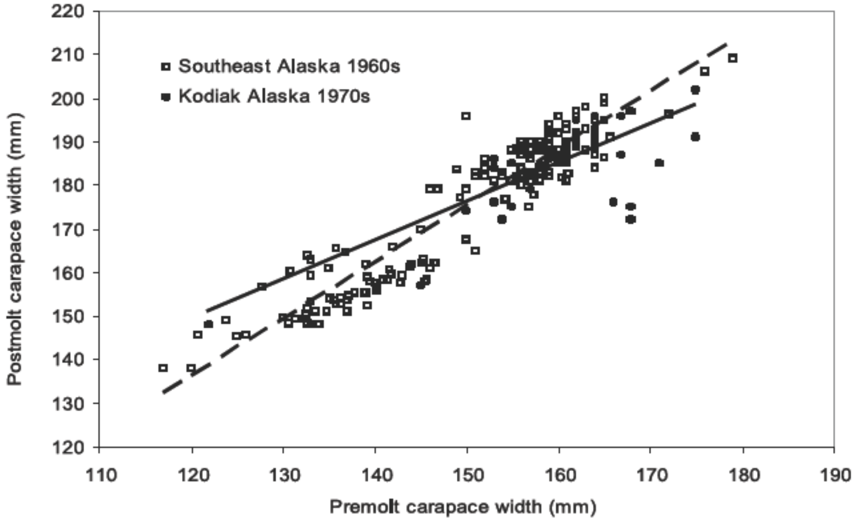

Figure 3. **Carapace width (mm) growth per molt tagging data for Southeast Alaska 1960s (open squares) and Kodiak Alaska 1970s (solid circles). Fitted linear regression models for growth per molt estimates are represented by the dotted line for Southeast Alaska 1960s ($y = 1.305x - 20.061$, $r^2 = 0.88$, $P < 0.0001$, $n = 362$) and the solid line for Kodiak Alaska 1970s ($y = 0.889x + 42.670$, $r^2 = 0.52$, $P < 0.0001$, $n = 59$).**

tional maturity at 112 mm CW and using the linear regression models for Kodiak Alaska 1970 and Southeast Alaska 1965 (Fig. 3), males of this size would molt two or three times respectively before recruiting to the fishery at ≥165 mm CW. It should be noted, however, that the smallest size available for the Kodiak regression was only 122 mm CW.

Discussion

To understand maturity in crabs it is necessary to determine both physiological and functional maturity. Crabs that are physiologically mature may not mate due to mating dynamics, male-male competition, and size at female maturity (Christy 1987; review by Elner and Beninger 1995; Sainte-Marie et al. 1995, 1997). Functional maturity is important when setting size limits for exploited Alaska crab stocks to insure males have the opportunity to mate at least once before recruiting to the fishery. This policy is thought to protect the reproductive potential of the crab stocks. The distinction between physiological and functional maturity has been reported for other commercially important brachyuran crabs (Adams 1982, Sainte-Marie et al. 1995).

In our study, the size at physiological maturity was estimated to be much smaller than previously reported for British Columbia (Butler 1960). Previous studies were limited by the ability to collect crabs at all size ranges and only examined crabs as small as 109 mm CW. We overcame these difficulties by capturing an adequate sample of small Dungeness crabs through the use of a small-mesh trawl net in very shallow waters. This sampling technique provided the sample sizes of males needed to determine a more accurate size at physiological maturity.

Measures of Dungeness crab functional maturity have varied between studies and have been limited to laboratory and field observations of mating pairs. Cleaver (1949) found the smallest male observed mating was 106 mm, while Butler (1960) based his estimated size at male functional maturity of 132 mm CW on field observations of clasping marks produced from males in a mating embrace. Our attempts to determine functional maturity in the wild were limited to observed mating pairs in pots. The minimum size male observed in a mating embrace was 157 mm CW, but this may be an artifact, since it is unlikely that a grasping pair would go into a pot. After genetic analysis of the extruded egg clutch in which the putative male contributed to the fertilization of eggs, we observed the minimum size of functional maturity to be 112 mm CW. Furthermore, males as small as 106 mm CW can physically mate as evidenced by their contributing sperm to the spermathecae. Our study offers a more direct measure of mating success and suggests that male Dungeness crabs have the potential to be both physiologically and functionally mature at a smaller size than previously reported.

In this study, the pooling of eggs allowed the extraction of enough DNA for analysis but could potentially lead to the masking of some low copy number alleles. Although genotyping individually developed eggs would allow for determination of Mendelian inheritance (Jensen and Bentzen 2004) and improve the detection rates of multiple paternity for individual eggs, pooling eggs did not mask the ability to detect the male parent alleles. When examining multiple paternity, the method of pooling eggs from different locations in the egg clutch can be used as a mechanism for screening large clutches for a minimum detection of one egg sired by a different father (Urbani et al. 1998, Gosselin et al. 2005).

Care must be taken in generalizing laboratory mating experiments to the conditions existing in the wild (Adams 1982, Paul 1992). Although our noncompetitive laboratory mating experiments eliminated some mating dynamics and competition, they did allow us to determine the size at which males are physically capable of successfully mating, which we defined as functional maturity. Size at female maturity can be a limiting factor in male functional maturity. In this study some females molted and mated, determined by the presence of male alleles in the sperm found in the female spermathecae, but did not extrude eggs in that reproductive season; they molted and extruded eggs the following year. These females may have been immature and needed to mature before extruding eggs, or the females may have been mature but did not extrude eggs annually as is seen in southeastern Alaska (Swiney and Shirley 2001, Swiney et al. 2003). If these females had been given the opportunity to mate with another male as would occur in the wild, the second mating would have precedence in egg fertilization and the initial mating would be less likely to sire a brood of eggs (Pamela Jensen, Alaska Fisheries Science Center, Seattle, 2008, pers. comm.). Our study illustrates the difficulties in determining male functional maturity due to the complexity of the mating dynamics of Dungeness crabs, which includes sperm storage, non-annual extrusion, the ability of immature females to mate, and the possibility of multiple paternity.

Our study was designed to focus on minimum size at functional maturity of male Dungeness crabs, so it did not address the ability of the males to mate with larger females. Typically, females mate with males larger than themselves (Shirley and McNutt 1989, Smith and Jamieson 1991), but this mating behavior becomes problematic when fisheries target larger males, leaving only sublegal sized males to fertilize the larger females. Smith and Jamieson (1991) concluded that females greater than 140 mm would go unmated in an intensively exploited male-only fishery, resulting in a loss of egg production. Conversely, Hankin et al. (1997) determined that if no large females could find mates, egg production would only be reduced between 2 and 25%. It is unknown whether the ability to mate is controlled by a physical limitation based on size difference or a behavioral preference. This issue needs to be investigated further.

Also, male polygamy is thought to play an important role in maintaining the reproductive potential of a crab stock (Cleaver 1949) and needs to be considered when heavily exploiting the large males of a population or decreasing legal size limits. Specifically, the ability and effectiveness of the small males to mate with more than one female must be demonstrated. Polygamy in Dungeness crabs has been observed in a laboratory setting (Cleaver 1949) and inferred through observations of abrasions on mating marks, but not studied under natural conditions (Butler 1960). Paul and Paul (1990) determined that breeding success of sublegal king crab decreases in successive matings. Further study would be necessary to determine if this also holds true for Dungeness crabs before reproductive potential can be incorporated into a change of management strategy.

Alaska size limits are based upon functional maturity of 132 mm CW, which assumes males mate at least once before reaching legal size, 165 mm CW (Cleaver 1949, Butler 1960, Miller 1976). Our observed minimum size at functional maturity of 112 mm CW would require 2 to 3 molts to reach legal size, but from our study we cannot infer how many molts males would undergo based upon size at 50 and 100% functional maturity. In addition, while no significant changes in growth increment have occurred in southeastern Alaska Dungeness crabs since the 1960s (Bishop et al. 2007), the effects of environmental changes on growth increment in the Kodiak area need to be considered when using these historic data for determining the relationship between maturity and the legal size limit.

Our study offers a first step toward evaluating the functional maturity and legal size limits of Dungeness crab, but until functional maturity can be defined in a competitive setting, a full functional maturity schedule is determined, and the importance of small males in the mating of larger females is examined, changing the size limit is not recommended. Furthermore, Dungeness crabs in Alaska are currently unsurveyed, so population dynamics of stocks are largely unknown and there is some question whether the market would accept a smaller product size.

Acknowledgments

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References

Adams, A.E. 1982. The mating behavior of *Chionoecetes bairdi*. In: International Symposium on the Genus *Chionoecetes*. Alaska Sea Grant College Program, University of Alaska, pp. 233-271.

Bishop, G.H., M.S.M. Siddeek, and J.M. Rumble. 2007. Growth of male Dungeness crabs in southeast Alaska. In: J.L. Nielsen, J.J. Dodson, K. Friedland, T.R. Hamon, J. Musick, and E. Verspoor (eds.), Am. Fish. Soc. Symp. 49:1339-1342.

Butler, T.H. 1960. Maturity and breeding of the Pacific edible crab (*Cancer magister*) Dana. J. Fish. Res. Board Can. 17:641-646.

Christy, J.H. 1987. Competitive mating, mate choice and mating associations of brachyuran crabs. Bull. Mar. Sci. 42:177-191.

Cleaver, F.C. 1949. Preliminary results of the coastal crab (*Cancer magister*) investigation. Washington Department of Fisheries Biol. Rep. 49A:47-82.

DeNise, S., E. Johnston, J. Halverson, K. Marshall, D. Rosenfeld, S. McKenna, T. Sharp, and J. Edwards, 2004. Power of exclusion for parentage verification and probability of match for identity in American kennel club breeds using 17 canine microsatellite markers. Anim. Genet. 35:14-17. doi:10.1046/j.1365-2052.2003.01074.x

Donaldson, W.E., and W.K. Donaldson. 1992. A review of the history and justification for size limits in Alaskan king, Tanner and snow crab fisheries. Alaska Department of Fish and Game. Fish. Res. Bull. 92-02. 21 pp.

Elner, R.W., and P.G. Beninger. 1995. Multiple reproductive strategies in snow crab, *Chionoecetes opilio*: Physiological pathways and behavioral plasticity. J. Exp. Mar. Biol. Ecol. 193:93-112. doi:10.1016/0022-0981(95)00112-3

Gosselin, T., B. Sainte-Marie, and L. Bernatchez. 2005. Geographic variation of multiple paternity in the American lobster, *Homarus americanus*. Mol. Ecol. 14:1517-1525. doi:10.1111/j.1365-294X.2005.02498.x

Hankin, D.G., T.H. Butler, P.W. Wild, and Q.-L. Xue. 1997. Does intense fishing on males impair mating success of female Dungeness crabs? Can. J. Fish. Aquat. Sci. 54:655-699.

Hankin, D.G., N. Diamond, M. Mohr, and J. Ianelli. 1989. Growth and reproductive dynamics of adult female Dungeness crabs (*Cancer magister*) in northern California. ICES J. Mar. Sci. 46:94-108. doi:10.1139/cjfas-54-3-655

Hines, A.H. 1989. Geographic variation in size at maturity in brachyuran crabs. Bull. Mar. Sci. 45:356-368.

Hoopes, D.T. 1973. Alaska's fishery resources: The Dungeness crab. U.S. National Marine Fisheries Service Extension Publ. Fish. Facts 6. 14 pp.

Jaffe, L.A., C.F. Nyblade, R.B. Forward, and S.D. Sulking. 1987. Phylum or subphylum Crustacea, class Malacostraca, order Decapoda, Brachyura. In: M.F. Strathmann (ed.), Reproductive and development of marine invertebrates of the northern Pacific Coast: Data and methods for the study of eggs, embryos and larvae. University of Washington Press, Seattle, pp. 451-465.

Jamieson, A. 1965. The genetics of transferrin in cattle. Heredity 20:419-441. doi:10.1038/hdy.1965.54

Jensen, P.C., and P. Bentzen. 2004. Isolation and inheritance of microsatellite loci in the Dungeness crab (Brachyura: Cancridae: *Cancer magister*). Genome 47:325-331.

Jensen, P.C., J.M. Orensanz, and D.A. Armstrong. 1996. Structure of the female reproductive tract in the Dungeness crab (*Cancer magister*) and implications for the mating system. Biol. Bull. 190:336-349. doi:10.2307/1543026

Lehman, C., and O. Osborn. 1970. Dungeness crab research. Alaska Department of Fish and Game, Commercial Fisheries Research and Development Act, Compl. Rep., Projects 5-10-R and 5-21-R, Juneau. 43 pp.

MacKay, D.C.G. 1943. The behavior of the Pacific edible crab *Cancer magister* Dana. J. Comp. Physiol. 36:255-268.

Methot, R.D. 1988. The management of cyclic resource: Dungeness crab fisheries of the Pacific coast of North America. In: J.F. Caddy (ed.), Marine invertebrate fisheries: Their assessment and management. Wiley and Sons, New York, pp. 205-224.

Miller, R.J. 1976. North American crab fisheries: Regulations and their rationales. Fish. Bull. 74:623-633.

Minitab. 2005. Minitab Inc. State College.

Oh, S.J., and D.G. Hankin. 2004. The sperm plug is a reliable indicator of mating success in female Dungeness crabs, *Cancer magister*. J. Crustacean Biol. 24:314-326. doi:10.1651/C-2389

Orensanz, J.M., and V.F. Gallucci. 1988. Comparative study of postlarval life-history schedules in four sympatric species of *Cancer* (Decapoda: Brachyura: Cancridae). J. Crustacean. Biol. 8:187-220. doi:10.2307/1548312

Paul, A.J. 1992. A review of size at maturity in male Tanner (*Chionoecetes bairdi*) and king (*Paralithodes camtschaticus*) crabs and the methods used to determine maturity. Am. Zool. 32:534-540.

Paul, J.M., and A.J. Paul. 1990. Breeding success of sublegal size male red king crab *Paralithodes camtschatica* (Tilesius, 1815) (Decapoda, Lithodidae). J. Shellfish Res. 9:29-32.

Poole, R., and D. Gotshall. 1965. Regulations and the market crab fishery. Outdoor California 26:1-2.

Raymond, M., and F. Rousset. 1997. GENEPOP: Population genetics software for exact tests and ecumenicism. J. Hered. 86:248-249.

Sainte-Marie, B., S. Raymond, and J. Brêthes. 1995. Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura: Majidae). Can. J. Fish. Aquat. Sci. 52:903-924. doi:10.1139/f95-091

Sainte-Marie, B., J. Sevigny, and Y. Gauthier. 1997. Laboratory behavior of adolescent and adult males of the snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) mated noncompetitively and competitively with primiparous females. Can. J. Fish. Aquat. Sci. 54:239-248. doi:10.1139/cjfas-54-2-239

Shirley, T.C., and L. McNutt. 1989. Precocious mating and trans-molt sperm retention by female Dungeness crabs. Abstract. Am. Zool. 29:131.

Smith, B.D., and G.S. Jamieson. 1991. Possible consequences of intensive fishing for males on the mating opportunities of Dungeness crabs. Trans. Am. Fish. Soc. 120:650-653. doi:10.1577/1548-8659(1991)120<0650:NPCOIF>2.3.CO;2

Snow, C.D., and J.R. Neilsen. 1966. Premating and mating behavior of the Dungeness crab (*Cancer magister* Dana). J. Fish. Res. Board Can. 23:1319-1323.

Somerton, D.A. 1981. Regional variation in the size of maturity of two species of Tanner crab (*Chionoecetes bairdi* and *C. opilio*) in the eastern Bering Sea, and its use in defining management subareas. Can. J. Fish. Aquat. Sci. 38:163-174. doi:10.1139/f81-022

Swiney, K.M., and T.C. Shirley. 2001. Gonad development of southeastern Alaskan Dungeness crab, *Cancer magister*, under laboratory conditions. J. Crustacean Biol. 21:897-904. doi:10.1651/0278-0372(2001)021[0897:GDOSAD]2.0.CO;2

Swiney, K.M., T.C. Shirley, S.J. Taggart, and C.E. O'Clair. 2003. Dungeness crab, *Cancer magister*, do not extrude eggs annually in southeastern Alaska: An in situ study. J. Crustacean Biol. 23:280-288. doi:10.1651/0278-0372(2003)023[0280:DCCMDN]2.0.CO;2

Toonen, R.J., M. Locke, and R. Grossberg. 2004. Isolation and characterization of polymorphic microsatellite loci from the Dungeness crab *Cancer magister*. Mol. Ecol. Notes 4:30-32. doi:10.1046/j.1471-8286.2003.00562.x

Urbani, N., B. Sainte-Marie, J.M. Sevigny, D. Zadworny, and U. Kuhnlein. 1998. Sperm competition and paternity assurance during the first breeding period of female snow crab (*Chionoecetes opilio*) (Brachyura: Majidae). Can. J. Fish. Aquat. Sci. 55:1104-1113. doi:10.1139/cjfas-55-5-1104

Wainwright, T., and D. Armstrong. 1993. Growth patterns in the Dungeness crab (*Cancer magister* Dana): Synthesis of data and comparison of models. J. Crustacean Biol. 13:36-50. doi:10.2307/1549121

Wild, P.W. 1983. Comparisons of ovary development in Dungeness crabs, *Cancer magister*, in central and northern California. California Department of Fish and Game Fish. Bull. 172:189-196.

Urban, J.D. 2010. Pacific Cod Predation on Tanner Crab in Marmot Bay, Alaska. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.03

Pacific Cod Predation on Tanner Crab in Marmot Bay, Alaska

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Abstract

Pacific cod (*Gadus macrocephalus*) have long been recognized as an important predator of Tanner crab (*Chionoecetes bairdi*). This study reports on Pacific cod predation on Tanner crab populations as determined from the stomach contents of Pacific cod sampled seasonally for a year in Marmot Bay off Kodiak Island, Alaska. This predator/prey relationship is of particular interest since both the predator and prey are commercially important species. Extrapolations from this 14 month study suggest that cod consumed over 365 million immature Tanner crab, mostly 10-45 mm carapace width, from four different cohorts. The cod per capita predation rate suggests moderate density-dependence on prey numbers, but cod were also confirmed to be opportunistic predators that rapidly switched from Tanner crab to alternative prey species. Without more extensive temporal and spatial data, the role cod predation plays in regulating crab populations is difficult to determine.

Introduction

For the last 60 years, population regulation has been an important and sometimes contentious topic in the ecological literature (reviewed in Murdoch 1994, Turchin 1995, Hixon et al. 2002). Population regulation, defined as a process that returns a population to its equilibrium level (Krebs 2002), is generally accepted to result from density-dependent stabilizing mechanisms (Murdoch 1994, Turchin 2003). A population can be considered regulated if it persists for many generations with bounded fluctuations around an equilibrium level, with a propensity to decrease when large and increase when small. Initially, density-dependent competition was considered to be the sole source of population regulation (Elton and Nicholson 1942), but it later became recognized that predation can also induce the regulation of prey populations (Sinclair and Pech 1996). In marine systems where competition is usually not evident, regulation of prey populations is often caused by predation (Hixon et al. 2002).

These largely theoretical considerations take on added importance when a commercially important species is a major predator of another commercially important species. Tanner crab *Chionoecetes bairdi* are a common prey of Pacific cod *Gadus macrocephalus* and in addition, both species support major fisheries in Alaska with a combined ex-vessel value over the last 10 years of more than US $635 million (Alaska Department of Fish and Game, fishticket database). Small Tanner crab are typically found in over 30% of Pacific cod stomachs (Jewett 1978, Albers and Anderson 1985, Yang and Nelson 2000). Predation rates of Pacific cod on small Tanner crab can be extremely high. It was estimated in a three year study, for example, that Pacific cod (hereafter simply cod) in a single year removed up to 94% of the age 1 Tanner crab from the Bering Sea (Livingston 1989).

There is some evidence from the three year Bering Sea study that cod prey on more Tanner crab when crab populations are high (Livingston 1989). Ideally, however, a population regulation study involving predation would consist of more than three data points and would last through many generations of the prey species (Harrison and Cappuccino 1995). For a study of a relatively long-lived marine species such as Tanner crab, which can live over 10 years (Donaldson et al. 1981), this is nearly impossible; but even studies over shorter time periods can be valuable as a method for examining the mechanisms that influence population dynamics (Meyers and Rothman 1995). A thorough understanding of basic predation mechanisms is needed for the construction of more comprehensive models of species regulation (Turchin 1999, Krebs 2002, Murdoch et al. 2003).

This study reports on a 14 month study with six sampling periods from a large bay in the northern Gulf of Alaska (Marmot Bay). The goal of this study was to establish if cod predation on Tanner crab is density-dependent when examined intensely over the course of a year. Tanner crab and cod population estimates, along with the estimate of the number of crab consumed as calculated from the analysis of cod stomach contents, were used to establish the relationship between consumption rates and crab populations. Specifically, the hypothesis is that because cod are opportunistic predators feeding on a large variety of species (Urban and Vining 2008), cod consumption rates on Tanner crab will vary independently of crab population densities.

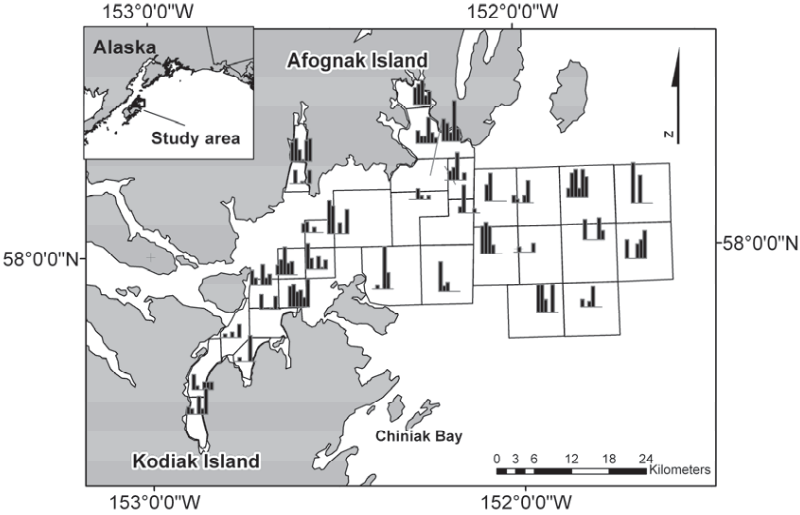

Figure 1. **Map of the Marmot Bay study area, between Kodiak and Afognak Islands in the Gulf of Alaska. Polygons represent the survey stations in Marmot Bay and bar graphs show the number of stomachs collected during each sampling period. The tallest bar equals 23 stomachs.**

Methods

Data collection

The Alaska Department of Fish and Game (ADFG) conducted six trawl surveys of 31 stations in Marmot Bay on the northeast corner of Kodiak Island (Fig. 1): June 20-24, 1998; August 24-29, 1998; October 26-31, 1998; January 7-17, 1999; March 30-April 5, 1999; and June 19-23, 1999. Cod were captured by the ADFG R/V *Resolution* towing a 400 Eastern otter trawl net targeting soft substrates. The vessel made one tow per station during each sampling period; the tow location within the station was determined by the vessel captain. The stations were established in 1988 by ADFG to include the most productive Tanner crab areas. Four stations in the outer bay were added specifically for this study (Fig. 1). The net was constructed with 10.2 cm stretch mesh in the mouth, 8.9 cm stretch mesh in the body, and a 3.2 cm stretch mesh liner in the cod end (Pengilly et al. 1999). Cod greater than 30 cm are retained in large numbers by the net although the selectivity of the net on cod of various lengths is not known (von Szalay and Brown 2001). Cod less than 30 cm consume few Tanner crab (Yang et al. 2006), which has also been shown for the morphologically similar Atlantic cod *Gadus morhua* predation on snow crab *Chionoecetes opilio* (Chabot et al. 2008). The catch was identified to species, counted, and weighed. Lengths were recorded for commercially important fish and crab species (Pengilly et al. 1999)

Cod stomachs were collected at sea following protocols established by the National Oceanic and Atmospheric Administration (NOAA) Alaska Fisheries Science Center, Resource Ecology and Fisheries Management Division. A maximum of 40 stomachs per station were collected, with a minimum sample size per station of five stomachs. Five specimens for every 10 cm size group per station were targeted. Fish that showed signs of either net feeding or regurgitation were not collected. Stomachs were preserved in 10% formalin and later transferred to 70% ethyl alcohol. Contents were identified to the lowest taxonomic level possible and enumerated. Wet weights were recorded to the nearest 0.1 g after the contents were blotted with paper towels. If carapaces were intact, Tanner crabs in the stomachs were measured to the nearest mm carapace width (CW). Fish were measured to the nearest cm fork length (FL).

Data analysis

Tanner crab consumption

Based on the work of previous studies (Livingston et al. 1986), cod were divided into two size groups for estimates of crab consumption: 30-59 cm FL and ≥60 cm FL. Cod become increasingly piscivorous beyond 60 cm FL, and mean stomach content weight as a percentage of total body weight is also much larger for cod ≥60 cm FL. Therefore, food habits and daily ration requirements should be calculated separately for the two size groups of cod. Crab consumption by cod during each sampling period was estimated according to Mehl and Westgard (1983):

$$C_i = DR_i \cdot D \cdot B_i \cdot P_i \,, \tag{1}$$

where C_i is the consumption by weight of crab by cod belonging to cod size group *i, DR_i* is the daily ration as a proportion of cod body weight by day of cod group *i*, *D* is the number of days in a sampling period where the actual sampling dates are considered the midpoint of the sampling period, B_i is the biomass of cod size group *i*, and P_i is the proportion by weight of Tanner crab in the diet of cod of size group *i.* Because *D* is calculated as the midpoint of the sampling period, the actual length of study becomes more than one year, extending from May 1998 to July 1999. The average weight of crab per sampling period and stratum was used to convert the biomass of crab consumed to numbers of crab. Average weight of the consumed crab was calculated as:

$$crabweight = 0.00029 \cdot (carapacewidth^{3.02}) \tag{2}$$

based on a conversion factor developed by ADFG for Kodiak Tanner crab (ADFG, unpubl. data). The daily ration for each cod group by sampling period was calculated following equations developed by Ursin et al. (1985) for the morphologically similar Atlantic cod *Gadus morhua*. Daily ration is described as mean stomach content weight (S) and a function of mean individual prey weight (w) in grams and bottom temperature (T) in °C:

$$DR = a \cdot S, \tag{3}$$

where $a = a_0 w^{a_1}$ and $a_0 = a_{00} e^{0.096T}$ and where $a_{00} = 0.33$ and $a_1 = -0.36$ as estimated by Ursin et al. (1985) for Atlantic cod.

Cod biomass and numbers

Cod biomass and numbers were estimated using the area-swept method, which takes the density of the catch within the area swept by the net and expands it to the area of the station under consideration. Length measurements collected from the trawl catch were used to apportion the catch at each station and sampling period between the two cod size groups. A positive fishing power correction factor of 1.72 was applied to the cod catch to adjust for the lower net opening on the ADFG trawl net, which is designed as a crab survey net, as compared to National Marine Fisheries Service nets, which are designed to survey groundfish (von Szalay and Brown 2001). Bottom temperatures were recorded at each station using a sensor attached to the trawl headrope.

Crab cohort analysis

To determine consumption by crab year class in each sampling period, measurements of Tanner crab carapace widths from all strata were combined by 2 mm groupings to determine size frequency modes. Mode sizes and length of time since a typical settlement date of July 1 (Incze 1983, Bunch and Highsmith 1998, Stevens 2003) were compared to size at age observed by Donaldson et al. (1981) around Kodiak and the northern Gulf of Alaska to determine instar number and settlement year. The proportions of Tanner crab by settlement year found in the stomach samples were used to calculate the total numbers of crab eaten by cod size group and by sampling period.

Predation density dependence

Because stomach samples were not evenly distributed across the study area either by station or across sampling periods, the study area was divided into three strata based on the bathymetry of the area (Fig. 2) and established survey strata of ADFG, which are thought to correspond to the stock structure of Tanner crab in the area. Stomachs were pooled within each stratum for each sampling period. The estimate of cod biomass in a stratum was the sum of the biomass for each station in the

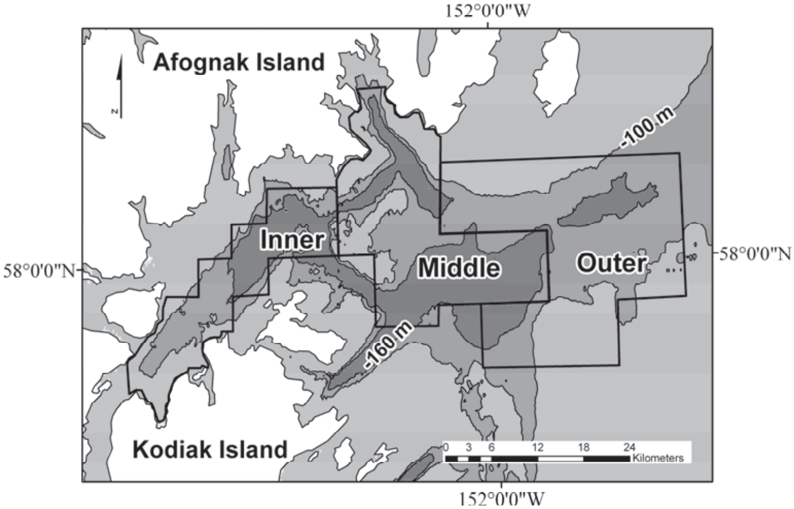

Figure 2. Map showing strata of the study area, with 100 and 160 m depth contours. The tow locations in the inner stratum averaged 74 m in depth, ranging from 33 to 109 m; the middle stratum averaged 95 m, ranging from 83 to 110 m; the outer stratum averaged 66 m, ranging from 32 to 66 m.

stratum. The inner stratum is separated from the rest of the bay by a large, relatively shoal area of hard substrate. The middle stratum lies to the east of the shoal and consists of deep stations over 160 m in depth. The outer stratum lies on the outer eastern edge of the study area and consists of shallower stations with a sandy mud substrate while the inner and middle strata are mainly silty mud. Six of the 31 stations were not considered to fall within any of the strata.

Tagging studies conducted by ADFG show that while adult Tanner crab movements within the strata are limited, cod are a mobile predator that range more widely (Donaldson 1983, ADFG unpubl. data). Therefore, it was assumed that cod feeding in any area during a sampling period were different individuals from those feeding in any other sampling period and the per capita consumption of crab during each period/stratum could be considered largely an independent event.

To test the strength of the relationship between cod predation rates on crab and crab populations, an ordinary least squares, model II linear regression analysis was conducted (Legendre and Legendre 1998). A model II regression is appropriate because the independent variable (crab population) could not be measured without error (Sokal and Rohlf 1995). The lmodel2 package (Legendre 2008) for R (R Development Core Team 2008)

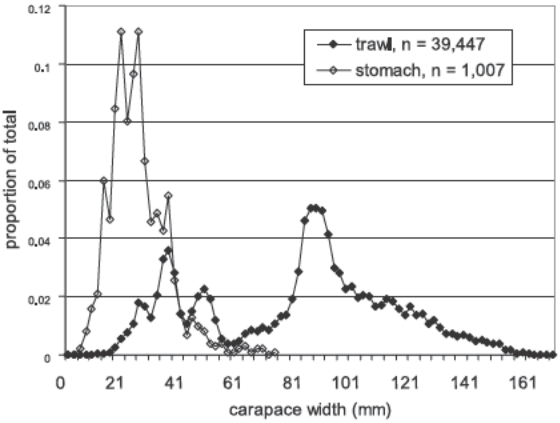

Figure 3. Size of Tanner crab taken from Pacific cod stomachs and captured by the Alaska Department of Fish and Game trawl survey.

was used for the analysis. A positive, significant regression would be an indication that cod predation on Tanner crab is density-dependent (Sinclair 1989, Sokal and Rohlf 1995). Regression analysis assumes bivariate normality of the data (Sokal and Rohlf 1995) so the crab population and predation rate data were log transformed to achieve more normal distributions.

Per capita consumption of crab was calculated by stratum and sampling period as the numbers of crab consumed calculated from the stomach analysis, divided by the area-swept estimate of cod numbers. Calculation of the population of crab available for consumption required that some assumptions be made. The size of Tanner crab eaten by cod are too small to be well surveyed by the standard survey trawl gear (Livingston 1989, Fig. 3), so the population of small crab (~10-45 mm CW) was reconstructed, as in Forney (1977) and Livingston (1989). The crab consumed during each sampling period were added to the population of Tanner crab at the start of the study to arrive at the new population estimate for the subsequent sampling period. This assumes that cod predation is the major source of mortality of these crab (Aydin et al. 2007, NPFMC 2008), and that virtually all predation mortality occurs in crab 10-35 mm CW (Livingston 1989). The population of crab at the start of the survey was calculated as the area-swept estimate of crab 33-45 mm CW (the growth increment of the 10-35 mm CW crab as predicted from Donaldson et al. 1981) from the June 2000 survey of Marmot Bay adjusted by the natural mortality of 0.51 between June 2000 and June 1999. The value of natural mortality of Tanner crab this size is unknown

Table 1. Total number and weight with percent frequency of occurrence of prey items identified to species, from 974 cod stomachs collected June 1998 to June 1999 in Marmot Bay, Alaska.

Prey items		Number	Grams	% Frequency
Arthropoda				
Malacostraca				
Decapoda				
	Argis lar	6	24.1	0.3
	Cancer oregonensis	2	3.2	0.2
	Chionoecetes bairdi	1,262	7,660.0	50.0
	Crangon communis	580	305.8	14.1
	Crangon dalli	23	14.2	0.9
	Eualus avinus	510	108.5	6.0
	Eualus biunguis	31	25.1	0.1
	Hyas lyratus	29	218.4	2.7
	Munida quadrispina	2	1.7	0.2
	Pagurus aleuticus	4	153.6	0.3
	Pandalopsis dispar	1	15.5	0.1
	Pandalus borealis	1,076	2,212.8	21.1
	Pandalus montagui tridens	3	12.8	0.2
Euphausiacea				
	Euphausia pacifica	28	6.5	1.2
	Thysanoessa inermis	1	0.1	0.1
	Thysanoessa spinifera	6	0.7	0.1
Echiura				
Echiuridae				
Echiuroinea				
	Echiurus echiurus	1	3.3	0.1
Mollusca				
Gastropoda				
Neogastropoda				
	Colus halli	1	0.4	0.1
	Fusitriton oregonensis	1	9.8	0.1

so the high end of the range of mortality estimates from the Bering Sea (NPFMC 2008, Zheng et al. 1998) for crab ≥93 mm CW was used.

Results

Stomachs were sampled from 974 Pacific cod (10-95 cm FL). The samples were distributed across the study area, although cod were not captured in all stations in all sampling periods (Fig. 1). Prey items from none phyla and 15 classes were identified from the stomach contents. Thirty-nine prey were identified to the species level (Table 1). By weight Tanner crab was the most consumed prey item followed by walleye pollock *Theragra chalcogramma*, northern shrimp *Pandalus borealis,* and arrowtooth flounder *Atheresthes stomias*. Euphausiids were the most

Table 1. (continued)

Prey items				Number	Grams	% Frequency
Sipuncula						
	Sipunculidea					
		Golfingiiformes				
			Golfingia margaritacea	4	27.4	0.4
Chordata						
	Osteichthyes					
		Clupeiformes				
			Clupea pallasii	4	223.5	0.4
		Gadiformes				
			Microgadus proximus	1	41.4	0.1
			Theragra chalcogramma	59	4654.4	5.5
		Osmeriformes				
			Mallotus villosus	2	11.6	0.2
			Thaleichthys pacificus	1	13.9	0.1
		Perciformes				
			Ammodytes hexapterus	1	1.3	0.1
			Cryptacanthodes aleutensis	7	42.8	0.7
			Lumpenella longirostris	1	8.2	0.1
			Lumpenus sagitta	2	19.7	0.2
			Lycodes brevipes	10	93.5	0.8
			Lycodes diapterus	1	88.3	0.1
			Poroclinus rothrock	9	35.5	0.6
		Pleuronectiformes				
			Atheresthes stomias	24	715.0	2.3
			Hippoglossoides elassodon	37	547.4	3.3
			Hippoglossus stenolepis	1	0.2	0.1
			Pleuronectes asper	5	253.7	0.4
			Reinhardtius hippoglossoides	3	1.1	0.3
		Scorpaeniformes				
			Dasycottus setiger	14	335.8	1.4
			Icelus spiniger	1	2.3	0.1
Empty stomachs				16		1.6

numerous prey item consumed, followed by Tanner crab, northern shrimp, Mysidacea, and unidentified *Eualus* shrimp.

Tanner crab consumption

Tanner crab were a principal prey item for cod in Marmot Bay, making up 26% of the cod prey by weight and 9% by number, and were found in 50% of the cod stomachs. Using equation 1 and the values found in Table 2 with a study length of 429 days, it was calculated that over 365 million crab were consumed (Table 2). In general, far fewer crab were consumed in the inner stratum, but fewer cod were seen there as well. In all strata, the numbers of crab consumed varied widely throughout the year with the coefficient of variation ranging from 58% in the inner stratum to 78% in the outer stratum (Fig. 4).

Table 2. Parameters (± SD) used to obtain consumption estimates of Pacific cod on Tanner crab populations in Marmot Bay. The inner, middle, and outer strata do not include all stations sampled.

Period/ stratum	Cod biomass (t)		Daily ration (% BWD)		% Crab in diet (by weight)		Number of crab consumed (millions)	
	<60 cm	≥60 cm	<60 cm	≥60 cm	<60 cm	≥60 cm	<60 cm	≥60 cm
Jun. 1998								
Inner	132	694	0.66 ± 0.33	0.43 ± 0.24	10.5 ± 1.0	9.7 ± 0.7	2.2 ± 1.1	2.8 ± 1.6
Middle	320	1,640	0.48 ± 0.30	0.40 ± 0.19	8.8 ± 0.5	16.8 ± 0.7	2.3 ± 1.5	9.0 ± 4.3
Outer	385	1,649	0.74 ± 0.41	0.34 ± 0.21	12.0 ± 1.6	10.7 ± 0.6	4.8 ± 2.8	4.5 ± 2.8
All stations	1,050	4,568	0.63 ± 0.36	0.40 ± 0.21	11.6 ± 0.2	12.8 ± 0.2	11.0 ± 6.0	17.8 ± 8.4
Aug. 1998								
Inner	122	1,156	0.47 ± 0.37	0.60 ± 0.28	1.0 ± 0.3	2.8 ± 0.3	<0.0 ± <0.0	0.8 ± 0.4
Middle	122	1,997	0.86 ± 0.68	0.58 ± 00.28	7.1 ± 1.1	28.5 ± 1.2	0.6 ± 0.5	15.2 ± 7.4
Outer	458	205	1.01 ± 0.57	0.54 ± 0.29	50.2 ± 2.8	56.6 ± 10.0	44.5 ± 25.2	11.1 ± 6.3
All stations	787	3,555	0.73 ± 0.51	0.64 ± 0.29	23.5 ± 0.8	20.2 ± 0.4	45.2 ± 10.1	28.7 ± 13.7
Oct. 1998								
Inner	17	325	0.53 ± 0.08	0.47 ± 0.21	26.1 ± 6.7	41.0 ± 3.0	0.4 ± 0.1	1.7 ± 0.8
Middle	303	2,057	0.82 ± 0.39	0.65 ± 0.37	31.3 ± 3.8	49.1 ± 1.7	5.2 ± 2.6	29.7 ± 16.9
Outer	554	1,862	1.37 ± 0.38	0.66 ± 0.39	41.9 ± 2.3	50.0 ± 2.0	34.6 ± 9.7	37.4 ± 22.1
All stations	912	5,295	1.13 ± 0.90	0.64 ± 0.34	38.4 ± 1.9	45.0 ± 0.7	40.4 ± 20.5	71.1 ± 29.9
Jan. 1999								
Inner	40	1,316	0.48 ± 0.15	0.37 ± 0.25	22.1 ± 4.0	38.0 ± 1.5	0.3 ± 0.1	2.5 ± 1.7
Middle	113	2,600	0.38 ± 0.25	0.33 ± 0.20	22.4 ± 5.3	41.8 ± 1.3	0.8 ± 0.6	17.9 ± 10.9
Outer	380	749	0.34 ± 0.70	0.31 ± 0.26	31.5 ± 5.7	14.2 ± 4.0	5.3 ± 11.0	2.6 ± 2.3
All stations	634	6,494	0.43 ± 0.60	0.36 ± 0.23	23.9 ± 2.1	30.1 ± .04	6.7 ± 6.2	27.3 ± 17.3
Mar. 1999								
Inner	38	311	0.71 ± 0.31	0.63 ± 0.37	7.2 ± 0.7	7.5 ± 0.6	0.6 ± 0.3	1.0 ± 0.6
Middle	125	352	0.19 ± 0.17	0.30 ± 0.26	42.4 ± 13.3	31.7 ± 5.4	1.5 ± 1.5	3.0 ± 2.3
Outer	485	2,097	0.83 ± 0.56	0.49 ± 0.60	28.9 ± 1.7	36.9 ± 2.0	15.9 ± 10.7	25.0 ± 30.8
All stations	801	3,611	0.83 ± 0.57	0.67 ± 0.40	28.8 ± 1.4	35.2 ± 1.0	23.7 ± 18.2	57.8 ± 37.2
June 1999								
Inner	91	847	0.49 ± 0.41	0.43 ± 0.21	54.4 ± 7.4	23.1 ± 1.1	3.8 ± 3.3	4.3 ± 2.1
Middle	111	648	0.49 ± 0.20	0.31 ± 0.24	36.2 ± 5.31	68.0 ± 12.6	2.4 ± 1.0	9.0 ± 7.2
Outer	1,125	879	0.21 ± 0.13	0.30 ± 0.32	17.1 ± 3.8	35.6 ± 6.4	5.1 ± 3.4	8.4 ± 9.2
All stations	1,487	2,786	0.44 ± 0.20	0.46 ± 0.25	37.1 ± 1.9	23.4 ± 0.6	11.6 ± 11.4	24.4 ± 9.9
Total	5,674	26,319	0.59 ± 0.55	0.41 ± 0.30	24.8 ± 0.2	28.4 ± 0.1	138.6 ± 16.3	227.2 ± 21.4

% BWD = percentage body weight daily.

Calculation of the propagation of error from Lindberg 2000.

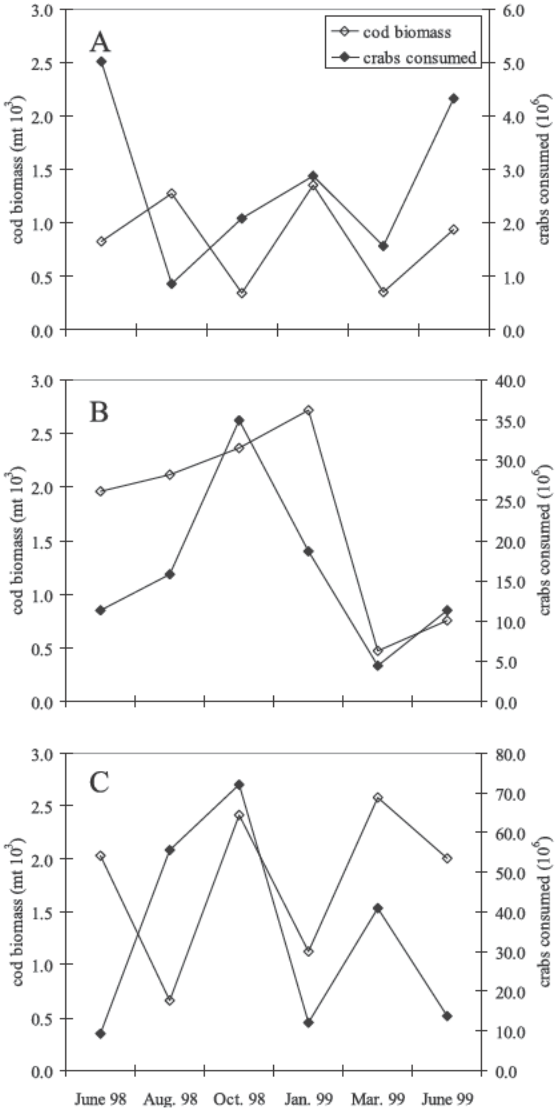

Figure 4. Changes by sampling period in cod biomass and crab consumed in the (A) inner, (B) middle, and (C) outer strata.

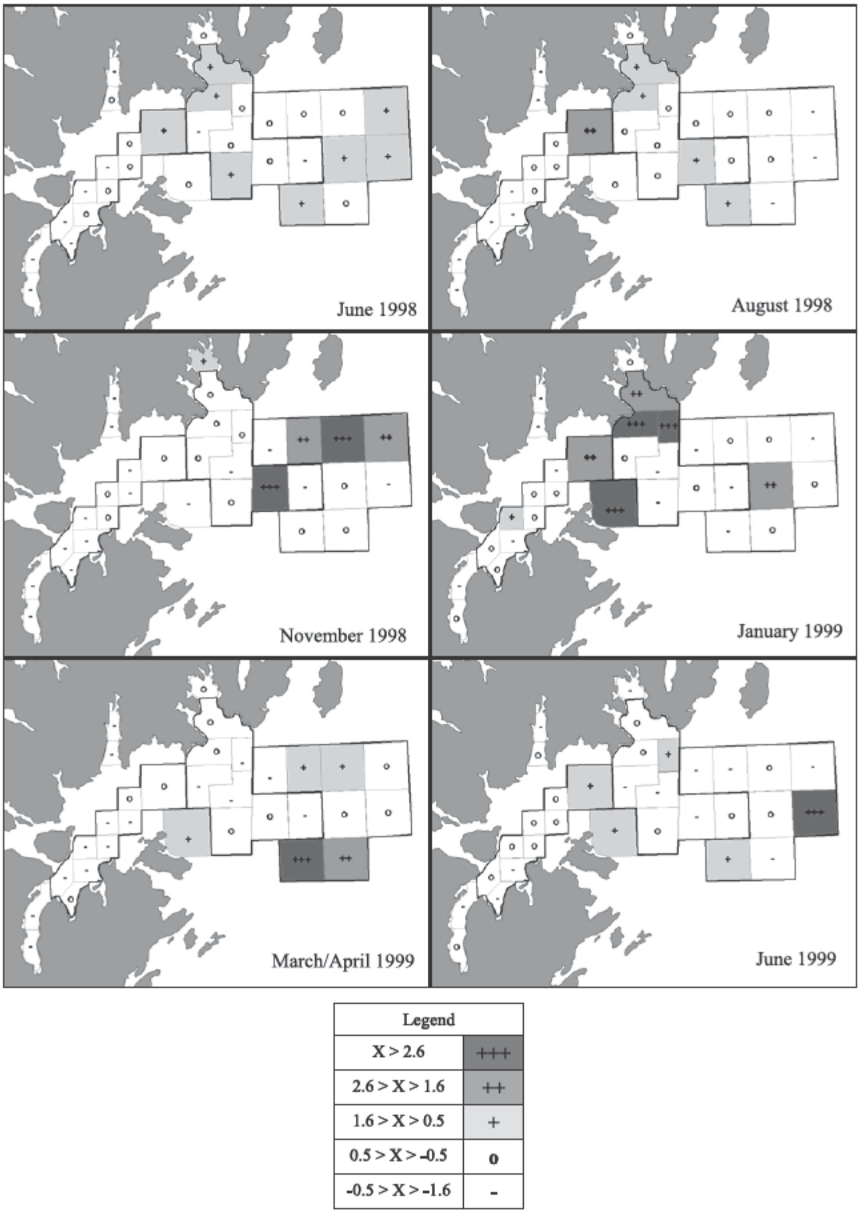

Figure 5. Anomalies in cod biomass by sampling period and survey station, with strata outlined in bold. Values are difference between the value at each station for each sample period and the grand mean of all stations and sampling periods, divided by the standard deviation of the grand mean.

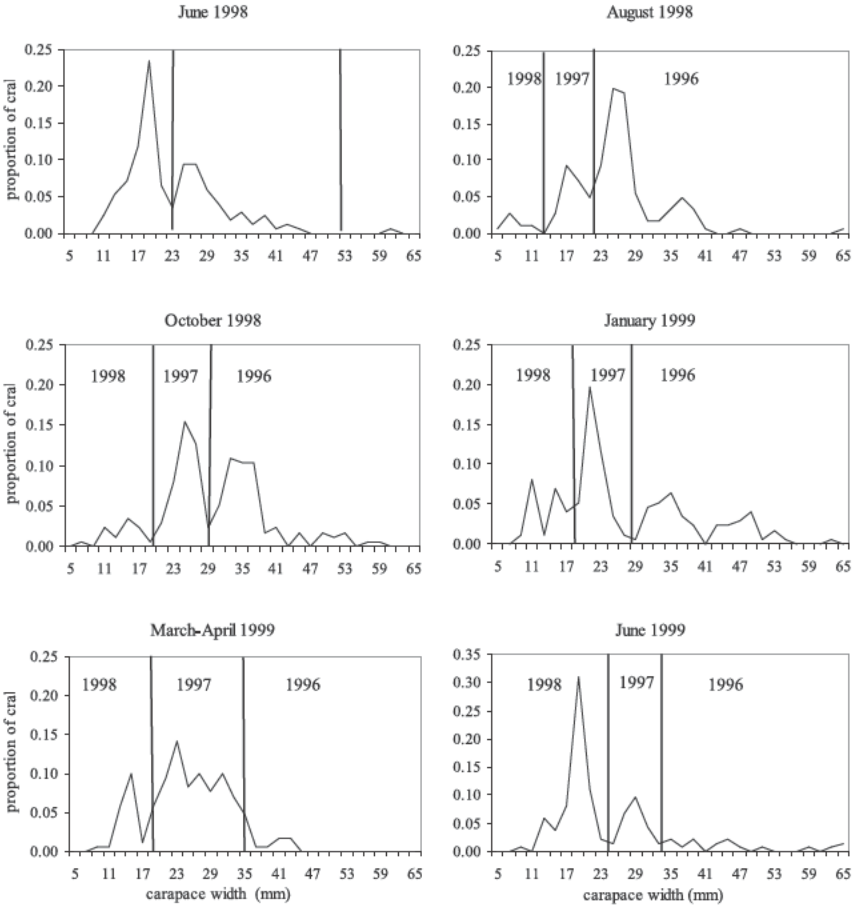

Figure 6. Width frequencies of Tanner crab taken from Pacific cod stomachs by sample period. Cohort settlement year is based on Donaldson et al. (1981) size at age tables with a settling date set as July 1.

The opportunistic foraging of cod may explain some of the variation in crab consumption rates. For example, one of the largest residuals in the regression analysis came during the August 1998 sampling in the inner stratum (Fig. 8). The numbers of pandalid shrimp consumed jumped to 65% of all prey items while Tanner crab consumption fell to <1%. By the following October, pandalids composed just 3% by number of the diet while Tanner crab consumption increased to 33%.

Cod also exhibited opportunistic feeding in the outer stratum during the March-April 1999 sampling period but this time the regression

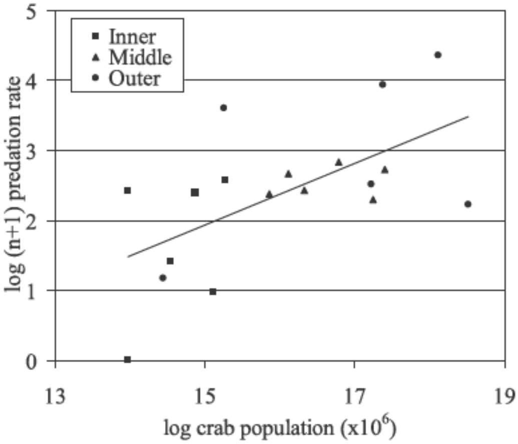

Figure 7. Regression plot of per capita crab consumption and crab population of the 1997 cohort ($r^2 = 0.38$, $F_{1,17} = 9.02$, $p = 0.008$). Each point represents a sampling period/stratum with the earliest sampling period by stratum represented by the highest population value on the crab population axis.

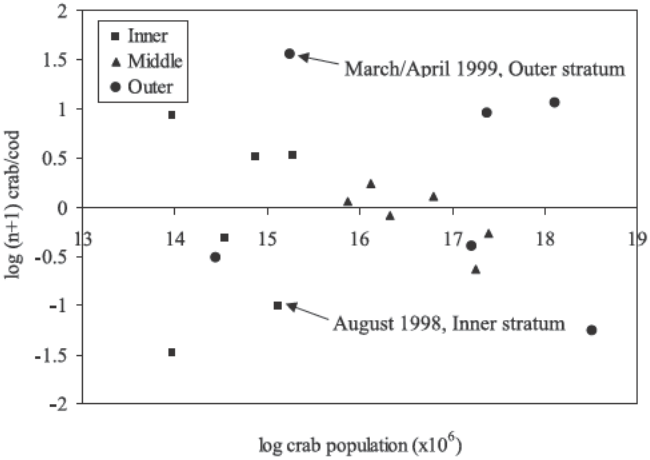

Figure 8. Residuals of a least squares fitted line of crab population and cod per capita crab consumption by stratum. (See text for a discussion of the annotated points.)

residual was strongly positive. Cod began to eat large numbers of euphausiids, up to 87% of the diet by number, perhaps corresponding to the peak spawning season for several common euphausiid species (Pinchuk et al. 2008). Cod aggregated in one of the largest concentrations seen during the survey (Fig. 5) perhaps due to the euphausiid concentrations. Crab fell from an average of 23% by number to 4% but were still consumed in larger than predicted numbers because of the concentration of predators. The available food habits data set is inadequate, however, to explain all the residuals in the regression.

Cod biomass

Cod were widespread, occurring in 87% of tows completed during the study with an average biomass per study period of over 5,300 t. Cod biomass varied widely both between stratum and between sampling periods (Figs. 4-5, Table 2). When anomalies from the grand mean of the cod population estimates from all stations and sampling periods are plotted on the study area by period, the location of cod aggregates changed with sampling periods and cod were more aggregated during the October and January sampling periods (Fig. 5).

Crab cohort analysis

Using a typical settling date of July 1, the size frequency modes seen in the Tanner crab taken from cod stomachs matched quite closely the size that would be expected at each sampling period based on work of Donaldson et al. (1981). During each period, cod were feeding on at least three cohorts of crab (Fig. 6). The 1997 year class was the only cohort well represented in the stomachs during all sampling periods (Fig. 6) and was also the year class that became vulnerable to the survey gear the following year during the ADFG survey in 2000. This made it the only cohort for which enough information was available for estimating its population size during the study; therefore it was the only cohort used in the correlation analysis. At the time of the 2000 survey, the 1997 cohort population estimate was 29.7 million crab and after accounting for natural mortality, a year earlier at the end of the study, the population would have been 47.5 million crab. Using the methods of Forney (1973) and Livingston (1989), it is estimated that cod removed 79.2% of the 1997 cohort over the 14 months of the study.

Predation density dependence

The per capita cod consumption of crab showed a significant, positive relationship with estimates of the population of the 1997 crab cohort ($r^2 = 0.38$, $F_{1,17} = 9.02$, $p = 0.008$), possibly indicating a density-dependent relationship (Fig. 7).

Discussion

The coefficient of determination of 0.38 relating predation rates to population levels of the 1997 Tanner crab cohort suggests the possible existence of a density-dependent predator/prey process, but other factors must also contribute to the unexplained variation in the predation rate. Measurement errors are always a problem. The trawl net is an imprecise sampling method and a number of factors can affect its performance (Weinberg and Kotwicki 2008) and the resulting estimates of Tanner crab and cod populations. Even though Tanner crab were a main prey item, cod were confirmed to be opportunistic predators with the ability to rapidly switch to other species when they became more attractive. In addition, environmental factors correlated with crab availability or affecting cod consumption rates may affect cod foraging behavior.

Consumption of the 1997 cohort was necessarily influenced by the numbers of the other cohorts which were of suitable size for cod predation during the study. Ideally a study of the role of cod predation on crab populations would involve data on the predation rates on individual cohorts over multiple years. The existing data did not allow this type of analysis, but 1997 was the dominate prey cohort during this study so the positive correlation value has some validity. Despite the uncertainties involved in this analysis, the data indicate that cod per capita consumption of crab may be dependent on crab numbers. The density-dependent demographic rate must only occur at "some place and time" during the life history in order to regulate and stabilize a population (Hixon and Carr 1997). At the same time, removal of 79% of a year class would also work to severely limit and suppress the Tanner crab populations. Ecologists have long struggled with the phenomenon of population stabilization (Murdoch 1994) because models of population dynamics (e.g., Nisbet et al. 1989, Turchin 2003) predict instability and large-amplitude population fluctuations under prey removal rates of this magnitude. Further long-term study of both cod food habits and population trends of Tanner crab and cod are needed to definitively determine the role cod play in Tanner crab population fluctuations and also to place these observations of a local predator/prey relationship within the context of a large marine ecosystem.

Reference

Albers, W.D., and P.J. Anderson. 1985. Diet of Pacific cod, *Gadus macrocephalus*, and predation on the northern pink shrimp, *Pandalus borealis*, in Pavlof Bay, Alaska. Fish. Bull. 83:601-610.

Aydin, K., S. Gaichas, I. Ortiz, D. Kinzey, and N. Friday. 2007. A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. NOAA Tech. Memo. NMFS-AFSC-178. 298 pp.

Bunch, T., and R.C. Highsmith. 1998. Genetic evidence for dispersal of larvae of Tanner crabs (*Chionoecetes bairdi*) by the Alaskan Coastal Current. Mol. Mar. Biol. Biotech. 7:153-159.

Chabot, D., B. Sainte-Marie, K. Briand, and J.M. Hanson. 2008. Atlantic cod and snow crab predator-prey size relationship in the Gulf of St. Lawrence, Canada. Mar. Ecol. Prog. Ser. 363:227-240. doi:10.3354/meps07384

Donaldson, W.E. 1983. Movements of tagged males of Tanner crab *Chionoecetes bairdi* Rathbun off Kodiak Island, Alaska. J. Shellfish Res. 3:195-201.

Donaldson, W.E., R.T. Cooney, and J.R. Hilsinger. 1981. Growth, age and size at maturity of Tanner crab, *Chionoecetes bairdi* M.J. Rathbun, in the northern Gulf of Alaska (Decapoda, Brachyura). Crustaceana (Leiden) 40:286-302. doi:10.1163/156854081X00750

Elton, C.S., and M. Nicholson. 1942. The ten-year cycle in numbers of the lynx in Canada. J. Anim. Ecol. 11:215-244. doi:10.2307/1358

Forney, J.L. 1977. Reconstruction of yellow perch (*Perca flavescens*) cohorts from examination of walleye (*Stizostedion vitreum vitreum*) stomachs. J. Fish. Res. Board Can. 34:925-932.

Harrison, S., and N. Cappuccino. 1995. Using density-manipulation experiments to study population regulation. In: N. Cappuccino and P. Price (eds.), Population dynamics, new approaches and synthesis. Academic Press, San Diego, pp. 131-147.

Hixon, M.A., and M.H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. Science 277:946-949. doi:10.1126/science.277.5328.946

Hixon, M.A., S.W. Pacala, and S.A. Sandin. 2002. Population regulation: Historical context and contemporary challenges of open vs. closed systems. Ecology 83:1490-1508. doi:10.1890/0012-9658(2002)083[1490:PRHCAC]2.0.CO;2

Incze, L.S. 1983. Larval life history of Tanner crabs, *Chionoecetes bairdi* and *C. opilio*, in the southeastern Bering Sea and relationships to regional oceanography. Ph.D. thesis, University of Washington, Seattle.

Jewett, S.C. 1978. Summer food of the Pacific cod, *Gadus macrocephalus*, near Kodiak Island, Alaska. Fish. Bull. 76:700-706.

Krebs, C.J. 2002. Beyond population regulation and limitation. Wildl. Res. 29:1-10. doi:10.1071/WR01074

Legendre, P. 2008. lmodel2: Model II regression. R package, version 1.6-3.

Legendre, P., and L. Legendre. 1998. Numerical ecology. No. 20. In: Developments in environmental modeling, 2nd edn. Elsevier, Amsterdam.

Lindberg, V. 2000. Uncertainties and error propagation. The Physics Source for Introductory Physics Courses. Accessed Dec. 2010: http:www.physicssource.org/items/detail.cfm?ID=7714.

Livingston, P.A. 1989. Interannual trends in Pacific cod, *Gadus macrocephalus*, predation on three commercially important crab species in the eastern Bering Sea. Fish. Bull. 87:807-827.

Livingston. P.A., D.A. Dwyer, D.L. Wenchker, M.S. Yang, and G.M. Lang. 1986. Trophic interactions of key fish species in the eastern Bering Sea. Int. N. Pac. Fish. Comm. Bull. 47.

Mehl, S., and T. Westgard. 1986. The diet and consumption of mackerel in the North Sea. ICES C.M. doc.1983/H:34.

Meyers, J.H., and L.D. Rothman. 1995. Field experiments to study regulation of fluctuating populations. In: N. Cappuccino and P. Price (eds.) Population dynamics, new approaches and synthesis. Academic Press, San Diego, pp. 229-250.

Murdoch, W.W. 1994. Population regulation in theory and practice. Ecology 75:271-287. doi:10.2307/1939533

Murdoch, W.W., C.J. Briggs, and R.M. Nisbet. 2003. Consumer-resource dynamics. Monographs in population biology, 36. Princeton University Press, Princeton. 459 pp.

Nisbet, R.M., W.S. Gurney, W.W. Murdoch, and E. McCauley. 1989. Structural population models: A tool for linking effect at individual and population levels. Biol. J. Linnaean Soc. 37:79-99. doi:10.1111/j.1095-8312.1989.tb02006.x

NPFMC. 2008. Stock assessment and fishery evaluation report for the king and Tanner crab fisheries of the Bering Sea and Aleutian Islands regions. North Pacific Fishery Management Council, Anchorage, Alaska. (Unpublished.)

Pengilly, D., J.E. Blackburn, and J.D. Urban. 1999. Bottom trawl assessment of seasonal distribution of Tanner crab, Pacific cod, and shallow water flatfish in Marmot Bay, Alaska. Final project report, NOAA Grant NA86FD0077. 78 pp. (Unpublished.)

Pinchuk, A.I., K.O. Coyle, and R.R. Hopcroft. 2008. Climate-related variability in abundance and reproduction of euphausiids in the northern Gulf of Alaska in 1998-2003. Prog. Oceanogr. 77:203-216. doi:10.1016/j.pocean.2008.03.012

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0. Accessed March 2010: http://www.R-project.org.

Sinclair, A.R.E. 1989. Population regulation in animals. In: J.M. Cherrett (ed.), Ecological concepts. Blackwell Scientific Publishers, Oxford, pp. 197-241.

Sinclair, A.R.E., and R.P. Pech. 1996. Density dependence, stochasticity, compensation and predator regulation. Oikos 75:164-173. doi:10.2307/3546240

Sokal, R.R., and F.J. Rohlf. 1995. Biometry: The principles and practice of statistics in biological research, 3rd edn. W.H. Freeman and Co., New York. 887 pp.

Stevens, B.G. 2003. Timing of aggregation and larval release by Tanner crabs, *Chionoecetes bairdi*, in relation to tidal currents patterns. Fish. Res. (Amst.) 65:201-216.

Turchin, P. 1995. Population regulation: Old arguments and a new synthesis. In: N. Cappuccino and P. Price (eds.), Populations dynamics, new approaches and synthesis. Academic Press, San Diego, pp. 19-40.

Turchin, P. 1999. Population regulation: A synthetic view. Oikos 84:153-159. doi:10.2307/3546876

Turchin, P. 2003. Complex population dynamics: A theoretical/empirical synthesis. Monographs in population biology, 35. Princeton University Press, Princeton. 450 pp.

Urban, D., and I. Vining. 2008. Variation in the trophic level of Pacific cod with changes in size and season. In: G.H. Kruse, K. Drinkwater, J.N. Ianelli, J.S. Link, D.L. Stram, V. Wespestad, and D. Woodby (eds.), Resiliency of gadid stocks to fishing and climate change. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 305-315. doi:10.4027/rgsfcc.2008.17

Ursin, E.M., M. Pennington, E.B. Cohen, and M.D. Grosslein. 1985. Stomach evacuation rates of Atlantic cod (*Gadus morhua*) estimated from stomach contents and growth rates. Dana 5:63-80.

von Szalay, P.G., and E. Brown. 2001. A performance evaluation of three estimators of fishing power correction between NMFS and ADFG demersal trawl survey vessels. Alaska Fish. Res. Bull. 8:85-95.

Weinberg, K.L., and S. Kotwicki. 2008. Factors influencing net width and sea floor contact of a survey bottom trawl. Fish. Res. 93:265-279. doi:10.1016/j.fishres.2008.05.011

Yang, M.-S., and M.W. Nelson 2000. Food habits of the commercially important groundfishes in the Gulf of Alaska in 1990, 1993, and 1996. NOAA Tech. Memo. NMFS-AFSC-112. 174 pp.

Yang, M-S., K. Dodd, R. Hibpshman, and A. Whitehouse. 2006. Food habits of groundfishes in the Gulf of Alaska in 1999 and 2001. NOAA Tech. Memo. NMFS-AFSC-164. 199 pp.

Zheng, J., G.H. Kruse, and M.C. Murphy. 1998. A length-based approach to estimate population abundance of Tanner crab, *Chionoecetes bairdi*, in Bristol Bay, Alaska, In: G.S. Jamieson and A. Campbell (eds.), Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Can. Spec. Publ. Fish. Aquat. Sci. 125, pp. 97-105.

Choi, J.S. 2010. Habitat Preferences of the Snow Crab, *Chionoecetes opilio*: Where Stock Assessment and Ecology Intersect. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.02

Habitat Preferences of the Snow Crab, *Chionoecetes opilio*: Where Stock Assessment and Ecology Intersect

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Abstract

The Scotian Shelf ecosystem (SSE) represents the southernmost distribution limit of snow crab in the northeast Atlantic. As a result, temperature variations can be expected to be an important factor in determining their spatial distribution. Temperature data from 1950 to the present were modeled as generalized additive models (GAMs) and used to reconstruct spatially explicit annual bottom temperatures. The influence of such temperature variations relative to other habitat factors such as substrate grain size, depth, and bottom slope and curvature is described with a binomial GAM and a 13-year data series of snow crab trawl surveys. Two main considerations result. First, explicit knowledge of habitat bounds must inform biomass estimation/stock assessment; otherwise, habitat bounds are implicitly assumed to be fixed and only density estimates are modeled. For the SSE, this type of assumption can result in errors of ±30% in biomass estimates relative to a methodology that accounts for environmental/habitat variations. Second, suitable habitat for snow crab has existed for many years prior to the late 1990s proliferation of snow crab in the SSE. It is hypothesized that alterations in food web structure, particularly the recent demise of demersal fish, was a primary factor in the recent expansion of the snow crab population. This potentially antagonistic relationship between demersal fish and snow crab provokes difficult questions for resource managers as the successful management of one species may have deleterious effects on others.

Introduction

Habitat preferences seem associated with variations in temperature, sediment type/granularity, depth, and light levels (Hooper 1986, Comeau et al. 1998, Sainte-Marie and Hazel 1992). Stock assessments for snow crab, as well most other species, generally ignore these factors and assume that the bounds of snow crab habitat are invariant with time. This effectively focuses assessments of abundance on variations in numerical or biomass density rather than total abundance or biomass. Standard fisheries models would therefore incorrectly attempt to absorb such surface area variations into catchability/selectivity coefficients or other sources of model or process error. When habitat factors such as temperature are homogeneous and/or stable, this may be an appropriate approximation. However, when they are more variable, this assumption may be altogether inappropriate, making the explicit modeling of habitat a necessary component of abundance estimation/stock assessment. This environmental variability is particularly problematic for stenothermic organisms such as snow crab (temperature preferences between 0.0 to 4.0°C and an upper metabolic limit in the range of 7.0°C; Foyle et al. 1989), especially in the current context of rapid global climate change and environmental uncertainty.

The Scotian Shelf ecosystem (SSE) off Nova Scotia, Canada, (Fig. 1) is on the southernmost distribution limit of snow crab in the northwest Atlantic of Canada. Three biologically significant management subareas relevant to snow crab are recognized, roughly following a variability gradient in interannual bottom temperatures: the northernmost area is a region of cold and low interannual variability (N-ENS, North-Eastern Nova Scotia); the southeastern area is a large and productive area (Fig. 2) with cold and intermediate interannual variability (S-ENS, South-Eastern Nova Scotia); and the southwestern area (CFA 4X; Crab Fishing Area 4X) is warmest and also highest in terms of interannual variability. Here, snow crab habitat preferences are explicitly modeled using data derived from a 13-year time series of trawl surveys. Because the abundance distributions of snow crab are zero-inflated and lognormal, a model of zero abundance locations (suitable habitat) and a secondary model of the positive-valued, lognormal abundance are used. The results and implications of such a hierarchical approach (Gelman and Hill 2006) are presented. To conclude, some of these results are applied to the question of what factors are responsible for the proliferation of the snow crab on the SSE over the last decade.

Methods

This analysis is primarily based on directed trawl surveys for snow crab (Choi and Zisserson 2007) and supplemented with other sources

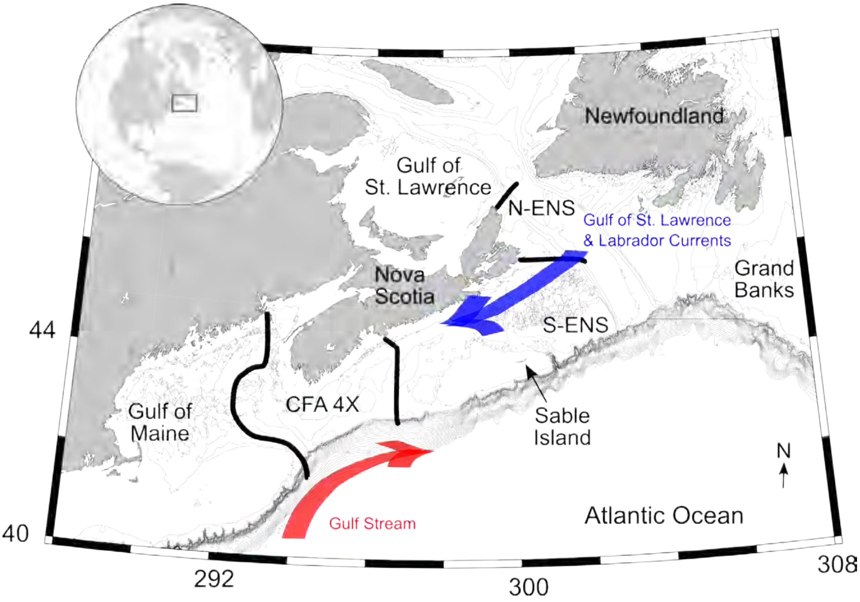

Figure 1. Map of the Scotian Shelf ecosystem (SSE) off Nova Scotia, Canada.

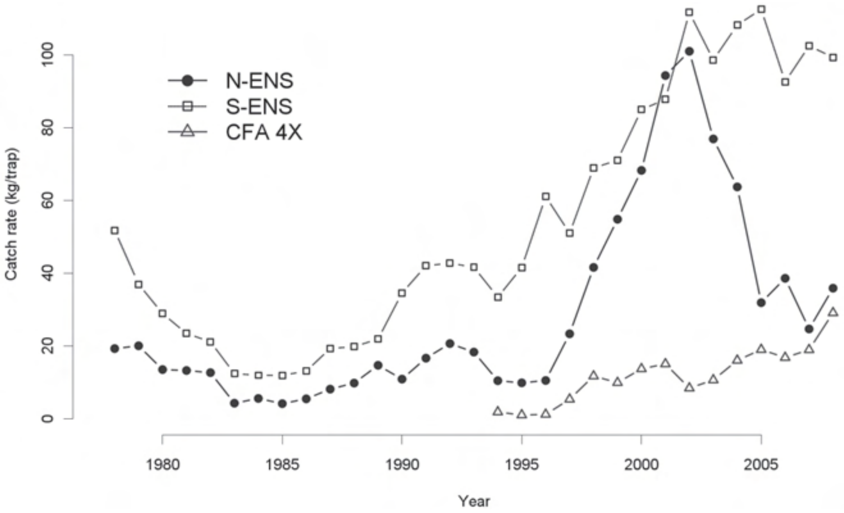

Figure 2. Historical variations in catch per unit effort indices (CPUE; kg per trap haul) of snow crab for the three management subareas in the SSE.

of information on bottom temperature conditions and substrate type (described below). A modified Bigouden *Nephrops* trawl net originally designed to dig into soft sediments for the capture of lobsters in Europe was used to sample snow crab (headline of 20 m, 27.3 m foot rope mounted with a 3.2 m long 8 mm chain, with a mesh size of 80 mm in the wings, 60 mm in the belly, and 40 mm in the cod-end). Tow duration was ~5 minutes with bottom contact monitored by Netmind sensors. The net width at the mouth was also monitored with Netmind sensors; warp length was ~3 times the depth. Vessel speed was maintained at ~2 knots. The positional and bottom water temperature measurements were recorded with a global positioning system and Minilog data recorders, respectively. The net's swept area was calculated from distance and net width information. All crab were enumerated, measured with calipers, and weighed with motion-compensated scales; for all crab shell condition was described, and claw hardness was determined with a durometer. This allowed direct biomass measurement. To date, 237,511 snow crab have been enumerated from 4,051 sampling events dispersed over 13 years. Snow crab in the SSE are observed at temperatures ranging from –0.5 to 14.7°C.

Detailed spatiotemporal records of bottom temperatures from 1950 to 2008 were discretized to a resolution of 1 km × 1 km and each grid point (199,663 locations in total) was modeled in time-series as a generalized additive model (GAM; Wood 2006). Model formulation was chosen based on the Akaike information criterion (AIC; Burnham and Anderson 2004) and analysis of variance; these time-series models generally accounted for about 70 to 90% of the temporal components of bottom temperature variations (seasonal and interannual) for any single grid point. The model specification was temperature ~s[cos(week), sin(week), year] + s(latitude, longitude), where "s" indicates a thin plate regression spline smoothing function, and longitude and latitude are UTM (universal transverse Mercator) region 20 planar coordinates. As the spatial coverage was sparse for the early part of the historical record, local spatial averaging to a spatial extent of 25 km radius with a 2-D smooth function of northing and easting was used. This distance range was chosen based on empirical variograms that indicated spatial-autocorrelation of bottom temperatures drop off asymptotically beyond 25 km on the SSE. The resultant models were used as a first-pass temporal interpolation of bottom temperature variations. A second-pass spatial interpolation used inverse-distance weighting to reconstruct the complete space-time bottom temperature series. From the space-time interpolated data, the mean annual temperatures, amplitudes, and the week number of temperature minima were estimated at each location for further covariate analysis with snow crab distributions (Fig. 3).

The natural logarithm (ln) of substrate granularity measured in millimeters (ln grain size mm); Kostylev and Hannah 2007; Fig. 3) was

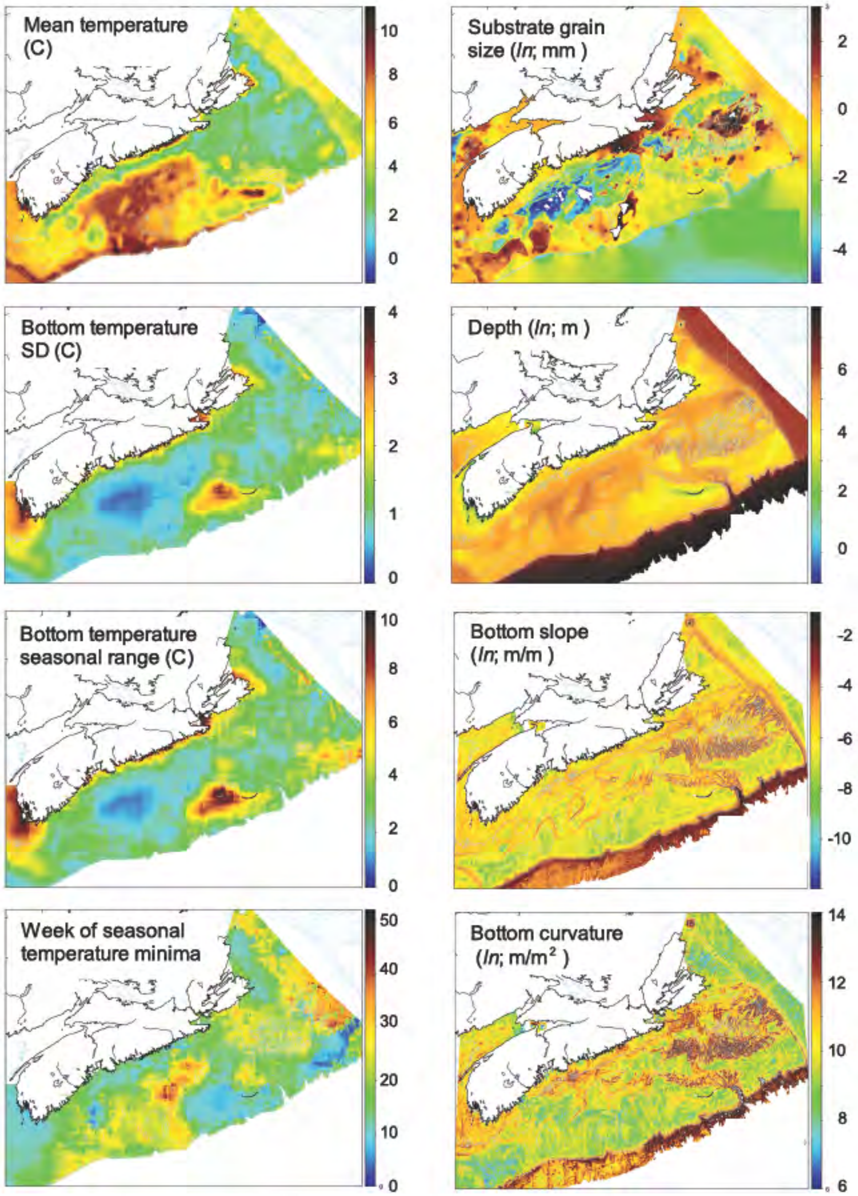

Figure 3. Interpolated and smoothed bottom temperature and substrate information used to predict snow crab habitat. Temperature data visualizations are the climatological means (1950 to 2008). For modeling and prediction, annual estimates were used.

used as a proxy for bottom type. Depths, measured in meters (m), were extracted from various sources, including the Canadian Hydrographic Service (15 arc-second resolution) and dedicated snow crab assessment surveys (Choi and Zisserson 2007). Estimates of bottom slope, ln(|m|/m), and bottom curvature, ln(|m|/m²), were computed and all data were discretized to a grid of 1 km × 1 km. The probability of finding snow crab, PSC = probability (snow crab biomass > 0), was determined based on the presence or absence of mature male snow crab in the directed snow crab trawl survey used for stock assessments. Female and immature crab are known to have different habitat preferences and their full elucidation will be reserved for a future study. On the SSE, males are sexually mature between the ages of 7-11 years and females between 7-8 years (Choi and Zisserson 2007).

Specifically, a binomial GAM with a logit link function (ln[*PSC*/(1–*PSC*)]) was used to describe this snow crab habitat:

$$\log it(p) = B_0 + \sum_{j=1}^{n} f_j(X_i)$$

where the B_0 is a constant; f_j are some nonlinear function (thin-plate regression splines were used) of the *n* covariates X_i: year, temperature, seasonal amplitude of bottom temperature, week of annual temperature minima, depth, substrate grain size, bottom slope, bottom curvature and a 2-D smooth of {latitude, longitude, expressed in planar coordinates, UTM zone 20}. Simpler, generalized linear models and mixed effects models were attempted. The GAM model outperformed the former based on AIC, mostly due to the nonlinear nature of many of the relationships; while the mixed effects model required more computational resources than were available (16 GB RAM). In this paper, predictions of the probability of finding snow crab on the whole of the SSE were made with the GAM model.

Abundance was estimated for those locations in which the lower 95% confidence bound for the probability of finding a mature male snow crab was greater than zero. Two methods were examined. The first was the simple areal expansion of the arithmetic mean biomass densities to a fixed area for each region—the mean value determined by the habitat model. The second method was an areal expansion to the annually varying surface area estimated for each region from the habitat model. All data analyses were conducted with statistical computing language and environment R (R Development Core Team 2008). Conversions between cartographic and Cartesian coordinate systems for analytical purposes were computed with the software PROJ (Evenden 1995) using the WGS84 geoid and the UTM grid for region 20. The surface area of potential snow crab habitat (*HAB*) was determined as the sum of all discretized locations where the predicted probability of observing a snow crab was greater than 0.5.

Results

The mean annual bottom temperatures from 1950 to 2008 varied between 0.0 to 11.0°C (Fig. 3). The warmer southwestern areas (>5.0°C) are influenced by the Gulf Stream, whereas the colder northeastern areas (<5.0°C) are influenced by the flow from the Gulf of St. Lawrence and the Labrador Current (Fig. 1). Seasonal range in bottom temperature varied form 0.0°C in some deep areas to 10.0°C (SD = 4.0°C) in the shallower areas. Phase shifts in seasonal cycles were indexed by the week at which bottom temperatures were at a minimum (Fig. 3). Minima occurred near week 10 in shallow areas and week 30 to 40 in deeper areas.

The habitat model explained approximately 35% of the total deviance (Table 1) in the survey data (4,051 sampling events). Significantly informative factors ($p < 0.0001$) included temperature, depth, substrate grain size, and a spatial component. The latter spatial component, a proxy of the unexplained spatial autocorrelation of snow crab presence/absence, was congruent with observed areas of snow crab fishing grounds.

Table 1. Analysis of deviance of the probability of snow crab presence based on a binomial generalized additive model. The "s(x)" indicates a smoothing by thin-plate regression splines for the factors longitude and latitude in planar coordinates (lon, lat), mean annual temperature (t), depth (Z), substrate grain size (grain), year (yr), weekly number of annual temperature minima (wmin), bottom curvature (ddZ), bottom slope (dZ), and annual amplitude of temperature oscillations (tamp).

Parametric coefficients					
	Estimate	SE	z value	Pr(>|z|)	
Intercept	1.0615	0.0487	21.8	<2e–16	***
Approximate significance of smooth terms					
	edf	Ref.df	Chi square	*p*-value	
s(lon, lat)	27.96	28.46	436.82	<2e–16	***
s(t)	2.44	2.94	92.71	<2e–16	***
s(Z)	3.22	3.72	74.55	1.6e–15	***
s(grain)	4.36	4.86	63.84	1.6e–12	***
s(yr)	8.06	8.56	57.54	2.6e–09	***
s(wmin)	7.39	7.89	31.71	9.6e–05	***
s(ddZ)	6.83	7.33	20.13	0.0066	**
s(dZ)	6.02	6.52	13.39	0.0495	*
s(tamp)	2.75	3.25	2.61	0.5010	

R-sq.(adj) = 0.345, Deviance explained = 30.7%, UBRE score = –0.095993, Scale est. = 1, n = 3877. edf = Estimated degrees of freedom, Rel.df = Reference degrees of freedom adjusted for the number of smoothing parameters. Significance codes: *** = 0.001, ** = 0.01, * = 0.05.

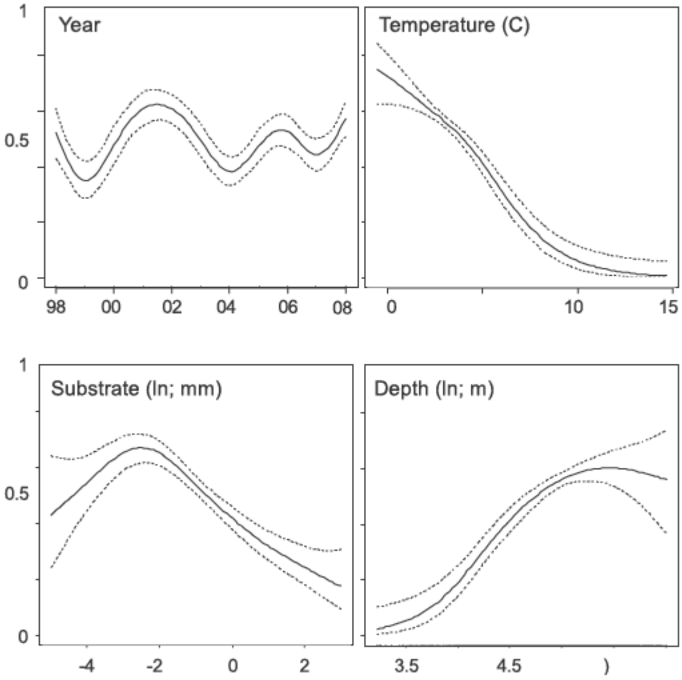

Figure 4. The empirically modeled relationship of snow crab habitat suitability as a function of the primary covariates; 95% CI are presented. Stippling on the x-axis represents data density.

The probability of finding snow crab declined rapidly with increasing temperatures to a limit of ~10ºC (Fig. 4). Snow crab fishing grounds exist in areas where mean annual bottom temperatures range from 1 to 4ºC. Surprisingly, the magnitude of seasonal fluctuations did not have a strong influence on delimiting potential snow crab habitat ($p = 0.5$). This is likely due to the snow crab surveys not extending very much beyond snow crab fishing grounds, resulting in a lack of sufficient contrast in the temperature range (~3ºC) to influence the model predictions. The strong correlation between seasonal temperature range and depth also likely reduced the magnitude of this potential influence. Snow crab fishing grounds exist in areas with seasonal standard deviations in temperature that range from 0.5 to 1.6ºC (seasonal temperature ranges of 1.0 to 4.0ºC). The time of year at which temperature minima were observed also contributed significantly to predicting snow crab habitat, with highest probabilities for weeks 15 to 25 (approximately April to May). This was also consistent with observed snow crab fishing grounds.

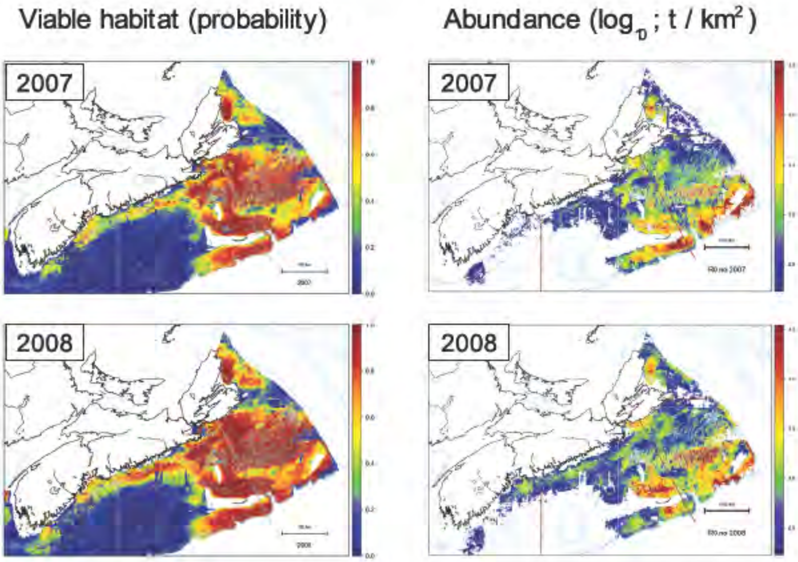

Figure 5. Predicted probabilities of viable habitat for snow crab (left) and the biomass densities of mature crab (right).

Depth was also an important determinant of habitat suitability ($p < 0.0001$) with very low probability of observing snow crab at locations shallower than 55 m and reaching a maximum near 220 m (Fig. 4). Bottom slope ($p = 0.05$) and curvature ($p = 0.007$) were less informative but retained in the model. Substrate grain size was informative ($p < 0.0001$) with high habitat suitabilities associated with intermediate grain sizes of 0.3 to 3.5 mm (Fig. 4). Interannual variations in the probability of finding suitable snow crab habitat were significant ($p < 0.0001$; Fig. 4). They show a damped oscillation with periodicities in the range of 4 and/or 8 years.

A spatiotemporal representation of predicted snow crab habitat based on these modeled relationships is presented in Fig. 5. The interannual variability is largely associated with interannual variations in temperature and also interannual habitat expansion/contraction associated with un-modeled processes such as density-dependence and predator/prey/disease fields (see year effect, above). The spatial variations show features that are generally stable between years and display good correspondence with fishing grounds and core abundance locations. The interannual variations in the surface area of these potential habitats (*HAB*) show similar temporal trends that are mostly in-phase across the various subregions. Peak habitat areas were

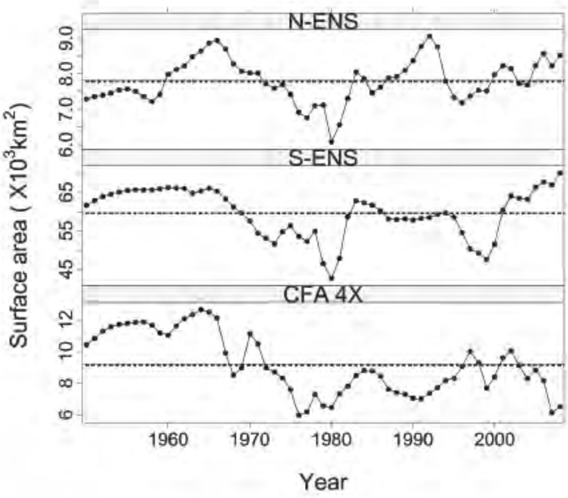

Figure 6. Predicted surface area of potential snow crab habitat (HA) during 1950-2008 in the N-ENS, S-ENS, and CFA 4X management areas of the Scotian Shelf ecosystem. The dashed horizontal lines indicates the long-term arithmetic mean surface area within each subarea.

observed in the mid 1960s, mid 1980s, and mid 2000s. Stronger amplitude variations have been evident since the late 1970s. Currently, *HAB* is 85 $\times 10^3$ km^2 for the SSE, about 11% higher than the long-term mean of 77 $\times 10^3$ km^2 (SD = 8 $\times 10^3$ km^2). In N-ENS (Fig. 1), *HAB* varied from 6 to 9 $\times 10^3$ km^2 (mean = 7.8 $\times 10^3$ km^2, $SD_{interannual}$ = 0.6 $\times 10^3$ km^2, CV = 8%); in S-ENS, *HAB* varied with similar oscillations, ranging from 40 to 70 $\times 10^3$km^2 since 1950 (mean = 59.7 $\times 10^3$ km^2, $SD_{interannual}$ = 6.2 $\times 10^3$ km^2, CV = 10%). In the southernmost region (4X), *HAB* was highly variable, ranging from 6 to 13 $\times 10^3$ km^2 (mean = 9.1 $\times 10^3$ km^2, $SD_{interannual}$ = 1.9 $\times 10^3$ km^2, CV = 21%). However, an important divergence in *HAB* trends has been evident since the late 1990s—declining rapidly in the south (CFA 4X and increasing in the more northern regions (N-ENS and S-ENS; Fig. 6). This divergence is associated with the greater influence of the warmer Gulf Stream in CFA 4X and the colder Labrador Current in N-ENS and S-ENS and suggests the operation of large-scale climatic processes and potentially a sign of what is to come with rapid climate change.

Average temperatures within the areas of suitable habitat have fluctuated over time (Fig. 7) with periods of approximately 4 and/or 8 years. While the southernmost area (CFA 4X) has historically shown similar periodicities in mean annual temperatures that were similar to the more northern areas, a divergence in temperature variations has been evident since the mid 1990s when high-amplitude decadal oscillations

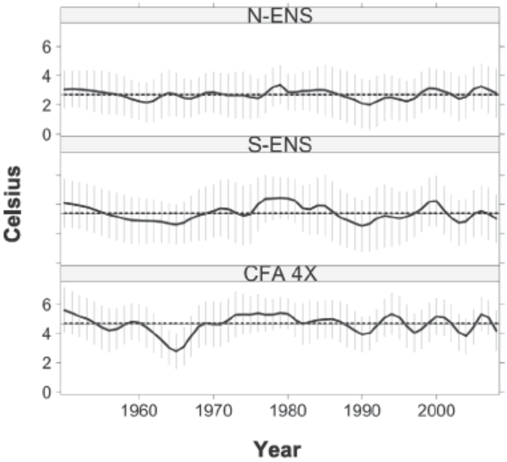

Figure 7. Annual mean bottom temperature within the predicted snow crab habitat, with 1 standard deviation error bars. The dashed horizontal line indicates the long-term arithmetic mean within each subarea.

were observed in the warmer area. The mean bottom temperature on the SSE snow crab habitat has been 3.5ºC (SD = 0.5ºC). Among subareas, the mean temperatures were 2.7ºC, 3.4ºC, and 4.6ºC, in N-ENS, S-ENS, and CFA 4X, respectively with respective interannual SD = 0.3, 0.5, and 0.6ºC. In the SSE, total biomass estimated assuming a constant habitat area, and those assuming annual variability in habitat area, deviate up to ±30% (Fig. 8). The degree of concordance between these two methods seems better at low abundance levels.

Discussion/conclusion

Snow crab habitat on the SSE was associated with temperature, depth, and substrate characteristics. Most of these habitat preferences have been previously documented (e.g., Hooper 1986, Sainte-Marie and Hazel 1992, Comeau et al. 1998). This is the first large-scale study to explicitly model habitat suitability as a probability of snow crab occurrence in a spatiotemporal context. The significance of this approach is that it allows a formal and objective means of describing the influence of one factor relative to another within and across systems.

In a stock assessment context, the results of similar habitat analyses can be used to flexibly model snow crab abundance in a hierarchical sense (Gelman and Hill 2006). Abundance estimation without accounting

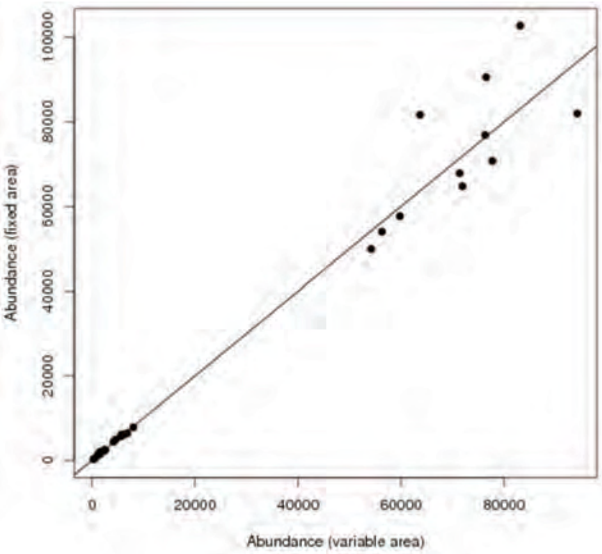

Figure 8. Abundance estimates based on a fixed area assumption (mean within each subarea) compared to a variable area assumption. Data points represent abundance estimates from the three separate fishing grounds: N-ENS, S-ENS, and CFA 4X from 1998 to 2008. The line of 1:1 correspondence is provided for visual comparison.

for variability in the bounds of snow crab habitat can result in errors in the range of ±30% of the biomass on the SSE (Fig. 8). If such fixed area indices are used to tune standard stock assessment models, the errors can be considerable and of the same order of magnitude as fishery exploitation rates.

Interannual variations in the probability of finding suitable snow crab habitat (Fig. 4) show a damped oscillation with periodicities in the range of 4 and/or 8 years. The exact causes of these periodicities are not clear; however, they are suggestive of large-scaled climatic fluctuations such as the El Niño/La Niña–type oscillations (see also Fig. 7). This interannual effect suggests that other processes may be operative: e.g., modulation of areal extent when temperature conditions result in higher availability of food or the alteration of the spatiotemporal distribution of predator or disease/parasite prevalence. These interannual patterns are unlikely to be associated with density-dependent processes as the variations in snow crab abundance/recruitment have had ~10-year periodicities, if any (Fig. 2).

The management implication for this variability in habitat space and ambient temperatures is simple: a more variable environment requires more conservative/precautionary management measures. This requirement is reinforced by the expectation of large-scale warming and temperature fluctuations associated with rapid global climate change. Strangely, the experience in CFA 4X, the region with the highest risk of such uncertainties, has been the converse. Because the fishery is in a "marginal" temperature environment, fishers perceive the fishery as a short-lived resource where the maximum economic benefit should be obtained as quickly as possible. Exploitation strategies have therefore been aggressive, with higher exploitation rates, extended fishing seasons (6 months), and high fishing effort that intercepts a large proportion of new recruits during the period of spring molt and reproduction (Choi and Zisserson 2007). It has proved difficult to dissuade fishers from the self-fulfilling expectation of a short-lived fishery and remains a challenge to plan for the long-term sustainability of this fishery.

The management implications are simpler for more stable temperature environments. The information-to-noise ratio in such "core" systems is relatively high with fewer environmental uncertainties to complicate the interpretation of biological dynamics. These areas also tend to be reproductive/nursery grounds that will sustain the population as a whole and reseed the more marginal environments following extreme environmental and/or fishery perturbations (MacCall 1990, Hanski and Gilpin 2008). Fishing practices that establish refugia in such areas would minimize disturbance of reproduction and recruitment in some subset of the core areas and so enhance the long-term conservation of the stock. Unfortunately the best catch rates also exist in the same areas.

Ecological/ecosystem context

At least two main hypotheses explain the increase of snow crab abundance since the late 1990s in the northwest Atlantic/SSE (Fig. 2): cold-bottom temperatures and predation release. The temperature hypothesis suggests that a major cooling period in the 1990s made the environment more favorable for the proliferation of cold-water species such as northern shrimp (*Pandalus borealis*) and snow crab. Anecdotal information from fishers, fishery-based catch rates, and some Fisheries and Oceans Canada research trawl surveys suggests that the abundance of snow crab on the SSE was low in the period prior to 1980 (Tremblay 1997). However, in the late-1980s and again in the late 1990s, increases in catch rates were observed throughout the shelf, presumably due to increased crab abundance (Fig. 2). Because snow crab require at least 10 years from larval settlement to grow to legal size (95 mm CW; Choi and Zisserson 2007), crab abundance in the late 1980s must result from reproduction as early as the late 1970s, and prior to the large temperature swings in the 1980s and 1990s (Fig. 7). Indeed, potential snow crab habitat on the SSE has been in existence throughout the historical record (Fig. 6) suggesting that strong temperature-related influences were not direct causes of the increase in snow crab abundance. It should, however, be noted that while the information supporting **direct** temperature- or climate-driven control of snow crab abundance may be weak, some **indirect** climate-driven mechanisms merit further exploration: e.g., the match-mismatch hypothesis (Cushing 1995) or the influence of temperature variations on juvenile crab.

The predation hypothesis suggests that the collapse of many demersal fish in the northwest Atlantic may have resulted in the proliferation of prey species due to reduced direct predation (e.g., Worm and Myers 2003, Frank et al. 2006) and indirectly, via reduced predation mortality on species that are potential prey for snow crab (Choi et al. 2005). On the SSE, known predators of snow crab include Atlantic halibut (*Hippoglossus hippoglossus*), skates (especially thorny skate (*Raja radiata*), Atlantic cod, American plaice (*Hippoglossoides platessoides*), seals, squids, and other crabs (Bundy 2004). In particular, Atlantic cod and thorny skates are noted for their high selectivity for early benthic stages of snow crab and their potential to weaken recruitment to commercial sizes (Bailey 1982; Lilly 1984; Robichaud et al. 1989, 1991). On the SSE, abundances of demersal fish were high prior to the 1990s but most have since collapsed with no recovery (Choi et al. 2005). The timing of these collapses (early 1990s) and the coincidental increase in snow crab abundance in the early 2000s corresponds with the time required for larval snow crab in early 1990 to recruit to the fishery in the early 2000s (Fig. 2). The direct influences of temperature variations on these species are thought to be minimal (Choi et al. 2005).

Interestingly, the highest snow crab densities have been found in the immediate vicinity of gray seal colonies (*Halichoerus grypus* on Sable Island; Choi et al. 2005). Therefore, the evidence indicating that seals have a negative influence on the SSE snow crab population is weak. In fact, it is quite possible that seals may be facilitating crab production by physically importing food and food waste (organic matter) from other more outlying areas to the immediate vicinity of Sable Island, and so indirectly "feeding" the snow crab, and second by removing potential predators of both pelagic and early benthic crab stages.

The coherence of the above temporal sequence of events suggests that predation release may be a more parsimonious factor controlling the abundance of snow crab than temperature/climate variability. If predation release has promoted the proliferation of snow crab, then management efforts to return demersal fish to former high levels of abundance may negatively impact the SSE snow crab. This potentially antagonistic relationship between demersal fish and snow crab presents a difficult conundrum. What criteria should be used to assess the "desirable" state—should they only be socioeconomic factors, purely ecological, or somewhere in between? How do we integrate into such a management context, basic biological considerations such as the temperature influence of growth/molt cycles, maturity ogives, egg development rates, metabolic thresholds, predation, competition, and conservation? With the increasing commitment of various nations, including the Canadian government, to move toward an integrated, ecosystem-based management of fisheries (Choi et al. 2005), such questions will become increasingly manifest, questions that we are far from being able to address at this time.

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References

Bailey, R. 1982. Relationship between catches of snow crab, *C. opilio* (O. Fabricius) and abundance of cod, *Gadus morhua* L. in the southwestern Gulf of St. Lawrence. Proceedings of the International Symposium on the Genus *Chionoecetes*. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 486-497.

Bundy, A. 2004. Mass balance models of the eastern Scotian Shelf before and after the cod collapse and other ecosystem changes. Can. Tech. Rep. Fish. Aquat. Sci. 2520.

Burnham, K.P., and D.R. Anderson. 2004. Multimodal inference: Understanding AIC and BIC in model selection. Sociological Methods and Research 33:261-304. doi:10.1177/0049124104268644

Choi, J.S., and B. Zisserson. 2007. An assessment of the snow crab resident on the Scotian Shelf in 2006. CSAS Research Document 2007/017.

Choi, J.S., K.T. Frank, B. Petrie, and W.C. Leggett. 2005. Integrated assessment of a large marine ecosystem: A case study of the devolution of the eastern Scotian Shelf, Canada. Oceanogr. Mar. Biol. Ann. Rev. 43:47-67.

Comeau, M., G.Y. Conan, F. Maynou, G. Robichaud, J.C. Therriault, and M. Starr. 1998. Growth, spatial distribution, and abundance of benthic stages of the snow crab, *Chionoecetes opilio*, in Bonne Bay, Newfoundland, Canada. Can. J. Fish. Aquat. Sci. 55:262-279. doi:10.1139/cjfas-55-1-262

Cushing, D.H. 1995. Population production and regulation in the sea: A fisheries perspective. Cambridge University Press, Cambridge.

Evenden, G.I. 1995. Cartographic projection procedures for the UNIX environment: A user's manual. Manual for PROJ 4.4.9. USGS Open File Report 90-284.

Foyle, T., R. O'Dor, and R. Elner. 1989. Energetically defining the thermal limits of the snow crab. J. Exp. Biol. 145:371-393.

Frank K.T., B. Petrie, N.L. Shackell, and J.S. Choi. 2006. Reconciling differences in trophic control in mid-latitude marine ecosystems. Ecol. Lett. 9:1096-1105. doi:10.1111/j.1461-0248.2006.00961.x

Gelman, A., and J. Hill. 2006. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York. 648 pp.

Hanski, I., and M. Gilpin. 2008. Metapopulation dynamics: Brief history and conceptual domain. Biol. J. Linn. Soc. 42:3-16. doi:10.1111/j.1095-8312.1991.tb00548.x

Hooper, R. 1986. A spring breeding migration of the snow crab, *Chionoecetes opilio* (O. Fabr.), into shallow water in Newfoundland. Crustaceana 50:257-264. doi:10.1163/156854086X00287

Kostylev, V.E., and C.G. Hannah. 2007. Process-driven characterization and mapping of seabed habitats. In: B.J. Todd and H.G. Greene (eds.), Mapping the seafloor for habitat characterization. Geol. Assoc. Can. Spec. Pap. 47:171-184.

Lilly, G. 1984. Predation by Atlantic cod on shrimp and crab off north-eastern Newfoundland in autumn of 1977-82. ICES CM 1984/G:53.

MacCall, A.D. 1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Accessed March 2010: http://www.R-project.org/.

Robichaud, D.A., R.F.J. Bailey, and R.W. Elner. 1989. Growth and distribution of snow crab, Chionoecetes opilio, in the southeastern Gulf of St. Lawrence. J. Shellfish Res. 8:13-23.

Robichaud, D.A., R.W. Elner, and R.F.J. Bailey. 1991. Differential selection of crab *Chionoecetes opilio* and *Hyas* spp. as prey by sympatric cod Gadus morhua and thorny skate *Raja radiata*. Fish. Bull. 89:669-680.

Sainte-Marie, B., and F. Hazel. 1992. Moulting and mating of snow crabs, *Chionoecetes opilio*, in shallow waters of the northwest Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 49:1282-1293. doi:10.1139/f92-144

Tremblay, M. 1997. Snow crab (*Chionoecetes opilio*) distribution limits and abundance trends on the Scotian Shelf. J. Northwest Atl. Fish. Sci. 21:7-22. doi:10.2960/J.v21.a1

Wood, S. 2006. Generalized additive models: An introduction with R. CRC Texts in Statistical Science Series, Vol. 67. Chapman and Hall.

Worm, B., and R. Myers. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology 84:162-173. doi:10.1890/0012-9658(2003)084[0162:MAOCSI]2.0.CO;2

Dew, C.B. 2010. Historical Perspective on Habitat Essential to Bristol Bay Red King Crab. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.04

Historical Perspective on Habitat Essential to Bristol Bay Red King Crab

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Abstract

The Alaska red king crab, *Paralithodes camtschaticus*, has one of the most information-rich assessment and exploitation histories of any species in the eastern Bering Sea. Yet unsound assumptions and misconceptions persist as to the species' basic biology, ecology, and habitat requirements. These include (1) temperature is the dominant factor governing the distribution and abundance of red king crab, making them so unpredictable in their movements that no particular habitat can be designated as more essential than another within their 150,000 km^2 Bering Sea range; (2) early no-trawl refuges (e.g., the Japanese Broodstock Sanctuary and the Pot Sanctuary) were implemented to resolve fishing-gear conflicts rather than to protect red king crab from trawling; (3) protection from bottom trawling is more important for juvenile red king crab than for the multiparous broodstock with its relatively high reproductive value; (4) all male red king crab with a carapace length of 120 mm or greater, regardless of their molt status, are capable of mating with one or more females each year; and (5) the Bristol Bay red king crab stock is assumed to be regulated largely by compensatory mechanisms that cause reproductive success to be highest when spawning-stock abundance is lowest, thus ensuring that the stock will recover from overfished abundance levels once fishing is halted. This paper uses information from surveys conducted as early as 1941 to examine these assumptions and to provide the detail and

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historical perspective needed to identify habitat essential to an intact population of Bristol Bay red king crab.

Introduction

The Bristol Bay red king crab stock has a long history of exploitation. According to Blackford (1979), the Japanese began fishing for king crab in the Bering Sea in the 1920s and, during the 1930s, were taking more than 13,000 t (metric tons) of whole crab per year from Bristol Bay north of the Alaska Peninsula. King crab fishermen from the Soviet Union entered the eastern Bering Sea in 1928, and by 1930 they were taking some 4,000 t annually (Blackford 1979). U.S. fishermen, encouraged by the findings of an exploratory survey conducted by the U.S. government (USFWS 1942), entered the Bristol Bay red king crab fishery in 1946. Although the Bering Sea produced most of the red king crab caught by American fishermen during the 1940s and early 1950s, the U.S. catch was small compared to that of Japan and Russia. By the mid 1950s, newly opened fishing grounds in the greater Gulf of Alaska (GOA) were out-producing the Bering Sea, and in 1966 the U.S. catch of 70,000 t (Orensanz et al. 1998) in the GOA dwarfed the U.S. Bering Sea catch of 450 t and was substantially larger than the Bering Sea catch of 19,000 t for Japan and the USSR combined (Otto 1981). However, in the early 1960s, it became clear that overfishing had begun to deplete Alaska's king crab resources. The Japanese reported in 1963 that their catch per unit of fishing effort in the Bering Sea had fallen by two-thirds since 1960. Also, the U.S. Alaska catch, 90% of which came from the GOA, peaked in 1966 and declined by 65-70% over the next three years (Blackford 1979).

By 1970, multiple conservation measures had been implemented, several of which were intended to reduce the direct effects of trawling on king crab. In 1959, Japan set aside a 67,000 km^2 area of Bristol Bay, where trawling by the Japanese fishing fleet was banned. In 1961, trawling as a crab fishing method was outlawed in all of Alaska's waters. In 1964, an international agreement was forged among the United States, Japan, and the USSR, whereby trawling was prohibited in a 20,000 km^2 tract of prime red king crab habitat in Bristol Bay waters, off the western end of the Alaska Peninsula. Also, during the 1960s, diplomatic pressure and evolving international conventions squeezed the Japanese and USSR king crab quotas until the harvest of Bering Sea king crab became essentially an American enterprise. As the GOA king crab stocks began to dwindle after 1966, U.S. fishermen turned to the Bering Sea, where the U.S. share of the king crab catch, less than 5% during 1958-1966, rose sharply to more than 50% by 1969 (Otto 1981). By 1970, the stage was set for an 11-year period (1970-1980) of escalating American exploitation unmatched in the history of Alaska fisheries—a period in which the Bering Sea king crab harvest increased exponentially, doubling every three years, until a cumulative, 11-year total of nearly 300,000 t and $3 billion worth of crab (in 2007 dollars) was extracted. Because managers have redefined the Bristol Bay red king crab population to be a population with no history prior to 1983, this highly exploitive 1970-1980 period, which provided considerable largesse to the state of Alaska and brought the Bristol Bay stock to the brink of commercial extinction, is presently excluded from the 1983-1997 baseline average used to evaluate whether the stock is overfished (Dew and McConnaughey 2005, p. 936).

The abrupt 1981 collapse of the Bristol Bay stock, the second largest king crab population in the world (Rodin 1990) and a stock that had been profitably exploited by three nations for half a century, was an unsettling event. However, the management community was confident that the size-sex-season management of Bering Sea king crab, whereby only large males (and no females) are harvested during a relatively short season, was sufficiently conservative that overfishing could not have been a significant factor in the collapse (Otto 1986, Wooster 1992). Therefore resource managers concluded that the 1977-1983 disappearance of more than 90% of the adult stock was a natural event unrelated to man's fishing and "largely beyond control" (Otto 1986, p. 105), despite record levels of fishing mortality (Dew and McConnaughey 2005). However, size-sex-season alone, without the support of reliable stock-size estimates (e.g., Dew 2008) and a well-developed understanding of the target species' behavior and ecology, cannot lead to fully informed management decisions.

There are several assumptions integral to the present management system that have persisted since the collapse and that create the potential for unexpected collapses in the future. Some of these assumptions are (1) within the geographic range of Bering Sea red king crab, no particular habitat is essential (NMFS 2005); (2) all male red king crab with a carapace length (CL) ≥120 mm are capable of mating with one or more females each year (Zheng et al. 1995); (3) the podding behavior of juvenile red king crab does not continue into adulthood (Powell and Nickerson 1965, Incze et al. 1986, Otto 1986, Armstrong et al. 1993, Witherell 1998, Ackley and Witherell 1999); and (4) the uncertainty associated with NMFS' red king crab population size estimates is sufficiently low (e.g., Otto 1986) that it can be ignored when setting harvest quotas. While all of these assumptions deserve attention, the primary purpose of this paper is to critically examine the assumption that, within the geographical range of Bristol Bay red king crab, no particular habitat is essential. This assumption is based on the rationale that changes in red king crab distribution and abundance are governed by unpredictable changes in water temperature and oceanographic regimes. Therefore the crab need all of the habitat available to them, and they are not dependent on any particular habitat within their general distribution (NMFS 2005).

Essential habitat

Since the inception of the Fishery Conservation and Management Act in 1976 (later amended, and known as the Magnuson-Stevens Act), habitat issues for species included within the fisheries of the United States have been of increasing concern. This concern culminated in 1996 with Congress enacting the Sustainable Fisheries Act (SFA), which expanded existing federal authority to identify and protect essential fish habitat (EFH). The SFA requires each regional fisheries management council, after receiving recommendations from the National Marine Fisheries Service (NMFS), to amend its fishery management plans (FMPs) to describe (in text) and identify (with maps) essential habitat for each species managed by the council. Perhaps understanding that animals are most abundant in their preferred habitat, NMFS (2005, Appendix E) recommended to the North Pacific Fishery Management Council (NPFMC) that relative abundance information, when available, should be used to designate EFH areas that are smaller than the general distribution for the species of interest. More narrow designations would help to prioritize management efforts and would be a more effective tool for habitat conservation. NMFS (2005, Appendix E) also reminded the NPFMC that defining EFH as a species' general distribution (the geographical range encompassing 95% of the population) is not consistent with the Magnuson-Stevens Act or the EFH regulations because the general distribution fails to distinguish EFH from total available habitat. Nevertheless, in the *Final Environmental Impact Statement for Essential Fish Habitat Identification and Conservation in Alaska*, hereafter referred to as the EFH EIS (NMFS 2005), EFH for red king crab and other FMP species in Alaska was defined as the general distribution. Among the reasons given for this approach to habitat evaluation was that the relative value of habitats inferred from a species' abundance within those habitats, as determined from stock-assessment surveys used to manage the species, is not based on the best available scientific information (DiCosimo 1999) because current survey information does not adequately address unpredictable annual differences in spatial distribution (NOAA 1999). According to the NPFMC, "The Council chose not to endorse Alternative 4 (Presumed Known Concentration), which NMFS had recommended (see Appendix E), because of concern that the narrower EFH designations resulting from Alternative 4 might not account for changes in habitat usage over time" (NMFS 2005, pp. 2-60).

Such concerns may be warranted for FMP species with relatively short, information-poor histories of assessment and exploitation. However, Alaska red king crab has one of the most information-rich assessment and exploitation histories of any species in the eastern Bering Sea (e.g., Zimmerman et al. 2009). Sometime in the late 1930s, Congress appropriated funds for a two-year (1940-41) survey of Alaska's fishery resources. The results of the eastern Bering Sea survey of 1941, which discovered very large concentrations of crab within 55 km from shore between Unimak Island and Port Moller, spurred the growth of the king crab industry in the early 1940s (Blackford 1979). Similarly, a second government survey in 1948 found its largest aggregations of crab located in nearshore waters between Amak Island and Port Moller. In 1949, relying on the federal government's exploratory work in 1941 and 1948, Deep Sea Trawlers, the first private-enterprise king crab venture in the United States and the precursor to Wakefield Seafoods, saved itself from probable bankruptcy by locating heavy concentrations of king crab off Amak Island, where government surveys predicted they would be. The company continued to trawl on the Amak crab for nine months, from April to December 1949, freeze-packing more red king crab weight (404,000 lbs, equivalent to about 800 t of whole crab) in 1949 than in 1947 and 1948 combined (Blackford 1979).

Thus, information from a decade of assessment surveys and commercial trawling operations in the southeastern Bering Sea during the 1940s suggests that, rather than being unpredictable, the preferred habitat of adult red king crab was well defined, extending from Unimak Island (Cape Serichef) to Port Moller, with its center near Amak Island. Further evidence for the persistence and stability of this habitat preference may be found in the fact that more than 20 years later this same area, north and west of Unimak Island and the western Alaska Peninsula to Nelson Lagoon near Point Moller, was set aside as a red king crab refuge where trawling and tangle-net fishing was prohibited and only pots could be used for crab fishing (Naab 1968a,b; 1971). Thus, America's first Bering Sea no-trawl zone, a 20,000 km^2 subset of the larger 67,000 km^2 Japanese no-trawl sanctuary, was established through negotiations with Japan and the Soviet Union to protect red king crab in habitat considered by the United States to be essential to the species in Alaska. To clarify, the American no-trawl zone, known as the Pot Sanctuary (Fig. 1, Table 1), is often confused in contemporary literature (e.g., Fredin 1987, Ackley and Witherell 1999, Dew and McConnaughey 2005) with the no-trawl sanctuary established by the Japanese to protect the red king crab broodstock (egg-bearing females) from Japan's trawl fleet. For lack of more accurate terminology, I will refer to the larger no-trawl zone as the "Japanese Broodstock Sanctuary" (Table 1).

History and purpose of no-trawl sanctuaries

It is important to understand that the primary objective of early no-trawl sanctuaries, namely the 1959 Japanese Broodstock Sanctuary and the 1964 Pot Sanctuary, was to protect Alaska's red king crab resource

Table 1. Additional information on the four red king crab no-trawl refuges of Fig. 1. The Japanese Broodstock Sanctuary and the Pot Sanctuary no longer exist, after being breached by trawling shortly after passage of the 1976 Fishery Conservation and Management Act. The southern 16-17% of the Red King Crab Savings Area is routinely subjected to trawling for flatfish in what is known as "bottom-of-the-box" trawling.

Refuge	Size (km^2)	Location	Protection	Years	Prohibited	Signatories
Japanese Broodstock Sanctuary	67,000	Coastal and offshore waters from 160°W to 165°W	Entire RKC broodstock	1959-1977	Japanese trawl fleet	Japan
Pot Sanctuary	20,000	Coastal waters from 162°W to 165°W	Highest-value RKC broodstock	1964-1977	All trawling, tangle nets	U.S., Japan, USSR
Red King Crab Savings Area	Nominal 14,000, actual 12,000	Offshore waters, 50-100 naut. mi. north of Amak I.	Adult (mostly male) RKC	1995 to present	Most trawling	U.S.
Bristol Bay Nearshore Trawl Closure	65,000	Bristol Bay east of 162°W	Juvenile RKC	1997 to present	All trawling	U.S.

from the effects of bottom trawling, considered to be so destructive of red king crab that, upon gaining statehood in 1959, Alaska quickly outlawed trawling as a king crab fishing method (Blackford 1979). However, according to contemporary accounts, the no-trawl sanctuaries of the late 1950s and early 1960s were established solely to resolve fishing gear conflicts (Fredin 1987, Ackley and Witherell 1999, NMFS 2005, Witherell and Woodby 2005). No mention is made in these accounts of the intended role of no-trawl sanctuaries in conserving Alaska's king crab resource (e.g., Naab 1968a). For example, Witherell and Woodby (2005, p. 3) state that the 1959 Japanese Broodstock Sanctuary was established "to limit interactions between its trawl fleet and its crab pot fleet." However, it is unlikely that the Japanese, considered to be the originators of the king crab industry in Alaska, and who had used tangle nets (Miller 1965), not pots, to pursue their Bristol Bay crab fish-

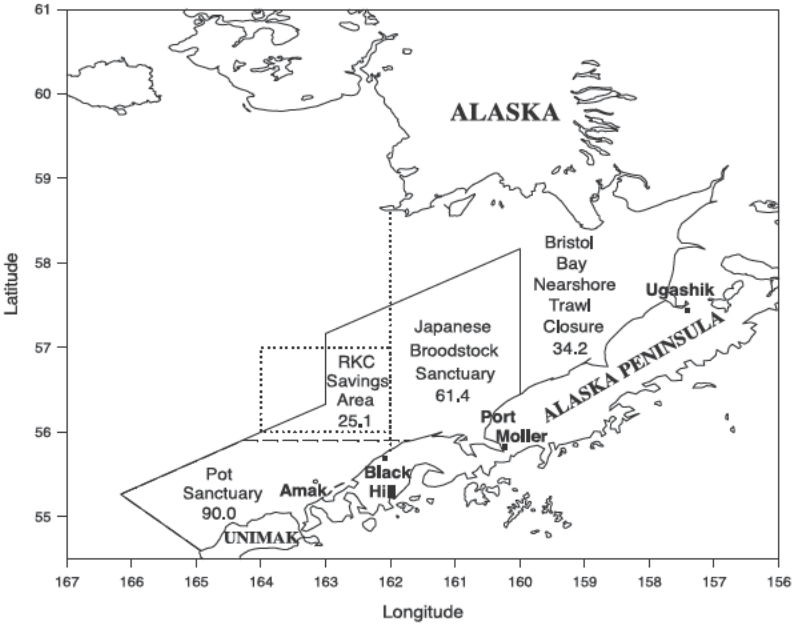

Figure 1. Refuges designed to protect the Bristol Bay red king crab population from the effects of trawling. Historic refuges (the 1959 Japanese Broodstock Sanctuary and the 1964 Pot Sanctuary) protected 89% of the baseline (1958) broodstock, while today's refuges (dotted lines) protect 48% (see Table 1 for additional information). The numbers in each refuge represent the baseline multiparous broodstock densities (number per hour of trawling in 1958).

ery since the 1920s (Blackford 1979), waited until 1959 to address gear conflicts. Moreover, the boundaries of the Japanese no-trawl sanctuary closely conformed to the Bristol Bay distribution of mature female king crab (Dew and McConnaughey 2005) but excluded the male molting grounds 150-200 km north of Unimak Island, which were the focal point of Japan's autumn tangle-net fishery (Takeshita et al. 1990). Because gear conflicts that might have existed among various Japanese fishing fleets would not have been resolved by the 1959 Japanese no-trawl zone (the autumn tangle-net fishery was outside the zone), it is more logical that the intent of the 67,000 km² sanctuary was to protect the broodstock from trawling. As precedent, the Japanese (Marukawa 1933) designed a similar reproductive refuge for Kamchatka red king crab, as pointed out by Dew and McConnaughey (2005).

The Pot Sanctuary

Unlike the Japanese Broodstock Sanctuary of 1959, intense international gear conflicts did play a prominent role in the formation of the 1964 Pot Sanctuary. After World War II, the Japanese resumed fishing in the Bering Sea in 1953, and USSR fleets re-entered the Bering Sea in 1959, touching off a fierce rivalry for Bristol Bay red king crab. The rapid escalation in competition resulted in increased fishing pressure, which alarmed Americans concerned about the future of Bering Sea red king crab (Blackford 1979). Gear conflicts arose because the Americans used mobile gear (bottom trawls) and the Japanese and Soviets used fixed gear (tangle nets) to fish for crab. American trawlers during the late 1940s discovered that king crab aggregations could be found at certain spots at particular times. After 1950, using new technology to take advantage of the crabs' predictable behavior, American trawlers devised "radar fishing" to help them stay on the foraging crab aggregations and, "with the assistance of naval polar plotting sheets, could systematically work over an area and clean out an entire school of crabs" (Blackford 1979, pp. 22-23). Problems arose as the Japanese (and the Soviets) adapted to the American strategy by surrounding the trawlers' radar-reflecting buoys with miles of tangle nets, thus obstructing further trawling. These conflicts occurred most frequently in waters within a 100 km radius of Amak Island, which in the early decades of America's king crab industry was the most productive king crab habitat in the Bering Sea.

By 1960, the king crab fishery off Unimak and the western end of the Alaska Peninsula was chaotic, with three nations (United States, Japan, and Soviet Union) fishing for the same resource at the same time, using three different types of fishing gear (pots, trawls, and tangle nets). The bottom trawl, which by 1953 was the main gear type used by Americans to take king crab (Miller 1965), was generally recognized as an inefficient, wasteful, and destructive way to fish. In 1961 the Alaska Department of Fish and Game banned trawling in all of the state's waters (within three miles of land) (Blackford 1979). Seven years previously, in 1954, the use of tangle nets in Alaska waters was also outlawed, although the federal government's 1941 survey demonstrated that tangle nets, because they were selective for the relatively mobile, hard-shell males sought by the fishery (USFWS 1942), caused substantially less collateral damage than trawls. Also, it was becoming evident that, for Americans (who disliked picking through tangle nets), pot fishing was the most efficient method of harvesting king crab in terms of productivity per man-hour worked (Miller 1965). Therefore, to impose some order on the fishery and to eliminate trawling on the richest king crab resource remaining in the Bering Sea and the Gulf of Alaska, the Pot Sanctuary at the western end of the Alaska Peninsula was established in 1964. Because of its importance as America's first trawl-free refuge established specifically for red king crab (e.g., Naab 1968a), and because of the confusion and inadvertent revisionism in the literature surrounding this conservation effort, the boundaries of the 1964 Pot Sanctuary are presented here (after Beale 1971): Cape Serichef (54.6°N, 164.93°W) northwest 108 km to 55.2667°N, 166.1667°W, then northeast 138 km to 55.9°N, 164.2833°W, then east 161 km to a point (55.9°N, 161.7°W) on the Alaska Peninsula between Black Hill and Nelson Lagoon (near Port Moller). That priorities have changed since the 1960s is evident from the fact that the former Pot Sanctuary, better known today as Cod Alley, is now the most heavily trawled area in the eastern Bering Sea (Dew and McConnaughey 2005); and the EFH EIS (NMFS 2005, p. L-17) tells readers that, as habitat for Alaska red king crab, the area north of Unimak ". . . was not particularly important prior to [the mid to late 1970s] and has not been important since."

Protection from trawling, then and now

"The diminution of future population increase produced by removing a single animal of a given age from a population may be termed the reproductive value of that individual." (Slobodkin 1961, p. 50). The reproductive value of an egg-bearing female is thus greater than that of a juvenile, whose probability of dying from natural mortality before contributing to the next generation is relatively high. Collectively, egg-bearing females form the broodstock, which is that part of the population with the greatest reproductive value, and it is the broodstock that should receive the highest priority in management plans to protect the reproductive potential of the stock from the effects of trawling. The Bristol Bay red king crab broodstock is most vulnerable to trawling after females have returned from spawning in relatively trawl-free nearshore waters to incubate their eggs in deeper waters during the next 11 months. But because the standard NMFS Bristol Bay survey is conducted during late May–early June while red king crab are spawning inshore, much of the broodstock is unavailable to the survey, and the distribution of post-spawning females remains largely unknown at the completion of the standard survey (Dew 2008). Of all the red king crab surveys since 1941 (when 64% of the crab were caught on spawning grounds well inshore of the NMFS survey boundary), only the two-stage survey of 1958 provided information sufficient to define the broodstock distribution in its relatively vulnerable egg-incubation phase (Dew 2008).

Using 1958 as the baseline with which to define a Bristol Bay broodstock configuration capable of sustaining an intact population suggests that today's refuge arrangement is inadequate to support a broodstock with a reproductive capacity sufficient to rebuild the stock. The historic no-trawl refuge consisted of the Japanese Broodstock Sanctuary and included the 20,000 km^2 Pot Sanctuary (Fig. 1, Table 1). This 67,000

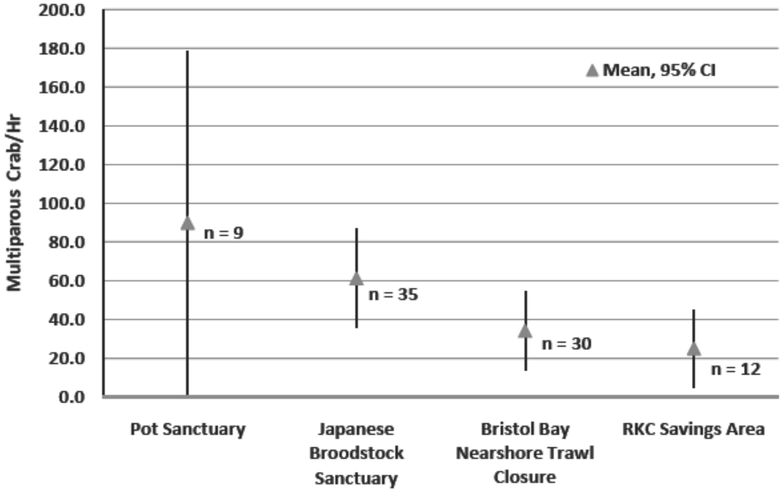

Figure 2. The June-July 1958 abundance trend of the Bristol Bay red king crab multiparous broodstock (females ≥100 mm CL), used here to rank the relative effectiveness of four no-trawl refuges (NMFS unpubl. data). Broodstock abundance was highest in the Pot Sanctuary (now Cod Alley) and lowest in today's refuges. n = number of tows.

km^2 area, implemented in 1959, provided a no-trawl refuge for some 89% of the baseline broodstock. By comparison, today's Bristol Bay Nearshore Trawl Closure (65,000 km^2) and the Red King Crab Savings Area (12,000 km^2), which together are 15% larger than the old Japanese no-trawl area, include less than half (48%) of the baseline broodstock. Ranked by the density (number per hour) of multiparous crab (Fig. 2), the Pot Sanctuary and the Japanese Broodstock Sanctuary were more effective at protecting the broodstock (and their preferred habitat) from trawling than today's refuges. The Pot Sanctuary protected not only the highest broodstock densities, but the multiparous females there were the largest females in Bristol Bay (Fig. 3). The relatively few multiparous females protected by today's Bristol Bay closure east of 162°W longitude were the smallest. The distribution of the 1958 broodstock resulted in a northeast to southwest gradient of increasing reproductive value from the relatively barren grounds east of Port Moller to the essential habitat of the western end of the Alaska Peninsula and Unimak Island—habitat that used to be protected from trawling by the Pot Sanctuary. This 1958 gradient, hypothesized to be the consequence of an endless-belt reproductive strategy, persisted some 20 years later as a distinctive

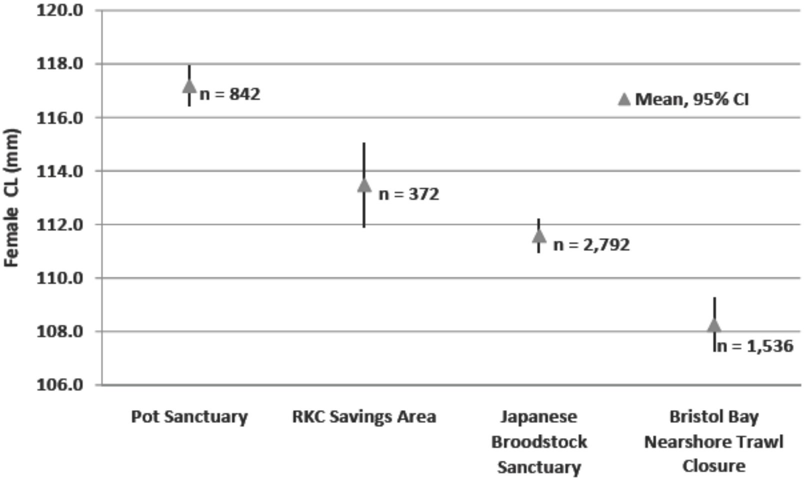

Figure 3. Size distribution among four no-trawl refuges of all measured female red king crabs collected from the baseline broodstock during late-phase sampling in June-July 1958 (NMFS unpubl. data). The largest females, i.e., those with the greatest reproductive value, were found in the Pot Sanctuary. The smallest females were found in today's Bristol Bay Nearshore Trawl Closure, east of 162°W latitude. n = number of crab.

feature of the 1975-1978 broodstock distribution, as pointed out by Dew and McConnaughey (2005).

The evidence suggests that the decision to abandon the relatively valuable Pot Sanctuary in favor of the Bristol Bay Nearshore Trawl Closure, an area largely uninhabited by the broodstock and only lightly plied by commercial trawlers, was based on considerations other than the preservation of the stock's reproductive potential. The stated purpose of the Bristol Bay closure was to protect juvenile red king crab and their habitat (Witherell and Woodby 2005), but this is a purpose inconsistent with the arithmetic of reproductive value (e.g., Fisher 1958, Slobodkin 1970, Wilson and Bossert 1971, Dew 1980). Moreover, survey data indicate that approximately half of the Bristol Bay closure comprises habitat of marginal value to, and only thinly populated by, juvenile and subadult king crab (Fig. 4). The relative sterility of a large proportion of the Bristol Bay closure was known as early as 1941 when a government survey reported that trawl catches along the Alaska Peninsula diminished moving from Port Moller eastward "until a drag off Ugashik (Fig. 4) resulted in a skunk haul" (USFWS 1942, p. 74).

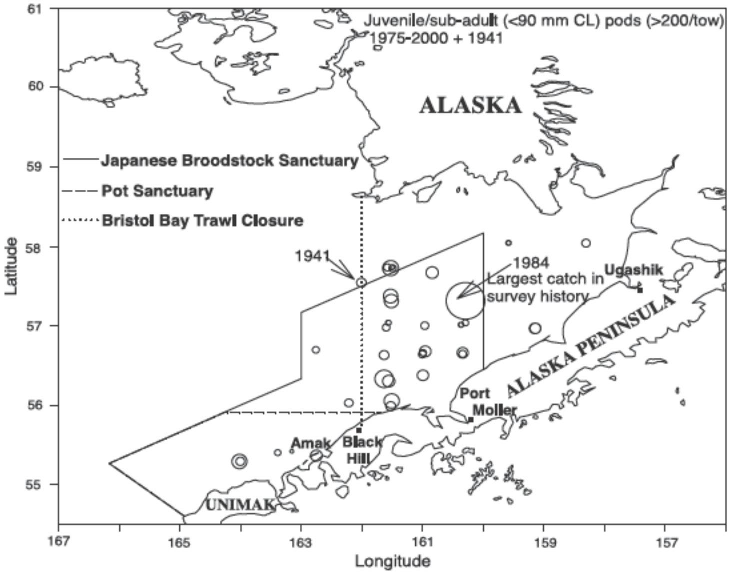

Figure 4. Location of juvenile pods of red king crab, 1975-2000, plus a single pod found in the 1941 survey (circle diameter indicates relative size of the aggregation). The Bristol Bay Nearshore Trawl Closure, designed specifically to protect juveniles and their habitat, included 87% of the podded juveniles; the Japanese Broodstock Sanctuary included 95%. Prime juvenile habitat does not extend east of 160°W.

Essential Fish Habitat Environmental Impact Statement misinformation

Once promulgated, an EIS is a legal document under NEPA (National Environmental Policy Act) and is used as a decision-making tool. Therefore, it is important to point out substantive error in the EFH EIS. There are several instances where the EFH EIS presents an inaccurate picture of the relative value of the historic no-trawl refuges and their respective roles in rebuilding a decimated red king crab stock. For example, the impression created by the following EFH EIS statement is incorrect and should be revised: "The area north of Unimak Island was very important habitat for red king crab females during the mid to late 1970s but was not particularly important prior to that time and has not been important since." (NMFS 2005, p. L-17). This statement is inconsistent with existing knowledge, including the 1958 multiparous-female distribution, when 34% of the entire Bristol Bay broodstock (and perhaps half of the stock's reproductive value) was located in the waters off Unimak Island. Also, it is unlikely that negotiating governments, scientists, and fishermen would have located the Pot Sanctuary, a trawl-free refuge established specifically for red king crab, in waters that were not particularly important to the species. Once it is understood that a habitat was important to red king crab some fifty years ago in 1958, as well as during the mid to late 1970s (Dew and McConnaughey 2005), there is no reason to suspect that the habitat is not equally important to the stock's reproductive potential today, regardless of man's choice to transform the area from a sanctuary for Alaska's most productive broodstock to a trawling ground largely uninhabitable by king crab. Based on today's trawl-closure boundaries, habitat essential to more than half of the ancestral (1958) broodstock remains unprotected from trawling, which may explain why today's stock cannot rebuild to even half of its former abundance. However, according to a December 7, 2004, letter to the Alaska Marine Conservation Council, it is the opinion of NMFS scientists that ". . . evidence linking trawl closure areas to king crab recovery is scant." (NMFS 2004). Building on this opinion the EFH EIS (NMFS 2005, p. L-19) states: "The abundance of red king crabs in the late 1970s was anomalously high and should not be viewed as a realistic goal for restoring the population." However, it is illogical to imply that trawl closures are ineffectual and then to say that red king crab were anomalously successful at a time when 89% of the broodstock (versus today's 48%) was being protected by a well-designed 67,000 km^2 trawl closure. While evidence linking trawl closures to king crab recovery may be scant (due in part to poorly designed closure areas), there is ample, quantitative evidence linking trawling to severe population declines of 88-99% after the Japanese Broodstock Sanctuary and the Pot Sanctuary were opened to commercial trawling (Dew and McConnaughey 2005). It may be logically indefensible to maintain that the impact of trawling in red king crab habitat is negligible (NMFS 2005, p. B-34), and simultaneously to aver that today's relatively unprotected Bristol Bay red king crab cannot be restored to earlier, "anomalously high" levels of abundance that occurred during a regime of effective protection from trawling.

Two management philosophies

Nearly a half-century ago, managers and scientists concerned for the future of Alaska's premier seafood resource believed that the spatial distribution of Bering Sea red king crab, as mediated through the species' habitat preferences, was predictable to the extent that more than 20,000 km^2 of habitat essential to king crab could be set aside as a trawl-free refuge (the Pot Sanctuary) to protect the king crab resource. In contrast, much of today's scientific and management community apparently believes that red king crab are so unpredictable in their movements that it is impractical and perhaps incautious to designate essential habitat with any precision greater than that required to draw a line around a 150,000 km^2 area encompassing the species' approximate geographical range within the Bering Sea (NOAA 1999, NMFS 2005).

The watershed event separating these two management philosophies was the 1981 collapse of the Bristol Bay red king crab stock, an event so sudden, unexpected, and catastrophic that managers were left without a plausible explanation until the regime-shift theory expanded to fill the void. Basically, the regime-shift theory advances the premise that, contemporary with record levels of fishing mortality (Dew and McConnaughey 2005), warmer water temperatures after 1976-77 acted, directly or indirectly, to increase the natural mortality of adult crab, thereby effecting a precipitous (1980-83) decline of more than 90% in the standing stock of Bristol Bay red king crab. Since the king crab collapse, reliance on the idea that temperature is the dominant ecological factor governing the distribution and abundance of crabs has become almost total (e.g., Loher and Armstrong 2005, Yeung and McConnaughey 2006). For example, in the EFH EIS, NMFS dismissed concerns that that the report did not adequately consider the effect of trawling on the distribution and abundance of crab, stating that ". . . changes in crab distribution and abundance appear to be attributable to changes in water temperature." (NMFS 2005, p. L-17). However, the relationship among abundance, distribution, and temperature is not well understood, and there is little agreement as to the directionality of the hypothesized relationship. Regime-shift proponents claim that the crab died off because of water temperatures slightly (2-3°C) warmer (e.g., Yeung and McConnaughey 2006) than the long-term mean; others (e.g., Loher and Armstrong 2005) claim that Bristol Bay red king crab avoid temperatures slightly (2-3°C) colder than the long-term mean. Taken together, these hypotheses require a degree of stenothermy uncharacteristic of a boreal species with an exceptionally wide temperature tolerance (Matishov et al. 2008). The species molts and grows during a six-month, winter-spring period, reproduces from January through June, forages and incubates its eggs during all months of the year, and conducts these major life functions in waters ranging from very shallow to greater than 100 m, a depth range within which temperature at any given time varies by several degrees. Also, as noted by Loher and Armstrong (2005), avoidance of low temperatures by red king crab does not explain the sudden loss of tens of millions of adult crab from the warmer southwestern sector of their Bristol Bay habitat near Unimak and Amak islands. Nor is there credible evidence for an unusual spike in fish predation or disease, mechanisms through which the regime shift, with its associated but transitory increase in temperature, is proposed to have acted to increase the natural mortality of adult king crab to catastrophic levels (Dew and McConnaughey 2005). Ultimately there is no hypothesis that can account for the spatially explicit disappearance of very large numbers of adult crab without including the lethal effects of bottom trawling within habitat essential to red king crab.

If it were true that water temperature was the dominant factor in determining where red king crab were found in the southeastern Bering Sea, then it would be difficult to designate any specific geographic location as essential habitat, given that bottom temperatures at the same location can vary substantially, even between consecutive years. For example, in Bristol Bay water 50-60 m deep off Black Hill, bottom temperature was 2.5 to 3.0°C in May 1958 and −0.5 to 0.0°C in May 1959 (McLaughlin 1963). At the same location 40 years later, the bottom temperature was 5-6°C in June 1998 and 1-2°C in June 1999 (Loher and Armstrong 2005). The idea of crab being driven from one location to another by "thermal forcing" (e.g., Loher and Armstrong 2005) is inconsistent with information from years of fishing and research surveys indicating that, regardless of interannual temperature variations, red king crab over the past half century have tended to use the same spawning, incubation, molting, foraging, and overwintering grounds from one year to the next, unless physically prevented from doing so.

Habitat selection evolves because organisms in some habitats leave more descendants than organisms in other habitats (Krebs 1978). But some historical perspective is needed to identify habitat essential to an intact population of crab but no longer habitable because of human activities. This can be accomplished by using data and information from surveys conducted at a time when a relatively unexploited Bering Sea red king crab population was spatially distributed within its environment in a way that maximized its reproductive potential. The EFH EIS uses data from 1987-2002 to evaluate habitat essential to Bristol Bay red king crab (NMFS 2005). However, using information from pre-1981 (precollapse) surveys might improve upon the exercise of evaluating habitat importance based on the spatial distribution of a remnant population in the aftermath of a collapse that all but eliminated the species from areas where it was previously abundant. There is a "ratchet effect" associated with a decision-making process that tends to cede historically important crab habitat to the trawling industry. For example, commenting on the importance to red king crab of Bristol Bay habitat south of 56°N—habitat which trawlers value as rock sole trawling grounds—NMFS reported that "no female crab have been taken in this area during the 1990-1994 trawl surveys" (NOAA 1995, p. 4867). Omitted from consideration is the fact that this same area was once (1964-1977) the Pot Sanctuary, recognized by scientists and fishermen of three nations as essential red king crab habitat that was to be protected from trawling. Now that the former Pot Sanctuary is the most heavily trawled bottom community in the eastern Bering Sea, it is not surprising that the area is no longer habitable by broodstock aggregations.

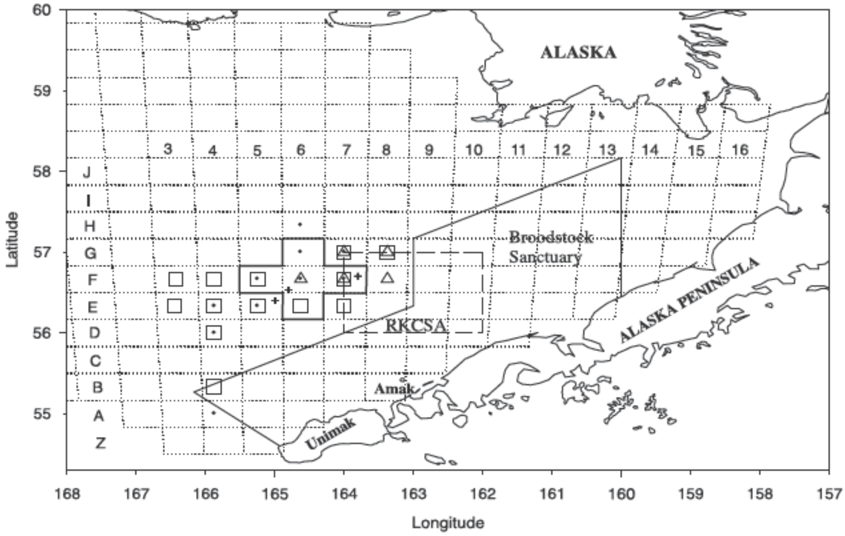

Figure 5. **Location of male-only habitat in relation to the Japanese Broodstock Sanctuary and today's Red King Crab Savings Area (RKCSA). To qualify, a station must have produced ≥100 red king crab during the time period under consideration, ≥94% of which must be males. Time periods: 1958-1961 (□); 1975-1980 (•); 1984-1999 (Δ). The (+) symbols represent the northeast-shifting, crab-weighted center of distribution for each time period. Numbers of survey-caught male and female red king crab at five contiguous stations (outlined in bold) during 1975-2000 are in Table 2. Note that the Japanese Broodstock Sanctuary was designed to exclude the male-dominated habitat, which was the focal point of Japan's autumn tangle-net fishery (Takeshita et al. 1990).**

Site fidelity

Site fidelity is an aspect of red king crab behavior that can be used to define essential habitat. When relatively dense concentrations of animals recur at a location year after year, irrespective of annual variations in water temperature, it is likely that some attribute of that particular habitat is essential. Because patterns of site fidelity can be disrupted or obliterated by fishing, it is important to search for such patterns using historical, pre-impact distribution and abundance data. A pattern of site fidelity notable for its stability over several decades is the recurrence of all-male molting aggregations west of the Japanese Broodstock Sanctuary (west of 163°W) and some 150-250 km north of Unimak Island. Using the criterion that 94 of 100 crab caught at a

Table 2. The cumulative sum of adult male (♂) and female (♀) red king crab and the proportion of males (p♂) collected during 1975-2000 within the male molting grounds west of 163°W. The 5,749 males collected at these five stations represent 21% of all mature males collected at the >100 Bristol Bay sampling stations during 1975-2000. This 26-year history indicates an overwhelming male dominance within this 6,860 km² area centered on station F6 (see Fig. 5).

	G6 ♂ = 237 ♀ = 1 p♂ = 1.00	
F5 ♂ = 501 ♀ = 4 p♂ = 0.99	F6 ♂ = 2,484 ♀ = 1 p♂ = 1.00	F7 ♂ = 1,402 ♀ = 26 p♂ = 0.98
	E6 ♂ = 1,125 ♀ = 142 p♂ = 0.89	

station must be male, survey data from 1958-1961 indicate that male habitat comprised 13 survey stations, generally within an 18,000 km² rectangle between 56-57°N and 163.5-166.5°W (Fig. 5). During 1975-1980 male habitat consisted of ten stations in a 14,000 km² rectangle between 56-57.3°N and 164-166°W. During the post-collapse years of 1984-1999, the habitat comprised five stations within a 7,000 km² area between 56.5-57°N and 163-165°W. During the period from 1958 to 2000 the male-only habitat area decreased by more than 60% and the center of distribution (+ symbols, Fig. 5) moved some 80 km to the northeast, away from regions of relatively heavy trawling to the south and west (Dew and McConnaughey 2005).

Despite a substantial reduction in its areal extent and a systematic shift in its geographical center, each of which may be an effect of fishing, the spatial and temporal persistence of this site fidelity over a 40 to 50 year period is an important indicator of essential habitat. Also noteworthy is the very narrow and consistent demographic character of the phenomenon. Virtually all (>99%) of the 12,447 red king crab collected at the stations indicated in Fig. 5 were adult (≥120 mm CL), recently molted, new-shell males (102 were females). Notwithstanding assertions that the relative importance of habitats cannot be evaluated using stock-assessment surveys (e.g., DiCosimo 1999, NOAA 1999), a 26-year (1975-2000) history of survey catches at five contiguous Bristol Bay stations demonstrates the stability and predictability of male dominance within this approximately 7,000 km² area of red king crab habitat (Table 2, Fig. 5).

Because the annual surveys that encountered the all-male aggregations were conducted during the April to July spawning of multiparous females, and because the habitat where the all-male aggregations were located is more than 100 km from nearshore spawning grounds, it is likely that the crab in these aggregations did not participate in multiparous mating in the year they were captured, as noted by Dew (2008). This interpretation of the data is consistent with the results of previous investigators (Korolev 1964; Chebanov 1965; Rodin 1970, 1990; Takeshita et al. 1990). Moreover, in 1958 the U.S. Bureau of Commercial Fisheries reported that the distribution of large new-shell males was different from that of old-shell males. The distribution of old-shell males was similar to that of mature females, particularly during the spring mating period, leading investigators to conclude that only old-shell males were capable of mating (USBCF 1959). Today's managers do not acknowledge this aspect of red king crab ecology and believe that all males ≥120 mm CL, regardless of their molt status, mate with one or more females every year (Zheng et al. 1995).

Crab as habitat

Because ecology is the study of interactions that determine the distribution and abundance of organisms (Krebs 1978), EFH concepts should be anchored firmly in ecological principles. Instead, the EFH EIS (NMFS 2005, p. L-17) maintains that ". . . mortality from bycatch is unrelated to habitat concerns" and that "Habitat effects on crab concern effects on prey and on living and non-living structures on and in the ocean bottom. Effects on the population due to bycatch in trawl fisheries are not included as a habitat effect." (NMFS 2005, p. B-31). However, by severing the link between crab and their habitat, this EFH approach sets itself apart from the discipline of ecology, of which a central tenet is that a habitat is altered by the presence (or absence) of its inhabitants. That is, a habitat whose components include a population of red king crab will not be the same if the crab are significantly reduced or eliminated from the habitat. Attempts to evaluate the habitat effects of trawling while excluding from consideration the effects of trawling on a major component of the habitat (the crab themselves) is, from the perspective of an ecologist, intellectually untenable.

Consider that each successfully molted crab leaves behind a cast shell. These shells are composed of chitin, a polysaccharide polymer embedded in a hardened proteinaceous matrix that may itself comprise more than a hundred different proteins such as resilin, a glycine- and proline-rich protein that confers high elasticity to the cuticle of hinge regions (Anderson and Weis-Fogh 1964, Hojrup et al. 1986, Merzendorfer and Zimoch 2003). My own in situ observations indicate that molting in subadult and adult red king crab is a nocturnal mass phenomenon, where large aggregations of crab molt synchronously in a single night.

Figure 6. Cast shells of red king crab resulting from a single night's mass molt. There are no live crab in the photo. Environmental conditioning occurs as the molted casts decay and become part of the sediment. (Photo by B. Dew at Kodiak, Alaska).

The location of a mass molt is marked by a layer of cast shells lying on the bottom (Fig. 6), ready to be broken down into their biochemical constituents by bacteria, largely of the genus *Vibrio* (Bassler et al. 1991, Yu et al. 1991). The annual decomposition of hundreds of tons of chitin and protein on molting grounds is likely to alter the composition of local sediments in a way that serves as a biochemical marker for crab returning to the habitat. In this way, habitats that optimize molting success, and any life functions associated with it, would be the most heavily marked, thus perpetuating site fidelity such as that observed on male molting grounds north of Unimak Island. Optimum spawning grounds would be similarly marked, given that mating female red king crab are obligate molters. Therefore, by virtue of the molting process, crab are an inextricable part of the habitat in which they are most successful; and the loss of crab as trawl bycatch is a habitat issue, not simply a bycatch issue as asserted in the EFH EIS (NMFS 2005).

Depensation

Like red king crab, some organisms, when present in sufficient numbers, are able to modify their environment in ways that increase survival or reproductive success (Liermann and Hilborn 2001). For example, much has been written about how the carcasses of spawned-out salmon provide marine-derived nutrients to spawning streams, thus increasing juvenile survival (e.g., Larkin and Slaney 1997, Cederholm et al. 1999) and perhaps aiding in homing and natal stream recognition. Less familiar is the concept that environmental conditioning is evidence of depensation in a population (Liermann and Hilborn 2001) because whatever advantages the mechanism confers to the population become less effective at low abundance levels. In a population where depensation is operative, reproductive success (recruits per unit of spawner biomass) is lowest when the abundance of the spawning stock is lowest. By contrast, in a population regulated largely by compensatory mechanisms, reproductive success is highest when spawning-stock abundance is lowest. Compensation is at the core of the models used to manage Bering Sea crab stocks and is the basis for the assumption that calling a halt to fishing will permit an overfished stock to recover from extremely low abundance levels. Depensatory models require a minimum viable stock size if the population is to grow or even to survive at all. Management models such as the Ricker and Beverton-Holt models, which exclude the possibility of depensation in populations where it may exist (Liermann and Hilborn 2001), are likely to fail when the population falls below its critical level.

Relatively strong depensation should be expected in populations of highly social species that assemble and conduct their life functions in large, dense aggregations (Wilson 1975, p. 83) and act together to condition their environment, as do red king crab. Also, depensation should be suspected when overexploited populations fail to recover after fishing mortality is reduced or eliminated. In 1966, the Gulf of Alaska (GOA) provided the bulk of the U.S. red king crab catch (70,000 t vs. 450 t from the Bering Sea). However, after a period of overfishing during which the estimated GOA harvest rate rose to about 70% of the legal male stock (Orensanz et al. 1998), the fishery collapsed and was closed in 1983. Although there has been no GOA commercial fishery since 1982, there is no sign of a GOA stock recovery, even after 27 years. A similar situation exists for the Bristol Bay population, stuck at less than 20% of its 1975-1980 abundance for the past 28 years since its abrupt 1981 collapse. For populations with strong depensation, the success of rebuilding plans that rely on reducing or eliminating fishing mortality to increase stock size may be increasingly thwarted as the population's minimum stock-size threshold is approached and may be completely nullified when the stock is driven below this threshold. Jennings et al. (2001, p. 84) provide the following warning: "If depensation exists, fishery managers should be extremely nervous because fished stocks may not recover after being fished to very low abundance, even when fishing is stopped."

Summary

The sudden, unexpected collapse of Alaska's Bristol Bay red king crab population in the early 1980s, after years of record harvests, came as a shock to those responsible for the well-being of the resource. Managers quickly decided that the collapse was due to natural causes related to climate change (regime shift) and unrelated to fishing (Otto 1986). However, as pointed out by Dew and McConnaughey (2005), it is difficult to make the case for natural causes without first accounting for the effects of fishing. But such accounting cannot be accomplished if underlying assumptions are invalid. For example, it is not likely that managers, modelers, and scientists would be able to differentiate between the effects of fishing and climate change without understanding that, based on available evidence, male red king crab do not molt and mate in the same year. Also, it may be difficult to invoke climate change as a primary cause of the decline and long refractory phase of a stock that has lost more than half of its reproductive potential over the past 30 years through the loss of essential habitat deemed by managers to be of no particular importance to the stock (NMFS 2005).

The EFH EIS (NMFS 2005) rationale that red king crab are unpredictably shunted about by regime shifts and temperature changes understates the role of fishing, especially bottom trawling, in shaping the spatial distributions observed today. It is possible that a species' contemporary distribution may reflect only those individuals that remain after fishing has rendered the prime grounds uninhabitable. The contemporary distribution may in fact consist only of marginal habitat rather than the habitat that was important to the ancestral stock. The EFH EIS uses no data earlier than 1987 to make its conclusions on habitat essential to red king crab. But by 1987, prime king crab habitat off the western end of the Alaska Peninsula had already been ceded to the bottom-fish industry and had become the most heavily trawled area in the eastern Bering Sea. Formerly this area was a red king crab no-trawl refuge known as the Pot Sanctuary, recognized by the scientists of three nations as habitat essential to the crab. But now the area is depauperate of crab and known as Cod Alley, and the EFH EIS declares that the area was not and is not important to red king crab.

According to those like Lowell Wakefield who risked their fortunes and lives in the pursuit of red king crab, the species' habitat preference and predictability were remarkable and obvious, as were the effects of trawling on red king crab aggregations (Blackford 1979). The crab could frequently be found at certain spots at particular times. Taking advantage of the podding and homing behavior of the crab, Wakefield's trawling crew devised "radar fishing" to help them stay on the foraging crab aggregations so they could work over an area and clean out an entire school. Some early observations from Wakefield's trawling operations, as inferred from Blackford (1979), should be of interest to today's managers: (a) the preferred habitat of red king crab was centered around Amak Island in the late 1940s and 1950s, and was predictable in time and space; (b) the behavior of red king crab, including podding and site fidelity, increases the species' vulnerability to trawling; (c) red king crab aggregations and local subpopulations can be wiped out by trawling; (d) after a red king crab fishery begins, the crab are first eliminated from habitats where they're most abundant; and (e) the longer the commercial-fishing history, the less useful is today's distribution in defining habitat essential to the crab. To a remarkable extent, the information and conclusions in the EFH EIS (NMFS 2005), a document that presumably reflects the best thinking of those responsible for the well-being of Alaska's red king crab stocks, are inconsistent with first-hand experiences and field observations recorded over the past 70 years.

References

Ackley, D., and D. Witherell. 1999. Development of a marine habitat protection area in Bristol Bay, Alaska. In: Ecosystem approaches for fisheries management. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 511-526.

Anderson, S.O., and T. Weis-Fogh. 1964. Resilin: A rubberlike protein in arthropod cuticle. Adv. Insect Physiol. 2:1-66. doi:10.1016/S0065-2806(08)60071-5

Armstrong, D.A., T.C. Wainright, G.C. Jensen, P.A. Dinnel, and H.B. Anderson. 1993. Taking refuge from bycatch issues: Red king crab (*Paralithodes camtschaticus*) and trawl fisheries in the eastern Bering Sea. Can. J. Fish. Aquat. Sci. 50:1993-2000. doi:10.1139/f93-223

Bassler, B.L., C. Yu, Y.C. Lee, and S. Roseman. 1991. Chitin utilization by marine bacteria: Degradation and utilization of chitin oligosaccharides by *Vibrio furnissi*. J. Biol. Chem. 266(36):24276-24286. PMid:1761533

Beale, S.T.W. 1971. The king crab industry of Alaska, 1953-1969: An economic analysis. M.A. thesis, University of Washington. 57 pp.

Blackford, M.G. 1979. Pioneering a modern small business: Wakefield Seafoods and the Alaskan frontier. Industrial development and the social fabric, Vol. 6. JAI Press. 210 pp.

Cederholm, C.J., M.D. Kunze, T. Murota, and A. Sibatani. 1999. Pacific salmon carcasses: Essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. Fisheries 24:6-15. doi:10.1577/1548-8446(1999)024<0006:PSC>2.0.CO;2

Chebanov, S.M. 1965. Biology of the king crab, *Paralithodes camtschatica* (Tilesius), in Bristol Bay. Soviet fisheries investigations in the Northeast Pacific, Part 4. TINRO 53:82-84.

Dew, C.B. 1980. Impact perspective based on reproductive value. In: L.D. Jensen (ed.), Proceedings of the Fifth National Workshop on Entrainment and Impingement. Ecological Analysts and Electric Power Research Institute, pp. 251-255.

Dew, C.B. 2008. Red king crab mating success, sex ratio, spatial distribution, and abundance estimates as artifacts of survey timing in Bristol Bay, Alaska. N. Am. J. Fish. Manage. 25:1618-1637. doi:10.1577/M07-038.1

Dew, C.B., and R.A. McConnaughey. 2005. Did trawling on the brood stock contribute to the collapse of Alaska's king crab? Ecol. Appl. 15:919-941. doi:10.1890/03-5231

DiCosimo, J. 1999. Essential fish habitat and closed areas in federal waters of the North Pacific. North Pacific Fishery Management Council, Anchorage, Alaska. Accessed August 2010: http://www.fakr.noaa.gov/npfmc/sci_papers/sci_papers.htm.

Fisher, R.A. 1958. The genetical theory of natural selection, 2nd edn. Dover Press, New York. 291 pp.

Fredin, R.A. 1987. History of regulation of Alaskan groundfish fisheries. Northwest and Alaska Fisheries Center Processed Report 87-07. 63 pp. NOAA, NMFS, AFSC, 7600 Sand Point Way NE, Seattle, WA 98115.

Hojrup, P., S.O. Anderson, and P. Roepstorff. 1986. Isolation, characterization, and N-terminal sequence studies of cuticular proteins from the migratory locust, *Locusta migratoria*. Eur. J. Biochem. 154:153-159. doi:10.1111/j.1432-1033.1986.tb09371.x

Incze, L.S., R.S. Otto, and M.K. McDowell. 1986. Recruitment variability of juvenile red king crab, *Paralithodes camtschatica*, in the southeastern Bering Sea. In: G.S. Jamieson and N. Bourne (eds.), North Pacific workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92:370-378.

Jennings, S., M.J. Kaiser, and J.D. Reynolds. 2001. Marine fisheries ecology. John Wiley and Sons, New York. 417 pp.

Korolev, N.G. 1964. The biology and commercial exploitation of the king crab, *Paralithodes camtschatica* (Tilesius), in the southeastern Bering Sea. In: Soviet fisheries investigations in the Northeast Pacific, Part 2. TINRO 49:102-108.

Krebs, C.J. 1978. Ecology: The experimental analysis of distribution and abundance, 2nd edn. Harper and Row, New York. 678 pp.

Larkin, G.A., and P.A. Slaney. 1997. Implications of trends in marine-derived nutrient influx to south coastal British Columbia salmonid production. Fisheries 22:16-24. doi:10.1577/1548-8446(1997)022<0016:IOTIMN>2.0.CO;2

Liermann, M., and R. Hilborn. 2001. Depensation: Evidence, models and implications. Fish Fish. 2:33-58. doi:10.1046/j.1467-2979.2001.00029.x

Loher, T., and D.A. Armstrong. 2005. Historical changes in the abundance and distribution of ovigerous red king crabs (*Paralithodes camtschaticus*) in Bristol Bay (Alaska), and potential relationship with bottom temperature. Fish. Oceanogr. 14:292-306. doi:10.1111/j.1365-2419.2005.00337.x

Marukawa, H. 1933. Biological and fishery research on Japanese king crab, *Paralithodes camtschatica* (Tilesius). Journal of the Imperial Experimental Station, Tokyo 4(37):24-31.

Matishov, G.G., V.S. Zenzerov, A.V. Emilina, and V.M. Muraveiko. 2008. Temperature resistance of the red king crab *Paralithodes camtschaticus* from the Barents Sea. Doklady Biological Sciences 420:198-200. doi:10.1134/S0012496608030162

McLaughlin, P. 1963. Survey of the benthic invertebrate fauna of the eastern Bering Sea. U.S. Fish and Wildlife Service Special Scientific Report No. 401. 75 pp.

Merzendorfer, H., and L. Zimoch. 2003. Chitin metabolism in insects: Structure, function, and regulation of chitin syntheses and chitinases. J. Exp. Biol. 206:4393-4412. doi:10.1242/jeb.00709

Miller, M.G. 1965. The development of the king crab industry in Alaska up to 1964. M.S. thesis, University of Alaska. 138 pp.

Naab, R.C. 1968a. The role of international agreements in Alaskan fisheries. Comm. Fish. Rev. 30:46-56.

Naab, R.C. 1968b. Revisions of international agreements affecting Alaskan fisheries. Comm. Fish. Rev. 31(6):30-34.

Naab, R.C. 1971. The growing role of international agreements in Alaskan fisheries. Comm. Fish. Rev. 33(9):27-40.

NMFS. 2004. Letter from NMFS (J.W. Balsiger) to Alaska Marine Conservation Council (B. Enticknap), December 6, 2004. NOAA National Marine Fisheries Service. Accessed August 2010: www.fakr.noaa.gov/habitat/letters/2004/dec/akmarineconservationresponse12-7-04.pdf.

NMFS. 2005. Final environmental impact statement for essential fish habitat identification and conservation in Alaska. NOAA, National Marine Fisheries Service, Alaska Region, Juneau. Accessed August 2010: http://www.fakr.noaa.gov/habitat/seis/efheis.htm.

NOAA (National Oceanic and Atmospheric Administration). 1995. Groundfish of the Bering Sea and Aleutian Islands area, North Pacific fisheries research plan. Trawl closure to protect red king crab. 50 CFR Parts 675 and 677. In: Federal Register. 60(16):4866-4870. Washington, D.C. Accessed August 2010: http://www.federalregister.gov/articles/1995/01/25/95-1777/groundfish-of-the-bering-sea-and-aleutian-islands-area-north-pacific-fisheries-research-plan-trawl.

NOAA. 1999. Fisheries of the exclusive economic zone off Alaska: Amendments for addressing essential fish habitat (EFH) requirements. 50 CFR Part 679. In: Federal Register 64 (26 April):20216-20220. Washington, D.C. Accessed August 2010: http://www.federalregister.gov/articles/1999/04/26/99-10408/fisheries-of-the-exclusive-economic-zone-off-alaska-amendments-for-addressing-essential-fish-habitat.

Orensanz, J.M., J. Armstrong, D. Armstrong, and R. Hilborn. 1998. Crustacean resources are vulnerable to serial depletion: The multifaceted decline of crab and shrimp fisheries in the greater Gulf of Alaska. Rev. Fish Biol. Fish. 8:117-176. doi:10.1023/A:1008891412756

Otto, R.S. 1981. Eastern Bering Sea crab fisheries. In: D.W. Hood and J.A. Calder (eds.), The eastern Bering Sea shelf: Oceanography and resources, Vol. 2. University of Washington Press, Seattle, pp. 1037-1066.

Otto, R.S. 1986. Management and assessment of eastern Bering Sea king crab stocks. In: G.S. Jamieson and N. Bourne (eds.), North Pacific workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92:83-106.

Powell, G.C., and R.B. Nickerson. 1965. Aggregations among juvenile king crabs (*Paralithodes camtschatica*, Tilesius), Kodiak, Alaska. Anim. Behav. 13:374-380.

Rodin, V.E. 1970. Some data on the distribution of king crab, *Paralithodes camtschatica* (Tilesius), in the southeastern Bering Sea. In: Soviet fisheries investigations in the Northeast Pacific, Part 5. TINRO 72:143-148.

Rodin, V.E. 1990. Population biology of the king crab, *Paralithodes camtschatica* Tilesius, in the North Pacific Ocean. In: Proceedings of the International Symposium on King and Tanner Crabs. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 133-144.

Slobodkin, L.B. 1961. Growth and regulation of animal populations. Holt, Rinehart and Winston, New York. 184 pp.

Slobodkin, L.B. 1970. Summary and discussion of the symposium. In: B.B. Parrish (ed.), Fish stocks and recruitment. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 164:7-14.

Takeshita, K., H. Fujita, and S. Matsuura. 1990. A note on population structure in the eastern Bering Sea adult red king crab, *Paralithodes camtschatica*. In: Proceedings of the International Symposium on King and Tanner Crabs. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 427-433.

USBCF. 1959. Progress report on king crab investigations 1959. U.S. Bureau of Commercial Fisheries, INPFC (International North Pacific Fisheries Commission) Document 316. 5 pp.

USFWS. 1942. Report of the Alaska crab investigation. Fishery Market News, May supplement 4(5a). U.S. Fish and Wildlife Service. 108 pp.

Wilson, E.O. 1975. Sociobiology: The new synthesis. Belknap Press, Cambridge. 697 pp.

Wilson, E.O., and W.H. Bossert. 1971. A primer of population biology. Sinauer Associates, Sunderland. 192 pp.

Witherell, D. 1998. King and Tanner crabs of the Bering Sea and Aleutian Islands area: Species profiles. Report to the North Pacific Fishery Management Council, 605 West 4th Ave., Suite 306, Anchorage, AK 99501.

Witherell, D., and D. Woodby. 2005. Application of marine protected areas for sustainable production and marine biodiversity off Alaska. Mar. Fish. Rev. 67:1-27.

Wooster, W.S. 1992. King crab dethroned. In: M.H. Glantz (ed.), Climate, variability, climate change and fisheries. Cambridge University Press, New York, pp. 14-30.

Yeung, C., and R.A. McConnaughey 2006. Community structure of eastern Bering Sea epibenthic invertebrates from summer bottom-trawl surveys 1982 to 2002. Mar. Ecol. Prog. Ser. 318:47-62.

Yu, C., A.M. Lee, B.L. Bassler, and S. Roseman. 1991. Chitin utilization by marine bacteria. A physiological function for bacterial adhesion to immobilized carbohydrates. J. Biol. Chem. 266(36):24260-24267. PMid:1761531

Zheng, J., M.C. Murphy, and G.H. Kruse. 1995. A length-based population model and stock-recruitment relationships for red king crab, Paralithodes camtschaticus, in Bristol Bay, Alaska. Can. J. Fish. Aquat. Sci. 52:1229-1246. doi:10.1139/f95-120

Zimmerman, M., C.B. Dew, and B.A. Malley. 2009. History of Alaska red king crab, *Paralithodes camtschaticus*, bottom trawl surveys, 1940-61. Mar. Fish. Rev. 71(1):1-22.

Sundet, J.H. and A.M. Hjelset. 2010. Seasonal Depth Distribution of the Red King Crab (*Paralithodes camtschaticus*) in Varangerfjorden, Northern Norway. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.20

Seasonal Depth Distribution of the Red King Crab (*Paralithodes camtschaticus*) in Varangerfjorden, Northern Norway

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Abstract

The red king crab was introduced to the Murman Fjord on the Kola Peninsula in the 1960s, and has since spread to most areas in the southern Barents Sea. Studies in its native areas in the North Pacific Ocean showed that red king crabs undergo seasonal migrations between shallow and deep waters. The degree to which the crab has adapted to its new environment is unknown, but knowledge of its seasonal behavior is essential to the design of stock assessment surveys and for evaluating the impact of the crab on the native fauna in the Barents Sea. Monthly samples of red king crabs taken at the same positions and at five depths in Varangerfjorden, northern Norway, indicated a different seasonal depth pattern among mature crabs of both sexes and a more patchy distribution among mature females than mature males. Mature males seem to enter shallow water in large numbers as early as November, while ovigerous females appear in shallow areas in December. Mature males are observed almost exclusively in deeper areas from June through September, while females are mainly caught in deep waters from June through November. There was no clear pattern in the catches of immature crabs. However, juveniles may not have been adequately sampled, because they are likely to be distributed in habitats shallower than 50 m. Based on this understanding of the seasonal depth distribution of red king crabs in Varangerfjorden, stock assessment surveys of mature crabs should be conducted in deep waters sometime between July and October. Seasonal movements in Varangerfjorden indicate that the crabs may impact benthic communities at all depths, but based on

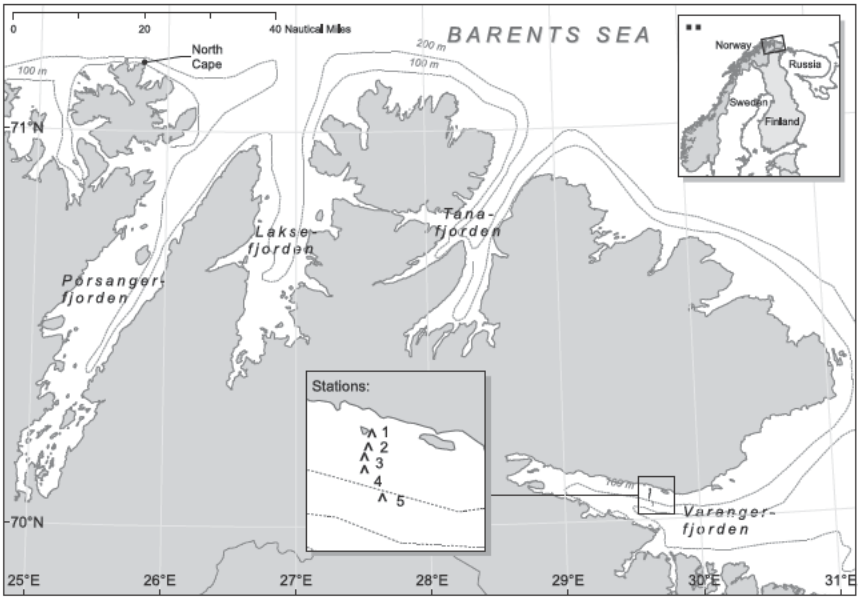

Figure 1. Map indicating the location of sampling stations in Varangerfjorden, northern Norway.

depth-specific residence time, deep-water fauna are most likely to be most affected.

Introduction

The red king crab (*Paralithodes camtschaticus*) was introduced to the Barents Sea in the 1960s, and although it has become invasive, it is unclear whether it is fully adapted to its new environment (Orlov and Ivanov 1978). Since 1992 this species has become increasingly abundant in Norwegian waters as it has spread westward from the Russian border along the coast of Finnmark, the most northeasterly county in Norway (Sundet 2009) (Fig. 1).

In Norway, the red king crab is regarded both as a valuable fishery resource and as an unwanted invasive species that may have a serious impact on the existing ecosystem (Anonymous 2007). The management of this species therefore entails at least two main demands for more knowledge: the size of the current standing stock and identification of ecosystem components that are most vulnerable to this non-native species.

Abundance estimation of red king crab involves population estimation models using fishery-independent surveys, catch enumeration, and biological sampling for sex, size, and shell condition (Otto 1986, Zheng et al. 1996). Because the crab undergoes seasonal migrations in its native habitat in the North Pacific (Wallace et al. 1949, Powell and Nickerson 1965), it is essential to understand their seasonal depth distribution while designing at-sea surveys in the Barents Sea. Adult red king crab in native areas perform seasonal migrations between deep and shallow waters, mainly governed by mating/molting and feeding behaviors (Marukawa 1933, Stone et al. 1992). Prior to our study, it was unknown whether red king crab have adapted a seasonal migration pattern in Norwegian waters.

A study by Sundet et al. (2000) revealed that the red king crab in Varangerfjorden mainly preyed upon solitary benthic animals. They primarily consumed soft-bottom species during autumn and winter (e.g., small bivalves and polychaetes) and typical shallow hard-bottom species (e.g., sea urchins and brittle stars) in spring, suggesting a shallow water distribution in spring. Bathymetric charts show that most shallow water in the fjords of Finnmark consist of steep slopes probably with a hard-bottom substrate, whereas the deep areas tend to be wide plain soft-bottom seafloor. Therefore, the relative amount of time spent by the crabs in deep and shallow waters should indicate whether soft- or hard-bottom communities are more likely to be influenced by their feeding activity.

The purpose of this study is to investigate the seasonal depth distribution of mature and immature red king crab to reveal whether they have adapted the same seasonal pattern as in their native areas. Such knowledge will provide scientific basis for designing future stock assessment surveys and studies of its impact on benthic communities.

Material and methods

Red king crab were sampled monthly at fixed stations and depths using baited traps in Varangerfjorden in eastern Finnmark (Fig. 1). Sampling depths were 50, 100, 150, 200, and 235 m; each depth was fished with a chain of three square collapsible traps (1.2 × 1.2 × 1.2 m) baited with whole herring (Stiansen et al. 2007). The intended soak time was 24 hours, but due to weather conditions actual soak times ranged from 10 to 66 hours, with a mean of 27.2 for all months (Table 1). To standardize catches each month we calculated catch per day (24 hrs) (CPUE) shown in Table 1. Carapace length (CL) of all crabs was measured to the nearest millimeter using a vernier caliper, and sex and presence of eggs were determined by visual inspection.

All data were grouped in terms of mature males and females, and immature males and females for further analysis. Data from stations at

Table 1. The total number, catch per day (24 h) (CPUE), and soak time of mature and immature red king crabs of each sex caught during the sampling period from September 2004 to August 2005, in Varangerfjorden, northern Norway.

	Mature crabs				Immature crabs				
Month	Females	CPUE females	Males	CPUE males	Females	CPUE females	Males	CPUE males	Soak time (h)
Jan	160	148	66	61	1	0.9	0	0.0	25.9
Feb	105	102	63	61	0	0.0	1	1.0	24.8
Mar	40	37	80	75	24	22.4	15	14.0	25.7
Apr	14	14	49	48	15	14.8	15	14.8	24.4
May	22	20	36	33	73	66.4	61	55.5	26.4
Jun	18	17	164	157	199	190.3	234	223.7	25.1
Jul	41	98	200	480	26	62.4	30	72.0	10.0
Aug	14	15	112	117	23	24.0	23	24.0	23.0
Sep	251	235	221	207	30	28.1	31	29.1	25.6
Oct	7	3	135	49	9	3.3	10	3.6	66.0
Nov	237	219	70	65	76	70.2	70	64.6	26.0
Dec	219	219	26	26	4	4.0	3	3.0	24.0
Total catch	1,128		1,222		480		493		

200 and 235 m depths showed similar trends and were therefore combined. Ovigerous female crabs are here synonymous to mature females and were classified based on the presence of external eggs. In males, size of maturation was based on morphological changes observed with maturation (Somerton 1980). Piecewise linear regression models revealed a change in the relative growth between chelae height and CL, at CLs between 103.5 mm and 116.5 mm (Rafter et al. 1996). For practical purposes we therefore chose 110 mm CL as a size of maturity for male red king crab.

An analysis of variance (ANOVA) was performed to identify significant differences ($P < 0.05$) in mean CL of mature females between April, March, and May at the deepest stations (>150 m). The significance level for rejecting the null hypothesis was set to 0.05 for all tests. All figures presenting results and statistical analysis were performed in R software

(R Development Core Team 2009), while ArcGis® was used for creating maps (Fig. 1).

Results

The number of mature females caught each month ranged between 7 and 251. The smaller catches (<50 crabs) were mainly caught from March to August; catches were generally high from September to February with the exception of October. From April to November, almost all mature female crabs were caught deeper than 100 m (Table 1). From December to March they were also found at the shallow station at 50 m (Fig. 2a). In April, all mature females caught at the deepest stations (≥150 m) had newly extruded eggs, and their mean CL was significantly smaller than that of females taken at the same depth in the adjacent months (113.2 ± 6.0 in April, versus 124.1 ± 11.5, $P = 0.002$, and 122.8 ± 6.8, $P = 0.007$, in March and May, respectively, DF = 38). All mature females caught at 50 m in January, February, and March had old eggs.

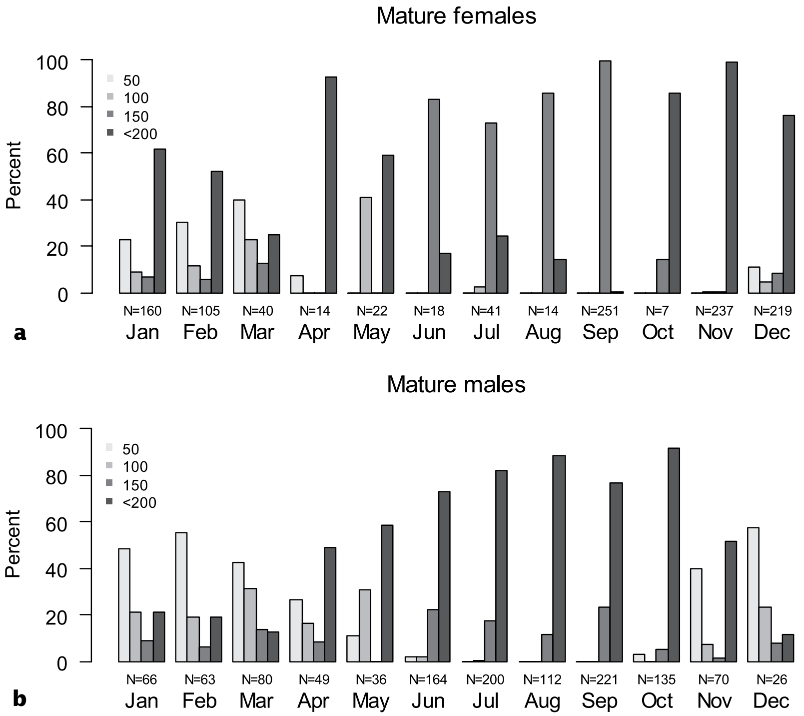

Figure 2. Relative catches (%) at different depths of mature female (a) and mature male (b) red king crabs each month during September 2004 to August 2005 in Varangerfjorden, northern Norway.

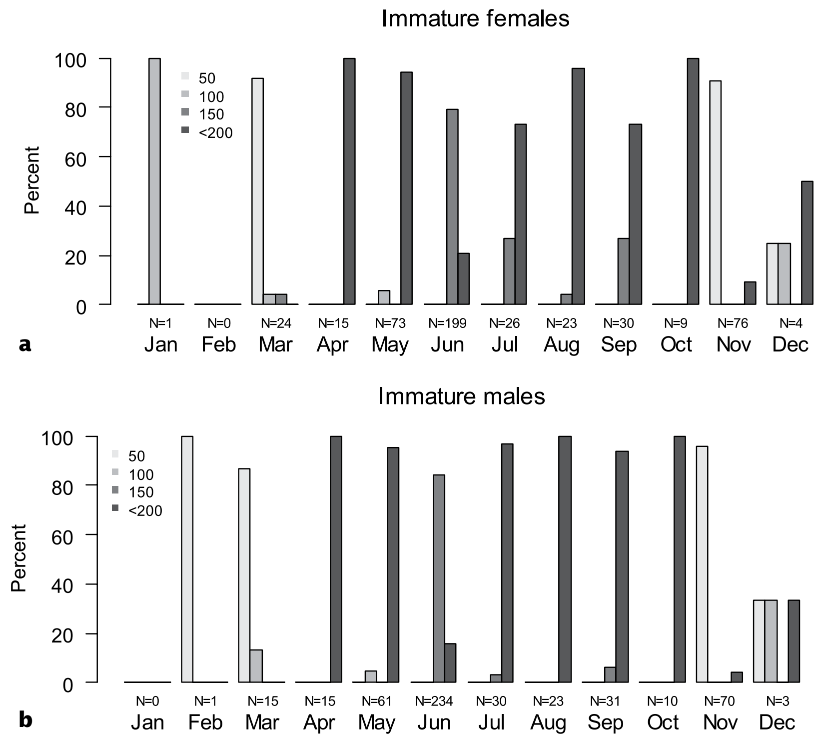

Figure 3. Relative catches (%) at different depths of immature female (a) and immature male (b) red king crabs caught at different depths each month during September 2004 to August 2005 in Varangerfjorden, northern Norway.

From June to October mature males were mainly caught at depths ≥150 m. On the other hand, males were most abundant at the shallowest (50 m) stations from November through May (Fig. 2b).

In general, fewer immature than mature crabs were caught, and monthly sample sizes ranged from only one to as many as 433. However, the sex ratio of immature crabs each month was almost 1:1 with the exception of January (Table 1). Most immature crabs were caught at or below 150 m, but there was no particular seasonal pattern of depth distribution in the samples of immature crabs throughout the year. Almost half of all the immature crabs were caught in the June sample (Fig. 3a and b).

Discussion

Soak time is crucial for the catchability in traps due to an increased tendency for crabs to escape after about 48 hours (Stiansen et al. 2007). This may have influenced catch rates in October when soak time was almost three times longer than planned (Table 1). Podding behavior in juvenile red king crab is common, but may also occur among adults (Dew 1990, 2010) and Stone et al. (1993) showed aggregating behavior among mature females. This phenomenon may therefore affect catchability of all sizes of crabs. However, the smallest juveniles are commonly distributed in very shallow waters and are probably beyond the effective fishing areas of the traps on our shallowest station (Dew 1990). High catches of mature females compared to males in some months and depths may be a result of this greater tendency for aggregation behavior among adult females compared to males, particularly at the deepest stations (Stone et al. 1993).

Catches of ovigerous females at the shallowest (50 m) station from December through March may indicate that multiparous females start migrating to shallow waters for reproduction as early as December, and continuing until March. The presence of old eggs show that all mature females caught at the shallowest station from January to March must be multiparous en route to the shallower areas. In the North Pacific, multiparous spawning takes place later (April-June) (Matsuura et al. 1972, Stone et al. 1993, Stevens and Swiney 2007, Dew 2008) than they were observed in Varangerfjorden. The observation of multiparous females at the shallowest stations in December may indicate that hatching and spawning takes place earlier in Varangerfjorden than in the North Pacific.

The sample of females with newly extruded eggs caught at the deepest station in April probably consists of primiparous crabs, which are the first to return to deep areas after spawning. Stevens and Swiney (2007) showed that primiparous females molt and mate earlier than their multiparous sisters. They will therefore probably enter the shallow areas sometime before multiparous females, thereby extending the period during which ovigerous females are found at such depths. Intensive reproductive activity might also explain the low numbers of both females and males caught at the shallowest station in April and May. Ovigerous females may need up to two weeks to complete hatching, egg extrusion, and mating. They probably do not feed during that period, rendering traps ineffective to capture them at this time of year (Cunningham 1969).

The largest numbers of mature males were caught from June to October, and all catches were made at the deep stations (Table 1, Fig. 2b). When these males appeared at the shallowest station in November, catches were substantially lower. During this period male crabs start spending much time molting and mating, and do not readily enter traps. Dew and McConnaughey (2005) hypothesized that not all mature males participate in mating activities every season, and this might explain the catches of a few large mature males at the deepest stations throughout the period of expected mating in Varangerfjorden (Fig. 2b). It is reasonable to believe that males that have molted are less capable of mating the same season, and that mating males mainly are skip-molters, as observed by others (Powell et al. 1973). A scrutiny of our data showed that males with shell age 3 and 4 (Donaldson and Byersdorfer 2005) dominated in the samples at 50 m from December through February, consistent with this hypothesis.

The lack of catches of mature males at the intermediate and shallow stations (<100 m) from June to October probably confirms that the male mating season is over and there is a general movement to deeper areas for foraging. In July, all mature males appear to have left the shallow areas and moved down to the deeper feeding areas where they were found until the upward movement started again in October/November (Fig. 2b) (Zhou and Shirley 1997).

Mature males tended to be caught at greater depths than mature females during the period outside mating. The depth distribution of ovigerous females is probably more dependent on temperature since they would seek temperatures that are optimal for embryonic development (Stone et al. 1993).

Podding behavior may explain the large variability in catches of immature crabs (Powell and Nickerson 1965, Dew 1990) (Table 1). This is probably also why almost all immature crabs were taken at a single depth in six out of twelve months (Fig. 3a and b). High catches may be a result when the traps are set close to a large aggregation or pod of crabs. Another striking observation is that the sex ratio was close to 1:1 every month, indicating that segregation between sexes has not yet occurred (Table 1).

Dew (2008) highlights the risk of carrying out surveys at a time of year when there exist a potential for systematic errors due to seasonal migrations of the red king crab. In this study we concluded that catchability of both mature males and females will be satisfactory for conducting area-swept assessment using trawl during July to October. The highly aggregated behavior of mature females may entail large variations in sample sizes, leading to imprecise estimates of the stock of females.

The seasonal residence time at different depths observed in this study suggests that deep-water soft-bottom communities will probably be most affected by the red king crab. Intensive feeding after molting and mating may, however, also have a significant impact on shallow waters, which usually host hard-bottom communities (Jewett and Feder 1982). Therefore, future studies should concentrate on revealing more knowledge about duration and feeding behavior of male and female crabs of various sizes at different depths to help elucidate details about the magnitude of red king crab effects and the responses of benthic communities.

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References

Anonymous. 2007. Stortingsmelding nr 40 (2006-2007) Forvaltning av kongekrabbe. Parliamentare white paper from the Ministry of Fisheries and Coastal Affairs, Norway. 144 pp. Accessed Dec. 2010: http://www.regjeringen.no/nb/dep/fkd/dok/regpubl/stmeld/2006-2007/stmeld-nr-40-2006-2007-.html?id=480559

Cunningham, D.T. 1969. A study of the food and feeding relationships of the Alaskan king crab *Paralithodes camtschatica*. Master's thesis, San Diego State College, California. 84 pp.

Dew, B.C. 1990. Behavioral ecology of podding red king crab, *Paralithodes camtschatica*. Can. J. Fish. Aquat. Sci. 47:1944-1958. doi:10.1139/f90-219

Dew, B.C. 2008. Red king crab mating success, sex ratio, spatial distribution, and abundance estimates as artifacts of survey timing in Bristol Bay, Alaska. N. Am. J. Fish. Manage. 26:1618-1637. doi:10.1577/M07-038.1

Dew, C.B. 2010. Podding behavior of adult king crab and its effect on abundance-estimate precision. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and management of exploited crab populations under climate change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.24

Dew, B.C., and R.A. McConnaughey. 2005. Did trawling on the broodstock contribute to the collapse of Alaska's king crab? Ecol. Appl. 15:919-941. doi:10.1890/03-5231

Donaldson, W.E., and S.C. Byersdorfer. 2005. Biological field techniques for lithodid crabs. Alaska Sea Grant College Program, University of Alaska Fairbanks. 76 pp.

Jewett, S.C., and H.M. Feder. 1982. Food and feeding habits of the king crab *Paralithodes camtschatica* near Kodiak Island, Alaska. Mar. Biol. 66:243-250. doi:10.1007/BF00397029

Marukawa, H. 1933. Biological and fishery research on Japanese king-crab *Paralithodes camtschatica* (Tilesius). J. Imp. Fish. Exp. Station 4:123-152.

Matsuura S., K. Takeshita, H. Fujita, and S. Kawasaki. 1972. Reproduction and fecundity of the female king crab, *Paralithodes camtschatica* (Tilesius), in the waters of western Kamchatka, II. Determination of the fecundity based on the counts of the ovarian eggs and of the spawned eggs attached to pleopods. Bull. Far Seas Fish. Res. Lab. 6:169-190.

Orlov, Y.I., and B.G. Ivanov. 1978. On the introduction of the Kamchatka king crab *Paralithodes camtschatica* (Decapoda: Anomura: Lithodidae) into the Barents Sea. Mar. Biol. 48: 373-375. doi:10.1007/BF00391642

Otto, R.S. 1986. Management and assessment of eastern Bering Sea king crab stocks. In: G.S. Jamieson and N. Bourne (eds.), North Pacific Workshop on Stock Assessment and Management of Invertebrates. Can. Spec. Publ. Fish Aquat. Sci. 92:83-106.

Powell, G.C., and R.B. Nickerson. 1965. Aggregations among juvenile king crabs (*Paralithodes camtschatica*, Tilesius) Kodiak, Alaska. Anim. Behav. 13:2-3. doi:10.1016/0003-3472(65)90058-8

Powell, G.C., B. Shafford, and M. Jones. 1973. Reproductive biology of young adult king crabs *Paralithodes camtschatica* (Tilesius) at Kodiak, Alaska. Proc. National Shellfish. Assoc. 63:77-87.

Rafter, E.E., E.M. Nilssen, and J.H. Sundet. 1996. Stomach content, life history, maturation and morphometric parameters of red king crab, *Paralithodes camtschaticus*, from Varangerfjord area, north Norway. ICES CM 1996/K:10. 16 pp.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Somerton, D.A. 1980. A computer technique for estimating the size of sexual maturity in crabs. Can. J. Fish. Aquat. Sci. 37:1488-1494. doi:10.1139/f80-192

Stevens, B.G., and K.M. Swiney. 2007. Hatch timing, incubation period, and reproductive cycle for captive primiparous and multiparous red king crab, *Paralithodes camtschaticus*. J. Crust. Biol. 27:37-48. doi:10.1651/S-2663.1

Stiansen, S., A. Fernø, D.M. Furevik, T. Jørgensen, and S. Løkkeborg. 2007. Efficiency and catch dynamics of collapsible square and conical pots used in the red king crab (*Paralithodes camtschaticus*) fishery. Fish. Bull. 106:40-46.

Stone, R.P., C.E. O'Clair, and T.C. Shirley. 1992. Seasonal migration and distribution of female red king crabs in a southeast Alaskan estuary. J. Crust. Biol. 12:546-560. doi:10.2307/1548836

Stone, R.P., C.E. O'Clair, and T.C. Shirley. 1993. Aggregating behavior of ovigerous female red king crab, *Paralithodes camtschaticus*, in Auke Bay, Alaska. Can. J. Fish. Aquat. Sci. 50:750-758. doi:10.1139/f93-086

Sundet, J.H., E.E. Rafter, and E.M. Nilssen. 2000. Sex and seasonal variation in the stomach content of the red king crab, *Paralithodes camtschaticus,* in the southern Barents Sea. Crustacean Issues 12:193-200.

Sundet, J.H. 2009. Kongekrabbe. Kysten og havet. Institute of Marine Research. (In Norwegian) Accessed Dec. 2010: http://www.imr.no/publikasjoner/andre_publikasjoner/kyst_og_havbruk/2009/nb-no.

Wallace, M.M., C.J. Pertuit, and A.R. Hvatum. 1949. Contribution to the biology of the king crab *Paralithodes camtschatica* (Tilesius). U.S. Fish. Wildl. Serv., Fish. Leafl. 340. 50 pp.

Zheng, J., G.H. Kruse, and M.C. Murphy. 1996. Comparision of abundance estimation methods for red king crabs in Bristol Bay and Kodiak. In: High lattitude crabs: Biology, management, and economics. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 283-294.

Zhou, S.J., and T.C. Shirley. 1997. Behavioural responses of red king crab to crab pots. Fish. Res. 30:177-189. doi:10.1016/S0165-7836(97)00005-2

Bechtol, W.R. and G.H. Kruse. 2010. Factors Affecting Historical Red King Crab Recruitment Around Kodiak Island, Alaska. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.18

Factors Affecting Historical Red King Crab Recruitment Around Kodiak Island, Alaska

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Abstract

Waters around Kodiak Island in the Gulf of Alaska once supported the world's largest fishery for red king crab *Paralithodes camtschaticus*. Commercial fisheries occurred at low levels beginning in 1937, but increased rapidly in the 1960s to a peak harvest of 42,800 t in 1965. Stock abundance declined in the late 1960s, moderated in the 1970s, and collapsed in the early 1980s, but a commercial fishery closure since 1983 has not resulted in stock recovery. We used a modified autocorrelated Ricker spawner-recruit model to examine crab recruitment patterns for the 1964-1999 brood years ($n = 36$ observations) in relationship to biotic and abiotic variables hypothesized to affect survival of early life stages of Kodiak red king crab. Our hierarchical approach for model selection used AIC_c, the Akaike Information Criterion corrected for small sample size. Results revealed a strong negative association between biomass of age 3+ Pacific cod *Gadus macrocephalus* and crab recruitment. The Kodiak stock of red king crab declined following a period of high harvest rates in the late 1960s that skewed sex ratios and compromised reproductive potential. Then in the late 1970s, it appears that predation on crab may have increased, possibly due to increased Pacific cod biomass combined with a nearshore shift in cod spatial distribution that resulted from warmer temperatures associated with a climate regime shift. Inclusion of percent cloud cover at Kodiak, Alaska, as a second ecological variable slightly improved model fit, but the associated mechanism is unclear.

Introduction

The Kodiak Island area in the northern Gulf of Alaska (Fig. 1) once supported the world's largest fishery for red king crab *Paralithodes camtschaticus*. Commercial harvests from this area first occurred in the 1930s, with exploratory harvests continuing into the late 1950s. These historical crab harvests largely occurred in winter by a small number of purse seine vessels (<18 m length overall) that harvested salmon in summer (Gray and Simon 1965, Spalinger 1992). However, small vessel size and lack of live tanks limited the fishery to low-level harvests in inshore, shallow waters close to landing facilities. With the introduction of vessels designed for crab fishing, annual landings increased rapidly in the 1960s to a peak harvest of 42,800 t (94.4 million pounds) in 1965, but harvest levels declined, and the commercial fishery fluctuated at low

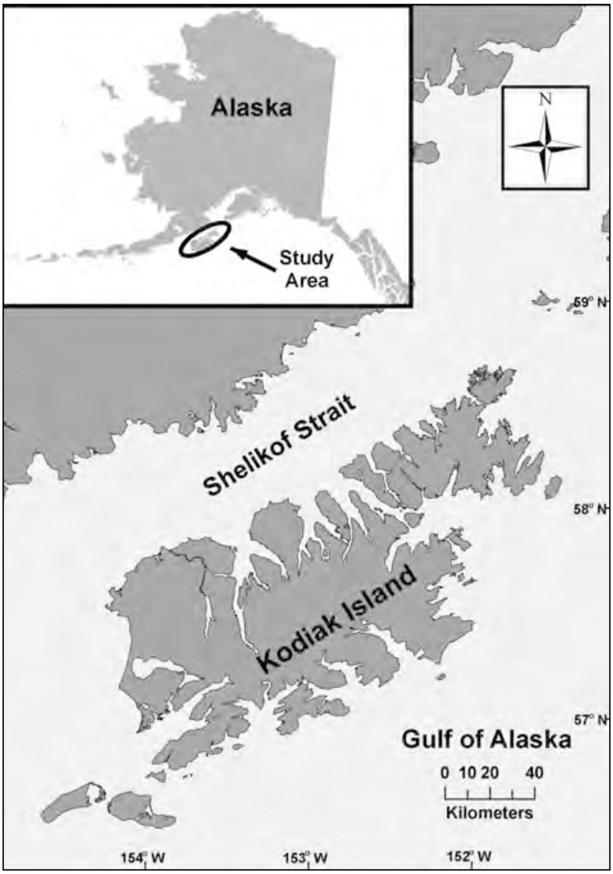

Figure 1. Location of the Kodiak study area in the northern Gulf of Alaska.

levels before being closed in 1983 (Spalinger and Jackson 1994, Bechtol and Kruse 2009a). Several management measures, such as time and area closures and adjusted minimum size limits, failed to stop the decline (Gray and Simon 1965, Spalinger 1992). A commercial fishery closure since 1983 has not resulted in recovery of this severely depleted stock.

Our study goal was to apply numerical modeling in a retrospective analysis to determine conditions that may have contributed to the rise, fall, and continued depressed status of the red king crab stock around Kodiak Island. Previous analyses of Alaska crab population dynamics focused on Bering Sea stocks, mainly red king crab and Tanner crab *Chionoecetes bairdi* in Bristol Bay and snow crab *Chionoecetes opilio* in the eastern Bering Sea (Zheng and Kruse 2000). Zheng and Kruse (2003) used a length-based analysis of trawl survey time series to investigate stock-recruit relationships for these three stocks. For Tanner crab and snow crab, cyclic patterns in the stock-recruit observations were believed to result from environmental forcing. For red king crab, stock-recruit relationships suggested density-dependent effects, although recruitment trends were also consistent with decadal climate shifts, so results were equivocal. In an analysis of recruitment patterns, seven of 15 crab stocks in the Gulf of Alaska and Bering Sea had trends consistent with decadal climate shifts, with periods of strong Aleutian lows coinciding with weak recruitment (Zheng and Kruse 2000). Red king crab from Bristol Bay to Cook Inlet, including Kodiak, generally shared this decadal pattern.

In previous analyses, we (1) reconstructed stock and recruitment abundances in Kodiak red king crab during 1960-2004 (Fig. 2; Bechtol and Kruse 2009a); and (2) examined potential stock-recruit relationships (Bechtol and Kruse 2009b). Although changes in abiotic and biotic factors may influence stock productivity at any red king crab life stage, these effects likely are most pronounced during early life history, particularly larval and early benthic stages. Here, we explored evidence of relationships between crab recruitment around the Kodiak archipelago and environmental and ecological factors. The application of models that combine population dynamics (stock-recruit) and ecological factors (e.g., predator-prey, fishery oceanography) allowed us to better assess conditions that contributed to the increase and subsequent collapse of the Kodiak king crab stock, as well as potential impediments to rebuilding (e.g., low spawning stock vs. predation vs. oceanographic conditions) that should be considered in ongoing restoration efforts.

Crab biology and ecological effects relevant to recruitment

Red king crab recruitment is believed to depend primarily on survival during early life history (Zheng and Kruse 2000). Adult females mate annually during March and April and the eggs are then incubated on the

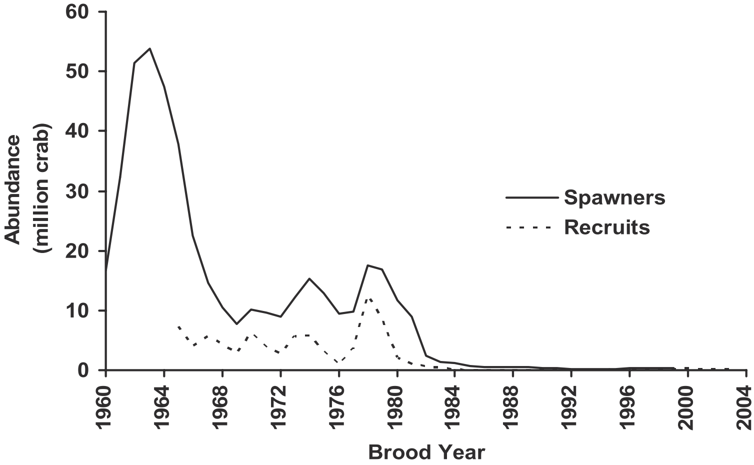

Figure 2. Annual estimated abundances of male spawners and lag-5 recruits for Kodiak red king crab, 1960-2004 (adapted from Bechtol and Kruse 2009a).

female's abdomen for approximately 300 days. Embryos hatch into pelagic larvae from March to May, inhabiting the water column at depths of less than 100 m. Larvae molt through four zoeal stages, lasting approximately two weeks each. Early instar zoea must feed within 2-6 days to survive, tending to be phytoplanktivorous with a preference for the diatom *Thalassiosira* sp. (Paul et al. 1989, Shirley and Shirley 1989). A stable, stratified water column and relatively cool sea surface temperatures promote a spring phytoplankton community dominated by *Thalassiosira* sp., thus supporting high zoeal survival (Ziemann et al. 1990, Bienfang and Ziemann 1995). Extensive cloud cover reflects significant amounts of solar radiation back to space (Weaver and Ramanthan 1996), which may delay and reduce the spring bloom (Bienfang and Ziemann 1995, Tyler and Kruse 1995, Cooney 2007) and also reduces surface water warming (Weingartner 2007). Surviving zoea metamorphose into glaucothoe that use a well-developed swimming ability to search for nearshore, rocky substrate with high-profile sessile fauna (Powell and Nickerson 1965, Armstrong et al. 1993, Stevens and Kittaka 1998, Loher 2001). Glaucothoe then molt into a benthic, largely solitary existence as the first red king crab instars, during May to July around Kodiak. At 1-2 years after settlement, the juvenile king crab begin to form pods and move to deeper water. A small size makes all juvenile king crab susceptible to predation, including cannibalism (Broderson et al. 1990). But predation risk increases for all life stages during the soft-shell period following molting. Red king crab undergo 7 to 8 molts the first year after settlement, decreasing to 1-2 molts in the fourth year (McCaughran and Powell 1977).

Methods

Estimates of spawners and recruits derive from a stage-based stock reconstruction of male and female red king crab using pot and trawl surveys from 1972 to 2004 and commercial harvests of male crab from 1960 to 1982 (Bechtol and Kruse 2009a). Male red king crab recruited into the model at 125 to 144 mm carapace length (CL), assumed to be one molt prior to legal size. Based on a growth analysis of Kodiak red king crab by McCaughran and Powell (1977), we assumed this pre-legal size is achieved 5 to 8 years after egg fertilization. A subsequent study (Bechtol and Kruse 2009b) of potential stock-recruit relationships determined the preferred model was a lag-5 autocorrelated Ricker with the time series separated into three periods representing brood years for 1960-1974, 1975-1984, and 1985-1996. We applied the same three productivity periods in this study. Following Bechtol and Kruse (2009b), we defined the spawning stock as male crab ≥125 mm CL because: (1) this is a male-only fishery (Pengilly and Schmidt 1995), so female abundance estimates were limited to survey years (1972-2004), whereas male estimates derived from commercial catch data extended from 1960 to 2004; and (2) the years of the highest population abundance, particularly the 1960s, are represented only by male data.

Following Tyler and Kruse (1996a,b), we explored an events-time modeling procedure that considers hypotheses about ecological factors operating during key life history stages. We specifically examined factors considered to be important to the larval to settlement stages, and to the juvenile benthic to recruitment stages. During the larval to settlement stages, the most critical factors were anticipated to be those affecting stratification and temperature of shallow, subsurface waters from March through June each year. These factors do not directly kill crab larvae, but are indices of conditions that promote or impede larval survival. We hypothesize that predation is the predominant factor controlling survival after glaucothoe settlement, although predation by planktivorous fish during the pelagic larval stage is also plausible. In addition, non-directed fishing activities (i.e., those not directed at red king crab) potentially affect survival of post-settlement crab stages through both habitat damage and direct mortality (Armstrong et al. 1993). We assembled 14 ecological data sets on variables for which associations with king crab recruitment were postulated (Table 1). The first nine data sets, representing factors potentially affecting stratification and temperature of marine surface and shallow, subsurface waters in the vicinity of Kodiak Island during the pelagic larval stage lasting from March through June, included the following:

Table 1. Ecological parameters examined for relationships to stock-recruit residuals.

Data series[a]	Abbreviation	Years considered	Data source
Kodiak wind speed cubed	WS3	1960-2004	http://www4.ncdc.noaa.gov/cgi-win/wwcgi.dll?wwDI~StnSrch~StnID~20021863
Pacific Decadal Oscillation	PDO	1960-2004	http://www.cgd.ucar.edu/cas/catalog/climind/soi.html
Gulf of Alaska freshwater discharge	DCG	1960-2004	Royer and Grosch (2007)
Kodiak cloud cover	CLD	1960-2004	http://www4.ncdc.noaa.gov/cgi-win/wwcgi.dll?wwDI~StnSrch~StnID~20021863
Kodiak sea surface temperature	SST	1960-2004	http://nomads.ncdc.noaa.gov/#climatencdc
GAK 1 water temperature	GAT	1970-2004	http://www.ims.uaf.edu/gak1/
GAK 1 salinity	GAS	1970-2004	http://www.ims.uaf.edu/gak1/
Trident Basin water temperature	TRI	1970-2004	C. Worton, Alaska Department of Fish and Game (pers. comm.)
Walleye pollock age 3+ female spawning biomass	POL	1961-2004	M. Dorn, National Marine Fisheries Service (pers. comm.)
Pacific halibut age 10+ biomass	HAL	1960-2004	S. Hare, International Pacific Halibut Commission (pers. comm.)
Pacific cod age 3+ biomass	COD	1964-2004	Thompson and Dorn (2005)
Arrowtooth flounder age 3+ biomass	ATF	1961-2004	Turnock et al. (2005)
Kodiak trawl shrimp harvest	SHR	1960-2004	G. Smith, Alaska Department of Fish and Game (pers. comm.)

[a] See text for details.

(1) sea level pressure at Kodiak, Alaska, as an index inversely related to storm activity and water column stratification;

(2) wind speed cubed as an index of surface wind energy and inversely related to water column stability;

(3) Pacific Decadal Oscillation as an index related to water column stability;

(4) freshwater discharge data for the Copper River and other Gulf of Alaska systems as an index of Alaska Coastal Current (ACC) flow and freshwater-driven water column stratification;

(5) percent cloud cover at Kodiak, Alaska, as an index inversely related to incident solar radiation and surface water warming;

(6) sea surface temperature in the area 55 to 60°N and 148 to 158°W as an index of shallow subsurface conditions off Kodiak;

(7) seawater temperature from the surface to 250 m at the GAK1 station off Seward, Alaska, as an index of surface and subsurface conditions in the ACC upstream of Kodiak;

(8) salinity from the surface to 250 m at the GAK1 station off Seward, Alaska, as an index of water column stratification in the ACC upstream of Kodiak; and

(9) seawater temperature at 10 m depth (MLLW, mean lower low water) in Trident Basin near the community of Kodiak as an index of shallow subsurface conditions on the southeast side of Kodiak.

Data were averaged from daily observations across March to June into annual estimates corresponding to the pelagic larval period.

Although numerous potential crab predators exist, few long-term stock assessments of potential predators are available. The next four data sets were treated as indices of potential predator populations in the Gulf of Alaska (Table 1):

(10) age 3+ spawning biomass of walleye pollock *Theragra chalcogramma* during 1961-2004 in the Gulf of Alaska;

(11) age 10+ abundance of Pacific halibut *Hippoglossus stenolepis* in International Pacific Halibut Commission Management (IPHC) Area 3A;

(12) age 3+ biomass of Pacific cod *Gadus macrocephalus* during 1961-2004 in the Gulf of Alaska; and

(13) age 3+ biomass of arrowtooth flounder *Atheresthes stomias* during 1964-2004 in the Gulf of Alaska.

Walleye pollock tends to be planktivorous and was hypothesized to feed on pelagic red king crab larvae, whereas Pacific halibut, Pacific cod, and arrowtooth flounder were hypothesized to prey on benthic stages of red king crab. Pacific herring *Clupea pallasii* is also a planktivorous species found in the nearshore during spring, but was not included in our analysis because of the lack of a formal time series of historical abundance or biomass for the Kodiak region.

The final data set, treated as an index of benthic trawl fishing impacts on benthic habitat and undocumented crab mortality, was

(14) pandalid shrimp catch biomass in the benthic trawl fishery during 1960-1985 (Table 1).

This trawl fishery has either been closed or attracted no harvesting effort since the mid 1980s due to low shrimp stock abundance (Jackson and Ruccio 2003). Although the fine-scale spatial overlap between juvenile red king crab and the trawl fishery is difficult to determine, it was assumed that greater trawl fishery removals resulted in greater impacts to crab and crab habitat. More direct estimates of trawling effort (e.g., number of trawl tows, area of seafloor trawled annually) were unavailable.

Standardized annual anomalies were developed for each data set by subtracting the grand mean from each year's observation, then dividing by the standard deviation. To examine potential relationships between crab recruitment and ecological variables, we incorporated ecological factors into the Ricker equation:

$$\begin{aligned} R_t &= \alpha S_{t-k} e^{-\beta S_{t-k} + \nu_t + \theta_t} \\ \theta_t &= \gamma_1 X_{1,t-k+j_1} + \cdots + \gamma_p X_{p,t-k+j_p} \ , \end{aligned} \tag{1}$$

where α is a parameter representing per-capita productivity at low stock size, β is a parameter controlling the degree of density dependence, R_t is recruit abundance in year t, S_{t-k} is stock size lagged k years from year t, $X_1 \ldots X_p$ are the time series of ecological anomalies with corresponding coefficients $\gamma_1 \ldots \gamma_p$, and $\{\nu_t\}$ is the set of random variables that account for unexplained variation (Ricker 1954, Quinn and Niebauer 1995, Pyper and Peterman 1998, Quinn and Deriso 1999). We note that theoretical peak recruitment occurs at a stock size (S_p) of $1/\beta$. The ecological anomalies are offset from the brood year by $j_1 \ldots j_p$ years, representing years after reproduction that the anomalies affect crab; e.g., a 0 offset corresponds to first year crab. To reduce the likelihood of spurious correlations, we limited the offsets for the first nine data sets and pollock, factors believed to primarily affect pelagic crab larvae (Table 1), to a range of 0-1; the offsets for the remaining predators and the shrimp fishery were limited to 1-5 years. Equation 1 incorporates autocorrelation effects, with ϕ representing the degree of autocorrelation among residuals, by letting $\nu_t = \delta_t + \phi \nu_t - 1$, where δ_t is environmental white noise, assumed to be distributed as $N(0,\sigma^2)$. Preliminary results suggested the inclusion of specific ecological data sets effectively eliminated the significance of the autocorrelation parameter, ϕ, as an explanatory variable, so we also fitted the data to a Ricker model without autocorrelations by setting $\phi = 0$. Note that setting $\phi = \gamma_i = 0$ results in a standard

Ricker model. We set $k = 5$, the lag providing the best S-R fits (Bechtol and Kruse 2009b). This equation was linearized by taking logarithms:

$$\ln\left(\frac{R_t}{S_{t-k}}\right) / \ln(\alpha)\ \beta S_{t-k} + \nu_t + \theta_t. \tag{2}$$

To provide comparable results among data sets of different lengths, only the 1964 to 1999 brood years were examined ($n = 36$). Per-capita productivity was examined among three critical time periods representing brood years 1964-1974, 1975-1985, and 1985-1999. In addition to examining residual patterns, model selection involved comparing the Akaike Information Criterion, corrected for small sample size (AIC$_c$; Burnham and Anderson 2004):

$$\begin{aligned} &\hat{\sigma} = \sqrt{\frac{RSS}{n-p}} \\ &-2\ln L = n\ln\left(2\pi\hat{\sigma}^2\right) + \frac{RSS}{\hat{\sigma}^2} \\ &AIC_c = -2\ln L + 2p + \frac{2p(p+1)}{n-p-1} \end{aligned} \tag{3}$$

where n is the number of observations, RSS is the residual sums of squares, and p is the number of parameters. According to Burnham and Anderson (2004), no credible evidence exists to eliminate competing models with AIC$_c$ differences ≤2, weak evidence exists for elimination with differences of 2-4, and definite evidence exists for differences ≥4. Our base model was the lag-5 autocorrelated Ricker model previously shown to be the most parsimonious model (Bechtol and Kruse 2009b).

Models were compared in a hierarchical approach starting with the base model and all models with a single ecological parameter. If a single ecological factor was found to improve model fit, a second ecological parameter was added. This process was repeated until no credible model improvement occurred. To simplify reporting of results, a given ecological data set and lag is signified by the Table 1 abbreviation combined with the offset, e.g., HAL-1 is halibut with a lag-1 year offset. Models were implemented in AD Model Builder (Otter Research Ltd., Sidney), with additional validation using Microsoft Excel. Relative precision of an estimated parameter was reported as the coefficient of variation *(CV)*, the standard error divided by the estimate. Standard errors were obtained as an estimate in the output from AD Model Builder, except that a bootstrap approach (Efron and Tibshirani 1993) with 1,000 replicates was used for models lacking autocorrelation.

After determining our preferred model, we examined the effects of the primary ecological factor on potential stock production and harvest

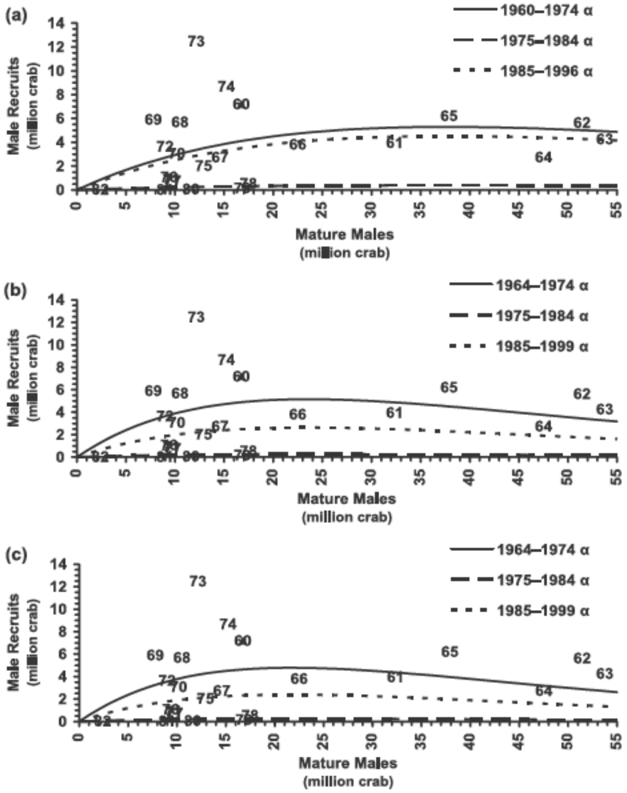

Figure 3. Spawner-recruit models configured with (a) no (base model), (b and d) one (COD-2), and (c and e) two (COD-2 and CLD-0) ecological parameters showing differences in productivity for the 1964-1974, 1975-1984, and 1985-1999 brood years; models d and e lack an autocorrelation parameter.

removals. By assuming the derived parameters represent the population in equilibrium, the maximum sustained catch (MSC) can be calculated as the maximum difference between recruitment (R_m) and the spawner abundance (S_m) needed to maintain the level of production (Quinn and Deriso 1999). For the Ricker curve, MSC occurs when

$$\alpha'\left(1-\beta S_m\right)e^{-\beta S_m}=1\ , \qquad \text{and} \qquad (4)$$
$$\alpha'=\alpha e^{\gamma X},$$

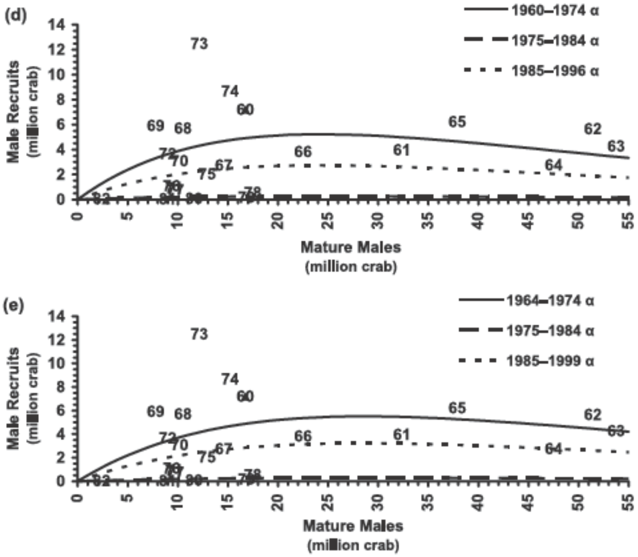

Figure 3. (continued)

where α, β, γ, and X are as in Equation 1. To represent current stock status, α and β were set equal to parameter estimates for brood years 1985-1999 from the preferred model. Finally, the harvest rate at MSC was calculated as μ_m = MSC/R_m. Given environmental variability, we estimated MSC at three levels of the environmental variable, representing the first three quartiles of the distribution of the environmental anomaly.

Results

Our model provided nonsensical results (e.g., $\beta < 0$ or unrealistically high S_p) when run with the GAK1 salinity and temperature, Trident Basin temperature, and shrimp harvest data sets, likely due to inconsistent overlaps with crab recruitment time series; these data were eliminated from further consideration.

Among models with a single ecological parameter, the smallest AIC$_c$ value was obtained with a Ricker curve lacking autocorrelation and lag-2 Pacific cod anomalies (COD-2; AIC$_c$ value of 96.9; Table 2), and a strongly negative effect indicated ($\gamma = -1.53$; CV = 0.22; Table 3). This model clearly outperformed the base model (AIC$_c$ = 106.8). However, AIC$_c$ differences of ≤2 suggest that the COD-2 model was not credibly better than the autocorrelated COD-2 (AIC$_c$ = 98.9) or the non-autocorrelated

Table 2. Comparison of AIC$_c$ values for selected lag-5 Ricker models with and without autocorrelation and incorporating (A) one, (B) two, and (C) three ecological parameters (defined in Table 1), with ecological effects lagged from 0 to 5 years. Models consider 1964-1999 brood years (n = 36 observations), with "F" indicating a fixed parameter to create a fuller model.

Parameter	Models without autocorrelation						Models with autocorrelation					
	Lag (years)						Lag (years)					
	0	1	2	3	4	5	0	1	2	3	4	5
A. One ecological parameter models												
SLP	114.6	114.6					109.7	109.8				
WS3	114.1	109.6					108.5	105.8				
PDO	111.0	114.6					107.0	109.6				
DCG	111.5	114.2					107.7	108.1				
CLD	113.6	114.2					104.3	109.7				
SST	111.8	114.5					107.1	109.7				
POL	101.4	108.7					102.2	106.2				
HAL		112.7	111.8	111.6	111.2	110.3		108.2	107.7	107.9	107.6	106.6
COD		100.5	96.9	98.3	99.2	100.4		102.5	98.9	100.5	101.0	102.2
ATF		110.1	111.4	112.6	113.3	113.8		106.8	107.2	107.9	108.2	108.4
B. Two ecological parameter models												
SLP	100.0	99.9					102.4	102.4				
WS3	95.0	99.7					98.1	101.9				
PDO	99.7	98.8					102.1	101.5				
DCG	97.2	99.3					99.9	101.6				
CLD	94.5	100.0					95.6	102.5				
SST	99.9	99.5					102.2	102.0				
POL	99.0	99.1					102.3	101.8				
HAL		99.5	99.6	99.9	100.0	100.0		101.8	102.3	102.4	102.4	102.4
COD		99.9	F	99.9	99.8	99.7		102.4	F	102.4	102.3	102.4
ATF		100.0	100.0	99.9	99.9	99.8		102.5	102.5	102.5	102.4	102.3
SLP	101.3	101.3					103.9	104.0				
WS3	97.9	101.0					101.1	103.4				
PDO	100.8	100.2					103.4	103.0				
DCG	99.0	101.0					101.9	103.4				
CLD	96.0	101.3					97.8	104.0				
SST	101.1	101.0					103.5	103.6				
POL	100.0	100.9					102.4	103.5				

Table 2. (continued)

Parameter	Models without autocorrelation						Models with autocorrelation					
	Lag (years)						Lag (years)					
	0	1	2	3	4	5	0	1	2	3	4	5
HAL		100.1	100.3	100.7	100.9	101.1		103.0	103.2	103.5	103.7	103.8
COD		101.0	99.9	F	101.2	101.2		103.6	102.4	F	103.8	103.9
ATF		101.3	101.4	101.4	101.3	101.3		104.0	104.0	104.0	104.0	104.0
C. Three ecological parameter models												
SLP	95.9	97.6					97.6	99.2				
WS3	94.6	97.5					96.8	98.5				
PDO	97.0	95.8					98.2	97.7				
DCG	92.6	96.6					93.8	97.3				
CLD	F	97.8					F	99.0				
SST	97.8	97.2					99.2	98.8				
POL	96.7	96.7					98.1	98.5				
HAL		97.8	97.8	97.8	97.7	97.6			99.2	99.2	99.0	99.1
COD		97.7	F	97.6	97.3	96.8			F	99.1	99.0	98.6
ATF		97.8	97.8	97.8	97.8	97.8			99.2	99.2	99.2	99.2
SLP	98.0	98.2										
WS3	F	96.5										
PDO	98.3	96.0										
DCG	96.3	96.6										
CLD	94.6	98.2										
SST	98.2	95.7										
POL	95.9	97.4										
HAL		98.3	98.4	98.3	98.1	98.0						
COD		98.2	F	98.4	98.2	97.4						
ATF		98.3	98.4	98.3	98.2	98.2						
SLP	98.2	99.2										
WS3	97.5	99.0										
PDO	98.2	97.4										
DCG	94.9	98.6										
CLD	F	99.3										
SST	99.4	98.8										
POL	98.0	98.7										
HAL		98.9	99.0	99.2	99.3	99.3						
COD		98.9	97.6	F	99.1	98.6						
ATF												

COD-3 models ($AIC_c = 98.3$). Therefore, these Pacific cod anomalies were examined as the first parameter of two ecological parameter models. We also noted that the non-autocorrelated COD-2 model showed only weak improvement over models with a single ecological parameter of COD-1, COD-4, or COD-5 without autocorrelation and the autocorrelated COD-3 (Table 2). Among models incorporating a second ecological parameter, weak model improvement was indicated by inclusion of CLD-0 with COD-2 without autocorrelation ($AIC_c = 94.5$; Table 2), although model fit did not differ from non-autocorrelated models of COD-2 with WS3-0 or COD-3 with CLD-0, or from autocorrelated CLD-0 with COD-2. Configurations with three ecological parameters that reduced the AIC_c value from the non-autocorrelated COD-2 with CLD-0 model included non-autocorrelated models of COD-2 and CLD-0 with either DCG-0 ($AIC_c = 92.6$) or WS3-0 ($AIC_c = 94.6$) and COD-3 with CLD-0 and DCG-0 ($AIC_c = 94.9$); and the autocorrelated COD-2 with CLD-0 and DCG-0, but AIC_c differences of <2 from the best two-parameter model suggested that model fits were not credibly different (Table 2). Models with four ecological parameters showed no improvement in AIC_c values.

Among models with the smallest AIC_c values for a given number of ecological parameters, the Pacific cod coefficient was consistently and strongly negative, ≤ -1.51 among the better fits within a parameter group, and exhibited reasonably good estimated precision (CVs generally ≤ 0.25; Table 3). The coefficient for cloud cover as a secondary ecological factor was weakly positive and, again, with reasonable precision ($\gamma = \sim 0.35$; CVs of 0.36-0.37; Table 3). There is weak evidence that either freshwater discharge (DCG-0) or wind speed cubed (WS3-0) are important, but there is also high uncertainty in these estimates.

Thus, it is apparent that Pacific cod is a primary component in the optimal model configuration. Pacific cod generally reduced overall variability by >20% compared to the base model with autocorrelation and no ecological factors (Table 4). Cloud cover may also be important, albeit to a lesser extent than Pacific cod; inclusion of cloud cover further reduced variability by about 8-10%. Inclusion of factors beyond these components is less definitive, with substantially reduced precision in the parameter estimates, suggesting increased likelihood of spurious correlations. On this basis, the optimal model included COD-2 and CLD-0 as ecological parameters in a lag-5 Ricker model without autocorrelation, although the consideration of these factors in an autocorrelated model cannot be ruled out.

Inclusion of ecological parameters resulted in several notable patterns in some parameter estimates. For example, with autocorrelation, per-capita productivity decreased from 0.38 to ≤0.11 for the 1964-1974 brood years (α_1) and increased substantially from 0.33 to >1.17 for the 1985-1999 brood years (α_3; Table 3). Density dependence increased with inclusion of ecological factors in autocorrelated models, but decreased

Table 3. Parameter estimates, and corresponding coefficients of variation (CV) for the (A) base model and selected models with and without autocorrelation and having (B) one, (C) two, or (D) three ecological parameters.

$\alpha 1$		$\alpha 2$		$\alpha 3$		β		ϕ		γ *parameter*		
Est.	CV	Est.	CV	Est.	CV	Est.	CV	Est.	CV	Effect	Est.	CV
Models with autocorrelation[a]												
A. Base model												
0.38	0.58	0.03	0.45	0.33	0.32	2.7×10^{-5}	1.10	0.45	0.27	None		
B. One ecological parameter												
0.10	0.55	0.03	0.32	1.42	0.40	4.3×10^{-5}	0.46	0.17	0.55	COD-2	−1.53	0.32
0.11	0.53	0.03	0.32	1.17	0.38	4.2×10^{-5}	0.46	0.16	0.95	COD-3	−1.39	0.23
C. Two ecological parameters												
0.08	0.60	0.02	0.36	1.61	0.44	5.2×10^{-5}	0.53	0.24	0.67	COD-2	−1.67	0.22
										CLD-0	0.33	0.36
0.09	0.58	0.03	0.35	1.29	0.40	4.3×10^{-5}	0.52	0.21	0.78	COD-3	−1.51	0.23
										CLD-0	0.32	0.37
D. Three ecological parameters												
0.06	0.62	0.02	0.38	1.70	0.44	3.9×10^{-5}	0.68	0.26	0.70	COD-2	−1.63	0.23
										CLD-0	0.38	0.32
										DCG-0	−0.27	0.45
Models without autocorrelation												
B. One ecological parameter												
0.09	0.83	0.02	0.28	1.49	0.46	4.1×10^{-5}	0.44	NA		COD-2	−1.56	0.22
0.10	0.62	0.03	0.32	1.24	0.42	4.1×10^{-5}	0.44	NA		COD-3	−1.44	0.22
C. Two ecological parameters												
0.07	0.59	0.02	1.70	0.29	0.37	3.5×10^{-5}	0.46	NA		COD-2	−1.70	0.17
										CLD-0	0.30	0.42
0.08	0.52	0.03	0.22	1.40	0.47	3.5×10^{-5}	0.43	NA		COD-3	−1.59	0.17
										CLD-0	0.30	0.38
D. Three ecological parameters												
0.05	0.72	0.02	0.29	1.81	0.33	2.6×10^{-5}	0.58	NA		COD-2	−1.65	0.19
										CLD-0	0.35	0.35
										DCG-0	−0.29	0.54
0.06	0.59	0.02	0.27	1.63	0.37	3.0×10^{-5}	0.50	NA		COD-2	−1.82	0.17
										CLD-0	0.24	0.50
										WS3-0	0.28	0.56

[a] Parameters are from Equation 1 in the text. The number following the dash in the γ parameter indicates the red king crab age, in years, when the parameter effect is assumed to occur. For example, COD-2 represents the correlation of Pacific cod biomass lagged to affect age-2 crab. Brood years are 1964-1974 for α_1, 1975-1984 for α_2, and 1985-1999 for α_3.

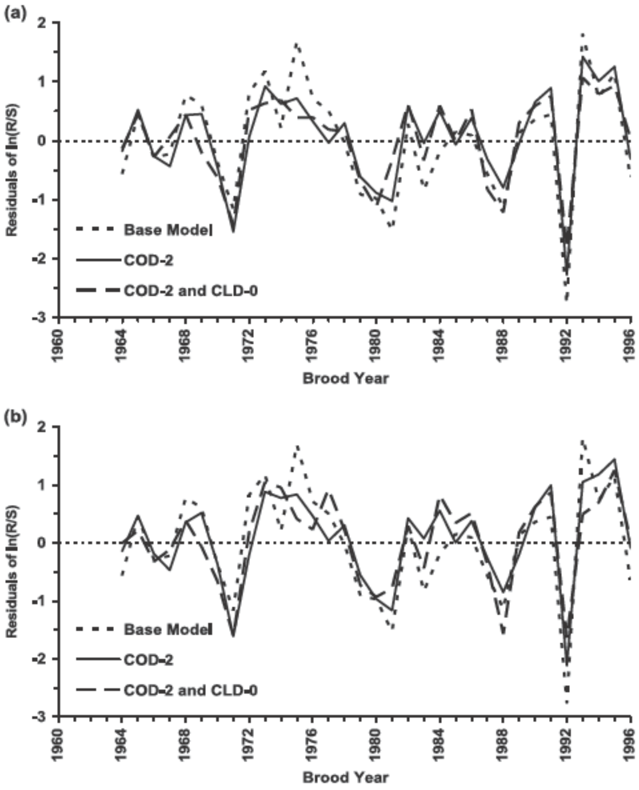

Figure 4. Trends in ln(R/S) residuals among models (a) with and (b) without autocorrelation configured with no (autocorrelated base model), one (COD-2), and two (COD-2 and CLD-0) ecological parameters.

or was unchanged in models without autocorrelation. Greater productivity and density dependence are exhibited in a slightly more pronounced dome-shape to the S-R curves with additional ecological factors (Fig. 3). The autocorrelation coefficient also decreased from 0.45 to ≤0.26 by including ecological factors. It is apparent the ecological factors provided substantial explanatory associations in models lacking an autocorrelation parameter (Fig. 4). Finally, peak spawning biomass, S_p, declined substantially from 37.6 million males for the base model to a range of 21.7-28.5 million males in most models that included ecological parameters, although models with three ecological parameters and lacking autocorrelation still had relatively high S_p values (Table 4; Fig. 3).

Trends in ln(R/S) residuals show relatively small, incremental improvement in model fit by inclusion of one and two ecological parameters (Fig. 4). In particular, augmenting the base

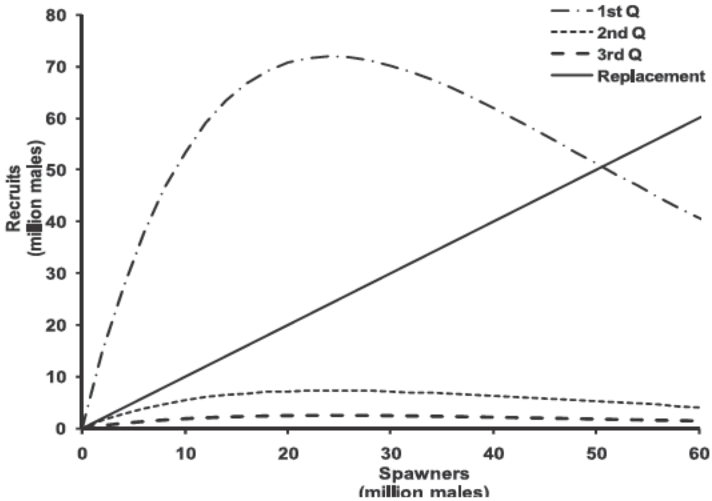

Figure 5. Spawner recruit curves based on α and β for the 1985-1999 brood years and showing separate curves for three quartiles of the Pacific cod anomaly distribution (inset shows origin).

model with a single ecological parameter of COD-2 reduced positive residuals in the late 1960s and mid 1970s and negative residuals during the 1980s. Inclusion of CLD-0 as a second parameter improved model fit for only a few brood years, such as 1969 and 1981, but residuals also increased in some years, such as 1988.

Based on the prevalence of Pacific cod as an ecological association, and given greater complexities and uncertainties with the inclusion of additional ecological factors, we ran the maximum sustained catch (MSC) analysis based on the COD-2 model (Table 5; Fig. 5). Results showed substantial variability in estimated stock abundance associated with maximum sustained catch under the 1985-1999 productivity and density dependence parameters. Essentially, there is no surplus production available at the median and third quartile of the distribution of Pacific cod anomalies. However, substantial catch is available if the first quartile of Pacific cod anomalies is assumed. Productivity at low stock abundance is substantial for the first quartile of Pacific cod anomalies, marginally above replacement for the second quartile, and insufficient to attain replacement for the third quartile (Fig. 5 inset).

Discussion

Previous studies found a strong relationship between red king crab recruitment and ecological factors operating on the larval crab stage

Table 4. Number of estimated parameters (*p*), residual sums of squares (RSS), RSS ratio, peak spawner abundance (S_p), and peak recruit abundance (R_p) for brood years 1964-1974, 1975-1984, and 1985-1999 for selected models (A) with and (B) without autocorrelation among different tiers of ecological effects.

A. Autocorrelated models

Ecological parameters	*p*	*RSS*	Reduction[a]	S_p[b]	R_p[b] by brood year		
					1964-1974	1975-1984	1985-1999
Base	5	29.0	NA	37,586	14,386	1,066	12,276
COD-2	6	21.4	26.2%	23,367	5,117	257	2,591
COD-3	6	22.4	22.8%	23,555	5,156	256	2,628
COD-2,CLD-0	7	17.8	38.6%	21,698	4,874	245	2,392
COD-3,CLD-0	7	18.9	34.8%	23,035	4,957	251	2,564
COD-2, CLD-0, DCG-0	8	15.3	47.1%	25,828	5,018	275	2,809
B. Models without autocorrelation							
None	4	36.0	124.1%[c]	32,769	5,825	318	3,684
COD-2	5	22.1	24.0%	24,233	807	222	13,288
COD-3	5	22.9	21.0%	24,353	938	304	11,093
COD-2,CLD-0	6	18.9	34.7%	28,430	685	224	17,765
COD-3,CLD-0	6	19.8	31.9%	28,581	797	316	14,722
COD-2, CLD-0, DCG-0	7	16.4	43.6%	38,299	740	282	25,468
COD-2, CLD-0, WS3-0	7	17.3	40.3%	33,452	786	259	20,104

[a] Ratio of the residual sums of squares relative to the base model.

[b] S_p and R_p are measured in thousands of crab (i.e., 37,586 is 37.586 million crab).

[c] Represents an increase in the *RSS* over the base model.

(Zheng and Kruse 2000, 2003). In contrast, we found the most prominent factor around Kodiak Island to be a consistent and a strong negative relationship between age-3+ Pacific cod biomass in the Gulf of Alaska and post-larval red king crab, with the strongest association for age-2 crab (Table 4). Inclusion of Pacific cod anomalies, particularly COD-2 or COD-3, into the S-R model for Kodiak red king crab substantially improved model fit compared to other models considered with a single ecological parameter (Table 4). The COD-2 and COD-3 models also provided a better fit than our base model, an autocorrelated Ricker model

Table 5. Estimates of male spawners, S_m, recruits, R_m, and catch, C_m, in thousands of males, and the exploitation rate, μ_m, at maximum sustainable catch under assumed values of productivity and density dependence and at three quartiles of the distribution of Pacific cod biomass.

Parameter[a]	1st quartile	Median	3rd quartile
a	1.49	1.49	1.49
b	4.13×10^{-5}	4.13×10^{-5}	4.13×10^{-5}
COD-2	–1.09	0.38	1.07
γ	–1.56	–1.56	–1.56
a'	8.072	0.819	0.281
S_m	17,939	None	None
R_m	69,066	None	None
C_m	51,128	None	None
μ_m	0.711	None	None

[a] "None" substituted for nonsensical solutions (e.g., S_m or $R_m < 0$).

($AIC_c = 106.8$), similar to that in Bechtol and Kruse (2009b), but limited to brood years 1964-1999.

While the mechanism of a negative relationship between juvenile king crab and Pacific cod cannot be confirmed from our analysis, predation on juvenile crab is most likely. Shallow nearshore waters are particularly important as rearing habitat for early juvenile stages of red king crab, but at about 1-2 years after settlement, red king crab become less solitary and begin to form pods as they move from shallow nearshore environments around Kodiak to deeper waters. Although crab cannot be aged, growth of juvenile red king crab is believed to be approximately linear up to 60 mm CL for both males and females, with a mean length of 13 mm and 33 mm after the first and second years of life, respectively (McCaughran and Powell 1977). Juvenile king crab at these sizes would certainly be vulnerable to predation by Pacific cod and other predatory fishes, and crab at these and larger sizes would also be most vulnerable during the soft-shell phase of their molt. The majority of red king crab observed in cod stomachs in the eastern Bering Sea have been soft-shell adult females (Livingston 1989), indicating that cod can even prey on adult crab, if the crab are in soft-shell condition. Predation impacts on king crab likely intensified around Kodiak Island in response to the general increase in the predator biomass observed in the Gulf of Alaska during the 1970s (Hollowed and Wooster 1992, Anderson and Piatt 1999, Hare and Mantua 2000, Ciannelli et al. 2005). Pacific cod are just one member of the suite of groundfish species that increased in abundance at this time. However, there has been little documentation of predation on any king crab life stage (Albers and Anderson 1985, Livingston 1989, Yang 1993, Dew and McConnaughey

2005, Yang et al. 2006, Zheng and Kruse 2006). Blau (1986) noted that only 77 of the 12,443 Pacific cod stomachs examined during ADFG pot surveys around Kodiak during 1972-1983 contained king crab. The lack of evidence of fish predation may result from systematic biases in the collection of diet data due to several factors: (1) few groundfish stomachs were historically sampled in nearshore, shallow waters inhabited by juvenile crab; (2) predator stomachs have typically been sampled from deeper waters in summer, not during late winter to spring when most adult crab undergo ecdysis and are most vulnerable to predation; and (3) extensive collection of diet data in recent years occurred when red king crab abundance was extremely low relative to alternative prey. We suspect that the majority of predation on red king crab cohorts occurs at age-2 and age-3 when they attain sizes too large for protection by bryozoans, mussel beds, polychaete tubes, and similar-sized biogenic habitats occupied as glaucothoe and young-of-the-year crab (Loher and Armstrong 2000). King crab are likely most vulnerable to predation in soft-shell condition after molting, which occurs multiple times per year at these young ages. We further suspect that predation risk declines, both as crab attain larger sizes and as molting frequency declines to once annually.

A spatial analysis of pot survey data shows strong increases in relative abundance of Pacific cod in nearshore waters around Kodiak at a time when the king crab population drastically declined (Bechtol 2009). Moreover, as king crab abundance declined, the crab population concentrated into nearshore areas as the centers of preferred habitat (Johnson 1990), perhaps as a density-dependent response (MacCall 1990). Anderson et al. (1997) suggested that warmer temperatures allowed cod to remain in inshore bays throughout winter, instead of migrating offshore as nearshore areas cooled. If true, this would have increased potential predator-prey interactions between these two species during the winter months. In the eastern Bering Sea, similar increases in near-bottom temperature resulted in changes to the spatial distribution of Pacific cod to the apparent detriment of the snow crab population, and the biomasses of yellowfin sole *Limanda aspera* and Pacific cod show significant inverse relationships with red king crab recruitment (Zheng and Kruse 2006). In the Gulf of St. Lawrence, Atlantic cod *Gadus morhua* fed on snow crab in the first four years post-settlement (Chabot et al. 2008).

Changes in Pacific cod biomass and distribution have also been linked to the collapse of northern shrimp *Pandalus borealis* populations in the Gulf of Alaska. For instance, a retrospective analysis found a strong increasing trend of natural mortality resulted in the crash of the northern shrimp stock in Kachemak Bay during the 1980s (Fu et al. 1999). A corresponding trend of increasing trawl survey catches of cod further suggests that intensified cod predation was likely responsible for the shrimp decline in Kachemak Bay (Fu and Quinn 2000). An examination of Pacific cod stomachs led Albers and Anderson (1985) to conclude that cod predation contributed to the lack of recovery of depressed stock of northern shrimp in Pavlof Bay, Alaska. Similarly, an analysis of North Atlantic stock found Atlantic cod biomass was positively related to ocean temperature and negatively related to northern shrimp biomass (Worm and Myers 2003).

Nevertheless, cod predation alone cannot explain Kodiak red king crab population dynamics (Collie and Kruse 1998, Orensanz et al. 1998). We suggest that increased Pacific cod biomass in the Kodiak area in the early 1980s further compromised an already depleted red king crab population. Very high harvest rates in the late 1960s were associated with a stock decline due to both direct fishery removals and subsequent reproductive failure associated with sex ratios skewed toward females (Bechtol and Kruse 2009a). Undoubtedly, environmental factors also played a role in the recruitment failures. Thus, the late 1970s increase in Pacific cod biomass, coupled with a temperature-driven nearshore shift in cod spatial distribution, likely increased crab predation, thereby exacerbating a decline in crab abundance originally triggered by fishing and other causes.

Although ecosystem response to environmental forcing is likely nonlinear (Hare and Mantua 2000), other evidence exists for roles of climate-driven changes in the physical environment on groundfish populations in the Gulf of Alaska and eastern Bering Sea. For example, Quinn and Niebauer (1995) found strong pollock recruitment in the eastern Bering Sea to be correlated with above normal air and bottom temperatures and reduced sea ice cover, factors that promote zooplankton production. Although sea ice is not a factor in the Gulf of Alaska, the pre-1976 regime was associated with low sea surface temperature and low biomasses of predatory groundfish, such as flatfishes and Pacific cod. During and immediately after the 1976 regime shift, a period of high sea surface temperature favored strong zooplankton production in the Gulf of Alaska, supporting strong pollock recruitment in the presence of continued low groundfish predation (Bailey 2000, Ciannelli et al. 2005). However, high zooplankton populations seem to have been detrimental to phytoplankton needed for first-feeding red king crab zoea, resulting in reduced crab recruitment, particularly beginning in the early 1980s (Fig. 2). Although sea surface temperature declined in the decade following the regime shift, ecosystem “maturation” resulted in increased biomass of predatory fishes, particularly Pacific halibut, arrowtooth flounder, flathead sole *Hippoglossoides elassodon*, and Pacific cod (Bailey 2000), further constraining recruitment. Since the 1989 regime shift, the ecosystem has been generally characterized by moderate sea surface temperature, but relatively high groundfish biomass (Hare and Mantua 2000, Mueter and Norcross 2002, Ciannelli et al. 2005). Thus, ocean temperature changes associated with the 1976 regime shift had substantial, but opposite, effects on the prey of red king crab compared to groundfishes, including Pacific cod. As a result, a compromised feeding environment for larval red king crab was coupled with intensified groundfish predation on juvenile crab.

Crab predators are not limited to groundfish species, although data on populations such as marine mammals are also sparse. For example, sea otters *Enhydra lutris* have been observed feeding on red king crab and Kvitek et al. (1992) documented restructuring of benthic habitat by an expanding sea otter distribution along the north shore of Kodiak Island in the 1980s; the intensity of habitat disturbance was related to the temporal gradient of sea otter occupancy. However, there are few long-term data on the spatial distribution and abundance of sea otters around Kodiak.

We also considered the greater scale of benthic habitat loss or restructuring, and corresponding crab discard mortality, associated with the bottom trawl fishery for shrimp that operated in the Kodiak area from the 1950s until 1986, a mechanism suggested to us by several former participants in the Kodiak crab fishery. However, analysis of the relationship between the shrimp fishery and red king crab recruitment was inconclusive due to the inconsistency in the data time series. Other fisheries historically occurred in the Kodiak area, notably the foreign fisheries targeting groundfish prior to implementation of the Exclusive Economic Zone in the mid 1970s. These fleets could legally fish up to 12 nautical miles from shore and likely had an impact on benthic habitat and organisms, including red king crab, but records on catch and discards are difficult to obtain and were not included in our analysis.

Secondary ecological effects of air temperature, wind speed cubed, freshwater discharge, and sea surface temperature, showed no improvement over the model with a single ecological factor of COD-2 (Table 2). However, improved model fit with the inclusion of cloud cover as a secondary ecological factor was somewhat unexpected, because of the seemingly contradictory effects of cloud cover: reduced cloud cover increases the incidental light to the benefit of photosynthetic phytoplankton, but also increases the water temperature to the benefit of zooplankton (Weingartner 2007). A possible interpretation is that a reduction in zooplankton predation pressure has a greater effect than the reduction in light for the phytoplankton serving as forage for crab larvae. Another possibility is that increased cloud cover reduced zooplankton predation pressure on crab larvae. Of course, the apparent effect of cloud cover could also be spurious. In any case, inclusion of cloud cover led to a minor improvement over our best single ecological parameter models based on cod biomass.

The role of currents on larval advection and/or retention may be important, but they are difficult to study in the Kodiak archipelago. The Alaska Coastal Current (ACC) is the primary ocean current in the area, but bathymetric features such as troughs and canyons can also affect localized flow patterns, including the formation of cyclonic eddies within embayments that facilitate larval retention (Allen et al. 2001, Stabeno et al. 2004). Increased freshwater discharge in the Gulf of Alaska not only increases mean current flow that can sweep larvae away from nursery areas, but also promotes eddies and other current instabilities that could lead to greater retention of crab larvae (Okkonen et al. 2003, Weingartner 2007). Ocean fronts (Logerwell et al. 2007) are another consideration, but their role, if any, on larval king crab retention or advection has yet to be investigated. In summary, it is not clear whether increased flow in the ACC is deleterious or advantageous to crab larval retention. Such ocean features tend to be highly localized, spatially and temporally, and a detailed analysis of their potential effects on long-term population recruitment is beyond the scope of our present study.

Our study is not without typical statistical limitations. Although the use of AIC_c values provides a means to compare the relative fit of competing models (Burnham and Anderson 2004), our analysis found that several model configurations produced similar AIC_c values. Pacific cod, particularly COD-2, was an important ecological factor in all models, and a large portion of the more complex models included CLD-0; the benefits of including other ecological factors were less clear. Given these aspects, combined with the recognition that a simpler model is less prone to spurious associations, a preferred model including COD-2 and CLD-0 is justified.

We also note that interpretation of the best model depends on the candidate models selected for comparison (Peterson et al. 2003). For example, had we not considered cod in our candidate set, the best fit with a single ecological parameter was POL-0, also showing strong improvement over our base model. Populations of pollock and Pacific cod both exhibited substantial increases in biomass in the Gulf of Alaska following the mid 1970s regime shift, but the subsequent ecosystem maturation appears to have had a somewhat negative effect on pollock versus a benefit on Pacific cod based on biomass trends (Bailey 2000, Ciannelli et al. 2005). As a result, biomass trends for these two species are consistent for some years and opposite for other years in the time period considered by our analysis, perhaps explaining why Pacific cod provided a better fit than pollock.

Alternative data sets beyond those we considered may have provided a stronger inference into red king crab population dynamics around Kodiak Island. But we also recognize that consideration of additional variables increases the potential for spurious associations. We have attempted to include variables that are biologically meaningful, subject to the limitation of being a reasonably long time series. Whereas several studies have explored relationships between various ecosystem components in the Gulf of Alaska (Hollowed and Wooster

1992, Anderson and Piatt 1999, Hare and Mantua 2000, Ciannelli et al. 2005, Mueter et al. 2007), the lack of long-term data sets has limited such analyses. Availability of long-term ecological data sets similarly constrained our analysis of Kodiak red king crab, a population that was fished heavily in the 1960s during a period of relatively high crab abundance (Fig. 2). There is a paucity of oceanographic observations prior to the 1970s, and red king crab abundance was already well into decline after oceanographic and stock assessment data were being systematically collected. In addition, the effect of short-term events on red king crab recruitment is difficult to assess but cannot be ruled out. For example, the 1964 Good Friday earthquake caused substantial damage to intertidal and shallow subtidal communities throughout southcentral Alaska (Spies 2007), but the impact on red king crab recruitment is difficult to assess.

In summary, we found a strong negative relationship between Gulf of Alaska biomass of age 3+ Pacific cod and recruitment of Kodiak red king crab, with the postulated causative mechanism being predation. Incorporation of Pacific cod biomass into the stock-recruit model substantially reduced the crab abundance estimated to produce peak recruitment (Table 4). Taken together, our research suggests the complicit effects of at least three key factors in the decline of Kodiak red king crab and the failure to recover: (1) stock depletion from high harvest rates in the late 1960s (Bechtol and Kruse 2009a); (2) compromised reproductive potential associated with resultant low stock size (Bechtol and Kruse 2009a,b); and (3) intensified predation owing to increased biomass of cod (and perhaps other groundfish predators) beginning in the 1980s and nearshore shifts in both the crab serving as prey (density-dependent response) and their groundfish predators (temperature response). The potential additional mechanism indexed by cloud cover is less clear and requires further investigation; it may signal a switch in conditions favoring zooplankton (prey of groundfish larvae) over phytoplankton (diatom prey of red king crabs), but alternatively it may be spurious. Thus, we offer here a relatively coherent scenario of the role of fishing, climate, and ecological factors on the decline of Kodiak red king crab as a point of departure for future investigations.

Our research has implications on ecosystem approaches to fishery management in the Gulf of Alaska. Namely, fishery management should particularly include the apparent negative influence of Pacific cod on red king crab recruitment. Experiments are under way to evaluate the ability of crab hatcheries to rehabilitate red king crab in the Gulf of Alaska. The effectiveness of such rehabilitation efforts, if implemented, may depend on the ability of enhancement efforts to increase king crab production sufficiently to swamp predation, which appears to be a current bottleneck to crab recovery. Although cod biomass has been declining since the mid 1980s, warm temperatures continue to favor a nearshore geographic distribution of these predators, perhaps to the detriment of the recovery of red king crab stocks.

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References

Albers, W.D., and P.J. Anderson. 1985. Diet of Pacific cod, *Gadus macrocephalus*, and predation on the northern pink shrimp, *Pandalus borealis*, in Pavlof Bay, Alaska Fish. Bull. 83:601-610.

Allen, S.E., C. Vindeirinho, R.E. Thomson, M.G.G. Foreman, and D.L. Mackas. 2001. Physical and biological processes over a submarine canyon during an upwelling event. Can. J. Fish. Aquat. Sci. 58:671-684. doi:10.1139/cjfas-58-4-671

Anderson, P.J., and J.F Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar. Ecol. Prog. Ser. 189:117-223. doi:10.3354/meps189117

Anderson, P.J., J.E. Blackburn, and B.A. Johnson. 1997. Declines of forage species in the Gulf of Alaska, 1972-95, as indicator of regime shift. In: Forage fishes in marine ecosystems. Alaska Sea Grant, University of Alaska Fairbanks, pp. 531-543.

Armstrong, D.A., T.C. Wainwright, G.C. Thomas, P.A. Dinnel, and H.B. Andersen. 1993. Taking refuge from bycatch issues: Red king crab *(Paralithodes camtschaticus)* and trawl fisheries in the eastern Bering Sea. Can. J. Fish. Aquat. Sci. 50:1993-2000. doi:10.1139/f93-223

Bailey, K.M. 2000. Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. Mar. Ecol. Prog. Ser. 198:215-224. doi:10.3354/meps198215

Bechtol, W.R. 2009. Abundance, recruitment, and environmental forcing of Kodiak red king crab. Ph.D. thesis, University of Alaska Fairbanks. 226 pp.

Bechtol, W.R., and G.H. Kruse. 2009a. Reconstruction of historical abundance and recruitment of red king crab during 1960-2004 around Kodiak, Alaska. Fish. Res. 100:86-98. doi:10.1016/j.fishres.2008.09.003

Bechtol, W.R., and G.H. Kruse. 2009b. Analysis of a stock-recruit relationship for red king crab off Kodiak Island, Alaska. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 1:29-44.

Bienfang, P.K., and D.A. Ziemann. 1995. APPRISE: A multi-year investigation of environmental variation and its effects on larval recruitment. In: R.J. Beamish (ed.), Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. 121:483-487.

Blau, S.F. 1986. Recent declines of red king crab (*Paralithodes camtschatica*) populations and reproductive conditions around the Kodiak archipelago, Kodiak. In: G.S. Jamieson and N. Bourne (eds.), North Pacific Workshop on Stock Assessment and Management of Invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92:360-369.

Broderson, C.C., P.M. Rounds, and M.M. Babcock. 1990. Diet influences cannibalism in laboratory-held juvenile red king crab *(Paralithodes camtschatica)*. In: Proceedings of the International King and Tanner Crab Symposium. Alaska Sea Grant, University of Alaska Fairbanks, pp. 377-382.

Burnham, K.P., and D.R. Anderson. 2004. Multimodal inference: Understanding AIC and BIC in model selection. Sociol. Methods Res. 33:261-304. doi:10.1177/0049124104268644

Chabot, D., B. Sainte-Marie, K. Briand, and J.M. Hanson. 2008. Atlantic cod and snow crab predator-prey size relationship in the Gulf of St. Lawrence, Canada. Mar. Ecol. Prog. Ser. 363:227-240. doi:10.3354/meps07384

Ciannelli, L., K.M. Bailey, K.-S. Chan, A. Belgrano, and N.C. Stenseth. 2005. Climate change causing phase transitions of walleye pollock *(Theragra chalcogramma)* recruitment dynamics. Proc. R. Soc. B 272:1735-1743. doi:10.1098/rspb.2005.3136

Collie, J.S., and G.H. Kruse. 1998. Estimating king crab (*Paralithodes camtschaticus*) abundance from commercial catch and research survey data. In: G.S. Jamieson and A. Campbell (eds.), Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Can. Spec. Publ. Fish. Aquat. Sci. 125:73-83.

Cooney, T. 2007. The marine production cycle. In: R.B. Spies (ed.), Long-term ecological change in the northern Gulf of Alaska. Elsevier, pp. 47-60.

Dew, C.B., and R.A. McConnaughey. 2005. Did trawling on the broodstock contribute to the collapse of Alaska's king crab? Ecol. Appl. 15:919-941. doi:10.1890/03-5231

Efron, B., and R.J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York. 456 pp.

Fu, C., and T.J. Quinn II. 2000. Estimability of natural mortality and other population parameters in a length-based model: *Pandalus borealis* in Kachemak Bay, Alaska. Can. J. Fish. Aquat. Sci. 57: 2420-2432. doi:10.1139/cjfas-57-12-2420

Fu, C., T.J. Quinn II, and M.D. Adkison. 1999. Retrospective projection using Monte Carlo simulation: An application of a length-based model to Kachemak Bay pink shrimp. In: Forage fishes in marine ecosystems. Alaska Sea Grant, University of Alaska Fairbanks, pp. 59-77.

Gray Jr., G.W., and R.J. Simon. 1965. Development of the king crab fishery off Kodiak Island. Alaska Department of Fish and Game, Inf. Leafl. 52. 15 pp.

Hare, S.R., and N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. 47:103-145. doi:10.1016/S0079-6611(00)00033-1

Hollowed, A.B., and W.S. Wooster. 1992. Variability of winter ocean conditions and strong year classes of Northeast Pacific groundfish. ICES Mar. Sci. Symp. 195:433-444.

Jackson, D.R., and M.P. Ruccio. 2003. Kodiak, Chignik, and south peninsula shrimp fisheries and their management: A report to the Alaska Board of Fisheries. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Rep. 4K03-7:31.

Johnson, B.A. 1990. Red king crab catch per unit effort and spatial distribution. In: Proceedings of the Section on Statistical Graphics. American Statistical Association, Alexandria, pp. 165-172.

Kvitek, R.G., J.S. Oliver, A.R. DeGange, and B.S. Anderson. 1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. Ecol. 73:413-428. doi:10.2307/1940749

Livingston, P.A. 1989. Interannual trends in Pacific cod, *Gadus macrocephalus*, predation on three commercially important crab species in the eastern Bering Sea. Fish. Bull. 87:807-827.

Logerwell, E.A., P.J. Stabeno, C.D. Wilson, and A.B. Hollowed. 2007. The effect of oceanographic variability and interspecific competition on juvenile pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*) distributions on the Gulf of Alaska shelf. Deep-Sea Res. II 54:2849-2868. doi:10.1016/j.dsr2.2007.08.008

Loher, T. 2001. Recruitment variability in southeast Bering Sea red king crab (*Paralithodes camtschaticus*): The role of early juvenile habitat requirements, spatial population structure, and physical forcing mechanisms. Ph.D. thesis, University of Washington. 436 pp.

Loher, T., and D.A. Armstrong. 2000. Effects of habitat complexity and relative larval supply on the establishment of early benthic phase red king crab (*Paralithodes camtschaticus* Tilesius, 1815) populations in Auke Bay, Alaska. J. Exp. Mar. Biol. Ecol. 245:83-109. doi:10.1016/S0022-0981(99)00157-4

MacCall, A.D. 1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle.

McCaughran, D.A., and G.C. Powell. 1977. Growth model for Alaska king crab *(Paralithodes camtschatica).* J. Fish. Res. Board Can. 34:989-995.

Mueter, F.J., and B.L. Norcross. 2002. Spatial and temporal patterns in the demersal fish community on the shelf and upper slope regions of the Gulf of Alaska. Fish. Bull. 100:559-581.

Mueter, F.J., J.L. Boldt, B.A. Megrey, and R.M. Peterman. 2007. Recruitment and survival of northeast Pacific Ocean fish stocks: Temporal trends, covariation, and regime shifts. Can. J. Fish. Aquat. Sci. 64:911-927. doi:10.1139/F07-069

Okkonen, S.R., T.J. Weingartner, S.L. Danielson, D.L. Musgrave, and G.M. Schmidt. 2003. Satellite and hydrographic observations of eddy-induced shelf-slope exchange in the northwestern Gulf of Alaska. J. Geophys. Res. 108:3033. doi:10.1029/2002JC001342

Orensanz, J.M., J. Armstrong, D. Armstrong, and R. Hilborn. 1998. Crustacean resources are vulnerable to serial depletion: The multifaceted decline of crab and shrimp fisheries in the Gulf of Alaska. Rev. Fish Biol. Fish. 8:117-176. doi:10.1023/A:1008891412756

Paul, A.J., J.M. Paul, and K.O. Coyle. 1989. Energy sources for first-feeding zoeae of king crab *Paralithodes camtschatica* (Tilesius) (Decapoda, Lithodidae). J. Exp. Mar. Biol. Ecol. 130:55-69. doi:10.1016/0022-0981(89)90018-X

Pengilly, D., and D. Schmidt. 1995. Harvest strategy for Kodiak and Bristol Bay red king crab and St. Matthew Island and Pribilof blue king crab. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Spec. Publ. 7. 18 pp.

Peterson, G.D., S.R. Carpenter, and W.A. Brock. 2003. Uncertainty and the management of multistate ecosystems: An apparently rational route to collapse. Ecol. 84:1403-1411. doi:10.1890/0012-9658(2003)084[1403:UATMOM]2.0.CO;2

Powell, G.C., and R.B. Nickerson. 1965. Aggregations among juvenile king crab *(Paralithodes camtschatica*, Tilesius) Kodiak, Alaska. Anim. Behav. 13:374-380. doi:10.1016/0003-3472(65)90058-8

Pyper, B.J., and R.M. Peterman. 1998. Comparison of methods to account for autocorrelation in correlation analysis of fish data. Can. J. Fish. Aquat. Sci. 55: 2127-2140. doi:10.1139/cjfas-55-9-2127

Quinn II, T.J., and R.B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York. 542 pp.

Quinn II, T.J., and H.J. Niebauer. 1995. Relation of eastern Bering Sea walleye pollock (*Theragra chalcogramma*) recruitment to environmental and oceanographic variables. Can. Spec. Publ. Fish. Aquat. Sci. 121:497-507.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559-623.

Royer, T.C., and C.E. Grosch. 2007. Update of a freshwater discharge model for the Gulf of Alaska. North Pacific Research Board Final Report 734. 12 pp.

Shirley, S.M., and T.C. Shirley. 1989. Interannual variability in density, timing and survival of Alaskan red king crab *(Paralithodes camtschatica)* larvae. Mar. Ecol. Prog. Ser. 54:51-59. doi:10.3354/meps054051

Spalinger, J.A. 1992. A brief synopsis of the history and development of the Kodiak king crab fishery. In: L.E. White and C. Nielsen (eds.), Proceedings of the International King Crab Rehabilitation and Enhancement Symposium. Alaska Department of Fish and Game, Fisheries Rehabilitation, Enhancement and Development Division Spec. Rep., pp. 5-8.

Spalinger, J.A., and D.R. Jackson. 1994. Annual management report for the shellfish fisheries of the Kodiak area, 1993. In: Annual management report for the shellfish fisheries of the westward region, 1993. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Regional Information Rep. 4K94-29, pp. 13-69.

Spies, R.B. 2007. Geophysical mechanisms. In: R.B. Spies (ed.), Long-term ecological change in the northern Gulf of Alaska. Elsevier, pp. 180-187.

Stabeno, P.J, N.A. Bond, A.J. Hermann, N.B. Kachel, C.W. Mordy, and J.E. Overland. 2004. Meteorology and oceanography of the northern Gulf of Alaska. Cont. Shelf Res. 24:859-897. doi:10.1016/j.csr.2004.02.007

Stevens, B.G., and J. Kittaka. 1998. Postlarval settling behavior, substrate preference, and time to metamorphosis for red king crab *Paralithodes camtschaticus*. Mar. Ecol. Prog. Ser. 167:197-206. doi:10.3354/meps167197

Thompson, G.G., and M.W. Dorn. 2005. Assessment of the Pacific cod stock in the Gulf of Alaska. In: Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, pp. 155-244. Accessed June 2010: http://www.afsc.noaa.gov/refm/docs/2005/GOAPcod.pdf.

Turnock, B.J., T.K. Wilderbuer, and E.S. Brown. 2005. Gulf of Alaska arrowtooth flounder stock assessment. In: Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, pp. 435-472.

Tyler, A.V., and G.H. Kruse. 1995. Report of the modeling workshop on year-class strength formation of red king crab. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Regional Information Rep. 5J95-11.

Tyler, A.V., and G.H. Kruse. 1996a. Process modeling and red king crab year-class strength in the Bristol Bay region of the Bering Sea. PICES Press 4(2):2-7.

Tyler, A.V., and G.H. Kruse. 1996b. Conceptual modeling of brood strength of red king crab in the Bristol Bay region of the Bering Sea. In: High latitude crabs: Biology, management, and economics. Alaska Sea Grant, University of Alaska Fairbanks, pp. 511-543.

Weaver, C.P., and V. Ramanthan. 1996. The link between summertime cloud radiative forcing and extratropical cyclones in the North Pacific. J. Clim. 9:2093-2109.

Weingartner, T. 2007. The physical environment of the Gulf of Alaska. In: R.B. Spies (ed.), Long-term ecological change in the northern Gulf of Alaska. Elsevier, pp. 12-47.

Worm, B., and R.A. Myers. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecol. 84:162-173. doi:10.1890/0012-9658(2003)084[0162:MAOCSI]2.0.CO;2

Yang, M-S. 1993. Food habits of the commercially important groundfishes in the Gulf of Alaska in 1990. NOAA Tech. Memo. NMFS-AFSC-22. 150 pp.

Yang, M-S., K. Dodd, R. Hibpshman, and A. Whitehouse. 2006. Food habits of groundfishes in the Gulf of Alaska in 1999 and 2001. NOAA Tech. Memo. NMFS-AFSC-164.

Zheng, J., and G.H. Kruse. 2000. Recruitment patterns of Alaskan crab and relationships to decadal shifts in climate and physical oceanography. ICES J. Mar. Sci. 57:438-451.

Zheng, J., and G.H. Kruse. 2003. Stock-recruitment relationships for three major Alaskan crab stocks. Fish. Res. 65:103-121. doi:10.1006/jmsc.1999.0521

Zheng, J., and G.H. Kruse. 2006. Recruitment variation of eastern Bering Sea crab: Climate-forcing or top-down effects? Prog. Oceanogr. 68:184-204.

Ziemann, D.A., L.D. Conquest, K.W. Fulton-Bennett, P.K. Bienfang. 1990. Interannual variability in the Auke Bay phytoplankton. In: D.A. Ziemann and K.W. Fulton-Bennett (eds.), APPRISE-Interannual variability and fisheries recruitment. The Oceanic Institute, Honolulu, pp. 129-170.

De Lestang, S., L.M. Bellchambers, N. Caputi, A.W. Thomson, M.B. Pember, D.J. Johnston, and D.C.Harris. 2010. Stock-Recruitment-Environment Relationship in a *Portunus pelagicus* Fishery in Western Australia. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.26

Stock-Recruitment-Environment Relationship in a *Portunus pelagicus* Fishery in Western Australia

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Abstract

Blue swimmer crab (*Portunus pelagicus*) fisheries in Western Australia have generally been considered robust to recruitment overfishing, as the minimum legal size for retention of these crabs in both the commercial and recreational crab fisheries are set well above the size at sexual maturity allowing crabs to spawn at least once before entering the fishery. However, the Cockburn Sound crab stock suffered a recruitment collapse, with three key factors: (a) the fishery is near the edge of this species distribution and hence vulnerable to environmental fluctuations; (b) a number of consecutive years of poor environmental conditions resulted in poor recruitments; and (c) high fishing pressure continued on these low recruitments. This study indicates that water temperatures at the start of the spawning season positively influence the strong stock-recruitment relationship for *P. pelagicus* in Cockburn Sound. Apparently, warm water temperatures at the onset of spawning result in the larger females producing additional broods of eggs, and therefore a far greater number of larvae over the short spawning season. This relationship produces catch predictions for this fishery a year ahead and provides information for the development of biological reference points for management.

Introduction

Large interannual variations in population size are common among crustaceans (Lipcius and van Engel 1990, Metcalf et al. 1995, Wahle et al. 2004). For those species that support fisheries, variation in population size is typically reflected in significant fluctuations in landings, which create uncertainty for managers and may consequently have an adverse effect on the livelihoods of commercial fishers (Zheng and Kruse 1999, Bellchambers et al. 2006).

Year-to-year variations in stock size are largely attributed to variations in recruitment (both larval and the emigration of adults) and fishing mortality (the removal of older, larger animals) (Ricker 1954, Beverton and Holt 1957). Although successful larval recruitment is reliant on adequate spawning biomass, the strength of this is usually influenced by various physical or biotic factors affecting the survivorship of both larval and juvenile stages prior to and after settlement (Cobb and Caddy 1989, Wahle 2003). For example, successful settlement of western rock lobster (*Panulirus cygnus*) pueruli along the coast of Western Australia is dependent on climatic conditions such as warm water temperatures, which influence growth/survival, and winds favorable to the transport of larvae toward the coast prior to settlement (Caputi et al. 2001).

Other environmental variables demonstrated to affect the survivorship and recruitment of decapods include water temperature (McConaugha et al. 1983), salinity (Anger et al. 1998), turbidity (Penn and Caputi 1986), habitat availability (Botero and Atema 1982), and oceanographic processes, including tidal velocities and prevailing currents (Goodrich et al. 1989, Caputi et al. 1995, Rabalais et al. 1995, Lee et al. 2004, Queiroga et al. 2006). Although recruitment may be influenced by any one of these environmental variables, the ability to model the relationship, and the relevance of the relationship to the management of the fishery, will be dictated by the strength of the recruitment correlation (Walters and Collie 1988, Basson 1999).

Water temperature has been implicated as an important factor in the majority of the recruitment-environment relationships and is often robust enough to persist over substantial time frames (Caputi et al. 1995, Uphoff 1998). This is particularly true of stocks located near the latitudinal limit of species distributions, where water temperatures can be outside the optimal range for successful recruitment (Myers 1998). Water temperature may affect recruitment in a variety of ways. For example, elevated water temperatures typically have a positive effect on decapod recruitment by accelerating larval development and reducing the duration of the larval phase and larval mortality (Bryars and Havenhand 2006, Fisher 2006). Elevated water temperatures prior to spawning may also directly affect the timing of larval release by controlling gonad development, mating, and the timing of spawning (Rosenkranz et al. 2001) as well as the larval habitat through changes to the abundances of larval foods and predators.

The blue swimmer crab (*Portunus pelagicus* [Linnaeus]) is distributed throughout the shallow marine and estuarine waters of the Indo-Pacific. Although predominantly a tropical or subtropical species, *P. pelagicus* is also found as far south as the temperate waters of southern Australia and differing environments throughout its large latitudinal range (26°N–34°S) have a major influence on its reproductive biology. de Lestang et al. (2003a) demonstrated that the spawning season of *P. pelagicus* in Shark Bay, where water temperatures remain above 18°C for a substantial part of the year, is considerably more protracted (spawns year-round) than in the temperate waters of Cockburn Sound where the spawning season is restricted to spring and summer. They suggested that water temperatures have a significant influence on egg production in blue swimmer crabs, and therefore the timing and longevity of the spawning period. Additionally, in the temperate waters of South Australia, Bryars and Havenhand (2006) demonstrated increased survivorship of *P. pelagicus* larvae at temperatures over 19°C and concluded that post-larval settlement would be greatest during abnormally warm summers. This highlights the influence water temperature can have on the life cycle of these crabs. It can affect the timing of spawning, which influences egg release times and the environment into which the larvae are released. Water temperatures during the larval cycle dramatically influence the length of larval life and therefore survival and the timing of juvenile recruitment, which can then impact on the ability of juvenile crabs to mature and mate the following year (Yatsuzuka 1962). Therefore, water temperatures during one only part of the life cycle can significantly alter population size and structure over a far greater timeframe.

Cockburn Sound, situated 30 km southwest of Perth, Western Australia (WA), was the second largest of the four main blue swimmer crab fisheries in WA. Commercial catch of blue swimmer crabs from Cockburn Sound is characterized by high interannual variability, ranging between 84 and 362 t from 1989/90 to 2004/05. Cockburn Sound, which is close to the Perth metropolitan area, also supports an important recreational crab fishery. Recreational surveys in the last 10 years have indicated an annual catch between 18 and 23 t. Although the variability in catch has been attributed to recruitment success (Bellchambers et al. 2006), the specific factors responsible for variation in recruitment strength have yet to be identified.

Blue swimmer crab fisheries in Western Australia have generally been considered robust to recruitment overfishing as the minimum legal size for the Cockburn Sound fishery for both the commercial and recreational crab fishery (130 and 127 mm carapace width [CW], respectively) are set well above the size at sexual maturity (98 mm CW) allowing crabs to spawn at least once before entering the fishery (de Lestang et al. 2003a). However, an extremely low catch (53 t) from high levels of effort in 2005/06, which signified high exploitation and the possibility of recruitment-overfishing, prompted managers to close the Cockburn Sound fishery for three seasons (2006/07, 2007/08 and 2008/09). The impact a management response such as this can have on the livelihoods of fishers and recreational interests of fishers highlights the pressing need for understanding the cause of the recruitment decline and improved management of the fishery.

The aim of the present study was to determine the combination of spawning stock and environmental effects that contributed to the collapse of this seemingly robust stock to enable an assessment of whether other similar fisheries may also be vulnerable.

Methods

Study site

Cockburn Sound (32.10°S, 115.43°E) is an embayment about 15 km long by 10 km wide and around 100 km^2 in area (Fig. 1).

Fishery-independent sampling

Crabs were sampled in Cockburn Sound using a small otter trawl net (tri-net), which was 5 m wide, 0.5 m high, and 5 m long, and had 51 mm mesh in the wings and 25 mm mesh in the bunt. The bridle was 13 m long, while the warp length was varied with water depth according to the equation, warp length = water depth × 3.5. For each replicate trawl, the net was towed at a speed of 3.5 km per hour for a distance of 750 m. A net efficiency factor was incorporated to adjust the effective spread of the net on the seabed (0.6 × net headrope length in meters) (de Lestang et al. 2003c). The area trawled at each site was then calculated by multiplying the distance covered by the effective net spread (de Lestang et al. 2003b). The otter trawl was used to collect *P. pelagicus* from three randomly spaced replicate sties in each of three separate areas of Cockburn Sound—the northern, middle, and southern portions of this embayment (Fig. 1), between April 1998 and May 2008. Although the sampling program was conducted in two separate periods due to changes in funding, the methodology and sampling was kept consistent to make the results comparable between the periods. The first sampling period was between April 1998 and March 2000 when sampling was conducted during hours of daylight on a monthly basis. The second sampling period was January to May in the seven years between 2002 and 2008 when each site was trawled both during the day and at night on a fortnightly basis. Each site was 1,000 m × 250 m

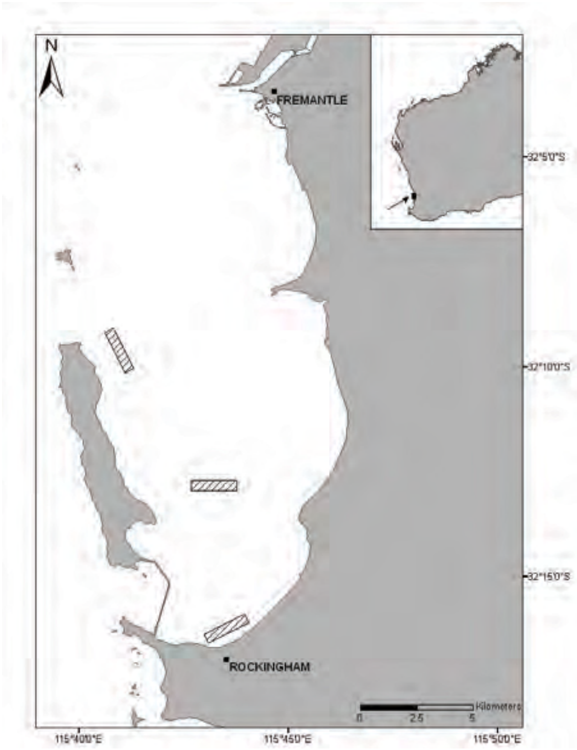

Figure 1. Map of Cockburn Sound, Western Australia. Cross-hatched boxes represent research trawling locations.

and was oriented in a southwest-northeast direction to accommodate local weather and sea conditions. The substrate at each site consisted of sparsely vegetated sand and silt, in depths ranging between 17 and 24 m. Additional fishery-independent trawl samples of *P. pelagicus* were obtained from opportunistic sampling conducted annually using a research trawler with twin 20 fm nets.

The carapace width (CW), the distance between the tips of the two lateral spines of the carapace, of each crab was recorded to the nearest millimeter. In addition, the crabs were sexed and the presence or absence of eggs recorded (see de Lestang et al. 2003a for more details).

Commercial catch monitoring

Monitoring of the commercial catch began in January 1999 and continued until June 2006. During this program, research staff joined three commercial "crab-trapping" vessels (represents approximately 20% of the fleet) for a day in each month of the fishing season (December-

September) to record details of the catch. When commercial fishing ceased in late 2006 due to the closure of the fishery, "commercial" catch monitoring was continued (since January 2007) via the charter of commercial vessels. These vessels were directed to fish in their normal pattern, and their catch was monitored and subsequently returned to the water.

Standardized egg production index

An index of egg production (*EPI*) for Cockburn Sound was developed using data derived from the three sampling methods (small and large research survey trawls and commercial trap-based sampling). An index of egg production is the most appropriate measure of breeding stock abundance as it directly relates to the abundance of eggs/larvae produced by the stock. Measures such as female abundance fail to account for the nonlinear relationship between crab size and eggs produced.

Each female crab captured during fishery-independent trawling and commercial crab-trap sampling was assigned a total potential egg production based on a batch frequency (*BFr*) to *CW* relationship ($BFr = 1+2/[1+\exp(-\log[19](CW-113.7)/13.8])$) and a batch fecundity (*BFe*) –*CW*($\log Bfe = 1.821 \log CW + 3.2862$) relationship (de Lestang et al. 2003a). For example, the above equations estimate a 100 mm CW female *P. pelagicus* will produce an average of 1.12 batches of eggs, each totaling 117,270 eggs in a spawning season, which equates to a total potential egg production of 129,230 eggs per season. This relationship was used to convert female catch rates (female crabs per m^2 trawled or per potlift, depending on the survey method) into potential egg catch rates (eggs per m^2 trawled or per potlift). A generalized linear model (GLM) was then used to produce a seasonal (July-June) potential egg catch rate estimate (*EPI*) (a GLM was used to standardize for an unbalanced sampling design and sampling methodology). The samples were also restricted to water depths ≥15 m, since the majority of breeding sized females are found in these water depths (Potter et al. 2001). The average egg production per sample (per m^2 or per trap) was log transformed to remove skewness from the data (Clark and Warwick 2001). Method of capture (small and large research trawl and crab trap), season, and month were treated as factors in the GLM with all two-way interactions. Back transformation of least-squares means of the seasonal estimates were used as the standardized *EPI*.

Water temperature

The monthly water temperature data incorporated into the stock-recruitment relationship was recorded at Warnbro Sound (10 km southwest of Cockburn Sound) as part of a survey of western rock lobster *Panulirus cygnus* recruitment conducted since 1984. Two replicate water temperature measurements are collected monthly using a mercury thermometer

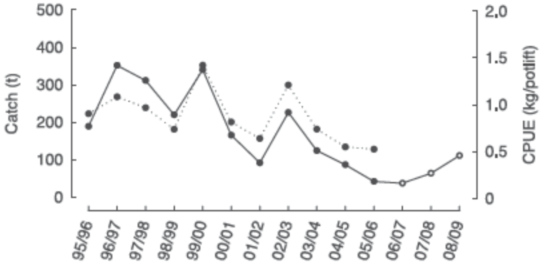

Figure 2. Annual commercial catch and CPUE of *Portunus pelagicus* in Cockburn Sound between 1995/96 and 2005/06. Estimated commercial catch (open circles) derived from a recruitment-catch relationship (Bellchambers et al. 2006) have been added for years when Cockburn Sound was closed to fishing.

from a boat in a standard location toward the center of the embayment at a depth of about 2 m. For the few years when both measurements are available Warnbro Sound water temperatures were found to be very similar to those experienced by crabs in Cockburn Sound ($r^2 = 0.86$, $P < 0.001$, d.f. = 31, data not shown).

Stock-recruitment relationship

A modified Beverton and Holt (1957) stock-recruitment equation, $Catch = (EPI \times \exp[Wtemp \times -a])/(b+c \times EPI)$, was used to describe the relationship between spawning stock ($EPI_{t/t+1}$), subsequent recruitment strength ($commercial\ catch_{t+1/t+2}$), and water temperatures (*Wtemp*) just before, during and after peak egg production, i.e., May_t to April_{t+1}. Commercial catch was used as a proxy for recruitment strength since the seasonal commercial catch (December to September) is mainly derived from a single 1+ year class (de Lestang et al. 2003b, Bellchambers et al. 2006). Although CPUE in the Cockburn Sound commercial blue swimmer crab fishery has followed similar patterns to total landings during recent years (Fig. 2), the use of annual landings as a measure of crab abundance was considered more appropriate than CPUE. This is because the fishery underwent major gear and effort changes in the early 1990s, and as such a consistent CPUE measure cannot be determined. Commercial catch on the other hand was considered a good proxy of settlement one year previously, since the legal population (mainly 1 year old crabs) are substantially depleted each fishing season to the point that fishing becomes no longer economically viable.

The relationship between spawning stock, recruitment, and water temperature in months before, during, and after peak egg production

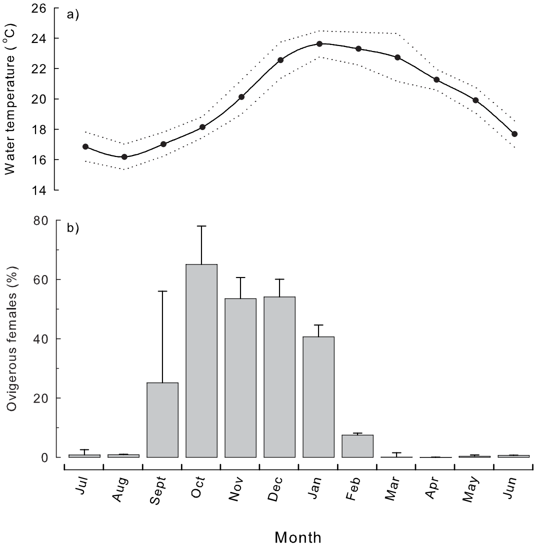

Figure 3. (a) Mean monthly water temperatures (solid line) (±1SD, dotted lines) from Warnbro Sound between 1996 and 2008. (b) Mean monthly percentage (+1SD) of ovigerous female *Portunus pelagicus* among all adult female *P. pelagicus* collected in Cockburn Sound from depths >15 m. Means are collated from research trawl samples and commercial catch monitoring data.

(and combinations of these months) was examined and the resultant r^2 values were examined to determine which of the monthly water temperatures (or combinations of months) have the strongest relationship with egg production and catch.

Results

The mean monthly water temperature cycle in Warnbro Sound (between 1996 and 2008) was lowest (16.1°C) in August, after which water temperature rose through spring and early summer to a maximum of 23.6°C in January (Fig. 3a). The mean percentage of female *Portunus pelagicus* that were ovigerous in any month demonstrates that the majority of reproductive activity in Cockburn Sound occurs during spring and summer, with the mean percentage of ovigerous crabs peaking in October and remaining high (>40%) until January (Fig. 3b).

Although the annual egg production index (*EPI*), which is a proxy for the size of the spawning stock each year, and the recruitment to the

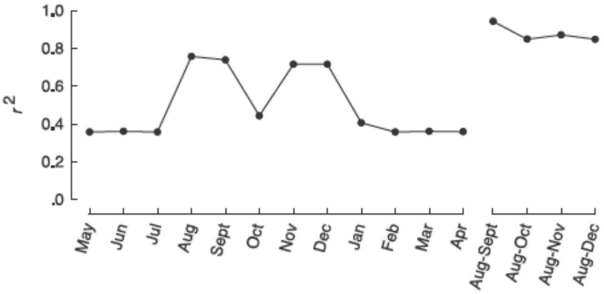

Figure 4. Coefficient of determination (r^2) between observed stock (egg production index) and recruitment (commercial catch) and the fitted the Beverton and Holt stock-recruitment relationship, using egg production and commercial catch (recruitment) of the following year, and water temperatures in different months, or combinations of months, near the spawning and larval period.

fishery (commercial catch) each season have both shown a general decline over the study period, fluctuations in *EPI* values alone explain little of the annual variation in subsequent commercial catches ($r^2 = 0.36$, $P = 0.05$, d.f. = 9). The incorporation of water temperatures from individual months during the early to mid spawning season into the stock-recruitment relationship (SRR) increased the fit of the model substantially. The best fit explained approximately 76% of the variation in the catches and was produced by using August water temperatures in the model (Fig. 4), although good fits were generally obtained for months, August to December. In addition to the individual months, average water temperatures for various combinations of months from August to December were also evaluated in the SRR. The r^2 derived from the SRR of the mean water temperature during each of the combinations of months tested was greater than for August alone (Fig. 4) and the best correlation ($r^2 = 0.94$, $P < 0.001$, d.f. = 9) was derived from using the average water temperature in August and September during the commencement of spawning (Fig. 5). The relationship between water temperature in individual months (and an average of months) and commercial catch without incorporating *EPI* in the model was also examined and the best relationship was not statistically significant ($r^2 = 0.26$, $P = 0.09$, d.f. = 9).

The strong influence of water temperature on the successful recruitment of crabs is demonstrated during the last decade, as the fishing seasons in which commercial landings were largest, i.e., 1997/98 and 1999/00 followed years 1996 and 1998, respectively, in which August/September water temperatures were elevated

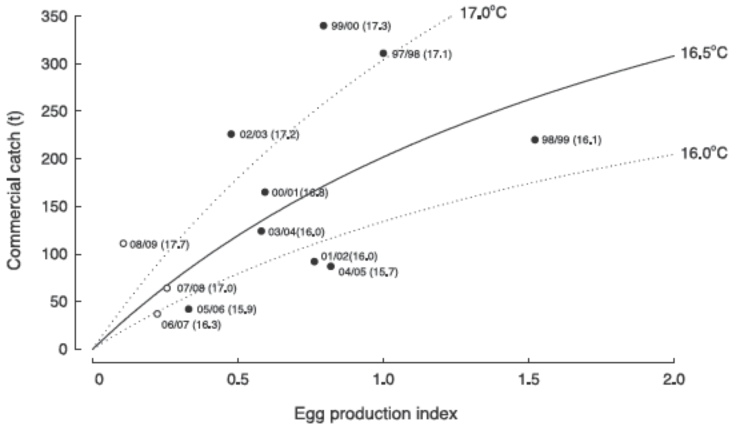

Figure 5. Beverton and Holt stock-recruitment relationship between commercial catch and egg production (preceding season) at three different water temperatures (mean August/September), i.e., 16.0, 16.5, and 17.0°C. Year (fishing season) and mean temperature during the preceding August and September (in parentheses) are indicated. Open circles represent estimated commercial catches for 2006/07, 2007/08, and 2008/09 seasons based on recruit-catch relationship developed by Johnston et al. (2011).

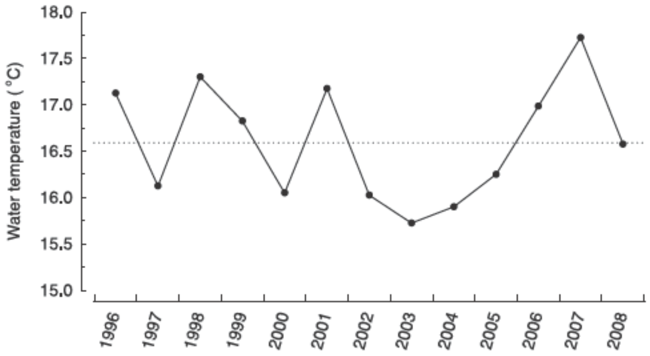

Figure 6. Mean water temperatures (solid line) for August-September recorded in Warnbro Sound for the period 1996-2008. The average August-September water temperature (16.6°C) for the entire period is also indicated (dotted line).

(>17°C) and the levels of egg production were moderate (Fig. 5). In contrast, when the mean August/September water temperatures were <16°C, e.g., 2003 and 2004, subsequent commercial landings in 2004/05 and 2005/06, respectively, were reduced, irrespective of the degree of egg production in the previous year (Fig. 5). Historically, the mean August/September water temperature in Warnbro Sound has fluctuated around the long-term average of 16.6°C, reaching a low of 15.7°C and a high of 17.7°C (Fig. 6). However, in recent years (2002-2005), mean August/September water temperatures remained below the long-term average for four consecutive years.

The initial reduction in catch in 2003/04 and 2004/05 appears to be mainly due to the environmental conditions (low water temperatures in 2002 and 2003), as the spawning stocks in the previous years (2002/03 and 2003/04) were at moderate levels (Fig. 5). The low recruitment to the fishery in these years, combined with fishing pressure, resulted in low levels of egg production in 2004/05. The subsequent low catch observed in 2005/06 along with the predicted low catches for 2006/07, 2007/08, and 2008/09 (based on juvenile abundance) may be due to the effect of low egg production.

The proportion of female crabs that are ovigerous in each month exhibit a similar annual pattern, increasing rapidly from a very low proportion in July and August to a peak two months later of between 0.5 and 0.9 in October (Fig. 7). Proportions remain high until January and then decline to essentially zero from March to June. Although this pattern remains similar between years, the magnitude of the proportions in a given month differ markedly following either a warm (>16.9°C) or cool (<16.3°C) mean August/September water temperature period (±0.3°C of the long term average 16.6°C). The most marked example of this is shown by the multiple spawning females (CW > 115 mm, see de Lestang et al. 2003a), with their proportions of ovigerous females being far greater (in some cases double) following a warm than cool August/September period (Fig. 7).

Discussion

We have demonstrated the importance of including environmental conditions (temperature) in the development of the SRR for blue swimmer crab in Cockburn Sound. Stock size alone, indexed by the *EPI*, explained a small proportion of the variance in recruitment ($r^2 = 0.36$). Similarly water temperature alone ($r^2 = 0.26$) was insufficient to explain recruitment. The poor recruitments, which occurred from 2004 to 2006, appears to be the result of high level of exploitation (Johnston et al. 2011) on a series of low recruitments that initially occurred due to poor environmental conditions. There is a strong correlation between water temperatures and recruitment success of *P. pelagicus* in Cockburn

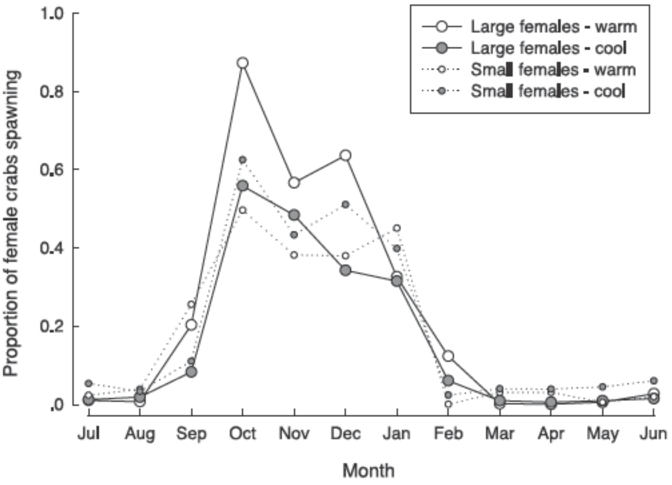

Figure 7. Variation in monthly proportions of small (CW 85-115 mm) and mainly single-brood producing females, and large (CW ≥ 115 mm) mainly multiple-brood producing females, following warm (>16.7°C) and cool (<16.1°C) August-September periods.

Sound, after taking into account the effect of the breeding stock. The marked influence of water temperatures on crab recruitment is not unexpected considering the tropical affinities of *P. pelagicus* and location of Cockburn Sound in the temperate waters of Western Australia. Bryars and Havenhand (2006) demonstrated that water temperature has an important influence on *P. pelagicus* larval duration and survival and predicted that post-larval settlement in the temperate waters of South Australia would be greatest during abnormally warm summers.

While water temperatures encountered by developing larvae in Cockburn Sound may influence larval survival and subsequent recruitment success, analysis of the r^2 values from the model demonstrate that water temperatures between August and December, i.e., at the beginning and during the spawning period, are more indicative of successful crab recruitment in the following year. This relationship suggests that recruitment success depends on a relationship between water temperature and the timing/magnitude of spawning.

The timing of spawning (more eggs released earlier) may contribute to strong recruitment in a number of ways. For example, early spawning may result in larvae being released at a time that allows them to take advantage of the particular food resources available at that time (e.g., Fisher 2006). It may also allow the larvae and subsequent juveniles more time in the warmer waters of spring/summer to grow faster and spend less time in small size classes that are most vulnerable to mortality (i.e., predation).

In addition, an early start to spawning or a greater proportion of mature females spawning at the beginning of the spawning season may lead to an increase in the total number of juvenile crabs produced by providing female crabs the opportunity to produce, incubate and hatch their maximum number (three) of egg batches (de Lestang et al. 2003a). Without prolonged periods of favourable conditions it is unlikely that female crabs will mature early enough, reach an adequate size or have sufficient time to hatch this many batches of eggs. The far greater proportion of large ovigerous females following a warm rather than a cool August/September indicates that these females carried an extra batch of eggs in these years, which supports the above scenario.

The apparent role of high fishing pressure during periods of low recruitment bring into question the assumption that blue swimmer crab fisheries in Western Australia are robust to recruitment overfishing. It appears that high levels of fishing pressure, coupled with three years of reduced recruitment due to unfavourable environmental conditions, resulted in a significant reduction in the levels of egg production (Fig. 5). This reduction is evident after 2003/04 and these levels have remained low in subsequent years. High exploitation rates were exacerbated by a shift by commercial fishers in 1993/94 from set nets to crab traps coincided with a marked increase in average total crab landings by the late 1990s (Johnston et al. 2011). The shift to crab traps resulted in an increase in the winter catch where there was high proportion of females caught. These females would have participated in their second year of spawning and their removal would have exacerbated the rate of decline in the *EPI* during periods of low recruitment.

Cockburn Sound is certainly not the first crab fishery thought erroneously to be resilient to overfishing. Chesapeake Bay blue crab fishery, once the most productive estuarine system in America, continues to report lower harvests each season since catches peaked in the early 1990s. These declines in catches are considered to be due to a combination of overfishing and adverse water quality and environmental conditions (Bunnell and Miller 2005, Lambert et. al. 2006a,b).

The SRR with environmental effects incorporated needs to be further tested because the time series of stock and recruitment data used to generate the relationship in this study is relatively short (only nine years). The key test should occur in the next few years as the fishery recovers. The time period for the recovery for this short-lived species is expected to be relatively fast (e.g., 3-4 years) especially with the favorable water temperatures recorded for 2006 and 2007. The recruitment-environment relationship also needs to be verified, as there are large numbers of environmental conditions that can be tested in space and time; this raises the risk of spurious correlations (Walters and Collie 1988). In the present study the water temperature time series at the nearest location near the spawning and larval period was the only variable tested, as it was considered the key indicator likely to influence the crab stock.

The stock-recruitment-environment relationship produced during this study allows catch predictions to be made for the Cockburn Sound crab fishery a year in advance. This forecasting capacity can be verified by the abundance of juvenile crabs sampled in March-August (Bellchambers et al. 2006, Johnston et al. 2011), reduces uncertainty for fisheries managers and enhances their ability to make sustainable management decisions. The early implementation of informed management actions significantly aids in the sustainable management of this fishery.

The development of an egg production index for Cockburn Sound provides managers with a baseline against which the level of *P. pelagicus* breeding stock can be assessed. However, these results demonstrate that, even at adequate levels of egg production, year to year variability in environmental conditions have a large influence on *P. pelagicus* recruitment. This variability is important to the resilience of the fishery and needs to be accounted for when developing robust biological trigger points (Johnston et al. 2011). This model, which quantifies the influence of water temperature on crab recruitment, will aid in the management of the fishery.

It is worth considering the combination of factors that has contributed to the collapse of this seemingly robust stock to enable an assessment of whether other similar fisheries may also be vulnerable. For the Cockburn Sound crab stock the key factors were (a) the fishery is near the edge of this species distribution and hence vulnerable to environmental fluctuations; (b) a number of consecutive years of poor environmental conditions resulted in poor recruitments; and (c) high fishing pressure continued to be applied to the stocks.

There have been two other crustacean fisheries where recruitment overfishing has occurred in Western Australia in the 1980s—the tiger prawn (*Penaeus esculentus*) stocks in Exmouth Gulf and Shark Bay (Penn and Caputi 1986, Caputi et al. 1998). There are some similarities with the crab collapse, as the tiger prawn was also near the edge of its distribution with a restricted spawning period compared to other prawn stocks in the region and subject to large fluctuations in abundance due to environmental conditions. Its life cycle was also contained within embayments with the spawning stock aggregating in the deep water and hence vulnerable to fishing throughout the life cycle. While there was no change in fishing method associated with these fisheries, there were significant increases in fishing power of the vessels and the introduction of prawn peeling machines that enabled the prawns to be targeted earlier in the season at a much smaller size. The tiger prawn stocks had two additional factors that contributed to their overfishing that do not occur in the crab fishery. The multispecies nature of the prawn fishery resulted in the tiger prawn stocks being fished at low abundance level because of the good abundance of the king prawn stocks. Secondly, the tiger prawn stocks were fished for a number of months before spawning commenced whereas the crab stocks are fished after the first spawning of the year class is completed.

While the stock-recruitment-environment relationship produced during this study is unique to *Portunus pelagicus* in Cockburn Sound, the factors contributing to the collapse are directly relevant to other highly exploited fisheries, particularly those whose catches are based on a single age class, e.g., blue crab in Chesapeake Bay, and stocks that are near the limit of their species distribution, e.g., South Australian blue swimmer crab stocks and Florida spiny lobsters (*Panulirus argus*).

Acknowledgments

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References

Anger, K., E. Spivak, and T. Luppi. 1998. Effects of reduced salinities on development and bioenergetics of early larval shore crab, *Carcinus maenas*. J. Exp. Mar. Biol. Ecol. 220:287-304. doi:10.1016/S0022-0981(97)00110-X

Basson, M. 1999. The importance of environmental factors in the design of management procedures. ICES J. Mar. Sci. 56:933-942. doi:10.1006/jmsc.1999.0541

Bellchambers, L., S. de Lestang, K.D. Smith, and A.W. Thomson. 2006. Catch prediction for the blue swimmer crab (*Portunus pelagicus*) in Cockburn Sound, Western Australia. Bull. Mar. Sci. 79:329-339.

Beverton, R.J.H., and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food G.B. (2 Sea Fish.) 19:1-533.

Botero, L., and J. Atema. 1982. Behaviour and substrate selection during larval settling in the lobster *Homarus americanus*. J. Crustac. Biol. 2:59-69. doi:10.2307/1548113

Bunnell, D.B., and T.J. Miller. 2005. An individual-based modeling approach to spawning-potential per-recruit models: An application to blue crab (*Callinectes sapidus*) in Chesapeake Bay. Can. J. Fish. Aquat. Sci. 62: 2560-2572. doi:10.1139/f05-153

Bryars, S.R., and J.N. Havenhand. 2006. Effects of constant and varying temperatures on the development of blue swimmer crab (*Portunus pelagicus*) larvae: Laboratory observations and field predictions for temperate coastal waters. J. Exp. Mar. Biol. Ecol. 329:218-229. doi:10.1016/j.jembe.2005.09.004

Caputi, N., C. Chubb, and A. Pearce. 2001. Environmental effects on recruitment of the western rock lobster, *Panulirus cygnus*. Mar. Freshw. Res. 52:1167-1174. doi:10.1071/MF01180

Caputi, N., R.S. Brown, and C.F. Chubb. 1995. Relationship between spawning stock, environment, recruitment and fishing effort for the western rock lobster, *Panulirus cygnus*, fishery in Western Australia. Crustaceana 68:213-226.

Caputi, N., J.W. Penn, L.M. Joll, and C.F. Chubb. 1998. Stock-recruitment-environment relationships for invertebrate species of Western Australia. In: G.S. Jamieson and A. Campbell (eds.), Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Can. Spec. Publ. Fish. Aquat. Sci. 125:247-255.

Clark, K.R., and R.M. Warwick. 2001. Change in marine communities: An approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth, UK. 172 pp.

Cobb, J.S., and J.F. Caddy. 1989. The population biology of decapods. In: J.F. Caddy (ed.), Marine invertebrate fisheries: Their assessment and management. Wiley, New York, pp. 327-374.

de Lestang, S., N.G. Hall, and I.C. Potter. 2003a. Reproductive biology of the blue swimmer crab, *Portunus pelagicus* (Decapoda: Portunidae) in five water bodies on the west coast of Australia. Fish. Bull. 101:745-757.

de Lestang, S., N.G. Hall, and I.C. Potter. 2003b. Do the age compositions and growth of the crab *Portunus pelagicus* in marine embayments and estuaries differ? J. Mar. Biol. Assoc. U.K. 83:1-8. doi:10.1017/S0025315403008166h

de Lestang, S., N.G. Hall, and I.C. Potter. 2003c. Changes in density, age composition, and growth rate of *Portunus pelagicus* in a large embayment in which fishing pressures and environmental conditions have been altered. J. Crust. Biol. 23:908-919. doi:10.1651/C-2376

Fisher, J.L. 2006. Seasonal timing and duration of brachyuran larvae in a high-latitude fjord. Mar. Ecol. Prog. Ser. 323:213-222. doi:10.3354/meps323213

Goodrich, D.M., J. van Montfrans, and R.J. Orth. 1989. Blue crab megalopal influx to Chesapeake Bay: Evidence for a wind-driven mechanism. Estuar. Coast. Shelf Sci. 29:247-260. doi:10.1016/0272-7714(89)90056-5

Johnston, D., D. Harris, N. Caputi, and A. Thomson. 2011. Decline of a blue swimmer crab (*Portunus pelagicus*) fishery in Western Australia: History, contributing factors and future management strategy. Fish. Res. doi:10.1016/j.fishres.2011.01.027

Lambert, D.M., J.M. Hoenig, and R.N. Lipcius. 2006a. Tag return estimation of annual and semiannual survival rates of adult female blue crabs. Trans. Am. Fish. Soc. 135(6):1592-1603. doi:10.1577/T05-318.1

Lambert, D.M., R.N. Lipcius, and J.M. Hoenig. 2006b. Assessing effectiveness of the blue crab spawning stock sanctuary in Chesapeake Bay using tag-return methodology. Mar. Ecol. Prog. Ser. 321:215-225. doi:10.3354/meps321215

Lee, J., J. Widdows, M.B. Jones, and R.A. Coleman. 2004. Settlement of megalopae and early juveniles of the velvet swimming crab *Necora puber* (Decapoda: Portunidae) in flow conditions. Mar. Ecol. Prog. Ser. 272:191-202. doi:10.3354/meps272191

Lipcius, R.N., and W.A. van Engel. 1990. Blue crab population dynamics in Chesapeake Bay: Variation in abundance (York River, 1972-1988) and stock-recruit functions. Bull. Mar. Sci. 46:180-194.

McConaugha, J.R., D.F. Johnson, A.J. Provenzano, and R.C. Maris. 1983. Seasonal distribution of larvae of *Callinectes sapidus* (Crustacea: Decapoda) in the waters adjacent to Chesapeake Bay. J. Crustac. Biol. 3:582-591. doi:10.2307/1547953

Metcalf, K.S., J. van Montfrans, R.N. Lipcius, and R.J. Orth. 1995. Settlement indices for blue crab megalopae in the York River, Virginia: Temporal relationships and statistical efficiency. Bull. Mar. Sci. 57:781-792.

Myers, R.A. 1998. When do environment-recruitment correlations work? Rev. Fish Biol. Fish. 8:85-305. doi:10.1023/A:1008828730759

Penn, J.W., and N. Caputi. 1986. Spawning stock-recruitment relationships and environmental influences on the tiger prawn, *Penaeus esculentus*, fishery in Exmouth Gulf, Western Australia. Aust. J. Mar. Freshw. Res. 37:494-505. doi:10.1071/MF9860491

Potter, I.C., S. de Lestang, and G.C. Young. 2001. The collection of biological data required for management of the blue swimmer crab fishery in the central and lower west coasts of Australia. Fisheries Research and Development Corporation Report, FRDC Project 97/137. Murdoch University, Perth. 112 pp.

Queiroga, H., M.J. Almeida, T. Alpuim, A.A.V. Flores, S. Francisco, I. Gonzàlez-Gordillo, A. Miranda, I. Silva, and J. Paula. 2006. Tide and wind control of megalopal supply to estuarine crab populations on the Portuguese west coast. Mar. Ecol. Prog. Ser. 307:21-36. doi:10.3354/meps307021

Rabalais, N.N., F.R. Burditt Jr., L.D. Coen, B.E. Cole, C. Eleuterius, K.L. Heck Jr., T.A. McTigue, S.G. Morgan, H.M. Perry, F.M. Truesdale, R.K. Zimmer-Faust, and R.J. Zimmerman. 1995. Settlement of *Callinectes sapidus* megalopae on artificial collectors in four Gulf of Mexico estuaries. Bull. Mar. Sci. 57:855-876.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559-623.

Rosenkranz, G.E., A.V. Tyler, and G.H. Kruse. 2001. Effects of water temperature and wind on year-class success of Tanner crabs in Bristol Bay, Alaska. Fish. Oceanogr. 10:1-12. doi:10.1046/j.1365-2419.2001.00153.x

Uphoff, J.M. 1998. Stability of the blue crab stock in Maryland. J. Crustac. Biol. 17:519-528.

Wahle, R.A. 2003. Revealing stock-recruitment relationships in lobsters and crabs: Is experimental ecology the key? Fish. Res. 65:3-32. doi:10.1016/j.fishres.2003.09.004

Wahle, R.A., L.S. Incze, and M.J. Fogarty. 2004. First projections of American lobster fishery recruitment using a settlement index and variable growth. Bull. Mar. Sci. 74:101-114.

Walters, C.J., and J.S. Collie. 1988. Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci. 45:1848-1854. doi:10.1139/f88-217

Yatsuzuka, K. 1962. Studies on the artificial rearing of the larval Brachyura, especially of the larval blur-crab, Neptunus pelagicus Linnaeus. Reports USA Marine Biological Station 9:1-88.

Zheng, J., and G.H. Kruse. 1999. Evaluation of harvest strategies for tanner crab stocks that exhibit periodic recruitment. J. Shellfish Res. 18:667-679.

Levings, A.H. and P.C. Gill. 2010. Seasonal Winds Drive Water Temperature Cycle and Migration Patterns of Southern Australian Giant Crab *Pseudocarcinus gigas.* In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.09

Seasonal Winds Drive Water Temperature Cycle and Migration Patterns of Southern Australian Giant Crab *Pseudocarcinus gigas*

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Abstract

The giant crab *Pseudocarcinus gigas* occurs along the continental shelf break of southern Australia. During the summer alongshore winds cause cooler water to upwell onto the shelf, and the crabs move from deeper water onto the shelf where there is more food. The combination of a preferred thermal niche and a depth-stratified food supply defines the favorable foraging environments that enhance the growth of *P. gigas.* Climate change is expected to cause a southerly shift of the austral subtropical high-pressure belt, and modelers have predicted more upwelling-favorable winds. The associated increase in the circulation of cooler water across the shelf is likely to provide *P. gigas* with an increased access to benthic food resources and their growth rate may increase in some regions.

Introduction

The giant crab *Pseudocarcinus gigas* (Fig. 1) became the target of a commercial fishery in 1992 at a time when little was known about the species. A legal minimum size was established in 1993 and in some areas the population was profiled as it was fished from a pristine state. Observations by fishermen indicated *P. gigas* occupied a relatively smooth muddy habitat, were nomadic, and were caught in similar depths at widely separated areas at the same periods of the year at southeastern Australian locations. For example, crabs off Kangaroo Island, South Australia, were behaving similarly to those off King Island,

Figure 1. Australian giant crab *Pseudocarcinus gigas*, caught off NW Tasmania, held by crewman Bo Jones.

northwest Tasmania. On shore, exporters found they were best kept alive in water temperatures from 10°C to 14°C. Most of the population lives at depths of 140 m to 400 m on the outer continental shelf and upper slope (Fig. 2) (Levings et al. 2001).

Diet analysis by Heeron and Mitchell (1997) found that *P. gigas* consumed anomura, asteroids, brachyurans, gastropods, and carrion. In summary, *P. gigas* is a scavenging carnivore that consumes a wide range of benthic prey, including its own species and carrion. Day et al. 1971, Rowe 1981, Maurer et al. 1982, Pérès 1982, Probert and Wilson 1984, Baba et al. 1986, Parry et al. 1990, and Ward and Blaber 1994 all found an increase in the richness of continental shelf benthic assemblages as the water became shallower. Australia's southern shelf has minimal input of nutrients from mainland rivers that pass through semi-arid areas (James et al. 1992), or off west Tasmania originate in peat bogs and have less nutrients than seawater (Crawford et al. 2000). This open shelf is subject to a unimodal swell and wind wave climate (Provis and

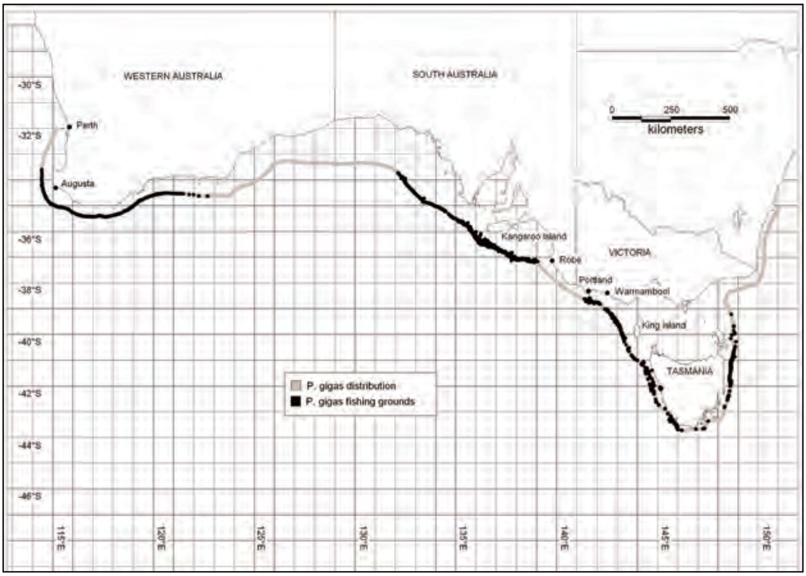

Figure 2. ***Pseudocarcinus gigas*** **distribution and commercial crab fishing grounds.**

Steedman 1985) that separates a muddy depositional environment from an erosive one at about 140 m, although storms can deepen the separation (James et al. 1992, James 1997). The density and biomass of macrobenthic fauna of this shelf (and potential *P. gigas* food resources) diminish with increasing depth, and the seafloor becomes increasingly barren as it becomes muddier on the upper slope (Boreen et al. 1993, James et al. 2001, Ward et al. 2006).

The two dominant features of the ocean along the southern Australian margin are a warm mixed-surface layer that is underlain by cooler Antarctic Intermediate Water (AAIW) (Newell 1961, Wyrtki 1971, Bye 1972, Callahan 1972, Newell 1974, Rochford 1977, Lewis 1981, Bye 1983, Godfrey et al. 1986, Hahn 1986, Schahinger 1987, Harris et al. 1987, Cresswell and Peterson 1993, Hufford et al. 1997). The mixed surface layer flows in a generally east-southeast direction and is known as the Leeuwin Current off west Australia, the Coastal Current off South Australia and Victoria, and the Zeehan Current off west Tasmania. An underlying counter-current of AAIW flows in a generally northwestward direction at a depth of about 400-600 m extending to approximately 1200 m (Wood and Terray 2005), and is known as the Leeuwin Undercurrent off west Australia and the Flinders Current off western Tasmania, western

Victoria, and South Australia (Middleton and Cirano 2002). This current feeds into shallower shelf circulations during summer when wind from the southeast forces the mixed surface layer offshore and triggers a compensatory upwelling of AAIW from greater depths (Hahn 1986, Schahinger 1987). Speculation by Rochford (1977) that summer water temperatures off western Victoria may have been linked with the Bonney Upwelling off South Australia, led to this collaborative investigation into linkages with the upwelling and distribution of *P. gigas* (reported here); and that of the blue whale *Balaenoptera musculus* (Gill 2004).

Materials and methods

The data set "Climatology of Australian Regional Seas" (CARS) is an archive of 40 years of measurements from Niskin bottles, continuous temperature depth transects, and expendable bathythermographs. The data were used to generate broad scale optimally interpolated isothermal maps of southern Australia at 50 m depth intervals for the winter and summer (G. Dunn, CSIRO Marine Research Laboratories, Hobart, pers. comm.). At a more focused spatial scale, temperature, salinity, and nitrate data for western Victoria were sorted from the CARS archive according to a seasonal scheme of winter, summer, and transitional. During winter the shelf waters are deeply mixed, and in summer are stratified (Rochford 1977, Lewis 1981, Bye 1983, Schahinger 1987). Transitional describes the two periods when the water changes from the winter to the summer state, usually in late spring; or the summer to the winter state, usually in mid autumn. The data were subjected to regression analysis to determine if there were correlations between temperature and salinity, and temperature and nitrate, during summer and winter.

Temperature logger studies

Following analysis of the CARS data, three inquiries were initiated.

Inquiry 1: Five subsurface arrays of StowAway TidbiTÔ temperature loggers were used to acquire a time series from western Victoria and were deployed at sites A to E (Fig. 3) for the period January 2001 to June 2002. Four of the arrays (B, C, D, and E) sampled at near surface (15 m), mid water (45 m), and near seafloor (80 m) depths. At the single shallow site (A) sampling intervals of 11 m, 25 m, and 50 m depth were used.

Inquiry 2: During the sampling period October 2005 to August 2006, two widely separated sites approximately 350 km apart at Cape Otway and west of Robe (Fig. 4) were used to check the connectivity of the seasonal water temperature signal between the two sites. At these sites loggers were mounted on a riser line at 45 m and 80 m depth.

Inquiry 3: A single logger array, with loggers at 15 m, 45 m, and 80 m, was maintained at location C (Fig. 3) for the period February 2001

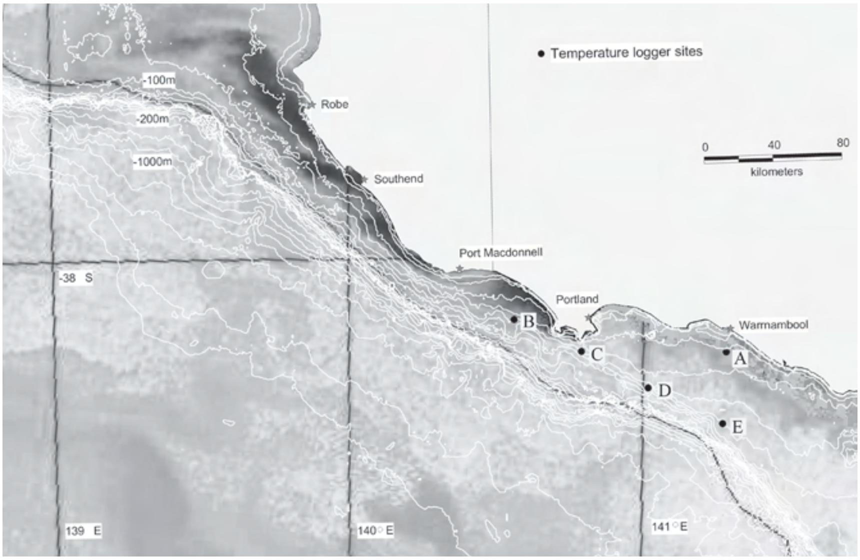

Figure 3. Temperature logger sites off western Victoria. An upwelling plume (dark area) reaches the surface inshore from sites B and C and extends to the northwest off Southend and Robe (SST image courtesy CSIRO Marine Research).

to March 2007 to record interannual variability of the start and the end of upwelling.

Integration with knowledge about P. gigas and its habitat

The CARS data and temperature observations were integrated with knowledge about *P. gigas* population structure, abundance, reproduction, movement, physiology, diet, growth and benthic composition (Levings 2008); to investigate relationships between ocean thermal structure and crab distribution, and to postulate the potential impacts of climate change on the growth and distribution of this species.

Results

CARS data analysis

The broad scale isothermal maps showed the seafloor temperature at the shelf break (200 m depth) was cooler in summer than in winter along the entire southern margin and that the western

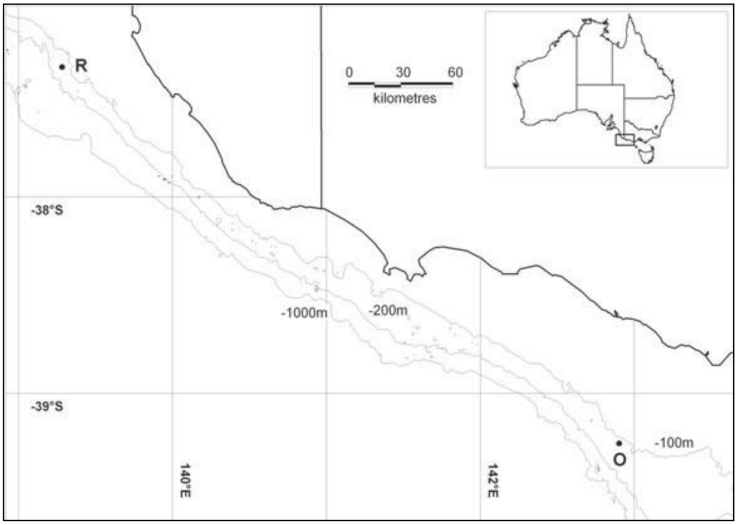

Figure 4. Mid-water (45 m depth) and near and bottom temperature loggers (80 m depth) were sited at Robe (R) and Cape Otway (O) sites during the period October 2005–August 2006.

Australian temperature was 3°C higher at this depth than off western Tasmania (Levings et al. 2001). At a more focused scale, the analysis of temperature, salinity, and nitrate data for western Victoria showed distinct stratification of the water column over the shelf in the summer. Although there was a scatter of salinity values in the surface layer ($r^2 = 0.22$) at depths from 0 to 80 m for temperatures >14.0°C, there was a very strong relationship ($r^2 = 0.96$) for waters at depths 80 m to 200 m and <14.0°C. The constant nature of salinity values for this depth range, typically 35.10 ppt at 12°C and 35.25 ppt at 13°C and the accompanying nitrate values of 6.0 to 7.0 µM, indicated the water was reheated Antarctic Intermediate Water (AAIW). The analysis, when applied to offshore waters for the depths 80-600 m, showed an even stronger relationship ($r^2 = 0.99$). Hence summer water at temperatures of <14.0°C was upwelled AAIW (Fig. 5) and therefore measurement of temperature alone was sufficiently robust to investigate for linkages between the Bonney Upwelling off South Australia and the shelf waters of western Victoria.

Temperature logger studies

Inquiry 1: Logger information, from all sites A-E, recorded a distinctly stratified water column off western Victoria during the summer of

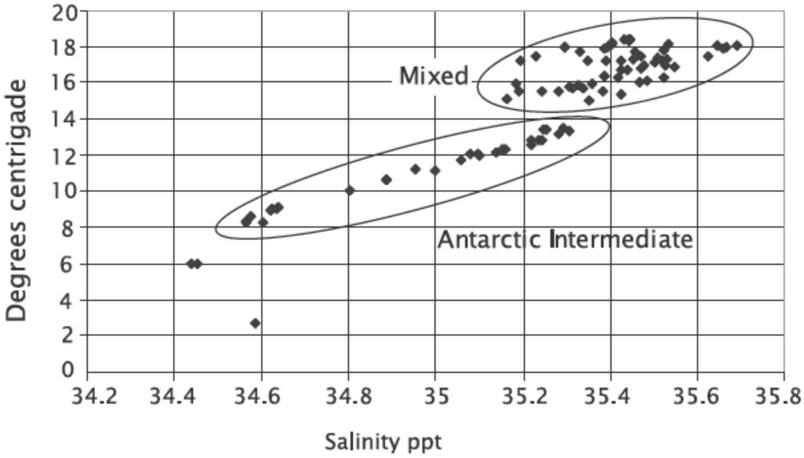

Figure 5. The temperature-salinity profile for summer for the region 38°.00S to 40°.00S and 141°.00E to 143°.00E shows that water of 14°C or less is Antarctic Intermediate Water.

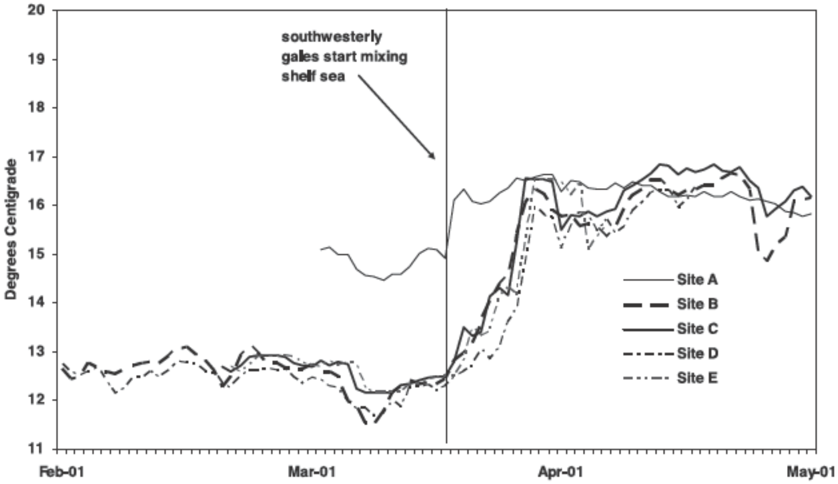

Figure 6. Seafloor temperature profiles from sites A-E off western Victoria during January to March 2001 show a clear temporal linkage as the summer stratification ended and well mixed conditions became established. Site A is at 50 m depth; sites B-E are at 80 m depth.

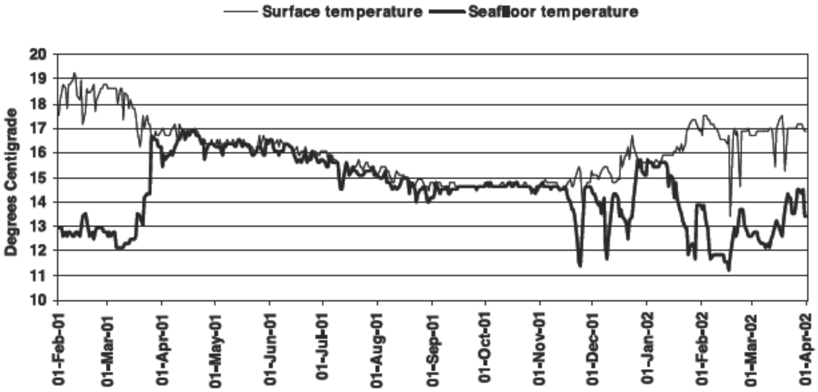

Figure 7. **The temperature profile for the seafloor and surface at site C off western Victoria shows the transitions from a stratified summer state to a well-mixed winter state, and then a return to a stratified summer state.**

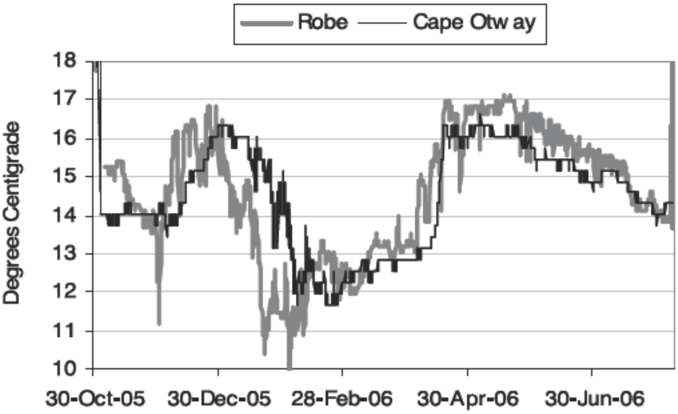

Figure 8. **Temperature loggers at 80 m depth at widely separated sites of Robe and Cape Otway showed highly correlated seasonal signals.**

2000-01. Seafloor water temperatures of 12.0°C to 13.0°C and surface temperatures of 18.0°C to 19.5°C were recorded. Occasionally, sharp downward spikes to 13.5°C were observed as the subducting layers of AAIW reached the surface at the westerly locations closer to the surface plume of the Bonney Upwelling. In mid March 2001 the onset of seasonal onshore winds from the southwest forced the warm surface layer shoreward and, by observation of the results from logger A compared to loggers B to E (Fig. 6), progressively displaced the over-shelf water volume from the shore outward. By the end of March the over-shelf water approached thermal homogeneity at all sites with the temperature at approximately 16.5°C. The mixed surface layer continued to cool to 14.5°C by August and remained at this level until upwelling favorable winds resumed in November 2001, triggering upwelling and dropping near bottom temperature to 12°C (Fig. 7). Thermal stratification for the summer season 2001-02 was weaker than the preceding year due to a lower incidence of upwelling favorable winds.

Inquiry 2: The sampling period October 2005 to August 2006 showed a highly correlated sequence of seafloor temperatures at the Robe and Otway locations, although a lag time of approximately 16 days was evident for the onset of the summer condition at the Otway site where the shelf is wider than at Robe. The onset of the winter condition at both sites was more rapid with very little lag time compared to summer (Fig. 8).

Inquiry 3: Some loss of data was experienced at the site C logger array due to shipping and foul weather (Fig. 9). Nonetheless the dominant feature of temperature for the period February 2001 to March 2007 was the recurring annual cycle of a stratified water column in summer—warm on the surface and cool on the seafloor—and a deeply mixed water column with warmer seafloor conditions during winter.

Integration of temperature data with knowledge about P. gigas and its habitat

Extensive population sampling (n = 75,456 crabs) and tagging (n = 19,012 crabs tagged, n = 3,243 recaptures) along the southern Australian region were conducted for the period 1993 to 2001 in a fishery-based study (Levings 2008). Mean length and catch rate (kg per pot per day) peaked in the autumn (ANOVA, $p = <0.0001$) at South Australian, Victorian, and Tasmanian locations as the adult population moved to deeper water. The South Australian data (n = 40,276 crabs), a continuous time series that profiled the population as it was fished from a pristine state, was sorted by season, and the distributions by depth by sex by size for winter and summer were plotted. This population is located at the center of the species range. The plots showed the population was most abundant at depths of 110-180 m on the outer shelf during summer and 190-400 m on the upper slope during winter (Fig. 10). A small

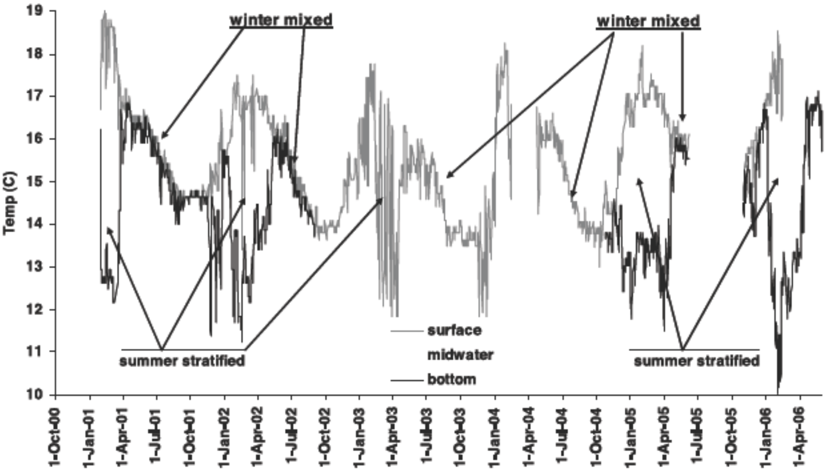

Figure 9. Winter mixing and summer stratification of the water column recur in an annual cycle during this six year series, although each annual winter-summer cycle shows variation in time of onset, cessation, and magnitude. The mid water plot has been omitted for clarity and some data gaps are evident where loggers were lost.

number of large male crabs taken during the summer as a bycatch of lobster fishing in shallower depths over the mid shelf are not accounted for in the summer data. Winter release and summer recapture of tagged crabs (or vice versa) for the same area also recorded a seasonal vertical migration, with a mean depth change of 182 m for the total of 39 recaptures. Western Victoria showed a similar migration for 67 recaptures, but the result, a depth change of 90 m, was biased by a narrower and shallower depth range of sampling in this area, where winter currents were stronger and the timely recovery of fishing gear more difficult from deeper water.

Examination of molt increments for 1,095 crabs across the species range (Levings 2008) found that western Australian *P. gigas* had a significantly smaller molt increment ($p = <0.001$) and a significantly larger intermolt period than the southeast Australian populations of Victoria and Tasmania (Tables 1 and 2). These extremes were at each end of a trend from smaller to larger molt increments and from longer to shorter intermolt periods. Larger molt increments and shorter intermolt periods were evident from areas where the thermal environment allowed the *P. gigas* population more access to richer food resources in shallower water.

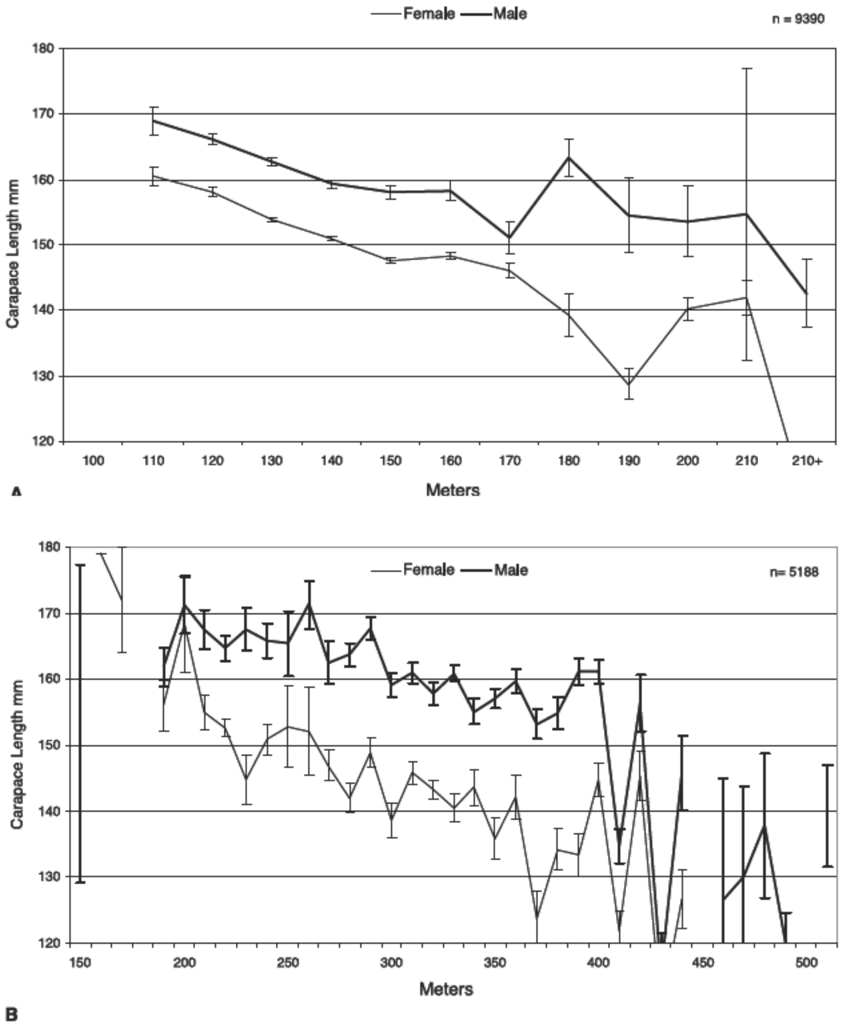

Figure 10. ***Pseudocarcinus gigas*** **are most abundant at depths of 110-180 m in summer (A) and 190-400 m in winter (B). The population is stratified by size by depth.**

Table 1. Comparisons of *Pseudocarcinus gigas* male and female molt increment.

	Female			Male		
	n	Mean ± SE	SD	n	Mean ± SE	SD
Western Australia						
111–120 mm	52	16.65 ± 0.31	2.28	18	19.97 ± 0.98	4.14
121–130 mm	62	14.70 ± 0.30	2.38	16	23.13 ± 0.83	3.30
131–140 mm	60	14.10 ± 0.29	2.24	8	21.88 ± 1.25	3.52
141–150 mm	12	13.21 ± 0.36	1.23	3	25.33 ± 1.20	2.08
South Australia						
111–120 mm	na	na	na	na	na	na
121–130 mm	15	20.07 ± 0.82	3.17	12	24.67 ± 0.84	2.93
131–140 mm	55	16.33 ± 0.45	3.31	39	23.95 ± 0.55	3.45
141–150 mm	98	15.55 ± 2.58	2.58	26	23.83 ± 0.54	2.74
Victoria						
111–120 mm	na	na	na	na	na	na
121–130 mm	10	23.40 ± 1.67	5.27	13	28.31 ± 0.56	2.01
131–140 mm	18	20.22 ± 1.07	4.52	11	26.64 ± 0.81	2.69
141–150 mm	7	18.71 ± 1.61	4.27	7	27.00 ± 1.29	3.42
Tasmania						
111–120 mm	21	25.14 ± 0.56	2.57	20	30.22 ± 0.42	1.87
121–130 mm	78	24.31 ± 0.70	6.20	25	29.72 ± 0.57	2.85
131–140 mm	124	21.32 ± 0.28	3.10	32	29.28 ± 0.54	3.07
141–150 mm	92	19.60 ± 0.33	3.18	21	28.24 ± 0.63	2.88

Table 2. Maximum number of years before *Pseudocarcinus gigas* of 121-150 mm carapace length molted after being tagged and released.

State	Maximum years to molt after tag and release	
	Female	Male
Western Australia	8	6
South Australia	6	5
Victoria	4	4
Tasmania	4	4

Discussion

Fishermen's observations and population sampling indicated a seasonal movement of *P. gigas* from shallow to deep water and vice versa at widely separated southeastern Australian locations. This suggested the presence of a mechanism or mechanisms of a similar spatial scale that regulated their distribution. Our study showed the existence of a water temperature linkage between the Bonney Upwelling and the waters of the western Victorian region. The seasonal wind field of the austral subtropical high-pressure belt is the major driver of water temperature in this area as the belt moves south in summer or north in winter (Linacre and Hobbs 1977, Sturman and Tapper 1996). In the summer when the belt is south of the Great Australian Bight, the combined effect of southeasterly winds and Coriolis force transports surface water offshore and triggers a compensatory flow of cool, nutrient-rich AAIW upward and onto the continental shelf. In areas where the shelf is narrow, this water shoals to the surface and becomes clearly visible in remote sensing imagery (Fig. 3); but where the shelf is wider, the water is masked by the warm mixed surface layer. In winter when the belt is over south-central Australia, onshore southwesterly winds force the surface layer against the shore, filling the shelf from the shore outward, displacing the cooler upwelled water of summer as an alongshore flow is established. Hence most of the seafloor of the southern Australian shelf is colder in the summer and warmer in the winter. Palaeo-ecologists Frakes and Kemp (1972) suggested that this pattern of ocean-atmosphere events has remained essentially the same for the last 20 million years since the establishment of the cold southern circumpolar current.

Faunal assemblages and sediment types of southern Australia are linked to the long period (approximately 13 s) unimodal swell of the area. The density and biomass of benthic macrofauna diminishes with increasing depth as the seafloor becomes muddier and increasingly barren (Rowe 1981, Boreen et al. 1993, Ward and Blaber 1994, Ward et al. 2006). Long period wave motion separates muddy from grainy sediments at a depth of approximately 140 m, often deeper to 250 m with storms (James et al. 1992, Boreen et al. 1993, Caires et al. 2005). Satellite derived maximum wave heights are 10-12 m off western Tasmania and Western Australia, and 8-10 m off South Australia (CSIRO Marine Research 2006). Shoreward of this separation, the turbulence of wave action exposes rocky reefs, gives anchor points for epifauna, and supports a higher abundance of larger prey items for *P. gigas*. The deeper environment beyond the reach of wave action favors the growth and accumulation of delicate-branching bryozoans, the major constituent of this deep shelf assemblage that also includes numerous sponges and ascidians (Chinnock 1996; Bone 1997; Bone and Campbell 1997; James et al. 2001; Williams et al. 2006, 2007). This assemblage provides food and refuge for small prey for *P. gigas* (Heeron and Mitchell 1997, Levings et al. 2001). Beyond the shelf break, the mud drape thickens to all mud with an attenuation of epifauna and for *P. gigas* most prey is either infauna or carrion (Levings 2008).

Population studies showed *P. gigas* in southeastern Australian locations move upward from the upper continental slope onto the shelf in the summer and downward onto the upper slope during the winter; such a movement keeps the species within a thermal niche of approximately 12°C to 14°C (Levings 2008). The depth range of the niche affects *P. gigas* accessibility to food resources; thus in southeastern Australia the population has access to richer food resources during the summer. However, off western Australia at the limit of the *P. gigas* range, the warm Leeuwin Current occupies the continental shelf, and the thermal niche is deeper over the muddy slope that is poorer in food. A robust competitor, the warm temperate crab *Hypothalassia acerba* occupies the richer environments of the shelf break and the outer shelf (Levings et al. 2001, Smith et al. 2004, Levings 2008). *P. gigas* from this area exhibit a comparatively smaller molt increment and longer intermolt period than all other populations of this species.

The prognosis for climate change for southern Australian waters by the CSIRO Global Climatic Model 3.5 (Gordon et al. 2002) is notable. Within a general global outlook of increasing sea surface temperatures, southern Australian waters are forecast to become cooler in the spring and summer due to an increase in the strength of upwelling-favorable winds. Autumn winds are expected to create more downwelling and winter is expected to be variable. The implication for *P. gigas* populations is an increased annual time of occupation of the food-rich outer and mid shelf areas and an increased growth rate off northwest Tasmania, western Victoria, and South Australia. The change in seafloor temperature is likely to extend laterally along the shelf and alter the western limit of the *P. gigas* range. The northeastern Tasmanian population may experience a slower growth rate as the East Australian Current becomes warmer; however, this may be offset by improved conditions on more southerly Tasmanian grounds where present temperatures appear to be too cold to sustain a large population of the species. Accompanying decreases in maximum wave height are likely to reduce the deep reach of storm turbulence (the storm wave base) and so muddiness may increase on the edge of the continental shelf. However, the average wave climate is an ever-present long period ground swell, a product of far distant subantarctic regions, and so the associated 140 m mud line (the swell wave base) may be less affected. The timing of biological responses such as migration, mating, egg incubation, and molting are expected to remain in broad synchrony with the austral climate cycle in an environment that has supported *P. gigas* evolution for the past 20 million years through multiple global warming and cooling cycles.

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References

Baba, K., K.I. Hayashi, and M. Toriyoma. 1986. Decapod crustaceans from the continental shelf and slope around Japan. Japanese Fisheries Resources Conservation Association, Tokyo.

Bone, Y. 1997. Bryozoans. Living biota to sedimentary fragments of limestones: How do oceanographic parameters of the Great Australian Bight affect this progression? In: M. Tomczak (ed.), Workshop on the Oceanography of the south east Indian Ocean and Great Australian Bight (GAB). Flinders Institute for Atmospheric and Marine Sciences, Technical Report No 14.

Bone, Y., and E. Campbell. 1997. Bryozoans from southern Australia: Some common sediment producing and environmentally significant species. Third Australian Marine Geoscience Conference, Department of Geology and Geophysics, University of Adelaide, Abstract.

Boreen, T., N. James, C. Wilson, and D. Heggie. 1993. Superficial cool-water carbonate sediments on the Otway continental margin, southeastern Australia. Mar. Geol. 112:35-56. doi:10.1016/0025-3227(93)90160-W

Bye, J.A.T. 1972. Oceanic circulation south of Australia. IN: D.E. Hayes (ed.), Antarctic oceanography II: The Australia–New Zealand sector. American Geophysical Union, Washington, D.C., Antarctic Series 9:95-100.

Bye, J.A.T. 1983. The general circulation in a dissipative ocean with longshore wind stresses. J. Phys. Oceanogr. 13:1553-1563. doi:10.1175/1520-0485(1983)013<1553:TGCIAD>2.0.CO;2

Caires, S., A. Sterl, G. Burgers, and G. Komen. 2005. ERA-40, forty-year European re-analysis of the global atmosphere ocean wave product validation and analysis. KNMI (Royal Netherlands Meteorological Institute). Accessed August 2010: http://www.knmi.nl/onderzk/oceano/waves/era40/index.html.

Callahan, E. 1972. The structure and circulation of deep water in the Antarctic. Deep-Sea Res. 19:563-576.

Chinnock, P. 1996. Calcareous benthic invertebrates and algae of the cool water shelves of WA and SA: Their significance in palaeoecological studies. B.S. honors thesis, University of Adelaide.

Crawford, C.M., G.J. Edgar, and G. Cresswell. 2000. The Tasmanian region. In: C.R.C. Sheppard (ed.), Seas at the millennium: An environmental evaluation. Pergamon, pp. 647-660.

Cresswell, G.R., and J.L. Peterson. 1993. The Leeuwin Current south of Western Australia. Australian J. Mar. Freshw. Res. 44:285-303.

CSIRO Marine Research. 2006. Maps produced for the Australian Government National Oceans Office, May 2006. http://www.cmar.csiro.au/datacentre

Day, J.H., J.G. Field, and M.P. Montgomery. 1971. The use of numerical methods to determine the distribution of the benthic fauna across the continental shelf of North Carolina. J. Anim. Ecol. 40:93-125. doi:10.2307/3333

Frakes, L.A., and E.M. Kemp. 1972. Influence of continental positions on early Tertiary climates. Nature 240:97-100. doi:10.1038/240097a0

Gill, P.C. 2004. Ecological linkages in the Bonney Upwelling blue whale feeding area. Ph.D. thesis, Deakin University, Warrnambool, Victoria, Australia.

Godfrey, J.S., D.J. Vaudrey, and S.D. Hahn. 1986. Observations of a shelf edge current south of Australia. J. Phys. Oceanogr. 16:668-679. doi:10.1175/1520-0485(1986)016<0668:OOTSEC>2.0.CO;2

Gordon, H.B., L.D. Rotstayn, J.L. McGregor, M.R. Dix, E.A. Kowalczyk, S.P. O'Farrell, L.J. Waterman, A.C. Hirst, I.G. Watterson, and T.I. Elliot. 2002. The CSIRO Atmospheric Research Mk 3.0 Climate Systems Model. CSIRO, Division of Atmospheric Research, Aspendale, Victoria, Technical Report No. 60. 118 pp. Accessed August 2010: http://www.cmar.csiro.au/e-print/open/gordon_2002a.pdf.

Hahn, S.D. 1986. Physical structure of the waters of the South Australian continental shelf. Ph.D. thesis, Flinders University of South Australia.

Harris G., C. Nilson, L. Clementson, and D. Thomas. 1987. The water masses of the east coast of Tasmania, seasonal and interannual variability. Australian J. Mar. Freshw. Res. 38:569-590. doi:10.1071/MF9870569

Heeron, T., and B.D. Mitchell. 1997. Morphology of the mouth parts, gastric mill and digestive tract of the giant crab *Pseudocarcinus gigas* (Decapoda: Oziidae). Australian J. Mar. Freshw. Res. 48:7-18. doi:10.1071/MF96026

Hufford, G.E., K.A. McCartney, and K.A. Donohue. 1997. Northern boundary currents and adjacent recirculations off southwestern Australia. Geophys. Res. Lett. 24(22):2797-2800. doi:10.1029/97GL02278

James, N.P. 1997. The cool water carbonate depositional realm. In: N.P. James and J.A.D. Clarke (eds.), Cool-water carbonates. Society for Sedimentary Geology (SEPM) Special Publication 56, Tulsa.

James, N.P., Y. Bone, L.B. Collins and T.K. Kyser. 2001. Surficial sediments of the Great Australian Bight: Facies dynamics and oceanography on a vast cool-water carbonate shelf. J. Sediment. Res. 71(4):549-567. doi:10.1306/102000710549

James, N.P., Y. Bone, C. Von Der Borch and V.A. Gostin. 1992. Modern carbonate and terrigenous sediments on a cool water, high energy, mid-latitude shelf: Lacepede, southern Australia. Sedimentology 39:877-903. doi:10.1111/j.1365-3091.1992.tb02158.x

Levings, A.H. 2008. A Life history model for the giant crab *Pseudocarcinus gigas.* Ph.D. thesis, Deakin University, Warrnambool, Victoria, Australia. 261 pp.

Levings, A.H., B.D. Mitchell, R. McGarvey, J. Mathews, L. Laurenson, C. Austin, N. Murphy, A. Miller, M. Rowsell, and P. Jones. 2001. Fisheries biology of the giant crab, *Pseudocarcinus gigas*. Deakin University, Final report to the Fisheries Research and Development Corporation, Australia, projects 93/220 and 97/132.

Lewis, R.K. 1981. Seasonal upwelling along the south-eastern coastline of South Australia. Australian J. Mar. Freshw. Res. 32:843-54. doi:10.1071/MF9810843

Linacre, E., and H. Hobbs. 1977. The Australian climatic environment. John Wiley.

Maurer, D., W. Leathem, and C. Menzie. 1982. Macrobenthic invertebrates from the middle Atlantic continental shelf. Int. Revue ges. Hydrobiol. 76:491-515.

Middleton, J.F., and M. Cirano. 2002. A boundary current along Australia's southern shelves: The Flinders Current. J. Geophys. Res. 107(C9). doi:10.1029/2000JC000701

Newell, B.S. 1961. Hydrology of south-east Australian waters. CSIRO Division of Fisheries and Oceanography, Technical Paper No. 10.

Newell, B.S. 1974. Distribution of oceanic water types off south eastern Tasmania, 1973. CSIRO Division of Fisheries and Oceanography, Report No. 59. 15 pp.

Parry, G.D., S.J. Campbell, and D.K. Hobday. 1990. Marine resources off East Gippsland, south eastern Australia. Marine Science Laboratories, Queenscliffe, Victoria, Tech. Report No. 72.

Pérès, J.M. 1982. Specific pelagic assemblages. In: O. Kinne (ed.), Marine ecology, vol. 5: Ocean management, part 1. John Wiley and Sons, Chichester, pp. 313-372.

Probert, P.K., and J.B. Wilson. 1984. Continental shelf benthos off Otago Peninsula, New Zealand. Estuar. Coast. Shelf Sci. 19:373-91. doi:10.1016/0272-7714(84)90032-5

Provis, D.G., and R.K. Steedman. 1985. Wave measurements in the Great Australian Bight. Unpublished paper presented at the Australasian Conference on Coastal and Ocean Engineering, IEAust, Christchurch, N.Z.

Rochford, D.J. 1977. A review of a possible upwelling situation off Port MacDonnell, S.A. CSIRO Division of Fisheries and Oceanography, Report No. 81. 15 pp.

Rowe, G.T. 1981. The deep sea ecosystems. In: A.R. Longhurst (ed.), Analysis of marine ecosystems. Academic Press, New York, pp. 235-267.

Schahinger, R.B. 1987. Structure of coastal upwelling events observed off the south-east coast of South Australia during February 1983–April 1984. Australian J. Mar. Freshw. Res. 38:439-459. doi:10.1071/MF9870439

Smith, K.D., I.C. Potter, and N.G. Hall. 2004. Biological and fisheries data for managing the deep-sea crabs *Hypothalassia acerba* and *Chaceon bicolour* in Western Australia. Fisheries Research and Development Council, Canberra, projects 1999/154 and 2001/055.

Sturman, A., and N. Tapper. 1996. The weather and climate of Australia and New Zealand. Oxford University Press.

Ward, T.J., and J.M. Blaber. 1994. Continental shelves and slopes. In: L.S. Hammond and R.N. Synnot (eds.), Marine biology. Longman Cheshire, Melbourne, pp. 333-343.

Ward, T.M., S.J. Sorokin, D.R. Currie, P.J. Rogers, and L.J. McLeay. 2006. Epifaunal assemblages of the eastern Great Australian Bight: Effectiveness of a benthic protection zone in representing regional biodiversity. Cont. Shelf Res. 26:25-40. doi:10.1016/j.csr.2005.09.006

Williams, A., N. Bax, and B. Barker. 2006. Integrating fishing industry knowledge of fishing grounds with scientific data on seabed habitats for informed spatial management and ESD evaluation in the SESSF. Final report to the Fisheries Research and Development Council, project 2000/153. 265 pp.

Williams, A., F. Althaus, B. Barker, C. Gardner and D. Mills. 2007. Understanding shelf-break habitat for sustainable management of fisheries with spatial overlap. Draft final report to the Fisheries Research and Development Council, project no. 2004/066. 250 pp.

Wood, J.D., and E. Terray. 2005. Ocean current, temperature, and wave observations at the Amrit-1 location offshore of southern Victoria, Australia. Final report April to October 2004. Ocean Data Technologies, Inc. technical report prepared for Santos, Ltd. and Unocal Corporation.

Wyrtki, K. 1971. Oceanographical atlas of the International Indian Ocean Expedition. National Science Foundation, Washington, D.C., November 1971. 531 pp.

Persselin, S. and B. Daly. 2010. Diet and Water Source Effects on Larval Red King Crab Cultivation. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.17

Diet and Water Source Effects on Larval Red King Crab Cultivation

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Abstract

King crab larval culture has expanded from small-scale research to hatchery and stock enhancement feasibility studies in Alaska. The goal of this project was to improve red king crab (*Paralithodes camtschaticus*) larval survival in culture by assessing diets and water sources in two separate experiments. Diet treatments included (1) newly hatched *Artemia* nauplii, and (2) newly hatched *Artemia* nauplii and the diatom *Thalassiosira nordenskioeldii*; both treatments were conducted at facilities in Kodiak and Seward, Alaska. The water source study was conducted at the Seward facility and treatments included (1) natural seawater from Resurrection Bay, and (2) artificial seawater made from (Instant Ocean®) sea salt.

At both facilities, mean survival to the glaucothoe stage was significantly higher and mean larval duration was significantly shorter for larvae fed the *Artemia*-diatom diet. Larval duration and survival to the glaucothoe stage were not significantly different between facilities. In Kodiak, larval survival and duration were carried through to the first juvenile stage (C1); all glaucothoe molted to C1 on the *Artemia*-diatom diet whereas only two glaucothoe molted to C1 on the *Artemia*-only diet by the termination of the experiment. In Seward, mean survival to glaucothoe and mean larval duration were not significantly different between larvae reared in artificial seawater and natural seawater. For higher yield

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in larval red king crab cultivation, a diet including *T. nordenskioeldii* is recommended while artificial seawater is likely unnecessary.

Introduction

Enhancement of red king crab (*Paralithodes camtschaticus*) populations has been promoted as a means for increasing the wild population in Alaska. After landings of red king crab peaked in the 1970s, catches of red king crab declined precipitously in the 1980s and have since remained depressed. Reasons for the decline and continued lack of recovery are still debated but may include egg predation (Kuris et al. 1991), disease, overfishing (Orensanz et al. 1998, Dew and McConnaughey 2005), climatic changes (Zheng and Kruse 2000), low survival through the juvenile life stage caused by predation (Blau 1986), drift of planktonic larvae from suitable habitat (Shirley and Shirley 1989), and insufficient food quantity or type (Paul et al. 1989). The successful establishment of red king crab in the Barents Sea in the 1960s provides evidence that red king crab populations can be enhanced by propagation (Kovatcheva et al. 2006). Whether this technique would work in the crab's endemic range in Alaska is unknown.

The collaborative Alaska King Crab Research, Rehabilitation and Biology (AKCRRAB) program was launched in 2006 to investigate the feasibility of king crab stock enhancement in Alaska. Success of small-scale larval culture techniques for red king crab and blue king crab (*Paralithodes platypus*) developed at the NOAA Alaska Fisheries Science Center, Kodiak Laboratory in Kodiak, Alaska (Persselin 2006, Stevens et al. 2008) formed the basis for developing large-scale diet and density studies for red and blue king crab larvae at the Alutiiq Pride Shellfish Hatchery (APSH) in Seward, Alaska. Initial results of this large-scale cultivation project, however, yielded poor overall survival (<1%) to the first juvenile instar; the combined effects of diet and density made it difficult to determine the source of the high mortality.

In the wild, female red king crabs carry their fertilized eggs for 11-12 months, releasing larvae over an average 32 day period in late winter to spring (Otto et al. 1990, Stevens and Swiney 2007). Larvae develop through four planktotrophic zoeal stages (Z1-Z4) and the nonfeeding glaucothoe stage before settling onto structurally complex habitat and molting into the first juvenile stage (C1) (Marukawa 1933). In the wild, newly hatched red king crab zoeae consume phytoplankton and zooplankton (Bright 1967). The diatoms *Thalassiosira* spp., present in the ocean during larval development, have been shown in the laboratory to support larval growth during the first zoeal stage (Paul et al. 1989, Paul and Paul 1990). At the Kodiak Lab, high survival (91.7%) to the first instar of *P. platypus* was achieved using a diet of newly hatched *Artemia franciscana* nauplii and the cold water diatom, *Thalassiosira nordenski-*

oeldii (Stevens et al. 2008). Although culture of larval *P. camtschaticus* and *P. brevipes* on a combination diet of *Artemia salina* nauplii and *Thalassiosira* spp. (dominated by *T. nordenskioeldii*) met with varied success (5.7%-87.2% survival in the zoeal stages), the results suggest that high survival on this diet is possible (Kittaka et al. 2002).

Fundamental parameters of larval culture such as temperature, water quality, and food availability can be more difficult to control in large rearing tanks than small systems where variables can be more precisely controlled and manipulated. In this small-scale study, we investigated diet and water source as factors contributing to poor survival in previous experiments and compared results for differences in survival at both the Kodiak Lab and University of Alaska Fairbanks Seward Marine Center, which is adjacent to APSH. Based on the success with blue king crab larvae, the *Artemia–T. nordenskioeldii* diet was selected for red king crab larvae at both facilities for this experiment (Stevens et al. 2008). Additional research suggests seawater contaminants such as hydrocarbons could have been a contributing factor in larval mortality at APSH (Duesterloh 2002). To address this, we compared larval survival using artificial and natural seawater. These controlled, small-scale experiments are a critical step in evaluating the feasibility of large-scale culture necessary for a stock enhancement program.

Materials and methods

Cultivation techniques were standardized between facilities. We used the same laboratory methods, fed the larvae identical diets from the same source of *Artemia* nauplii and *Thalassiosira nordenskioeldii*, held the larvae at the same temperatures, kept identical larval densities, and used larvae from the same broodstock cohort. The only difference between facilities was the additional comparison of natural and artificial seawater sources at the Seward Marine Center.

Eighteen ovigerous crabs were collected with commercial crab pots in Bristol Bay, Alaska, during November 2007. Six crabs were retained at the Kodiak Laboratory in flow-through, ambient seawater tanks with a temperature range of 2.4 to 7.7°C (mean 4.05°C, SE = 0.1). Twelve crabs were shipped to holding tanks at the Seward Marine Center and held in flow-through, ambient seawater with a temperature range of 3.4 to 8.0°C (mean 5.15°C, SE = 0.1). Crabs were fed to satiation with squid and herring twice per week at both locations.

Newly hatched larvae (less than 24 hours old) were collected on April 21, 2008, at the Kodiak Lab and on April 4, 2008, at Seward Marine Center from three female crabs that had been isolated in separate hatching bins. Four larvae from each female were placed in 1 L glass beakers for a total of 12 larvae per beaker. The project consisted of two experiments: (1) the effect of diet on larval survival and duration, and

Table 1. Treatments and study locations for diets and water sources investigated for effect on survival and duration of red king crab *Paralithodes camtschaticus* larvae.

Treatment name	Treatment definition	Location of study
ArtK	Natural seawater with newly hatched *Artemia* nauplii	Kodiak Lab
ThalK	Natural seawater with newly hatched *Artemia* nauplii + *Thalassiosira nordenskioeldii*	Kodiak Lab
ArtS	Natural seawater with newly hatched *Artemia* nauplii	Seward Marine Center
ThalS	Natural seawater with newly hatched *Artemia* nauplii + *Thalassiosira nordenskioeldii*	Seward Marine Center
ASW	Artificial seawater with a diet of newly hatched *Artemia* nauplii	Seward Marine Center

(2) the effect of natural vs. artificial seawater on larval survival and duration. The diet experiment, conducted at the Kodiak Lab and the Seward Marine Center, consisted of two treatments: (1) larvae receiving *Artemia* nauplii (ArtK, ArtS), and (2) larvae receiving *Artemia* nauplii plus live *T. nordenskioeldii* microalgae (ThalK, ThalS) (Table 1). The seawater experiment, conducted at the Seward Marine Center, consisted of two treatments: (1) larvae receiving *Artemia* nauplii in natural seawater (ArtS), and (2) larvae receiving *Artemia* nauplii in artificial seawater (ASW) (Table 1). All *Artemia* nauplii were newly hatched, collected at less than 24 hours after initial hydration. Treatments comprised five replicates of 12 zoeae per beaker held in a temperature-controlled room at 7°C. Larvae were fed approximately 1750 *Artemia* nauplii per beaker (2.2 *Artemia* nauplii per ml) daily and were maintained on a 12 hour dark:12 hour light photoperiod cycle at 70 lux using indirect fluorescent lighting. Larvae were placed inside a 150 mm long 75 mm diameter PVC tube, with 675 µm nylon screen glued to the bottom (Persselin 2006, Stevens et al. 2008). For the diet experiment, each tube was set into a beaker filled with 800 ml of seawater that was filtered to 5 µm and UV-sterilized (ArtK, ArtS) or 800 ml of filtered and sterilized seawater containing 10,000 cells per ml of *T. nordenskioeldii* (ThalK, ThalS). For the seawater experiment each tube was set into a beaker filled with 800 ml of seawater that was filtered to 5 µm and UV-sterilized (ArtS) or 800 ml artificial seawater made using deionized water and Instant Ocean® sea salt (ASW). Salinity of natural and artificial seawater was 31 ppt. Tubes containing larvae were transferred to clean beakers with new seawater daily prior to feeding. Feeding was terminated when all zoeae in the beaker molted to the glaucothoe stage. Molts and mortalities were

recorded and removed daily. Final survival and duration to glaucothoe was determined when the last larva in each replicate had molted to glaucothoe (Seward Marine Center and Kodiak Lab). Final survival and duration to C1 (Kodiak Lab only) was determined when the last glaucothoe in each replicate had molted to C1 or died.

San Francisco Bay strain *Artemia* cysts (Brine Shrimp Direct, Ogden) from the same batch were used at the Kodiak Lab and the Seward Marine Center to eliminate the effect of *Artemia* quality on the treatments. *Artemia* cysts were hatched daily in aerated seawater sterilized as above. Newly hatched (<24 hours old) *Artemia* nauplii were collected and rinsed in freshwater prior to feeding to larvae.

The chain-forming diatom *T. nordenskioeldii* (15-27 µm long), obtained from the Center for Culture of Marine Phytoplankton at Bigelow laboratory for Ocean Sciences (West Boothbay Harbor), has been under cultivation at the Kodiak Lab since 2002. A starter culture was shipped to the Seward Marine Center for cultivation. Diatoms were cultured under a 16 hour light:8 hour dark photoperiod cycle in a temperature-controlled room at 7°C in seawater filtered to 5 µm, UV-sterilized, chlorinated with 6% sodium hypochlorite and dechlorinated with sodium thiosulfate. The seawater was enriched with f/2 algal culture formula (Kent Marine, Franklin), and sodium metasilicate.

Analysis of variance (ANOVA) and post-hoc comparisons (Tukey's HSD) were used to determine significance in larval survival and duration. Survival and duration to C1 at the Kodiak Laboratory was compared using Student's *t*-test. For the water source experiment, survival and duration to glaucothoe were compared between treatments using Student's *t*-test. Significance was determined with an alpha level of 0.05. Means with standard error (SE) are reported.

Results

Diet

Larval survival

For survival, the main effect of diet was significant (Table 2). Survival to glaucothoe was higher when *Thalassiosira nordenskioeldii* was included in the diet at both locations (Tukey's HSD, $p < 0.001$). When fed *Artemia* nauplii only, overall survival was 30.7% (SE = 5.3) with mean survival of 29.8% (SE = 6.8) at the Kodiak Laboratory (ArtK) and 31.7% (SE = 10.3) at the Seward Marine Center (ArtS) (Fig. 1A and B, Table 3). When *T. nordenskioeldii* was included in the diet, overall survival was 84.4% (SE = 5.6) with mean survival of 93.8% (SE = 4.1) at the Kodiak Lab (ThalK) and 75.0% (SE = 7.0) at the Seward Marine Center (ThalS) (Fig. 1A and B, Table 3). The main effect of site was not significant and there was no diet site interaction (Table 2).

Table 2. Analysis of variance (ANOVA) for survival and duration of red king crab *Paralithodes camtschaticus* larvae.

	Effect	SS	d.f.	MS	*F*	*p*-value
Survival	Diet	13540.8	1	13540.8	47.96	<0.001
	Site	335.3	1	335.3	1.19	0.293
	Diet × site	500.1	1	500.1	1.77	0.203
	Residual	4234.7	15	282.3		
Duration	Diet	786.14	1	786.14	50.49	<0.001
	Site	16.54	1	16.54	1.06	0.319
	Diet × site	96.36	1	96.36	6.19	0.025
	Residual	233.55	15	15.57		

SS = sum of squares; d.f = degrees of freedom; MS = mean square.

Table 3. Survival rates of red king crab *Paralithodes camtschaticus* larvae in each replicate of diet and seawater treatments conducted in Kodiak and Seward, Alaska.

		Replicate						
		A	B	C	D	E	Total	
Treatment[a]	Stage[b]	% survival	% survival	% survival	% survival	% survival	Mean %	SE[c] %
ArtK	G	33	25	8	50	33	29.8	6.8
ArtK	C1	[d]	[d]	[d]	8	8	3.2	2.0
ThalK	G	100	100	92	[g]	83	93.8	4.1
ThalK	C1	33	100	75	[g]	42	62.5	15.4
ArtS	G	42	8	25	67	17	31.7	10.3
ThalS	G	67	75	100	58	75	75.0	7.0
ASW	G	33	8	33	33	50	31.7	6.7

[a] Treatments: see table 1 for treatment definitions.

[b] Stages: G = glaucothoe; C1 = first juvenile.

[c] Standard error.

[d] No molts to C1.

[e] 1 molt to C1 on day 79.

[f] 1 molt to C1 on day 77.

[g] Replicate dropped due to unexplained mortality not observed in any of the other replicates.

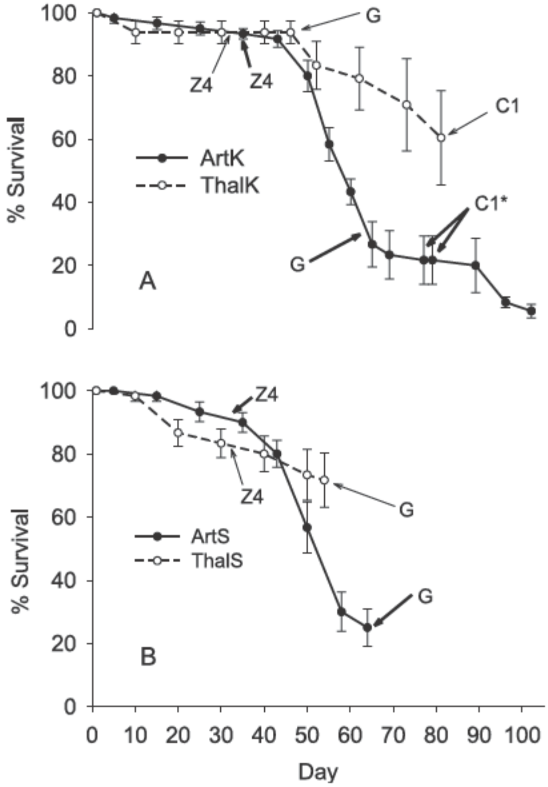

Figure 1. Mean percent survival of red king crab *Paralithodes camtschaticus* larvae in diet treatments in (A) Kodiak through C1 stage, and (B) Seward through glaucothoe stage. ArtK and ArtS are the newly hatched *Artemia* nauplii diets, and ThalK and ThalS are the newly hatched *Artemia* nauplii plus *Thalassiosira nordenskioeldii* diets. Arrows designate the mean day of molt with darker arrows for ArtK and ArtS and lighter arrows for ThalK and ThalS. Z4 is the molt to the zoea 4 stage, G is the molt to glaucothoe stage, C1 is the molt to the first juvenile crab stage, and C1* designates the two days when a molt occurred in the ArtK treatment.

Mean survival of all ArtK larvae to C1 was 3.2% (SE = 2.0), while mean survival of ThalK larvae to C1 was 62.5% (SE = 15.4) (Fig. 1A, Table 3). Survival to C1 was higher (d.f. = 7, $t = 4.31$, $p = 0.004$) when *T. nordenskioeldii* was included in the diet.

One of five replicates of the ThalK treatment experienced unexplained mortality on days 30 and 31. Survival dropped from 100% to 50% on day 30, and to 33% on day 31 at which point it remained constant for the rest

Table 4. Duration of red king crab *Paralithodes camtschaticus* larval development in each replicate of diet and seawater treatments conducted in Kodiak and Seward, Alaska.

		Replicate						
		A	B	C	D	E	Total	
Treatment[a]	Stage[b]	Days	Days	Days	Days	Days	Mean	SE[c]
ArtK	G	61	69	67	60	59	63.2	2.0
ArtK	C1	[d]	[d]	[d]	[e]	[f]	–	–
ThalK	G	46	46	45	[g]	46	45.6	0.3
ThalK	C1	74	74	74	[g]	81	75.8	1.8
ArtS	G	55	60	64	51	54	56.8	2.3
ThalS	G	47	48	48	54	45	48.4	1.5
ASW	G	51	52	57	49	45	50.8	2.0

[a] Treatments: see table 1 for treatment definitions.

[b] Stages: G = glaucothoe; C1 = first juvenile.

[c] Standard error.

[d] No molts to C1.

[e] 1 molt to C1 on day 79.

[f] 1 molt to C1 on day 77.

[g] Replicate dropped due to unexplained mortality not observed in any of the other replicates.

of the experiment. This abrupt increase in mortality was not observed in any of the other replicates and is attributed to causes other than the diet being tested. We did not include this replicate in the analysis.

Larval duration

For larval duration, the main effect of diet was significant. Larval duration to glaucothoe was shorter when *T. nordenskioeldii* was included in the diet (Tukey's HSD, $p < 0.001$). When fed *Artemia* nauplii only, overall duration was 60.0 days (SE = 1.3). At the Kodiak Lab (ArtK), the duration for all larvae to reach glaucothoe was 69 days; however, mean duration was 63.2 days (SE = 2.0) (Fig. 1A, Table 4). At the Seward Marine Center (ArtS), duration for all larvae to reach glaucothoe was 64 days, but mean duration was 56.8 days (SE = 2.3) (Fig. 1B, Table 4). When *T. nordenskioeldii* was included in the diet, overall duration was 47.1 days (SE = 1.3). At the Kodiak Lab (ThalK), duration for all larvae to reach glaucothoe was 46 days, with a mean duration of 45.6 days (SE = 0.3) (Fig. 1A, Table 4). At the Seward Marine Center (ThalS), duration for all larvae to reach glaucothoe was 53 days; however, mean duration was 48.4 days (SE = 1.5) (Fig. 1B, Table 4). The main effect of site was not significant, but there was a significant diet site interaction (Table 2). When fed *Artemia* nauplii only, the duration to reach glaucothoe was longer at the Kodiak

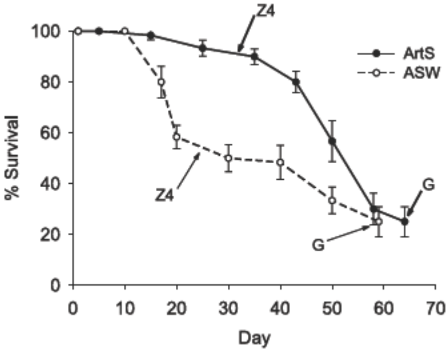

Figure 2. Mean percent survival of red king crab *Paralithodes camtschaticus* larvae in artificial and natural seawater treatments in Seward through the glaucothoe stage. ArtS is the natural seawater treatment with larvae fed a diet of newly hatched *Artemia* nauplii, and ASW is the artificial seawater treatment (Instant Ocean® Sea Salt) with larvae fed a diet of newly hatched *Artemia* nauplii. Arrows designate the mean day of molt with darker arrows for ArtS and lighter arrows for ASW. Z4 is the molt to the zoea 4 stage and G is the molt to glaucothoe stage.

Lab (ArtK) (63.2 days, SE = 2.0) than at the Seward Marine Center (ArtS) (56.8 days, SE = 2.3) (Tukey's HSD, $p = 0.022$) (Table 2).

Duration for all ArtK larvae to reach C1 could not be calculated because only two glaucothoe molted to C1; one glaucothoe in one replicate on day 77 and one glaucothoe in a second replicate on day 79 (Fig. 1A, Table 4). All other glaucothoe had died by day 103. Duration for all ThalK larvae to reach C1 was 81 days, but mean duration was 75.8 days (SE = 1.8).

Water source

Mean survival to glaucothoe was 31.7% (SE = 10.3) in natural and 31.7% (SE = 6.7) artificial seawater (Fig. 2, Table 3). Duration for all larvae to reach glaucothoe was 64 days in natural seawater (ArtS) and 56 days in artificial seawater (ASW); however, mean duration was similar and took 56.8 days (SE = 2.3) in natural seawater and 50.8 days (SE = 2.0) in artificial seawater (d.f. = 8, $t = 1.98$, $p = 0.083$) (Fig. 2, Table 4).

Discussion

Effect of diet on larval survival and duration

A diet limited to newly hatched *Artemia* was inferior to a diet of newly hatched *Artemia* and *Thalassiosira nordenskioeldii* microalgae for rearing red king crab larvae. The addition of *T. nordenskioeldii* promoted higher survival and a shorter larval duration. By the termination of the Kodiak Lab experiment, all glaucothoe had molted to C1 when fed *Artemia* and *T. nordenskioeldii*, while only two glaucothoe had molted to C1 when fed *Artemia* only (Fig. 1A, Table 4). The low survival and prolonged duration on the *Artemia*-only diet would not support successful small- or large-scale larval rearing to the juvenile crab stage.

Artemia nauplii are commonly used in fish and crustacean larval culture due to their availability, ease of culture, and acceptability as a prey item by larvae. Newly hatched *Artemia* nauplii have commonly been used as a food source in culturing red king crab larvae in the laboratory but survival and development have been variable and generally suboptimal (Kurata 1960, Kittaka et al. 2002, Kovatcheva 2002, Epelbaum and Kovatcheva 2005, Kovatcheva 2006, Persselin 2006). *Artemia* have little, if any, of the highly unsaturated fatty acids (HUFAs) docosahexaenoic acid (DHA, 22:6*n*-3) or eicosapentaenoic acid (EPA, 20:5n-3) that are considered crucial for the normal development and survival of crustacean larvae (Levine and Sulkin 1984; McConaugha 1985; Navarro et al. 1991, 1993; Anger 2001; Evjemo et al. 2001; Kogane et al. 2007).

Interestingly, diets with and without *T. nordenskioeldii* had similarly high survival until after reaching the Z4 stage, at which point mortality increased in treatments without diatoms (Fig. 1). This suggests that development at the Z4 stage is highly sensitive to diet. At the Kodiak Lab, survival in the *Artemia*-only treatment plummeted at the same time the ThalK larvae molted to glaucothoe, suggesting that the ArtK Z4 stage larvae had passed a critical point for molting successfully to glaucothoe. Larval duration was also affected by the absence of diatoms. Development to glaucothoe was prolonged in the ArtK Z4 stage larvae and only two glaucothoe molted to C1. The ArtS Z4 stage larvae also experienced prolonged development to glaucothoe and a more extreme increase in mortality than the ThalS Z4 stage larvae. The extended larval duration and increased mortality in the *Artemia*-only treatments suggest that king crab larvae require additional nutrients for successful and timely molting to the C1 stage. Kittaka et al. (2002) observed that lipid accumulation during zoeal stages is critical for glaucothoe survival in king crab. Lipid accumulation also appears necessary for successful larval development in other crab species. Larval mud crab (*Scylla serrata*) had lower survival and a prolonged intermolt period to the C1 stage when fed only *Artemia,* while larvae fed *Artemia* enriched with EPA or DHA had shorter intermolt periods (Suprayudi et al. 2004).

EPA and DHA were significant in promoting successful development to the megalopa stage (comparable to glaucothoe) of the mud crab (*Eurypanopeus depressus*) and EPA was found to maintain the survival rate and DHA to accelerate the intermolt period in larval swimming crab (*Portunus trituberculatus*) (Levine and Sulkin 1984, Takeuchi et al. 1999). Though it is unknown what levels of EPA and DHA are optimal for red king crab larval development, previous fatty acid analysis of *T. nordenskioeldii* suggested that it would provide an adequate amount (Kittaka et al. 2002).

Warm-water microalgae species such as *Isochrysis galbana* and *Nannochloropsis* spp. are typically used in aquaculture, including blue crab (*Callinectes sapidus*) larval culture, to provide essential fatty acids and other nutrients and to maintain water quality (Zmora et al. 2005). However, the cold-water species *T. nordenskioeldii* was chosen for this experiment because it is likely a component of the natural diet of red king crab larvae (Bright 1967, Shirley and Shirley 1989, Paul et al. 1989). Experiments conducted by Kittaka et al. (2002) indicated that combining *Thalassiosira* sp. with *Artemia* nauplii could provide increased survival to glaucothoe in red king crab; however, results were variable, ranging from 0% to 87.2%. Duration to the glaucothoe stage ranged from 27.9 to 35.0 days, with a mean of 29.7 days, at 8-10°C (Kittaka et al. 2002). Larval duration on the combination diet was longer in our experiment likely due to the cooler culture temperature. With blue king crab larvae, the *T. nordenskioeldii–Artemia* nauplii diet produced high survival (91.7%) to the C1 stage (Stevens et al. 2008). Although the species are similar, the difference in survival may indicate different nutritional requirements. However, one ThalK replicate achieved 100% survival to C1, suggesting other factors may have contributed to mortality such as initial larval fitness or exposure to contaminants during culture. Survival in this replicate provides evidence that the addition of *T. nordenskioeldii* can promote optimal survival.

We also compared survival between facilities to test for location effects. Because larval survival was similar between the Kodiak Lab and the Seward Marine Center, seawater source was likely not the principal cause of the Seward Marine Center's low survival in 2007. Mortality may have been attributed to other factors such as fluctuating water flow and temperature, food presentation and nutritional quality, and larval rearing density. We noted a difference in larval duration between facilities in *Artemia*-only treatments despite attempts to duplicate temperature and light exposure and intensity at both locations. There were no differences in duration between facilities when *T. nordenskioeldii* was included in the diet. Slight differences in temperature and light parameters between facilities may have become significant over the longer duration of the *Artemia*-only treatments and contributed to the increased larval duration at the Kodiak Lab.

Effect of seawater source on larval survival and duration

Artificial seawater was not beneficial in terms of survival and larval duration when compared to natural seawater for rearing larvae to the glaucothoe stage. Zoeal survival declined much more rapidly in artificial seawater than natural seawater; however, the numbers of animals surviving to glaucothoe were similar. The cause of this difference in zoeal mortality rate is unknown and warrants further investigation should the use of artificial seawater become necessary.

Interest in using artificial seawater arose due to water quality concerns at the Seward Marine Center facility after initial cultivation attempts in 2007 resulted in lower than expected survival. A study conducted in 2001 found polyaromatic compound contamination in the Seward Marine Center seawater supply at levels reported to cause genetic damage to fish embryos (Rice et al. 2001, Duesterloh 2002). Artificial seawater is used for culture in facilities without access to natural seawater or to control seawater purity and has been used to successfully rear blue crab (*Callinectes sapidus*), red king crab, and other species (Cadman and Weinstein 1988, Konishi et al. 2002, Kovatcheva 2002, Xiao et al. 2003, Epelbaum and Kovatcheva 2005, Kovatcheva 2006, Zmora et al. 2005). Red king crab larvae previously reared in artificial seawater and on a diet of *Artemia* nauplii had an average larval duration of 39 days to the glaucothoe stage and an average survival to glaucothoe of 30.8% in 1 L beakers at 7-8°C (Epelbaum and Kovatcheva 2005). Our results are consistent with these findings.

Conclusion

Although newly hatched *Artemia* nauplii provide an easily obtained and reared food source for red king crab larvae, they alone do not provide a diet adequate for producing high survival or timely development to the C1 stage. The addition of *Thalassiosira nordenskioeldii* increases survival and shortens larval duration likely due to essential fatty acids necessary for proper development. Further analysis of lipid content and fatty acid composition of *Artemia*, *T. nordenskioeldii,* and red king crab would help clarify the role of *T. nordenskioeldii* in larval development. A better understanding of these components would aid selection of the most feasible diet for large-scale culture. *Thalassiosira nordenskioeldii* is a slow-growing, cold-water species; a fast-growing, warm-water microalgae or a formulated enrichment product with a similar nutrient and fatty acid profile could be substituted to decrease costs in labor and time.

Artificial seawater does not increase larval survival when compared to natural seawater and our results suggest that inter-site variability in water quality was not the principal cause for reduced survival in previous Seward experiments. This finding is advantageous to large-scale culture, as using natural seawater in a large-scale system eliminates the expense of artificial salts and the associated space, filtration, and labor requirements.

This research advances our understanding of larval culture parameters, informs the refinement of large-scale culture technique, and provides impetus for further research into improving the feasibility of large-scale larval production of king crab for stock rehabilitation.

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References

Anger, K. 2001. The biology of decapod crustacean larvae. Crustacean issues 14. A.A. Balkema, Lisse, p. 420.

Blau, S.F. 1986. Recent declines of the red king crab (*Paralithodes camtschatica*) populations and reproductive conditions around the Kodiak archipelago, Alaska. In: G.S. Jamieson and N. Bourne (eds.), North Pacific workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92:360-369.

Bright, D. 1967. Life histories of the king crab, *Paralithodes camtschatica*, and Tanner crab, *Chionoecetes bairdi*, in Cook Inlet, Alaska. Ph.D. thesis, University of Southern California, Los Angeles. 265 pp.

Cadman, L., and M.P. Weinstein. 1988. Effects of temperature and salinity on the growth of laboratory-reared juvenile blue crabs *Callinectes sapidus* Rathbun. J. Exp. Mar. Biol. Ecol. 121:193-207. doi:10.1016/0022-0981(88)90088-3

Dew, C.B., and R.A. McConnaughey. 2005. Did trawling on the broodstock contribute to the collapse of Alaska's king crab? Ecol. Appl. 15:919-941. doi:10.1890/03-5231

Duesterloh, S. 2002. The role of copepods in the distribution of hydrocarbons: An experimental approach. Ph.D. thesis, University of Alaska Fairbanks. 182 pp.

Epelbaum, A.B., and N.P. Kovatcheva. 2005. Daily food intakes and optimal food concentrations for red king crab (*Paralithodes camtschaticus*) larvae fed *Artemia* nauplii under laboratory conditions. Aquacult. Nutr. 11:455-461. doi:10.1111/j.1365-2095.2005.00374.x

Evjemo, J.O., T.L. Danielsen, and Y. Olsen. 2001. Losses of lipid, protein and n-3 fatty acids in enriched *Artemia franciscana* starved at different temperatures. Aquaculture 193:65-80. doi:10.1016/S0044-8486(00)00470-1

Kittaka, J., B.G. Stevens, S. Teshima, and M. Ishikawa. 2002. Larval culture of the king crabs *Paralithodes camtschaticus* and *P. brevipes.* In: A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley, and D. Woodby (eds.), Crabs in cold water regions: Biology, management, and economics. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 189-209.

Kogane, T., S. Dan, and K. Hamasaki. 2007. Improvement of larval rearing technique for mass seed production of snow crab *Chionoecetes opilio*. Fish. Sci. 73:851-861. doi:10.1111/j.1444-2906.2007.01406.x

Konishi, K., T. Matsumoto, and R. Tsujimoto. 2002. The complete larval development of *Chionoecetes japonicus* under laboratory conditions. In: A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley, and D. Woodby (eds.), Crabs in cold water regions: Biology, management, and economics. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp.135-146.

Kovatcheva, N. 2002. Observations on rearing red king crab (*Paralithodes camtschaticus*) zoea and glaucothoe in a recycling water system. In: A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley, and D. Woodby (eds.), Crabs in cold water regions: Biology, management, and economics. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 273-282.

Kovatcheva, N. 2006. Red king crab (*Paralithodes camtschaticus*) reproduction and cultivation in artificial conditions in Russia. In: B.G. Stevens (ed.), Alaska crab stock enhancement and rehabilitation: Workshop proceedings. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 15-22.

Kovatcheva, N., A. Epelbaum, A. Kalinin, R. Borisov, and R. Lebedev. 2006. Early life history stages of the red king crab *Paralithodes camtschaticus* (Tilesius, 1815). VNIRO Publishing, Moscow. 115 pp.

Kurata, H. 1960. Studies on the larva and post-larva of *Paralithodes camtschatica,* II. Feeding habits of the zoea. Bull. Hokk. Reg. Fish. Res. Lab. 21:1-8.

Kuris, A.M., S.F. Blau, A.J. Paul, J.D. Shields, and D.E. Wickham. 1991. Infestation by brood symbionts and their impact on egg mortality in the red king crab, *Paralithodes camtschatica*, in Alaska: Geographic and temporal variation. Can. J. Fish. Aquat. Sci. 48:559-568. doi:10.1139/f91-071

Levine, D.M., and S.D. Sulkin. 1984. Nutritional significance of long-chain polyunsaturated fatty acids to the zoeal development of the brachyuran crab, *Eurypanopeus depressus* (Smith). J. Exp. Mar. Biol. Ecol. 81:211-223. doi:10.1016/0022-0981(84)90141-2

Marukawa, H. 1933. Biological and fishery research on Japanese king crab, *Paralithodes camtschatica* (Tilesius). J. Imp. Fish. Exp. St. (Tokyo) 37:1-152.

McConaugha, J.R. 1985. Nutrition and larval growth. In: A.M. Wenner (ed.), Larval growth. Crustacean issues 2. A.A. Balkema, Rotterdam, pp. 127-154.

Navarro, J.C., F. Amat, and J.R. Sargent. 1991. A study of the variations in lipid levels, lipid class composition and fatty acid composition in the first stages of *Artemia* sp. Mar. Biol. 111:461-465. doi:10.1007/BF01319419

Navarro, J.C., R.S. Batty, M.V. Bell, and J.R. Sargent. 1993. Effects of two *Artemia* diets with different contents of polyunsaturated fatty acids on the lipid-composition of larvae of Atlantic herring (*Clupea harengus*). J. Fish Biol. 43:503-515.

Orensanz, J.M.L., J. Armstrong, D. Armstrong, and R. Hilborn. 1998. Crustacean resources are vulnerable to serial depletion: The multifaceted decline of crab and shrimp fisheries in the greater Gulf of Alaska. Rev. Fish Biol. Fish. 8:117-176. doi:10.1023/A:1008891412756

Otto, R.S., R.A. MacIntosh, and P.A. Cummiskey. 1990. Fecundity and other reproductive parameters of female red king crab (*Paralithodes camtschatica*) in Bristol Bay and Norton Sound, Alaska. In: Proceedings of the International Symposium on King and Tanner Crabs. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 65-90.

Paul, A.J., and J.M. Paul. 1990. Growth of stage I king crab larvae of *Paralithodes camtschatica* (Tilesius) (Decapoda: Lithodidae) in natural communities. J. Crustac. Biol. 10:175-183. doi:10.2307/1548479

Paul, A.J., J.M. Paul, and K.O. Coyle. 1989. Energy sources for first-feeding zoeae of king crab *Paralithodes camtschatica* (Tilesius) (Decapoda, Lithodidae). J. Exp. Mar. Biol. Ecol. 130:55-69. doi:10.1016/0022-0981(89)90018-X

Persselin, S. 2006. Cultivation of king crab larvae at the Kodiak Fisheries Research Center, Kodiak, Alaska. In: B.G. Stevens (ed.), Alaska crab stock enhancement and rehabilitation: Workshop proceedings. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 9-14.

Rice, S.D., R.E. Thomas, M.G. Carls, R.A. Heintz, A.C. Wertheimer, M.L. Murphy, J.W. Short, and A. Moles. 2001. Impacts to pink salmon following the *Exxon Valdez* oil spill: Persistence, toxicity, sensitivity, and controversy. Rev. Fish. Sci. 9:165-211. doi:10.1080/20016491101744

Shirley, S.M., and T.C. Shirley. 1989. Interannual variability in density, timing, and survival of Alaskan red king crab *Paralithodes camtschatica* larvae. Mar. Ecol. Prog. Ser. 54:51-59. doi:10.3354/meps054051

Stevens, B.G., and K.M. Swiney. 2007. Hatch timing, incubation period, and reproductive cycle for primiparous and multiparous red king crab *Paralithodes camtschaticus* (Tilesius, 1815). J. Crustac. Biol. 27:37-48. doi:10.1651/S-2663.1

Stevens, B.G., S. Persselin, and J. Matweyou. 2008. Survival of blue king crab *Paralithodes platypus* Brandt, 1850, larvae in cultivation: Effects of diet, temperature, and rearing density. Aquacult. Res. 39:390-397. doi:10.1111/j.1365-2109.2007.01798.x

Suprayudi, M.A., T. Takeuchi, and K. Hamasaki. 2004. Essential fatty acids for larval mud crab *Scylla serrata*: Implications of lack of ability to bioconvert C18 unsaturated fatty acids to highly unsaturated fatty acids. Aquaculture 231:403-416. doi:10.1016/S0044-8486(03)00542-8

Takeuchi, T., N. Satoh, S. Sekiya, T. Shimizu, and T. Watanabe. 1999. The effect of dietary EPA and DHA on the molting rate of larval swimming crab *Portunus trituberculatus*. Nippon Suisan Gakk. 65:998-1004.

Xiao, G., L. Pan, Z. Luan, H. Wang, and G. Wang. 2003. Impact of water quality adjustment technology on *Eriocheir sinensis* breeding in Sanila. Mar. Sci. 27:1-4.

Zheng, J., and G.H. Kruse. 2000. Recruitment patterns of Alaskan crabs in relation to decadal shifts in climate and physical oceanography. ICES J. Mar. Sci. 57:438-451. doi:10.1006/jmsc.1999.0521

Zmora, O., A. Findiesen, J. Stubblefield, V. Frenkel, and Y. Zohar. 2005. Large-scale juvenile production of the blue crab *Callinectes sapidus.* Aquaculture 244:129-139. doi:10.1016/j.aquaculture.2004.11.012

Zheng, J., D. Pengilly, R. Foy, and D. Barnard. 2010. Stock Assessment Model Evaluation for St. Matthew Blue King Crab. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.27

Stock Assessment Model Evaluation for St. Matthew Blue King Crab

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Abstract

A catch-survey analysis was developed with trawl survey data from 1978 to 2009, triennial pot survey data from 1995 to 2007, and commercial catch data from 1978 to 2009 to assess St. Matthew Island blue king crab abundances. A maximum likelihood approach was used to estimate abundance and recruitment. Because of the sharp decline of survey abundance in 1999, five model scenarios with different combinations of natural mortality (M) and trawl survey catchability were evaluated. The evaluation criteria include likelihood ratio tests and fits of abundance and biomass. Scenarios 1-3 with estimating M separately for 1999 resulted in a significant improvement in fit from scenarios 4 and 5 with a constant M. Among the five scenarios, with a p-value of 0.05, scenario 1 with fixed M for both 1978-1998 and 2000-2008 ($M = 0.18$ per year) and trawl survey catchability ($Q = 1$) with M estimated by the model in

1999 is the best model, and scenario 4 with a fixed constant $M = 0.18$ per year for the whole time series is the worst one.

Introduction

Blue king crab, *Paralithodes platypus* (Brant 1850), are sporadically distributed throughout their range in the North Pacific Ocean from Hokkaido, Japan to southeastern Alaska. In the eastern Bering Sea, small populations are distributed around St. Matthew Island, the Pribilof Islands, St. Lawrence Island, and Nunivak Island. Isolated populations also exist in cold water areas of the Gulf of Alaska at Olga Bay–Kodiak Island and at Port Wells–Prince William Sound, Russell Fjord, Glacier Bay, Lynn Canal, and Endicott Arm–Southeast Alaska (Somerton 1985). Adult blue king crab are found at depths less than 180 meters and in average bottom water temperatures of 0.6°C (NPFMC 1998). Genetic and tagging studies show that blue king crab off St. Matthew Island are a separate stock from blue king crab off the Pribilof Islands (Otto and Cummiskey 1990). The management area of St. Matthew Island blue king crab includes the waters north of the latitude of Cape Newenham (58°39N) and south of the latitude of Cape Romanzof (61°49N) (Bowers et al. 2008).

The St. Matthew Island fishery developed subsequent to baseline ecological studies associated with oil exploration (Otto 1990). Only large, legal males can be retained by the fishery. The fishery started in 1977, and harvests peaked in 1983 when 164 vessels landed 4,288.26 t. The fishing seasons were generally short, lasting less than a month. This fishery was declared overfished and closed in 1999 when the stock size estimate was below the minimum stock size threshold (MSST) of 4,989.52 t as defined by the fishery management plan (FMP) for the Bering Sea/Aleutian Islands king and Tanner crabs (NPFMC 1998). In November 2000, Amendment 15 to the FMP for the Bering Sea/Aleutian Islands king and Tanner crabs was approved to implement a rebuilding plan for the St. Matthew Island blue king crab stock. The rebuilding plan included an Alaska Board of Fisheries–approved harvest strategy and area closures to control bycatch as well as gear modifications and an area closure for habitat protection. During 2000-2009, the abundance estimates calculated from the National Marine Fisheries Service (NMFS) annual eastern Bering Sea shelf survey data have not met the harvest strategy threshold defined in the rebuilding plan, although 2006 and 2007 abundance estimates were above MSST and the stock is considered rebuilding (Bowers et al. 2008). The blue king crab fishery reopened in 2009/2010 in the St. Matthew Island district after the harvest strategy threshold was removed.

Zheng and Kruse (2002) hypothesized a high level of natural mortality in the St. Matthew blue king crab stock from 1998 to 1999 as an explanation for the low catch per unit effort (CPUE) in the 1998 commercial fishery and in the 1999 ADFG nearshore pot survey (Blau 2000), as well as the low numbers across all crab size groups caught in the eastern Bering Sea NMFS annual trawl survey from 1999 to 2005. To examine this hypothesis, five scenarios of the stock assessment model were evaluated in this study, with combinations of natural mortality and trawl survey catchability either fixed or estimated.

Methods

Data

NMFS has conducted annual summer trawl surveys of St. Matthew Island blue king crab since 1978. The survey stations used to assess the St. Matthew Island blue king crab stock are located within the St. Matthew Island section of the Alaska Department of Fish and Game (ADFG) northern district. From 1978 to 1982, 40 stations centered in 20 × 20 nm (37.04 × 37.04 km) cells were sampled in a total area of 16,040 nm^2. From 1983 to 2008, two strata were identified with low and high density of stations. The low-density strata consisted of 28 stations within an 11,228 nm^2 area and the high density strata consisted of 29 stations in a 7,619 nm^2 area. Total area calculations for each stock management unit uses an area of 401 nm^2 for each 20 × 20 nm cell due to a spherical projection of the grid surface in an area as large as the eastern Bering Sea.

The fishing gear used from 1978 to 1980 was a 400-mesh eastern otter trawl with an effective path width of 12.2 m, and in 1981 was an 83-112 trawl towed by the R/V *Chapman* with an effective path width of 18 m. From 1982 to 2008 a standardized 83-112 eastern otter trawl with an 83 ft (25.3 m) headrope and a 112 ft (34.1 m) footrope (Acuna and Lauth 2008) was used and net width was measured from net mensuration equipment during each tow. Each tow was approximately 0.5 hour in duration and 1.5 nm (2.8 km) in length at a speed of 3 knots (1.5 m per second) (Stauffer 2004). Fishing power was assumed to be equal between vessels if more than one vessel were used.

Crab density (number per nm^2) was estimated at each station for pre-recruit 1 (105-119 mm carapace length [CL]), pre-recruit 2 (90-104 mm CL), recruit (newshell 120-133 mm CL), and post-recruit (oldshell ≥ 120 mm CL and newshell ≥ 134 mm CL) males. The area swept by the trawl was calculated as the product of the distance traveled while the net had bottom contact by the effective width. Distance traveled by the trawl was determined from ship positions recorded at the beginning and end of each tow using LORAN or GPS equipment. Total crab population abundance within the St. Matthew Island section management unit was estimated by averaging crab densities among all stations, multiplying by the total area of the strata, and then adding strata within the management unit (Fig. 1). Variance was estimated by summing the individual stratum variances weighted by squared area of each stratum in each year.

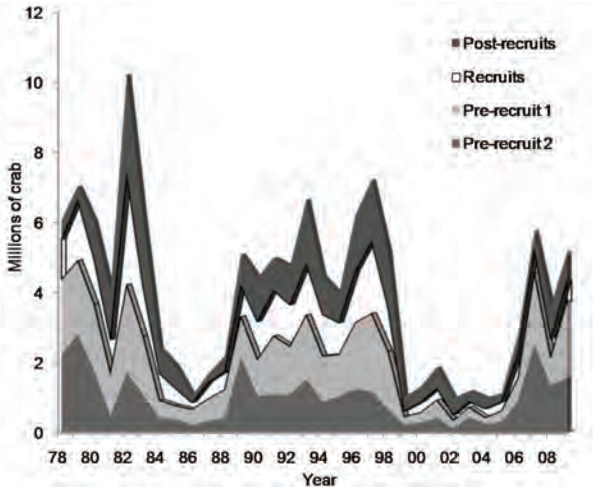

Figure 1. Area-swept abundance by stage (pre-recruit 2, pre-recruit 1, recruits, and post-recruits) from trawl surveys from 1978 to 2009 for St. Matthew Island blue king crab.

ADFG performed a triennial pot survey for St. Matthew Island blue king crab in 1995, 1998, 2001, 2004, and 2007 (Watson 2008), which was able to sample from areas of important habitat for blue king crab, particularly females, that the NMFS trawl survey cannot completely sample. The pot surveys were usually conducted during late July and August with a chartered commercial crab pot vessel. The 2007 survey station grid encompassed the 2,850 nmi^2 area between 59°30-60°30N and 172°00-174°00W and contained 141 primary stations and 24 secondary stations (Watson 2008). Watson (2008) described the detailed survey design, pot structures, and biological sampling. Ninety-six stations were fished in common in each of the five surveys (Watson 2008). The CPUE indices and variances from these 96 stations were used in the catch survey analysis.

Commercial catches in number and weight and CPUE for the directed pot fishery were obtained from ADFG. In this study, total annual retained catches (including dead-loss) were used in the catch-survey analysis.

Catch-survey model

A four-stage catch survey analysis (CSA) is principally similar to a full length-based analysis (Zheng et al. 1995) with the major difference being coarser length groups for the CSA. Only male crab abundance is modeled by the CSA for St. Matthew Island blue king crab because the summer trawl surveys do not catch females very well. Male crab abundance was divided into four groups: pre-recruits 2 ($P2$), pre-recruits 1 ($P1$), recruits (R), and post-recruits (P). To be of legal size, St. Matthew Island male king crab must be ≥140 mm carapace width (regulatory measurement), corresponding to males ≥120 mm carapace length (CL). The average growth increment per molt is about 14 mm CL for adult male blue king crab (Otto and Cummiskey 1990). We modeled St. Matthew Island male blue king crab with four stages: $P2$ (90-104 mm CL), $P1$ (105-119 mm CL), R (newshell 120-133 mm CL), and P (oldshell ≥120 mm CL and newshell ≥134 mm CL). $P2$ and $P1$ include both newshell and oldshell crab.

For each stage of crab, the molting portions of crab "grow" into different stages based on a growth matrix, and the non-molting portions of crab remain in the same stage or become post-recruits. The model links the crab abundances in four stages in year t+1 to the abundances and catch in the previous year through natural mortality, molting probability, and the growth matrix:

$$
\begin{aligned}
P2_t^b &= (P2_t e^{-0.5M} - hc2_t e^{-(0.5-y_t)M_t})\, e^{-0.5M_t - st_2 Ft_t - sf_2 Ff_t},\\
P1_t^b &= (P1_t e^{-0.5M_t} - hc1_t e^{-(0.5-y_t)M_t})\, e^{-0.5M_t - st_1 Ft_t - sf_1 Ff_t},\\
P2_{t+1} &= P2_t^b[(1-m2_t) + m2_t\; G_{P2,P2}] + N_{t+1},\\
P1_{t+1} &= P1_t^b[(1-m1_t) + m1_t\; G_{P1,P1}] + P2_t^b\; m2_t\; G_{P2,P1},\\
R_{t+1} &= P2_t^b\, m2_t\; G_{P2,R} + P1_t^b\, m1_t\; G_{P1,R},\\
P_{t+1} &= [(P_t + R_t)e^{-0.5M_t} - rc_t e^{-(0.5-y_t)M_t}]e^{-0.5M_t - Ft_t - Ff_t},
\end{aligned}
\tag{1}
$$

where $P2_t^{\,b}$ and $P1_t^{\,b}$ are pre-recruit 2 and pre-recruit 1 abundances after handling mortality in year t, $hc2_t$ and $hc1_t$ are pot bycatches for pre-recruits 2 and pre-recruits 1, st_2, st_1, sf_2, and sf_1 are selectivities for pre-recruits 2 and pre-recruits 1 bycatches from groundfish trawling and groundfish fixed gear fisheries, N_t is new crab entering the model in year t, $m2_t$ and $m1_t$ are molting probabilities for pre-recruits 2 and pre-recruits 1 in year t, $G_{i,j}$ is a growth matrix containing the proportions of molting crab growing from stage i to stage j, M_t is natural mortality in year t, rc_t is estimated commercial catch in year t, and y_t is the time lag from the survey to the midpoint of the fishery in year t. By definition, all recruits become post-recruits in the following year.

The retained catch is estimated to be

$$
\begin{aligned}
rc_t &= (P_t + R_t)hr_t\\
hr_t &= 1.0 - e^{-Fp_t},
\end{aligned}
\tag{2}
$$

where hr_t is the legal harvest rate at the survey time in year t, and Fp_t is the fishing mortality for the directed pot fishery in year t. The pot bycatches from the directed fishery are

$$\begin{aligned} hc2_t &= sp_2\, hr_t\, P2_t\, h, \\ hc1_t &= sp_1\, hr_t\, P1_t\, h, \end{aligned} \tag{3}$$

where sp_2 and sp_1 are selectivities for pre-recruit 2 and pre-recruit 1 bycatches from the directed pot fishery, and h is the handling mortality rate for the directed pot fishery. The bycatches from the groundfish fisheries are computed as

$$\begin{aligned} tc2_t &= (P2_t e^{-0.5M_t} - hc2_t e^{-(0.5-y_t)M_t})(1 - e^{-st_2\, Ft_t}), \\ tc1_t &= (P1_t e^{-0.5M_t} - hc1_t e^{-(0.5-y_t)M_t})(1 - e^{-st_1\, Ft_t}), \\ tc_t &= [(P_t + R_t) e^{-0.5M_t} - rc_t e^{-(0.5-y_t)M_t}](1 - e^{-Ft_t}), \\ fc2_t &= (P2_t e^{-0.5M_t} - hc2_t e^{-(0.5-y_t)M_t})(1 - e^{-sf_2\, Ff_2}), \\ fc1_t &= (P1_t e^{-0.5M_t} - hc1_t e^{-(0.5-y_t)M_t})(1 - e^{-sf_1\, Ff_1}), \\ fc_t &= [(P_t + R_t) e^{-0.5M_t} - rc_t e^{-(0.5-y_t)M_t}](1 - e^{-Ff_t}), \end{aligned} \tag{4}$$

Where $tc2_t$, $tc1_t$, tc_t, $fc2_t$, $fc1_t$ and fc_t are crab bycatches of pre-recruits 2, pre-recruits1, and legals from the trawl and fixed gear fisheries.

Trawl survey biomass, Bt_t, and pot survey biomass index, Bp_t, are estimated as

$$\begin{aligned} Bt_t &= (str_2\, P2_t\, w_1 + str_1\, P1_t\, w_2 + R_t\, w_3 + P_t\, w_4)\, Q, \\ Bp_t &= (spo_2\, P2_t\, w_1 + spo_1\, P1_t\, w_2 + R_t\, w_3 + P_t\, w_4) / q, \end{aligned} \tag{5}$$

where str_2, str_1, spo_2, and spo_1 are selectivities for pre-recruit 2 and pre-recruit 1 crab for the trawl and pot surveys, w_i is a mean weight for stage I, and q is the pot survey catchability.

Four sets of logistic function parameters (f and w) were used in the model to estimate selectivities st_2, st_1, sf_2, sf_1, sp_2, sp_1, str_2, str_1, spo_2, and spo_1: trawl survey (ϕ_{ss} and ω_{ss}), pot survey (ϕ_{sp} and ω_{sp}), groundfish trawl bycatch (ϕ_{st} and ω_{st}), and fixed gear bycatch (ϕ_{sf} and ω_{sf}):

$$S_l = \frac{1}{1 + e^{-\phi(l-\omega)}}. \tag{6}$$

S_l was scaled to be 1.0 for all legal males.

We modeled molting probability for pre-recruits 2, $m2_t$, as a random walk process:

$$m2_{t+1} = m2_t e^{\eta_t}, \tag{7}$$

where η_t are independent, normally distributed random variables with a mean of zero. This allows us to model the changes in molting probability under a constraint condition. Molting probability for pre-recruits 1, $m1_t$, is a function of $m2_t$:

$$m1_{t+1} = m2_{t+1} / mo12, \tag{8}$$

where $mo12$ is a parameter. Molting probability for pre-recruits 2 in the first year was estimated as mo_0.

Model scenarios

Five scenarios of the model were developed for St. Matthew Island blue king crab, depending on parameters estimated independently and conditionally. In scenarios 1 and 4, both *M* for 1978-1998 and 2000-2009 and *Q* were fixed and *M* for 1999 was independently estimated for scenario 1 and fixed for scenario 4. In model scenarios 2 and 5, *M* was estimated conditionally whereas *Q* was fixed and *M* was constant for the whole time series for scenario 5 and a different *M* value was independently estimated for 1999 for scenario 2. In model scenario 3, *Q* was estimated conditionally and *M* was fixed for 1978-1998 and 2000-2009 and estimated for 1999:

	Scenario				
	1	2	3	4	5
M for 1978-1998, 2000-2009	0.18	Estimate	0.18	0.18	Estimate
M for 1999	Estimate	Estimate	Estimate	0.18	Same as above
Q	1.0	1.0	Estimate	1.0	1.0

Parameter estimation

Estimated parameters include natural mortality (*M*), molting probability parameters (mo_0, $mo12$), catchabilities (*Q*, *q*), selectivity parameters (ϕ_{ss}, ω_{ss}, ϕ_{sp}, ω_{sp}, ϕ_{st}, ω_{st}, ϕ_{sf}, ω_{sf}), directed fishing mortalities (Fp_t), bycatch fishing mortalities (Ft_t, Ff_t), *M* in 1999, crab entering the model for the first time each year except the first (N_t), and total abundance in the first year (TN_{78}). Depending on the model scenario, *M* and *Q* may be estimated conditionally. If *M* is not estimated, *M* is assumed to be 0.18 per year in this study, based on a maximum age of 25 and the 1% rule (Zheng 2005).

A maximum likelihood approach was used to estimate parameters. For length (stage) compositions ($p_{l,t,s,sh}$), the likelihood functions are

$$Rf=\prod_{l=1}^{L}\prod_{t=1}^{T}\frac{\left\{\exp\left[-\frac{(p_{l,t}-\hat{p}_{l,t})^2}{2\sigma^2}\right]+0.01\right\}}{\sqrt{2\pi\sigma^2}},$$
$$\sigma^2=\left[\hat{p}_{l,t}(1-\hat{p}_{l,t})+0.01\right]/n, \tag{9}$$

where L is the number of stage groups, T is the number of years, $p_{l,t}$ is observed proportions of stage l and year t, $\hat{p}_{l,t}$ is estimated proportions of stage l and year t, and n is the effective sample size, which was estimated to be 50% of observed sample sizes with a maximum cap of 100.

The weighted negative log-likelihood functions are:

$$\begin{aligned}
&\textit{Length compositions}: \quad -\sum_i \ln(Rf_i),\\
&\textit{Biomasses other than survey}: \quad \lambda_j\sum_t[\ln(C_t/\hat{C}_t)^2],\\
&\textit{NMFS trawl survey biomass}: \quad \sum_t[\ln(Bt_t/\hat{B}t_t)^2/(2\ln(CVt_t^2+1))],\\
&\textit{Pot survey biomass index}: \quad \lambda_p\sum_t[\ln(Bp_t/\hat{B}p_t)^2/(2\ln(CVp_t^2+1))],\\
&N\ \textit{variations}: \quad \lambda_R\sum_t[\ln(N\ \textit{deviations})^2],\\
&\textit{Fishing mortality deviations}: \quad \lambda_s\sum_t[\ln(F\ \textit{deviations})^2],\\
&\textit{Molting probability deviations}: \quad \lambda_m\sum_t \ln(\eta_t^2).
\end{aligned} \tag{10}$$

Weighting factors are set as: λ_j = 100 (retained catch) and 2 (trawl bycatch), λ_p = 0.2, λ_R = 0.1, λ_s = 0.1, and λ_m = 20. Using AD Model Builder (Otter Research Ltd. 1994), we estimated parameters using the quasi-Newton method to minimize –ln(L).

The growth matrix was estimated from tagging data (Table 1, Otto and Cummiskey 1990). To reduce the number of parameters estimated, we assumed that the relative frequencies of length groups from the first-year trawl survey data approximate the true relative frequencies. Thus, we did not need to conditionally estimate length-specific abundance for the first year. Handling mortality rates for the directed pot

Table 1. Growth matrix (*G*) for St. Matthew Island blue king crab.

	Pre-recruits 2	Pre-recruits 1
Pre-recruits 2	0.11	0.00
Pre-recruits 1	0.83	0.11
Recruits	0.06	0.83
Post-recruits	0.00	0.06

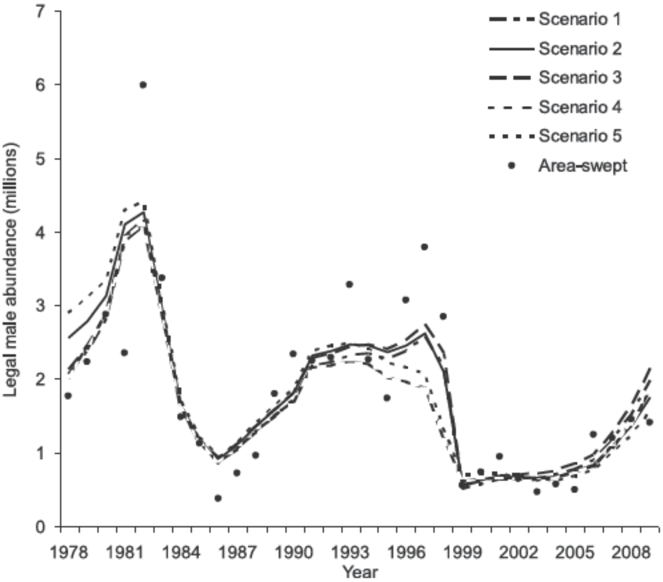

Figure 2. Comparison of legal male abundance estimates of St. Matthew Island male blue king crab with five scenarios of the catch-survey analysis.

fishery, the groundfish fixed gear fisheries, and the groundfish trawl fisheries were assumed to be 0.2, 0.5, and 0.8 (Zheng and Siddeek 2008). Observer coverage was very limited for the directed fishery, and only 1-3 out of 90-131 vessels were covered from 1995 to 1998 (Moore et al. 2000). Due to limited observer data, fishery selectivities of pre-recruits 2 and 1 in the directed pot fishery were assumed to be 0.4 and 0.6 relative to legal crab, respectively, based on the results of the Bristol Bay red king crab (*Paralithodes camtschaticus*) stock assessment (Zheng and Siddeek 2008).

Results

Estimated survey selectivities, catchabilities, and natural mortalities are summarized in Table 2. Estimated natural mortality in 1999 was much higher than that in 1978-1998 and 2000-2008. Estimated natural mortalities were much higher than the assumed value of 0.18 per year. When natural mortality was estimated for all years (scenarios 2 and 5), high natural mortality values resulted in lower estimated trawl survey selectivities (Table 2). The ratio (*mo12*) of the molting probability of pre-recruits 2 to that of pre-recruits 1 was constrained by the lower

Table 2a. Natural mortality and trawl survey catchability parameters and negative log likelihood values for a catch-survey analysis of St. Matthew Island blue king crab with data from 1978 to 2009 for five scenarios.

	Model scenario				
Parameter	1	2	3	4	5
Natural mortality for years other than 1999	fix	0.25	fix	fix	0.29
		(0.03)			(0.03)
Natural mortality in 1999	1.42	1.30	1.45	fix	0.29
	(0.21)	(0.22)	(0.21)		(0.03)
Trawl survey catchability (Q)	fix	fix	0.92	fix	fix
			(0.09)		
Negative log likelihood components					
Trawl survey biomass	15.52	15.53	15.63	20.66	21.10
Pot survey biomass	12.25	10.78	12.23	12.66	10.21
Retained catch biomass	1.07	1.11	1.02	1.47	1.36
Trawl bycatch biomass	0.18	0.17	0.22	0.13	0.14
Fixed gear bycatch biomass	0.08	0.08	0.08	0.08	0.09
Trawl survey length component	–196.7	–195.7	–197.1	–193.2	–193.7
Pot survey length component	–38.30	–40.06	–38.15	–34.06	–39.24
Trawl bycatch length component	–15.88	–15.90	–15.89	–15.80	–15.86
Fixed gear bycatch length component	–45.94	–46.39	–46.01	–44.87	–45.27
Other penalty	14.90	14.79	14.81	15.85	15.85
Total	–252.8	–255.6	–253.2	–237.1	–245.4
Total number of parameters	145	146	146	144	145

An *M* value is estimated for 1999 with the "2 *Ms*" scenario. A value of "fix" indicates that it is fixed in the model. Standard deviations are in parentheses below the estimated values.

bound of 1.0 for all scenarios (Table 2); the molting probability of the younger stage must be equal to or greater than the older stage to be biologically meaningful. Scenario 2 resulted in the lowest negative log likelihood value, and scenario 4 had the highest negative log likelihood (Table 2). The Chi-square test was used to compare scenarios with different numbers of degrees of freedom. Scenario 2 resulted in a significant improvement in fit from scenarios 1 with a p-value of 0.09. With a p-value of 0.05, scenario 1 is the best model, and scenario 4 is the worst one. Scenarios 2 and 3 also improved the fits significantly from scenarios 4 and 5 with p-values <0.001. Scenario 5 significantly fit the data better than scenario 4 (p-value of 0.004). Overall, scenarios 1 and 2 fit the data very well and were significant improvements in fit from the other three scenarios.

Table 2b. Estimated parameters and standard deviations (SD) for a catch-survey analysis of St. Matthew Island blue king crab with data from 1978 to 2009 for five scenarios.

	Model scenario									
Parameter	1		2		3		4		5	
	Value	SD	Value	SD	Value	SD	Value	SD	Value	SD
mo_0	0.522	0.211	0.492	0.094	0.520	0.096	0.562	0.094	0.499	0.095
$mo12$	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000
ϕ_{ss}	0.131	0.042	0.110	0.020	0.135	0.048	0.162	0.081	0.105	0.015
ω_{ss}	98.62	2.793	102.2	3.635	98.54	2.881	96.56	1.396	103.0	3.317
ϕ_{sp}	0.132	0.020	0.130	0.017	0.133	0.020	0.131	0.022	0.127	0.017
ω_{sp}	110.8	2.613	113.0	2.641	110.7	2.696	109.2	2.649	113.9	2.482
ϕ_{st}	0.187	0.116	0.189	0.112	0.189	0.118	0.180	0.112	0.185	0.106
ω_{st}	120.8	5.940	121.4	6.049	120.6	5.835	120.8	6.013	121.9	6.175
ω_{sf}	0.101	0.018	0.104	0.018	0.102	0.018	0.086	0.018	0.096	0.018
ϕ_{sf}	125.5	3.742	126.7	3.717	125.2	3.712	129.2	5.219	129.8	4.447
q	0.246	0.031	0.242	0.030	0.267	0.042	0.190	0.021	0.197	0.022
$\ln(TN_{78})$	8.921	0.120	9.139	0.156	8.951	0.124	8.912	0.115	9.266	0.157

Mortality and recruitment parameters are not presented in this table. Pot survey catchability is q and initial abundance in 1978 is N_{78}.

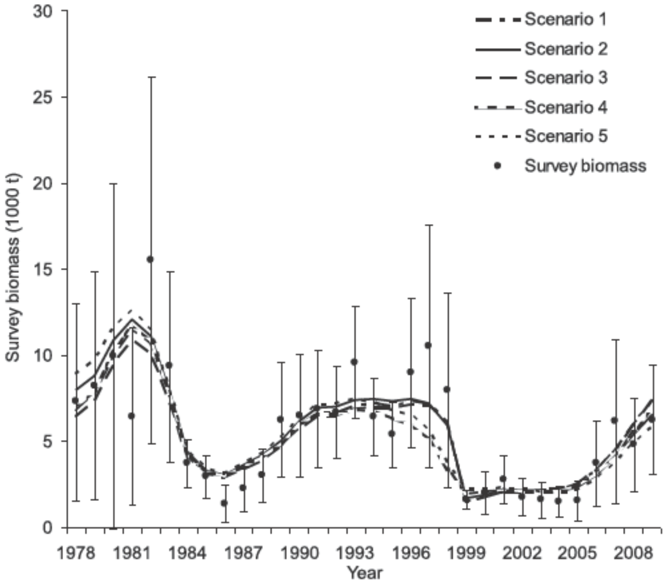

Figure 3. Comparison of trawl survey male biomass estimates of St. Matthew Island male blue king crab with five scenarios of the catch-survey analysis with 95% confidence intervals.

Scenarios 1-3 with estimating natural mortality in 1999 resulted in similar relative biomass and abundance estimates over time (Figs. 2 and 3). As a comparison, estimated male survey biomass and legal male abundance were much lower than the area-swept estimates during 1996-1998 and higher during 1978-1982 with scenarios 4 and 5 (Figs. 2 and 3). The trends of estimated relative abundance indices for pot surveys with scenarios 1-3 were also similar, and different with scenarios 4 and 5 (Figs. 4 and 5). All scenarios indicate an increasing abundance and biomass since 1999, and estimated legal abundance and mature male biomass in 2009 were the highest values since 1999 (Figs. 2 and 3).

Observed and model estimated retained catch and trawl bycatch biomasses were very close to each other for all five scenarios (Fig. 6). Trawl bycatch biomass (not shown here) was very low relative to the retained catch. The highest retained catches occurred during the early 1980s and the fishery was closed during 1999-2008. Estimated bycatch biomass from the directed fishery was small, relative to the retained catch, and scenarios 2 and 5 with an estimated M resulted in higher bycatch biomass estimates than the other three scenarios (Fig. 7).

Legal harvest rates were adjusted to be the ratio of retained catch to estimated legal abundance adjusted by natural mortality to the midpoint of each fishing season, illustrated in Fig. 8. Estimated legal harvest rates were very high during 1982-1985, above 50%. Because of low abundance estimates during the mid and late 1990s, estimated legal harvest rates were higher for scenarios 4 and 5 than the other three scenarios during this period (Fig. 8). Estimated bycatch fishing mortalities from the groundfish fisheries were very small and generally less than 0.002 per year.

New crab enter the model through pre-recruit 2 stage and are called recruitment to the model, to be distinct from the recruit stage that is the recruitment to the legal population. Estimated recruitment to the model somewhat relates to M values; higher M values generally resulted in higher estimated values of recruitment to the model (Fig. 9). Scenario 4 with the overall lowest M produced the smallest estimates of recruitment to the model, whereas the high M for scenarios 2 and 5 resulted in overall high estimates of recruitment to the model (Fig. 9).

Retrospective analyses are based on leaving one year's data out at a time to evaluate how well the current model performs with fewer data. Scenarios with estimating natural mortality in 1999 performed very well with only a small bias of abundance estimates (Fig. 10). Because of relatively low legal abundance from the trawl survey data during the early 2000s, the estimated legal males and mature male biomass (not shown here) during the terminal years tended to be higher during this period than those estimated with the terminal year of 2009 for scenario 1 (Fig. 10). This bias is slightly less for scenarios 2 and 3 than for scenario 1. The trajectories of biomass and abundance from the assessments made

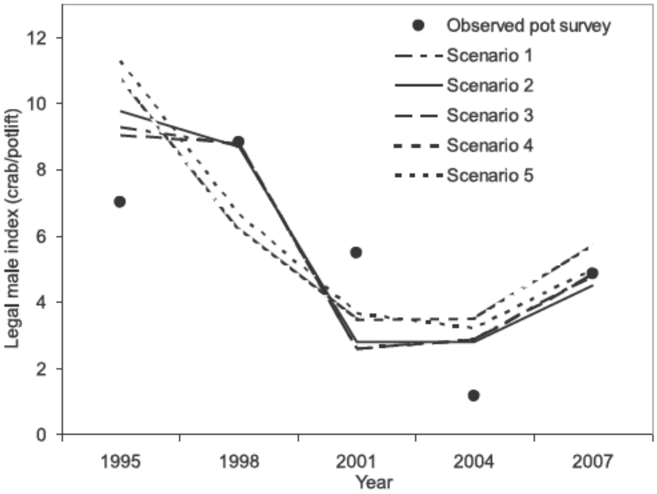

Figure 4. Comparison of relative pot survey legal male abundance estimates of St. Matthew Island male blue king crab with five scenarios of the catch-survey analysis.

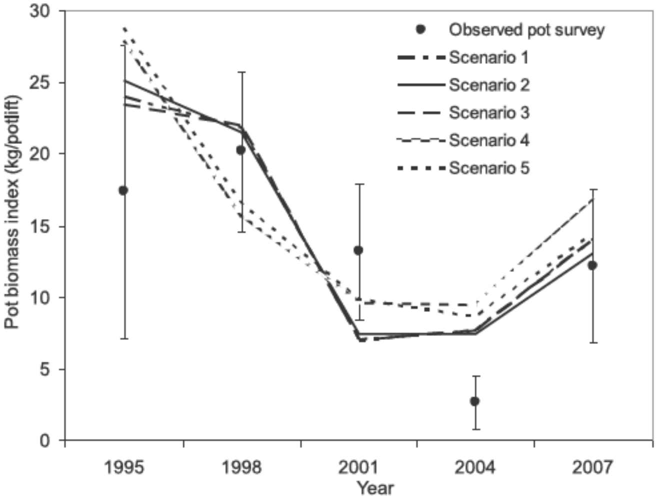

Figure 5. Comparison of pot survey male biomass (kg per potlift) of St. Matthew Island male blue king crab with five scenarios of the catch-survey analysis, with 95% confidence intervals.

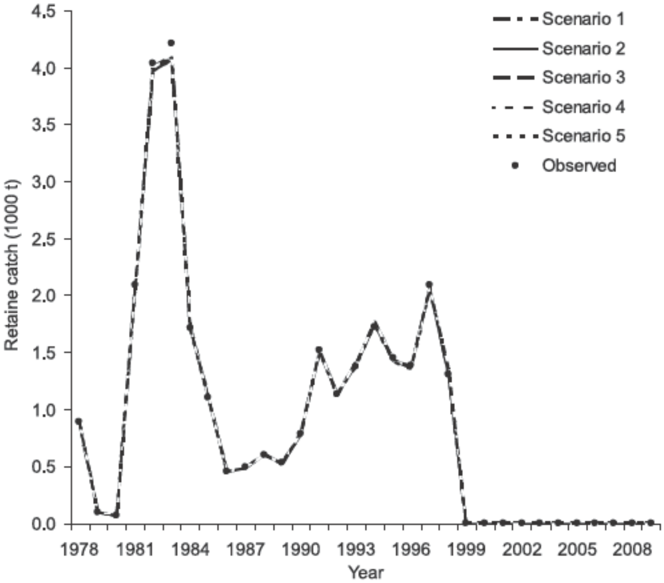

Figure 6. **Comparison of retained catch estimates of St. Matthew Island male blue king crab with five scenarios of the catch-survey analysis from 1978 to 2009.**

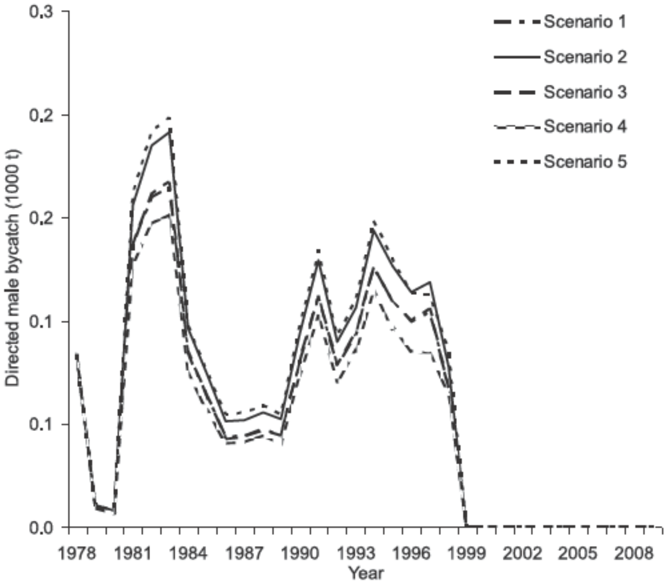

Figure 7. **Comparison of directed male bycatch estimates of St. Matthew Island male blue king crab with five scenarios of the catch-survey analysis from 1978 to 2009, with a handling mortality rate of 20%.**

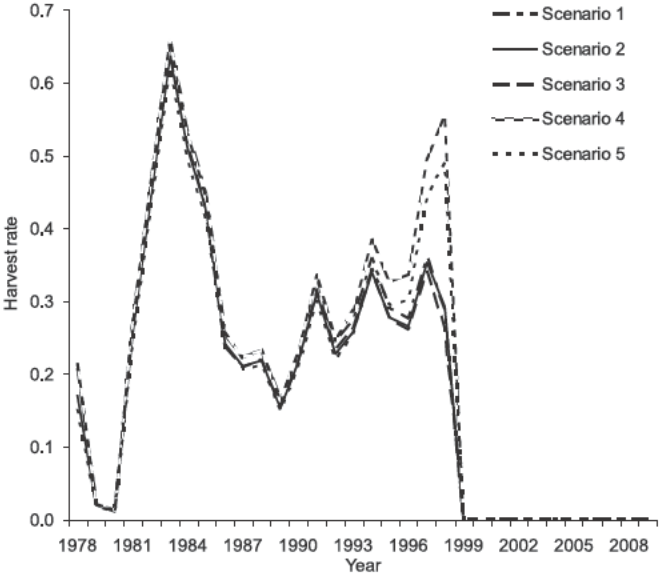

Figure 8. Comparison of estimated harvest rates for the directed pot fishery of St. Matthew Island male blue king crab at fishing time, with five scenarios of the catch-survey analysis.

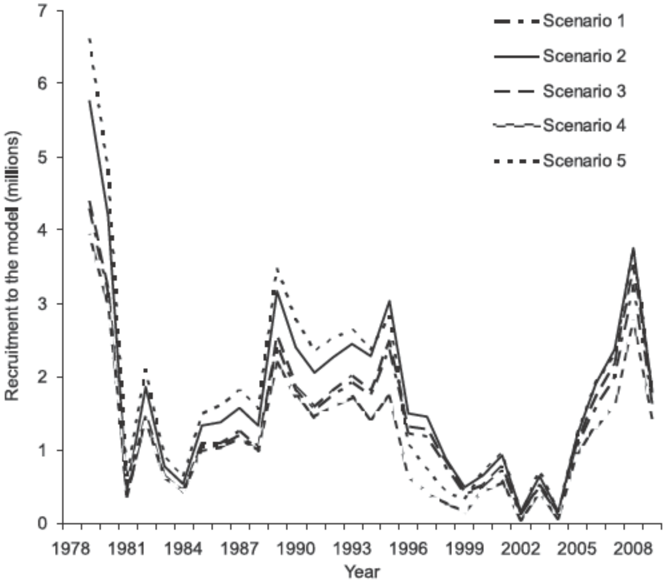

Figure 9. Comparison of estimated recruitments to the model of St. Matthew Island male blue king crab with five scenarios of the catch-survey analysis.

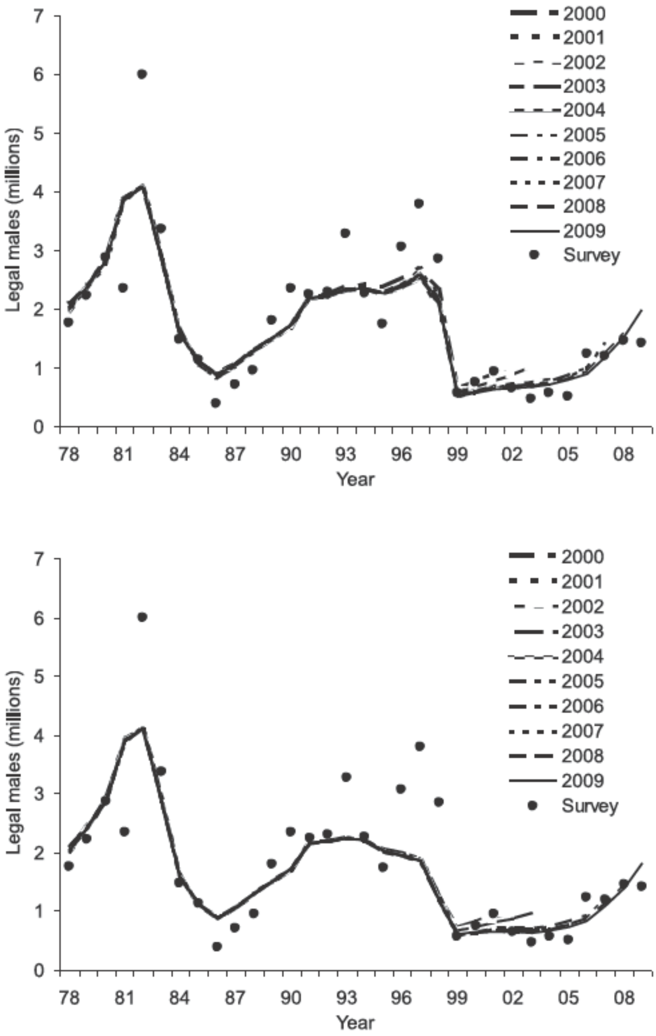

Figure 10. Comparison of estimates of legal male abundance of St. Matthew Island blue king crab with terminal years 2000-2009 with scenario 1 (upper plot) and scenario 4 (lower plot).

during 2000-2008 were very close to each other and close to those made in 2009 with scenarios 1-3. Since scenario 2 has been used to manage the fishery during the last ten years, the performance of scenario 2 is similar to the historical performance. Scenario 4 with fixed natural mortality for the whole period and trawl survey catchability overestimated the abundance greatly in the terminal year of 1999. Model estimated abundance and biomass were overall much lower than the area-swept estimates during 1990s with scenario 4 (Fig. 10).

Likelihood profiles for estimated legal male abundance and mature male biomass in 2009 are illustrated in Fig. 11. For scenario 1, the 95% confidence intervals for legal male abundance are 1.371 million to 2.653 million of crab; the 95% confidence intervals for mature male biomass in 2009 with the assumed fishing mortality of 0.18 per year are 3,903 t to 7,912 t. The shapes of the likelihood profiles are similar among five scenarios, but the modes are different (Fig. 11). Scenario 5 has the lowest abundance and biomass estimates and scenario 3 has the highest estimates in 2009 (Fig. 11).

Discussion

Two kinds of uncertainty greatly affect the stock assessment for St. Matthew Island blue king crab. The first is parameter uncertainty for natural mortality and survey catchability. The second uncertainty is how to interpret the big decline of trawl survey abundance in 1999. We used five model scenarios to compare and assess the estimated abundances under different assumptions of natural mortality, survey catchability, and abundance in 1999. Our results show that scenarios 1 and 2, which estimated a natural mortality for 1999 and fixed trawl survey catchability to be 1, are significant improvements in fit compared to the other three scenarios. Scenario 4 with a fixed natural mortality to be 0.18 per year and trawl survey catchability to be 1 is the worst model among the five scenarios.

As expected, estimated trawl survey catchability and natural mortality are confounded, like the results from the previous studies (Zheng et al. 1997, Collie et al. 2005). It is unlikely that we are able to satisfactorily estimate both parameters simultaneously from the current available survey and catch data. Independent data or assumptions for one parameter are needed for estimating both parameters. Under assumptions that maximum age is 25 years and that only 1% of crab survive to this maximum age when not subject to fishing mortality, natural mortality is estimated to be 0.18 per year. Trawl survey catchability for mature males is estimated to be 0.92 with this natural mortality, lower than that of Collie et al. (2005), who estimated trawl survey catchability to be 1.105 with an assumed natural mortality of 0.3 per year. Because the trawl survey abundance estimates are derived from an area-swept

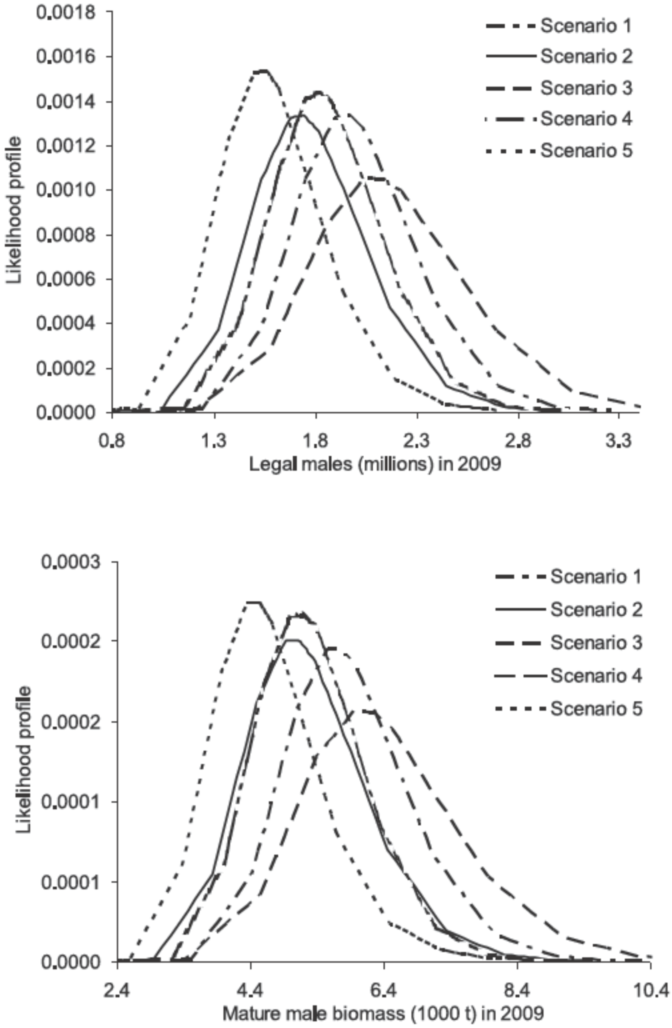

Figure 11. **Likelihood profiles for estimated legal male abundance (upper plot) and mature male biomass (lower plot) in 2009 by scenario.**

approach, estimated trawl survey catchability should intuitively be equal to or less than 1.

It is a challenge to stock assessment and fishery management when the survey estimate of stock abundance falls sharply in a given year. It is a common practice in stock assessments that a constant natural mortality is assumed and the stock assessment models would provide much higher estimates than the survey results. If natural mortality for a given year has increased greatly, the assumption of a constant natural mortality would greatly overestimate the stock abundance during the terminal year and lead to overfishing. The stock assessment scientists and fishery managers faced this problem for St. Matthew Island blue king crab in 1999. Instead of blindly assuming a constant natural mortality, Zheng and Kruse (2002) considered the possibility that natural mortality had changed when a decline in survey abundance far exceeded the level explained by estimated survey measurement errors in the past. They proposed three steps to deal with such situations: (1) auxiliary information should be collected to gauge whether a massive die-off has occurred; (2) a model should be used to evaluate different assumptions of natural mortality in the terminal year; and (3) future population projections should be made and risks of different assumptions should be evaluated (Zheng and Kruse 2002). The assumption made 10 years ago that natural mortality was much higher in 1999 than other years is supported by the subsequent trawl survey data. With an additional 10 years of survey data, a model scenario with this assumption statistically fits the data significantly better than those without the assumption. The St. Matthew blue king crab stock assessment in 1999 provided an example on how to handle a sharp decline of population abundance occasionally: high natural mortality or changes in survey catchability.

No environmental factors have been identified as a cause for high natural mortality in 1999. Although crab abundance also declined sharply in the early 1980s, the decrease could be explained by the high fishing mortalities. Directed and nondirected fishing mortalities could not explain the sharp decline in 1999. The decline in 1999 occurred for all segments of the population and both sexes. The decline in survey abundance could not be explained by the survey catchability since the missing crab did not occur in the subsequent surveys. Therefore, the sharp decline in 1999 is attributed to high natural mortality.

Another important factor influencing abundance and natural mortality estimates is the handling mortality rates. In Alaska, harvest policies allow harvest of legal-sized male crab only, and sublegal male and female crab caught during fishing have to be returned to the sea. Handling mortality reduces future recruitment to fisheries by reducing both pre-recruit abundance and spawning biomass. Besides mortality, handling may also produce sublethal effects on crab, such as reduced growth (Kruse 1993). Based on limited observer data, bycatch of sublegal male and female crab from the directed blue king crab fishery off St. Matthew Island was relatively high, and total bycatch was often twice as high as or higher than total catch of legal crab (Moore et al. 2000). But observer data were extremely limited for the directed pot fishery for St. Matthew Island blue king crab. We assumed fishery selectivities to be 0.4 and 0.6 for pre-recruits 2 and pre-recruits 1 and the handling mortality rate to be 0.2 for the directed pot fishery, based on the results for Bristol Bay red king crab (Zheng and Siddeek 2008). Although estimated recruitment to the model is affected by handling mortality, handling mortality rates ranging from 0 to 50% do not affect legal male abundance and mature male biomass estimates much.

Changes in spatial distributions may explain some differences between the trawl and pot surveys of St. Matthew Island blue king crab. Vining et al. (2001) show that spatial distributions of blue king crab off St. Matthew Island were different between 1995 and 1998. Crab were more spread out and much more broadly distributed in 1998 and than in 1995. The population center of St. Matthew Island blue king crab is likely located in shallow inshore waters where the crab density is highest and juvenile crab are concentrated. According to MacCall's (1990) "basin model," the range of a stock expands or contracts around its center as a function of overall stock abundance and large-scale changes in density-independent factors. Since trawl surveys cover a broader area than pot surveys and pot surveys cover the shallow inshore waters off St. Matthew Island where trawl surveys do not completely access, the decline in stock abundance showed up earlier in the trawl surveys than the pot surveys. This agrees with the basin model that the declines occur last in the center of the population. A combination of trawl and pot surveys helps us better track the crab abundance changes over time.

Besides St. Matthew blue king crab, catch survey analysis has been used to assess Pribilof Islands blue king and red king crab stocks. Catch survey analysis is simple and useful for a small stock with limited sample sizes to construct an adequate length frequency. Numbers of crab measured during trawl surveys are too small to have a full length-based model for St. Matthew Island and Pribilof Islands king crab stocks. Catch survey analysis is also useful for data-limited situations since it does not require data on the full age compositions. Sensitivity of and bias in catch survey analysis estimates of stock abundance for fish stocks were evaluated by Mesnil (2005).

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References

Acuna, E., and R.R. Lauth. 2008. Results of the 2007 eastern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrate resources. NOAA Tech. Memo. NMFS-AFSC-181. 195 pp.

Blau, S.F. 2000. Nearshore blue king crab survey St. Matthew Island, 1999. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report No. 4K00-42, Kodiak.

Bowers, F.R., M. Schwenzfeier, S. Coleman, B. Failor-Rounds, K. Milani, K. Herring, M. Salmon, and M. Albert. 2008. Annual management report for the commercial and subsistence shellfish fisheries of the Aleutian Islands, Bering Sea and the westward region's shellfish observer program, 2006/07. Alaska Department of Fish and Game, Fishery Management Report No. 08-02, Anchorage. 230 pp.

Collie, J.S., A.K. Delong, and G.H. Kruse. 2005. Three-stage catch-survey analysis applied to blue king crabs. In: G.H. Kruse, V.F. Gallucci, D.E. Hay, R.I. Perry, R.M. Peterman, T.C. Shirley, P.D. Spencer, B. Wilson, and D. Woodby (eds.), Fisheries assessment and management in data-limited situations. Alaska Sea Grant, University of Alaska Fairbanks, pp. 683-714.

Kruse, G.H. 1993. Biological perspectives on crab management in Alaska. In: G.H. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II (eds.), Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. Alaska Sea Grant, University of Alaska Fairbanks, pp. 355-384.

MacCall, A.D. 1990. Dynamic geography of marine fish populations. Washington Sea Grant and University of Washington Press, Seattle. 153 pp.

Mesnil, B. 2005. Sensitivity of, and bias in, catch-survey analysis (CSA) estimates of stock abundance. In: G.H. Kruse, V.F. Gallucci, D.E. Hay, R.I. Perry, R.M. Peterman, T.C. Shirley, P.D. Spencer, B. Wilson, and D. Woodby (eds.), Fisheries assessment and management in data-limited situations. Alaska Sea Grant, University of Alaska Fairbanks, pp. 757-782

Moore, H., L.C. Byrne, and D. Connolly. 2000. Alaska Department of Fish and Game summary of the 1998 mandatory shellfish observer program database. Alaska Department of Fish and Game, Commercial Fisheries Division, Regional Information Report 4J00-21, Kodiak. 146 pp.

NPFMC. 1998. Fishery management plan for Bering Sea/Aleutian Islands king and Tanner crabs. North Pacific Fishery Management Council, Anchorage.

Otter Research Ltd. 1994. An introduction to AD Model Builder: For use in nonlinear modeling and statistics. Otter Research Ltd., Nanaimo, British Columbia.

Otto, R.S. 1990. An overview of eastern Bering Sea king and Tanner crab fisheries. In: Proceedings of the International Symposium on King and Tanner Crabs. Alaska Sea Grant, University of Alaska Fairbanks, pp. 9-26.

Otto, R.S., and P.A. Cummiskey. 1990. Growth of adult male blue crab (*Paralithodes platypus*). In: Proceedings of the International Symposium on King and Tanner Crabs. Alaska Sea Grant, University of Alaska Fairbanks, pp. 245-258.

Somerton, D.A. 1985. The disjunct distribution of blue king crab, *Paralithodes platypus*, in Alaska: Some hypotheses. In: Proceedings of the International King Crab Symposium. Alaska Sea Grant, University of Alaska Fairbanks, pp. 13-21.

Stauffer, G. 2004. NOAA protocols for groundfish bottom trawl surveys of the nation's fishery resources. NOAA Tech. Memo. NMFSF/SPO-65.

Vining, I., F. Blau, and D. Pengilly. 2001. Evaluating changes in the spatial distribution of blue king crab near St. Matthew Island. In: G.H. Kruse, N. Bez, A. Booth, M.W. Dorn, S. Hills, R.N, Lipcius, D. Pelletier, C. Roy, S.J. Smith, and D. Witherell (eds.), Spatial processes and management of marine populations. Alaska Sea Grant, University of Alaska Fairbanks, pp. 327-348.

Watson, L.J. 2008. The 2007 triennial St. Matthew Island blue king crab survey and comparisons to historic surveys. Alaska Department of Fish and Game, Fishery Management Report No. 08-41, Anchorage. Accessed Dec. 2010: www.sf.adfg.state.ak.us/FedAidPDFs/fmr08-41.pdf.

Zheng, J. 2005. A review of natural mortality estimation for crab stocks: Data-limited for every stock? In: G.H. Kruse, V.F. Gallucci, D.E. Hay, R.I. Perry, R.M. Peterman, T.C. Shirley, P.D. Spencer, B. Wilson, and D. Woodby (eds.), Fisheries assessment and management in data-limited situations. Alaska Sea Grant, University of Alaska Fairbanks, pp. 595-612.

Zheng, J., and G.H. Kruse. 2002. Assessment and management of crab stocks under uncertainty of massive die-offs and rapid changes in survey catchability. In: A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley, and D. Woodby (eds.), Crabs in cold water regions: Biology, management, and economics. Alaska Sea Grant, University of Alaska Fairbanks, pp. 367-384.

Zheng, J., and M.S.M. Siddeek. 2008. Bristol Bay red king crab stock assessment in fall 2008. In: Stock assessment and fishery evaluation report for the king and Tanner crab fisheries of the Bering Sea and Aleutian Islands regions; 2008 BSAI Crab SAFE. Compiled by the Plan Team for the King and Tanner Crab Fisheries of the Bering Sea and Aleutian Islands. North Pacific Fishery Management Council, pp. 77-166. http://www.fakr.noaa.gov/npfmc//membership/plan_teams/CRAB_team.htm.

Zheng, J., M.C. Murphy, and G.H. Kruse. 1995. A length-based population model and stock-recruitment relationships for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. Can. J. Fish. Aquat. Sci. 52:1229-1246. doi:10.1139/f95-120

Zheng, J., M.C. Murphy, and G.H. Kruse. 1997. Application of catch-survey analysis to blue king crab stocks near Pribilof and St. Matthew islands. Alaska Fish. Res. Bull. 4:62-74.

Bishop, G.H., C.E. Siddon, and J.M. Rumble. 2010. Change-in-Ratio and Index-Removal Population Estimation of Dungeness Crab in Southeastern Alaska. In: G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby (eds.), Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.16

Change-in-Ratio and Index-Removal Population Estimation of Dungeness Crab in Southeastern Alaska

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Abstract

The fishery for Dungeness crab, *Cancer magister*, in southeastern Alaska is passively managed with regulations governing size, sex, and season. In response to concerns regarding the timing of the commercial season and high exploitation rates, a pot survey program was conducted to investigate the utility of abundance-based management tools. Pre (June) and post-season (August/September) surveys were conducted in seven survey areas: Stikine Flats, Duncan Canal, Port Camden, Berners Bay, Peril Strait, Tenakee Inlet, and St. James Bay from 2000 through 2002. Data were modeled using change-in-ratio and index-removal methods to estimate legal population size, catchability, and exploitation rates.

Change-in-ratio population size estimation yielded exploitation rates averaging 93% and 99% respectively, for Stikine Flats and Duncan Canal open escape ring pots, and 83% each for Peril Strait and Tenakee Inlet closed escape ring pots. In Port Camden, St. James Bay, and Berners Bay, low, variable, and even negative exploitation rates were estimated, probably as a result of inseason recruitment molts, which violate the assumption of a closed population. The index-removal method produced exploitation rate estimates that were biased low due to catchability increasing between the two survey periods.

The variable success of the two methods applied here demonstrates a high level of spatial and temporal variability in Dungeness crab life history timing, and makes their assessment very difficult. We suggest that increased variability in life history timing could be a general effect

of climate change and result in associated decreases in the precision of stock assessments.

Introduction

Management of the fishery for Dungeness crab, *Cancer magister*, in southeastern Alaska is passive, and regulations govern minimum size, sex, and season. The minimum size is 165 mm carapace width (CW), measured immediately in front of the 10th anterolateral spine; only males may be taken, and there is a 4-month season split between summer (June 15–August 15) and fall (October 1–November 30) for major fishing areas. The season timing partially overlaps both male (February-July) (Lehman and Osborn 1970) and female (July-September) molt periods (Shirley and Shirley 1988). Approximately 80% of annual harvest is currently taken during the summer season. The fishery has intensified (mean harvest was 0.65, 2.34, and 3.26 million pounds respectively in the 1970s, 1980s, and 1990s, and 4.7 million pounds from 2000/01 to 2007/08 [Hebert et al. 2008]), and currently relies primarily on a single year class. In response to concerns about high exploitation rates, we investigated the feasibility of developing abundance-based management tools for this fishery.

Pot survey data collected before and after the summer season were analyzed using change-in-ratio (CIR) (Dawe et al. 1993, Pollock and Hoenig 1998a) and index-removal (IR) (Dawe et al. 1993, Pollock and Hoenig 1998b) methods to estimate population size.

Materials and methods

Field

Survey

Pot surveys were conducted before and after the summer season (June 1-13 and August14-September 24) for Stikine Flats, Duncan Canal, Port Camden, Peril Strait, Tenakee Inlet, St. James Bay, and Berners Bay of southeastern Alaska (Fig. 1) for 2000, 2001, and 2002, and before the summer season only in 2003 and 2004. Together, these seven areas produced 47% of the Dungeness crab harvest in southeastern Alaska for the 2000/01-2002/03 commercial seasons. Dungeness crab pots 96.5 cm in diameter, with two tunnels and two 11.1 cm inside diameter escape rings were used. The escape rings were wired closed on half of the pots to fully retain prerecruit and female Dungeness crabs. Pots were set between 1400 h and 1700 h, and pulled between 0700 h and 1200 h on the following day, to achieve a standard 17 to 20 h soak time.

Individual pot cluster locations along the 18.3 m isobath were determined in ArcGIS using a systematic sampling scheme with a random start location (Thompson 1992). Clusters consisted of one pot each from

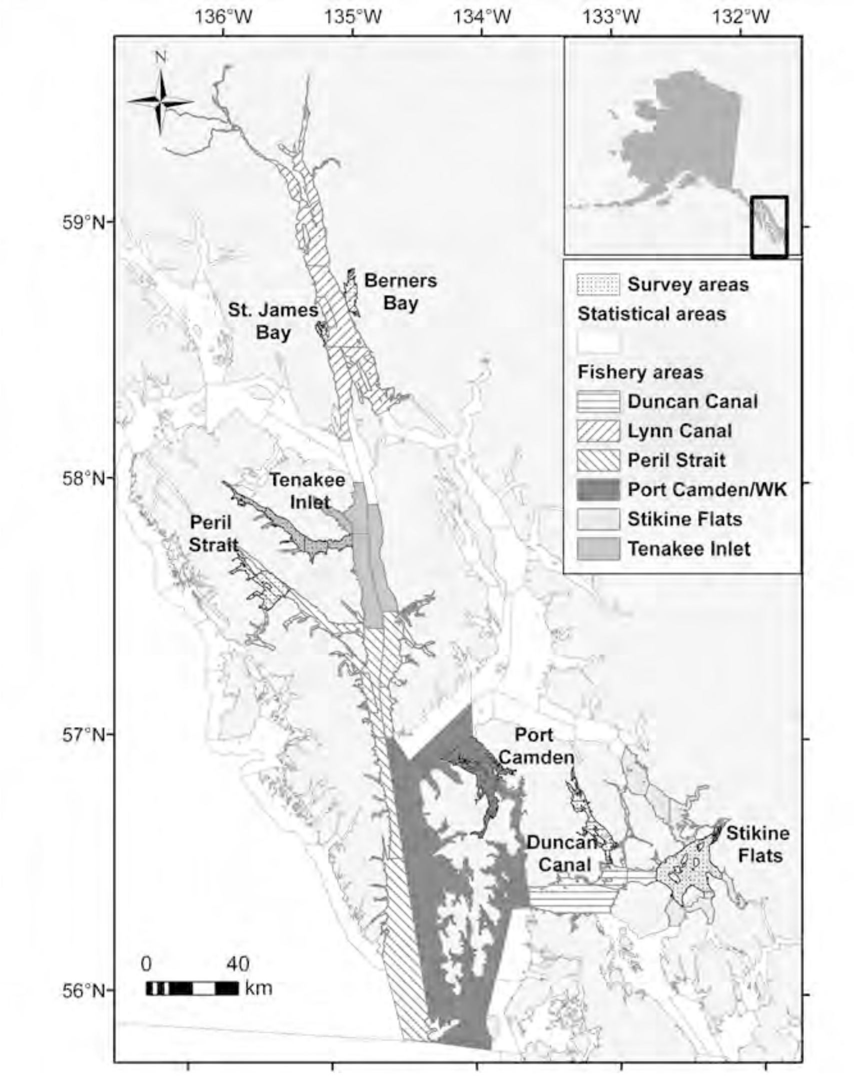

Figure 1. Seven Dungeness crab survey areas (dotted) and six fishery areas (other fill patterns) in southeastern Alaska.

three depth strata: "shallow" (5.5-16.5 m), "medium" (18.3-25.6 m), and "deep" (27.4-34.7 m); an additional pot from a "very deep" (36.6-73.2 m) strata was included in some clusters. Depth was measured relative to mean lower low water. Target depths were randomly selected within each stratum. After navigating by Differential Global Positioning System to the cluster location, precise pot locations were located by driving offshore or onshore to the selected depth. A total of 74-82 pots were set and retrieved over the course of two days in each survey area, except for the postseason Berners Bay survey, and St. James Bay surveys, where 41 pots were set over a single day. Postseason pot locations duplicated preseason locations as precisely as possible.

After collection in pots, Dungeness crab carapace widths (CW) were measured to the nearest millimeter immediately anterior to the 10th anterolateral spine, and shell age was determined. A few pots containing large numbers of crabs were subsampled for size and shell age.

Mean catch per unit effort (CPUE), in terms of number per pot, and its standard error were determined by escape ring configuration, survey period, survey area, and year for legal and prerecruit males.

Soak time

In 2002, an experiment was conducted pre- and post-season in Duncan Canal to investigate the effect of soak time on catch. During each survey period, six replicates of eight pots (half with escape rings closed and half open with soak times of 12, 24, 36, or 48 h) were set systematically at 150 m intervals along the 18.3 m isobath. Treatment order was randomly determined within each 8 pot replicate. We conducted two 3-way ANOVAs, one each for prerecruit and legal male CPUE, to determine the effect of soak time, escape ring configuration, and survey period.

Tagging

Crabs were tagged during surveys from 2000 to 2004. During tagging, a Floy double T-bar anchor tag (FD-94) was inserted into the posterior margin of the epimeral suture on the right side between the fourth and fifth legs. A Mark II pistol-grip garment tagging gun with a regular needle having a ⅝ inch insertion depth was used for tagging. The vast majority of recaptures were accomplished through the commercial fishery. The primary objective of tagging was growth; molt increment and molt interval have been reported separately (Bishop et al. 2008) and were not addressed further here. Of interest to this study is the proportion of prerecruit males that molted into the summer fishery; this was determined for each survey area and year as the product of the ratios of prerecruit:legal number recovered and legal:prerecruit number tagged.

Commercial catch sampling

Commercial Dungeness crab landings were sampled to characterize harvest dockside in Ketchikan, Wrangell, Petersburg, Sitka, Juneau, and Haines. Samples of 50 or 75 crabs per trip were taken from 4 to 142 trips in each of six fishery areas annually. Fishery areas do not wholly coincide with survey areas (Fig. 1). Recruit crabs were defined as new shell males >164 mm CW and ≤194 mm CW based on the molt increment determined in Bishop et al. (2008). Recruit composition was calculated as the mean of the proportion recruit in *n* trips.

Recruit composition from dockside sampling is used as an independent approximation of exploitation rate to corroborate and check exploitation rates estimated through CIR and IR modeling.

Modeling

CIR and IR methods were used to model data to produce population estimates, catchability coefficients, and exploitation rates for each survey area. These methods share two major assumptions: (1) the population is closed, and (2) the removals of each size class (prerecruit and legal) are known exactly. They each have two additional assumptions that differ slightly. CIR assumes that (1) the catchability between survey periods can vary, but not by size class, and (2) both size classes of crab have the same catchability. This latter assumption affects only estimates of prerecruit population size, which we did not estimate, as we were uncertain of its veracity. IR assumes that (1) all animals have the same catchability, and (2) catchability does not vary between survey periods.

Change-in-ratio (CIR)

The change in the proportion of legal Dungeness crabs before and after the summer season was used to estimate preseason total ($\hat{N}_1$) and legal ($\hat{X}_1$) male population sizes in numbers (Dawe et al. 1993, Pollock and Hoenig 1998a) using:

$$\hat{N}_1 = \frac{\hat{R}_x - \hat{P}_2\hat{R}}{\hat{P}_1 - \hat{P}_2}$$

and

$$\hat{X}_1 = \hat{P}_1\hat{N}_1$$

where $\hat{R}_x$ is total number of legal crabs removed by the fishery; $\hat{P}_1$ is proportion of total male crab that are legal before the fishery; $\hat{P}_2$ is proportion that are legal after the fishery; and $\hat{R}$ is total (prerecruit + legal) removals.

Prerecruit crabs are those that will become legal after their next molt (all males ≥135 mm and ≤164 mm CW). Legal removals were estimated from harvest, recorded in pounds on Alaska Department of Fish and Game (ADFG) fish tickets converted to abundance using average weight and decremented by the proportion of harvest that is prerecruit (illegal harvest). Average weight and proportion prerecruit data come from dockside sampling. Separate estimates were obtained for pots with open and closed escape rings. Legal exploitation rate ($\hat{u}_x$) was estimated by dividing legal removals by legal population size as:

$$\hat{u}_x = \frac{\hat{R}_x}{\hat{X}_1}$$

Finally, pre and postseason legal catchability coefficients (q_1 and q_2) were estimated by dividing legal CPUE at survey period t ($\hat{c}_{x1}$) by legal population size at survey period t as:

$$\hat{q}_x = \frac{\hat{c}_{x1}}{\hat{X}_1}$$

Variance for the estimate of legal population size ($\hat{V}[\hat{X}_1]$) was calculated as:

$$\hat{V}[\hat{X}_1] = (\hat{P}_1 - \hat{P}_2)^{-2}\{\hat{N}_1^2 P_2^2 \hat{V}[\hat{P}_1] + \hat{N}_2^2 \hat{P}_1^2 \hat{V}[\hat{P}_2]\}$$

where $\hat{N}_2$ is postseason legal population size. Variance of exploitation rate was calculated as:

$$\hat{V}[\hat{u}_x] = \frac{\hat{f}^2(\hat{f} - \hat{P}_2)^2 \hat{P}_2^2 \hat{V}[\hat{P}_1] + \hat{P}_1^2 \hat{f}^2(\hat{f} - \hat{P}_1)^2 \hat{V}[\hat{P}_2] + \hat{P}_1^2(\hat{P}_1 - \hat{P}_2)^2 \hat{P}_2^2 \hat{V}[\hat{f}]}{\hat{P}_1^4(\hat{f} - \hat{P}_2)^4}$$

These estimates were simplified from Dawe et al. (1993) by assuming that the variance of removals ($\hat{R}_x$) and of the proportion of illegal crabs caught in the fishery ($\hat{f}$) were zero, and that $\hat{f}$ and $\hat{P}_2$ were independent.

Index removal (IR)

Decline in survey CPUE of legal male Dungeness crabs before ($\hat{c}_1$) and after ($\hat{c}_2$) the summer season was related to magnitude of legal removal ($\hat{R}$) by the fishery to estimate preseason legal population size ($\hat{N}_1$) (Dawe et al. 1993, Pollock and Hoenig 1998b) as:

$$\hat{N}_1 = \hat{R}\frac{\hat{c}_1}{\hat{c}_1 - \hat{c}_2}$$

Legal removals were estimated as previously described. Additionally, the catchability coefficient ($\hat{q}$) was calculated as:

$$\hat{q} = \frac{\hat{c}_1}{\hat{N}_1}$$

and exploitation rate ($\hat{u}$) as:

$$\hat{u} = \frac{\hat{R}}{\hat{N}_1}$$

Variance for the estimate of legal crab abundance ($\hat{V}[\hat{N}_1]$) was estimated using formulae provided in Dawe et al. (1993) with the simplifying assumption that variance of $\hat{R}$ was zero and that $\hat{c}_1$ and $\hat{c}_2$ were independent, as follows:

$$\hat{V}[\hat{N}_1] = \frac{\hat{N}_1^{\,2}\hat{V}[\hat{c}_2] + \hat{N}_2^2\hat{V}[\hat{c}_1] + \hat{c}_1^2\hat{V}[\hat{R}]}{(\hat{c}_1 - \hat{c}_2)^2}$$

Variance of u is calculated as:

$$\hat{V}[\hat{u}] = \frac{\hat{c}_2^2}{\hat{c}_1^4}V[\hat{c}_1] + \frac{1}{\hat{c}_1^2}\hat{V}[\hat{c}_2]$$

Separate estimates were obtained for pots with open and closed escape rings. All analyses were done using JMP® statistical software version 7.0.1 (SAS Institute 2007).

Results

Survey CPUE was highly variable by survey area and survey period, the highest CPUE for legals were generally in Duncan Canal, Stikine Flats, and Port Camden during June surveys and for prerecruits in Stikine Flats, Duncan Canal, and Port Camden during postseason surveys in closed escape ring pots (Table 1).

Soak time experiment

The 3-way ANOVA showed significant effects only of escape rings and survey period (Table 2). The direction of effects differed between legal and sublegal, with CPUE generally greater in open pots and in June for legals but in closed pots and in August/September for prerecruits (Fig. 2).

Tagging

We estimate that 10.9%, 4.1%, and 14.2% of prerecruits molted into the fishery after June tagging for Peril Strait in 2001 and 2002, and Tenakee Inlet in 2001, respectively (Table 3). Estimates are unavailable for other areas due to either insufficient prerecruit tag recoveries or no legal tagging; however, it is known to be above zero, as June-tagged prerecruits molted into the same season fishery in Stikine Flats, Duncan Canal, and Port Camden (Table 3).

Table 1. Dungeness crab mean CPUE and its standard error by size class, escape ring, survey period, and survey area in surveys from 2000 to 2002.

Escape rings	Survey period	Survey area	Legal CPUE (no./pot)						Prerecruit CPUE (no./pot)					
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
			2000	2000	2001	2001	2002	2002	2000	2000	2001	2001	2002	2002
Closed	June	Stikine Flats			5.7	0.42	4.1	0.45			7.5	1.09	2.2	0.30
		Duncan Canal			7.1	0.65	7.0	0.7			5.0	0.59	2.4	0.36
		Port Camden			1.4	0.28					5.3	0.89		
		Berners Bay			0.8	0.18	0.7	0.43			1.5	0.29	1.0	0.37
		Peril Strait			2.9	0.54	2.4	0.43			2.4	0.46	1.7	0.27
		Tenakee Inlet			3.6	0.69	2.8	0.54			1.8	0.42	0.9	0.24
		St. James Bay					2.9	0.55					1.7	0.43
	Aug./Sep.	Stikine Flats	1.2	0.21	1.3	0.22	3.2	0.38	11.2	1.05	14.0	1.02	6.7	0.85
		Duncan Canal	0.7	0.20	1.4	0.20	1.7	0.23	8.7	0.86	10.5	0.97	4.5	0.60
		Port Camden			2.5	0.37					12.3	1.85		
		Berners Bay			1.3	0.38					2.3	0.49		
		Peril Strait			2.1	0.30	1.0	0.18			6.0	1.00	1.7	0.41
		Tenakee Inlet			2.3	0.39	1.3	0.28			3.9	0.77	3.6	0.73
		St. James Bay					2.5	0.6					1.5	0.45
Open	June	Stikine Flats	4.0	0.27	7.6	0.56	5.3	0.48	0.7	0.08	2.6	0.39	1.1	0.26
		Duncan Canal	3.1	0.28	7.2	0.64	8.3	0.86	0.8	0.12	1.9	0.30	0.8	0.14
		Port Camden			1.6	0.36					0.8	0.23		
		Berners Bay			0.7	0.20	0.8	0.28			1.0	0.14	0.8	0.21
		Peril Strait			2.8	0.42	2.8	0.57			1.2	0.22	0.8	0.20
		Tenakee Inlet			3.5	0.66	2.8	0.54			1.2	0.25	0.5	0.12
		St. James Bay					2.1	0.62					0.9	0.22
	Aug./Sep.	Stikine Flats	1.8	0.22	1.3	0.15	3.9	0.40	1.2	0.26	3.3	0.53	2.5	0.37
		Duncan Canal	1.2	0.23	1.9	0.24	1.7	0.24	1.8	0.26	2.1	0.33	1.3	0.20
		Port Camden			2.9	0.48					1.6	0.32		
		Berners Bay			1.2	0.26					0.5	0.16		
		Peril Strait			1.7	0.28	1.4	0.31			0.8	0.19	0.7	0.17
		Tenakee Inlet			2.8	0.41	1.8	0.27			1.2	0.23	0.7	0.14
		St. James Bay					3.0	0.55					1.0	0.37

Table 2. Results of a 3-way ANOVA of effects of escape rings, survey period, and soak time on legal and prerecruit Dungeness crab survey CPUE in Duncan Canal in 2002.

Y	Source	DF	SS	*F*	Prob > *F*
Legal	Full model	5	2164.58	37.78	<0.0001
	Escape rings	1	60.17	5.25	0.0243
	Survey period	1	2035.04	177.58	<0.0001
	Soak time	3	69.38	2.02	0.1170
Prerecruit	Full model	5	485.54	9.33	<0.0001
	Escape rings	1	376.04	36.12	<0.0001
	Survey period	1	100.04	9.61	0.0026
	Soak time	3	9.46	0.30	0.8233

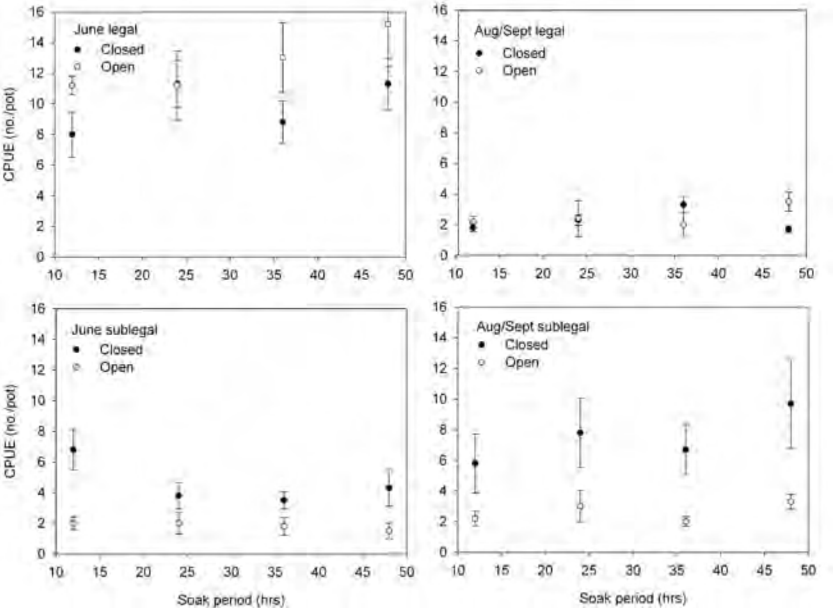

Figure 2. Results of an experiment to investigate effects of soak time and escape ring on CPUE of Dungeness crabs before and after the summer season, conducted in Duncan Canal in 2002.

Table 3. Number of prerecruit and legal male Dungeness crabs tagged during the June survey and number of prerecruits recovered during summer and fall portions of subsequent commercial season from 2000 to 2004.

Survey area	Tag survey period	Year	Number tagged		Number recovered during same season		% Prerecruits recovered	% Prerecruits molting into fishery
			Legal	Prerecruit	Legal	Prerecruit		
Stikine Flats	Aug./ Sep.	2000	103	241				
		2001	103	667				
		2002	0	364				
	June	2003	0	84	0	5	6.0%	
		2004	1	61	0	1	1.6%	
Duncan Canal	Aug./ Sep.	2000	73	290				
		2001	119	452				
		2002	0	446				
	June	2003	0	152	0	9	5.9%	
		2004	0	48	0	3	6.3%	
Port Camden	Aug./ Sep.	2001	179	398				
	June	2003	0	55	0	2	3.6%	
Peril Strait	June	2001	249	116	158	8	6.9%	10.9%
	Aug/ Sep.	2001	151	254				
	June	2002	6	74	4	2	2.7%	4.1%
	Aug./ Sep.	2002	0	88				
	June	2003	2	73	0	0	0.0%	
Tenakee Inlet	June	2001	289	94	63	3	3.2%	14.2%
	Aug./ Sep.	2001	209	199				
	June	2002	1	41	0	0		
	Aug./ Sep.	2002	0	163				
	June	2003	1	236	0	3	1.3%	
		2004	0	121	0	0	0.0%	
St. James Bay	June	2002	0	40	0	0		
Berners Bay	June	2001	57	32	17	0		
	Aug./ Sep.	2001	52	53				
	June	2002	0	9	0	1		

Commercial catch sampling

From dockside sampling the mean proportion newly recruited crabs during 2000/01-2002/03 was estimated at 90%, 86%, 79%, 82%, 89%, and 81% respectively, for Stikine Flats, Duncan Canal, Peril Strait, Tenakee Inlet, Port Camden, and Lynn Canal (St. James Bay and Berners Bay) fishery areas (Table 4).

Modeling

CIR modeling produced population estimates 8-280% smaller than IR for pots with closed escape rings, and 15-173% smaller for pots with open escape rings, excluding Port Camden, St. James Bay, and Berners Bay, Peril Strait, Tenakee Inlet open escape ring pots (Table 5, Figs. 3 and 4).

Table 4. Proportion of commercial harvest consisting of recruit Dungeness crabs, determined from dockside sampling in seven fishery areas from 2000/01 to 2002/03 commercial seasons.

Fishery area	Survey area	Season	% Recruit		
			Mean	SE	N (landings)
Stikine Flats	Stikine Flats	2000/01	89%	0.012	39
		2001/02	89%	0.009	70
		2002/03	92%	0.007	58
		Mean	90%		
Duncan Canal	Duncan Canal	2000/01	76%	0.018	67
		2001/02	90%	0.006	142
		2002/03	91%	0.005	106
		Mean	86%		
Port Camden/ West Kuiu	Port Camden	2000/01	83%	0.012	68
		2001/02	90%	0.007	66
		2002/03	93%	0.004	85
		Mean	89%		
Peril Strait	Peril Strait	2000/01	67%	0.055	13
		2001/02	79%	0.025	29
		2002/03	91%	0.021	7
		Mean	79%		
Tenakee Inlet	Tenakee Inlet	2000/01	78%	0.051	4
		2001/02	82%	0.019	16
		2002/03	85%	0.028	7
		Mean	82%		
Lynn Canal	St. James Bay and Berners Bay	2000/01	77%	0.052	6
		2001/02	76%	0.057	10
		2002/03	91%	0.021	9
		Mean	81%		

Table 5. Dungeness crab harvest, and legal male population size estimate and its standard error using change-in ratio and index removal methods for pots with open and closed escape rings in seven survey areas from 2000/01 to 2002/03 commercial seasons.

Survey area	Season	Summer harvest (no.)	Fall harvest (no.)	Escape rings closed				Escape rings open			
				CIR		IR		CIR		IR	
				Legal population estimate (no.)	SE	Legal population estimate (no.)	SE	Legal population estimate (no.)	SE	Legal population estimate (no.)	SE
Stikine Flats	2000/01	143,607						184,884	19,554	260,694	231,801
	2001/02	295,463	33,124	311,375	9,976	386,374	132,116	307,137	9,586	355,259	62,388
	2002/03	468,222	79,149	604,369	44,174	2,298,544	9,194,576	630,980	77,362	1,719,504	3,957,038
Duncan Canal	2000/01	60,939	7,856					68,731	3,673	99,981	105,451
	2001/02	343,089	38,583	345,144	6,354	423,626	104,750	384,817	23,487	462,049	152,902
	2002/03	329,224	20,064	369,492	10,519	436,377	147,838	360,710	13,839	415,272	118,766
Port Camden	2001/02	130,944	53,168	570,134	445,505	−154,658	510,570	604,192	843,840	−171,786	670,277
Peril Strait	2001/02	24,692	5,876	33,574	3,814	91,806	377,603	623,153	4,593,801	64,120	152,480
	2002/03	35,912	8,150	58,376	11,337	63,016	74,284	70,818	31,106	71,824	137,021
Tenakee Inlet	2001/02	36,350	5,809	50,859	6,207	102,993	299,009	187,179	220,106	180,580	1,140,782
	2002/03	27,613	9,067	31,124	1,530	51,950	84,207	48,106	13,270	75,936	202,983
St. James Bay	2002/03	11,879	6,015	211,181	1,574,575	83,155	658,923	−40,244	100,891	−28,761	162,171
Berners Bay	2001/02	3,683	0	−31,458	127,187	−5,426	22,747	−913	677	−4,603	19,112

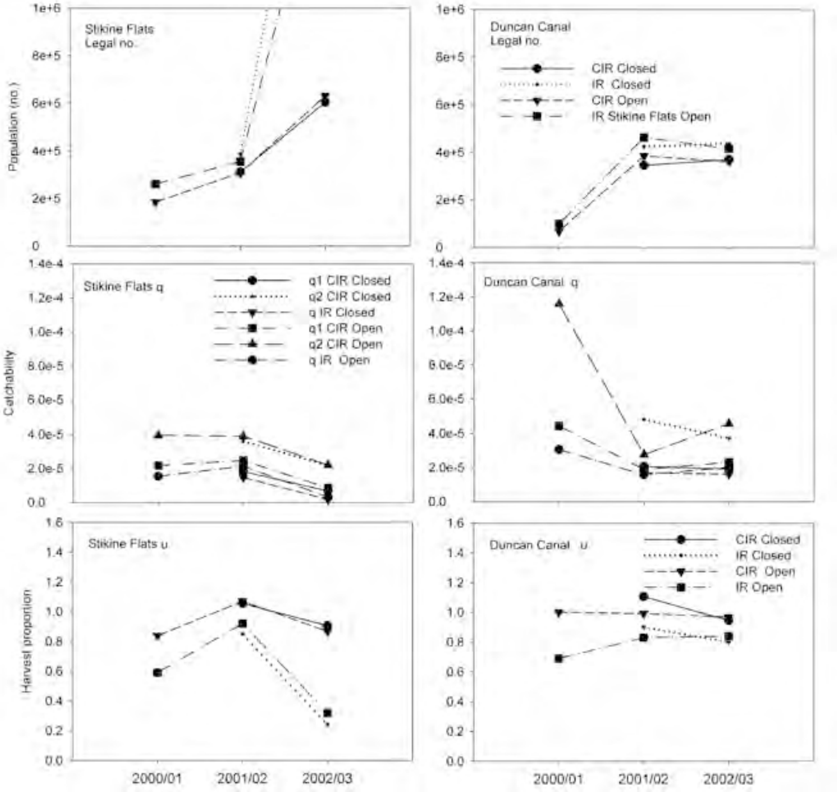

Figure 3. Estimates of population size, catchability, and exploitation rate from CIR and IR modeling for Stikine Flats and Duncan Canal.

The CIR method produced negative population estimates for Berners Bay and St. James Bay in open escape ring pots. CIR produced estimates with very large standard errors for Peril Strait open escape ring pots, and for Port Camden and St. James Bay (Table 5). Using the IR method, five of 24 population estimates were negative and all except six estimates had very large standard errors (Table 5). For Stikine Flats and Duncan Canal there was very little difference (–33.7-10.3%) between population estimates from open and closed escape ring pots using either method, but for Peril Strait and Tenakee Inlet open escape ring pots produce 18-95% larger population estimates for CIR and –43-43% larger estimates for IR.

Catchability coefficients estimated using CIR modeling varied by survey area, escape ring configuration, and survey period. Postseason catchability coefficients (q_2) were consistently 5-60% higher than preseason catchability coefficients (q_1) for closed escape ring pots except

Table 6. Dungeness crab catchability coefficient and its standard error using change-in ratio and index removal methods for pots with open and closed escape rings in seven survey areas from the 2000/01-2002/03 commercial seasons.

Survey area	Season	Escape rings closed				Escape rings open			
		CIR		IR		CIR		IR	
		*q*1	*q*2	*q*	SE	*q*1	*q*2	*q*	SE
Stikine Flats	2000/01					2.20E-05	4.00E-05	1.50E-05	2.30E-05
	2001/02	1.80E-05	3.60E-05	1.50E-05	1.00E-05	2.50E-05	3.90E-05	2.10E-05	1.20E-05
	2002/03	6.70E-06	2.20E-05	1.80E-06	7.90E-06	8.40E-06	2.20E-05	3.10E-06	8.40E-06
Duncan Canal	2000/01					4.40E-05	1.20E-04	3.10E-05	5.60E-05
	2001/02	2.10E-05	4.80E-05	1.70E-05	1.20E-05	1.90E-05	2.80E-05	1.60E-05	1.20E-05
	2002/03	1.90E-05	3.70E-05	1.60E-05	1.40E-05	2.30E-05	4.60E-05	2.00E-05	1.70E-05
Port Camden	2001/02	2.40E-06	5.60E-06	–8.80E-06	2.10E-05	2.70E-06	6.00E-06	–9.60E-06	2.80E-05
Peril Strait	2001/02	8.60E-05	2.20E-04	3.10E-05	1.60E-04	4.40E-06	2.80E-06	4.30E-05	1.40E-04
	2002/03	4.10E-05	4.30E-05	3.80E-05	8.10E-05	4.00E-05	3.90E-05	3.90E-05	1.10E-04
Tenakee Inlet	2001/02	7.00E-05	1.50E-04	3.50E-05	1.30E-04	1.90E-05	1.80E-05	1.90E-05	1.40E-04
	2002/03	8.90E-05	3.60E-04	5.30E-05	1.40E-04	5.90E-05	8.70E-05	3.70E-05	1.40E-04
St. James Bay	2002/03	1.40E-05	1.30E-05	3.50E-05	3.00E-04	–5.20E-05	–5.70E-05	–7.30E-05	3.30E-04
Berners Bay	2001/02	–2.50E-05	–3.80E-05	–1.40E-04	9.90E-04	–7.50E-04	–2.80E-04	–1.50E-04	9.10E-04

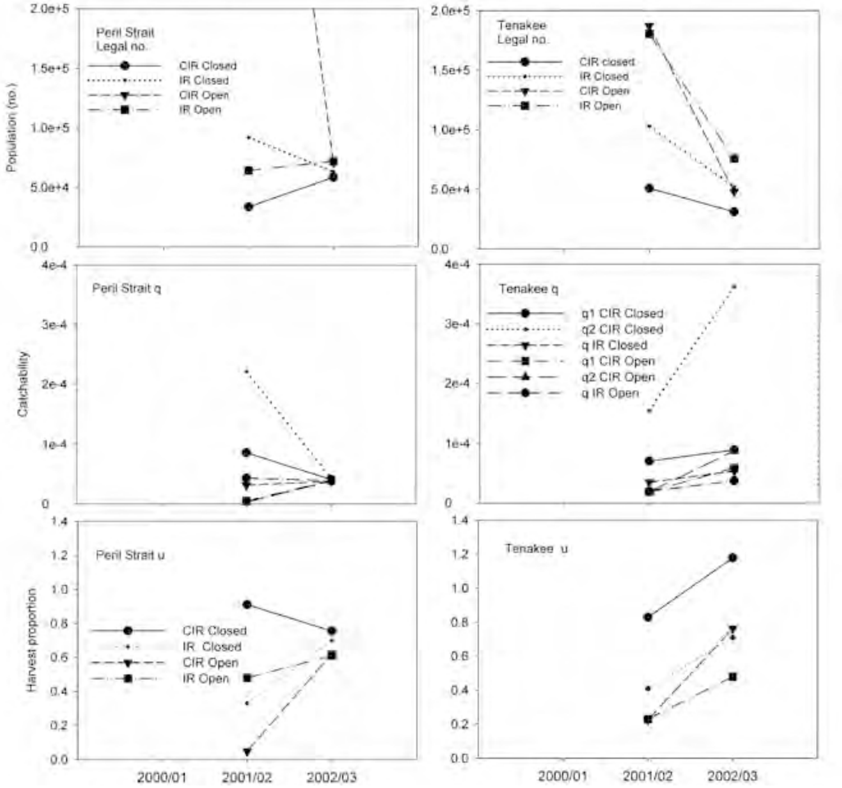

Figure 4. Estimates of population size, catchability, and exploitation rate from CIR and IR modeling for Peril Strait and Tenakee Inlet.

in St. James Bay. Open escape ring pots also had 9-60% higher q_2 than q_1 except in Peril Strait, Tenakee Inlet, and Berners Bay (Table 6, Figs. 3 and 4). Negative catchability coefficients were calculated for St. James Bay in pots with open escape rings and in Berners Bay for both escape ring configurations (Table 6, Figs. 3 and 4). The CIR q_1 was higher than the IR q for both closed (7-500%) and open (0-500%) escape ring pots (Table 6) except for Port Camden, St. James Bay, and Berners Bay where negative IR catchability coefficients were obtained.

CIR exploitation rate estimates were consistently 15-50% higher than those obtained by IR methods. There was very little difference between estimates from closed and open escape ring pots for Stikine Flats and Duncan Canal, while for Peril Strait and Tenakee Inlet, closed escape ring pots generally produced 13-95% higher exploitation rate estimates than open (Table 7; Figs. 3 and 4).

Table 7. Dungeness crab exploitation rate (*u*) and its standard error using change-in-ratio and index removal methods for pots with open and closed escape rings in seven survey areas from the 2000/01-2002/03 commercial seasons.

Survey area	Season	Escape rings closed				Escape rings open			
		CIR		IR		CIR		IR	
		u	SE	*u*	SE	*u*	SE	*u*	SE
Stikine Flats	2000/01					84%	8.0	59%	49.3
	2001/02	106%	2.8	85%	25.9	107%	2.8	92%	14.6
	2002/03	91%	5.5	24%	79.8	87%	8.9	32%	63.3
Duncan Canal	2000/01					100%	4.6	69%	63.1
	2001/02	111%	1.7	90%	20.3	99%	5.1	83%	24.9
	2002/03	95%	2.5	80%	25.5	97%	3.5	84%	22.7
Port Camden	2001/02	32%	16.8	−119%	265.9	30%	28.3	−107%	310.7
Peril Strait	2001/02	91%	8.1	33%	109.3	05%	28.4	48%	89.7
	2002/03	75%	11.5	70%	65.7	62%	21.4	61%	95.4
Tenakee Inlet	2001/02	83%	8.6	41%	101.1	23%	22.5	23%	127.3
	2002/03	118%	4.3	71%	85.1	76%	15.8	48%	98.5
St. James Bay	2002/03	08%	41.4	22%	115.3	−44%	73.0	−62%	233.7
Berners Bay	2001/02	−12%	43.6	−37%	304.1	−403%	282.3	−43%	369.6

Discussion

The variable success of the two methods employed here to estimate population parameters for Dungeness crab in southeastern Alaska suggests that the importance of violations of model assumptions varied spatially, most likely due to differences in crab life history timing and density. Specifically, model results became less believable with increased latitude. This is probably because of delays in completion of the recruitment molt and of male crabs becoming active, with increasing latitude; however, latitude alone does not explain the patterns, as Port Camden is at the same latitude as Duncan Canal. On a larger scale, delays in timing of Dungeness crab life history events with increasing latitude from California to British Columbia have been documented; megalopae settlement occurs in April and May for Oregon, May through June for Washington, and May through September for British Columbia (Mackay 1942, Cleaver 1949, Butler 1956, Lough 1976, Stevens 1982). Thus, the smaller spatial scale differences in life history timing that we describe are interesting, but not surprising. Increased variability in life history timing could be a general effect of climate change and result in associated increases in variability of stock assessments.

Because movement of mature male Dungeness crab between areas is known to be limited (O'Clair et al. 1990), there is no reason to believe that a large number of crabs immigrated to the study areas between survey periods. Thus, the negative population and exploitation rate estimates, and high standard errors obtained for some areas, indicate that one or more model assumptions were violated there. First, differing catchability coefficients between survey periods for the CIR model suggest that the IR assumption of constant catchability between survey periods was violated. Second, reduced legal CPUE, observed in closed relative to open escape ring pots preseason but not postseason during the Duncan Canal soak time experiment, suggests that gear saturation was occurring. This would reduce q preseason for closed escape ring pots only, and would be important for areas where, and survey periods or years when, crab density was high. Finally, inseason recoveries of prerecruit crabs tagged preseason indicate that the CIR and IR assumption of a closed population was violated for some areas and years.

Increases in q between pre and postseason survey periods would not affect CIR results, but would bias IR population estimates high and exploitation rates low. Low crab activity level during the June survey could cause this. In a tagging study in Fritz Cove, Stone and O'Clair (2001) found that Dungeness crabs were active in April associated with movement to shallow water, followed by a quiescent period from May through June, succeeded by a very active period from July through October. Increases in catchability between spring and summer surveys were also observed in a study comparing pot and dive survey CPUE in Glacier Bay (Taggart et al. 2002). Having recently molted would also decrease activity level, and a high proportion of recently molted crabs were observed during the June survey in some areas and years.

If gear saturation affected legals and prerecruits equally, then q_2 would increase for both, and CIR results would not be affected, but IR population estimates would be biased high for gear-saturated, closed escape ring pots. The fact that population estimates from open and closed escape ring pots were very similar for Stikine Flats, Duncan Canal, and Port Camden, where preseason legal CPUE was high, suggests that gear saturation was not a significant issue.

Violation of the assumption of a closed population would bias both CIR and IR population estimates high, and exploitation rate estimates low. Tag recovery estimates of prerecruit molt rates confirmed this violation for Peril Strait and Tenakee Inlet.

Despite many violations of assumptions, these methods provide fairly believable results for several survey areas, as determined by comparisons of exploitation rates with percent recruit from dockside sampling. In addition, both CIR and IR methods documented a large population increase for Duncan Canal and Stikine Flats associated with the record 7.3 million pound harvest in 2002/03 (Hebert et al. 2008). The best fit of model and escape ring type varies by survey area. For Stikine Flats and Duncan Canal, open escape ring CIR is best, producing exploitation rates averaging respectively 93% and 99%. For Port Camden, none of the models provide believable results. For Peril Strait and Tenakee Inlet, the closed escape ring CIR estimate is most reasonable; exploitation rates averaged 83% in each area, when the 2002/03 Tenakee Inlet estimate was excluded. Closed escape ring pots performed better for these areas, probably because those pots caught a more consistent number of prerecruits. For St. James Bay and Berners Bay, the negative population sizes estimated from each model are not believable results.

The high exploitation rates estimated are not unprecedented in Dungeness fisheries along the west coast of North America. Smith and Jamieson (1989) estimated exploitation rates at 99-100% ($F = 5.1\text{-}6.9$) from tagging in British Columbia, while in northern California, Jow (1965) found exploitation rates of 100% ($F = 7.9$).

In conclusion, because of spatial variation in timing of the recruitment molt, any stock assessment survey for Dungeness crab in southeastern Alaska would need to be fine-tuned to specific survey area. CIR modeling could be used to assess stocks for some survey areas, particularly if the start of summer season were delayed to provide sufficient time for crab in all areas to complete the recruitment molt. Even if season timing were delayed, it might prove difficult to find a summer season in which no recruitment molting was occurring due to the extended molt period. Thus, preseason tagging of both legals and prerecruits should be a regular part of a survey program in order to quantify the level of ongoing recruitment to adjust the population estimate. A larger pot with closed escape rings should be employed to guard against gear saturation, particularly in very high abundance areas. Bottom water temperature data should be collected throughout the year at each survey area to provide insights into interannual variation in molt timing.

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References

Bishop, G.H., M.S.M. Siddeek, and J.M. Rumble. 2008. Growth of male Dungeness crabs in southeastern Alaska. In: J. Nielsen et al. (eds.), Reconciling fisheries with conservation: Proceedings of the Fourth World Fisheries Congress. American Fisheries Society, Vancouver, pp. 1339-1342.

Butler, T.H. 1956. The distribution and abundance of early post-larval stages of the British Columbia commercial crab. Fish. Res. Board Can. 107:22-23.

Cleaver, F.C. 1949. Preliminary results of the coastal crab, *Cancer magister*, investigation. Washington Department of Fisheries, Biological Report 49-A, pp. 48-82.

Dawe, E.G., J.M. Hoenig, and X. Xucai. 1993. Change-in-ratio and index-removal methods for population assessment and their application to snow crab (*Chionoecetes opilio*). Can. J. Fish. Aquat. Sci. 50:1456-1476. doi:10.1139/f93-167

Hebert, K., J. Stratman, K. Bush, G. Bishop, C. Siddon, J. Bednarski, and A. Messmer. 2008. 2009 Report to the Board of Fisheries on region 1 shrimp, crab, and scallop fisheries. Alaska Department of Fish and Game, Fisheries Management Report 08-62. 210 pp.

Jow, T. 1965. California cooperative tagging study. Pacific Marine Fisheries Commission, 16th and 17th Annual Report. 51-52 pp.

Lehman, C., and O. Osborn. 1970. Dungeness crab research. Alaska Department of Fish and Game, Commercial Fisheries Research and Development Act Completion Report 5-10-R and 5-21-R, Juneau. 42 pp.

Lough, R.G. 1976. Larval dynamics of the Dungeness crab, *Cancer magister*, off the central Oregon coast, 1970-71. Fish. Bull. 74:353-375.

Mackay, D.C.G. 1942. The Pacific edible crab, *Cancer magister*. Fish. Res. Board Can. 32 pp.

O'Clair, C.E., R.P. Stone, and J.L. Freese. 1990. Movements and habitat use of Dungeness crabs and the Glacier Bay fishery. In: A.M. Milner, and J.D. Wood (eds.), Proceedings of the Second Glacier Bay Science Symposium. U.S. National Park Service, Gustavus, pp. 74-77.

Pollock, K.H., and J.M. Hoenig. 1998a. Change-in-ratio estimators. In: S. Kotz, C.B. Read, and D.L. Banks (eds.), Encyclopedia of statistical sciences update volume. John Wiley and Sons, New York, pp. 109-112.

Pollock, K.H., and J.M. Hoenig. 1998b. Index-removal methods. In: S. Kotz, C.B. Read, and D.L. Banks (eds.), Encyclopedia of statistical sciences update volume. John Wiley and Sons, Inc., New York, pp. 342-346.

SAS Institute. 2008. JMP version 8.0. SAS Institute Inc., Cary, North Carolina.

Shirley, S.M., and T.C. Shirley. 1988. Appendage injury in Dungeness crabs, *Cancer magister*, in southeastern Alaska. Fish. Bull. 86(1):156-160.

Smith, B.D., and G.S. Jamieson. 1989. Exploitation and mortality of male Dungeness crabs (*Cancer magister*) near Tofino, British Columbia. Can. J. Fish. Aquat. Sci. 46:1609-1614.

Stevens, B.G. 1982. Distribution, abundance, and food habits of the Dungeness crab, *Cancer magister*, in Grays Harbor, Washington. Ph.D. thesis, University of Washington. 205 pp.

Stone, R.P., and C.E. O'Clair. 2001. Seasonal movements and distribution of Dungeness crabs, *Cancer magister*, in a glacial southeast Alaska estuary. Mar. Ecol. Prog. Ser. 214:167-176. doi:10.3354/meps214167

Taggart, S.J., C.E. O'Clair, T.C. Shirley, and J.M. Mondragon. 2002. Estimating Dungeness crab, *Cancer magister* abundance, crab pots and dive transects compared. Fish. Bull. 102(3):488-497.

Thompson, S.K. 1992. Sampling. Wiley Interscience, New York. 343 pp.

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New Management Control Rules for Bering Sea and Aleutian Islands Crab Fisheries

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Abstract

Amendment 24 to the U.S. federal Fishery Management Plan (FMP) for Commercial King and Tanner Crab Fisheries in the Bering Sea and Aleutian Islands was made in 2007 and implemented for the 2008 fisheries. The amended FMP specifies a five-tier system to which each stock under the purview of the plan is assigned and which is used for setting the overfishing and overfished levels. The primary differences between the amended FMP and the preceding FMP are twofold: (1) the biomass currency (mature male biomass vs. total male plus female mature biomass); and (2) the limit catch (total removal from all fisheries vs. retained catch removal from the directed fishery). Thus, the amended FMP considers the effect of total removals from the ecosystem on stock productivity and also the direct impact of fishery removal of

males on reproductive output. In this paper, in addition to providing some guidance for developing control rules under the amended FMP, we compare the merit of the amended control rule over the old control rule considering two major crab fisheries, Bristol Bay red king crab, *Paralithodes camtschaticus*, a recovered stock, and eastern Bering Sea snow crab, *Chionoecetes opilio*, a depleted and recovering stock. We discuss the regime shift consideration made when developing the old and amended FMPs.

Introduction

The living resources in the Exclusive Economic Zone waters of the United States are managed under the Fishery Conservation and Management Act (Magnuson-Stevens Act) and as subsequently amended (Restrepo and Powers 1999). The latest revision to the federal guidelines for National Standard 1 (Federal Register 74[11], January 16, 2009) provides additional prescriptions for preventing overfishing by requiring that fishery management plans establish a mechanism to specify annual catch limits and accountability measures aimed at the conservation and effective utilization of the stock. Since its enactment in 1976, the impact of changes made to the Magnuson-Stevens Act, in addition to evolving prescriptions to the National Standard guidelines, collectively serve to achieve a more precautionary approach to management. The operational tenets of the first of the 10 National Standards embodies the precautionary management approach by requiring management to prevent overfishing while achieving optimum yield on a continuing basis for each stock (Restrepo and Powers 1999). The Bering Sea and Aleutian Islands (BSAI) crab fishery management plan (FMP) implemented in 1989, subsequently amended in 1999 (NPFMC 1999) and 2007 (NPFMC 2007) adhere to these principles.

The 1999 amendment to the crab FMP (hereafter known as the old FMP) defined the control rule (CR), known as a maximum sustainable yield (MSY) control rule (or limit CR), by a constant overfishing level fishing mortality (F_{OFL}), independent of biomass, equating F_{MSY} (F_{OFL}) to natural mortality M. It defined the overfished reference point by the minimum spawning stock threshold (MSST), equal to one-half the MSY total male plus female mature stock biomass (total mature biomass, TMB) (NPFMC 1999). If the stock declined below MSST, the stock was deemed overfished. In this plan, the MSY stock size (TMB_{MSY}) was estimated as the average TMB enumerated by the National Marine Fisheries Service (NMFS) summer bottom trawl survey over the 15-year period from 1983 to 1997, which was considered to be an ecologically stable period (NPFMC 1999). The old FMP defined the overfishing limit as sustainable yield equal to $TMB \times M$. If the retained catch in any year exceeded sustainable yield, overfishing occurred. The use of this sustainable yield designation was arbitrary and no underlying theory was shown that linked BSAI crab dynamics to sustained retained catch removals from the legal male stock at the rate $TMB \times M$. The applicability of M and average TMB as proxies for F_{MSY} and MSY biomass, respectively, in BSAI crab management has been criticized for lack of analytical support (Siddeek 2002). The 2007 amended FMP (hereafter known as the new FMP) (NPFMC 2007) was developed to address the technical limitations in the old FMP in terms of the overfishing limits by defining F_{OFL} as F_{MSY} or a proxy of F_{MSY}, $F_{x\%}$ (F corresponding to x% virgin spawning biomass-per-recruit) and MSY biomass as B_{MSY} or a proxy of B_{MSY}, $B_{x\%}$ (spawning biomass at $F_{x\%}$). Because of the complicated reproductive dynamics of crabs and the male-only fishery, mature male biomass (MMB) was selected as the proxy for spawning biomass, B, in the new FMP, which is likely to have a greater impact on the fishery than TMB that consists of both sexes.

The limit CRs (or F_{OFL} CRs) specify thresholds of stock or fishery metrics (e.g., biomass or fishing mortality rate) that, if exceeded, invoke specified status determination (e.g., overfished or overfishing) and management responses. Target CRs specify stock or fishery levels to be achieved without specified status determination or management consequences, if not achieved.

The new FMP considers the effect of total fishery removals from the ecosystem on stock productivity and also the direct impact of fishery removal of males on reproductive output. In this paper, in addition to providing some guidance for developing limit and target control rules under the new FMP, we compare the merit of the new control rule over the old control rule considering two major crab stocks: Bristol Bay red king crab, *Paralithodes camtschaticus* (recovered stock) and eastern Bering Sea snow crab, *Chionoecetes opilio* (depleted and recovering stock). We discuss how the 1976-77 regime shift was accounted for when developing the old and the new FMPs.

Methods

General approach followed to develop control rules in the two Fishery Management Plans (FMPs)

Old limit control rule

The National Standard 1 of the Magnuson-Stevens Act is implemented using an MSY control rule, which uses a constant F_{OFL} independent of biomass (Fig. 1). The 22 Bering Sea and Aleutian Islands (BSAI) crab stocks that were subject to the provisions of the old plan are grouped into three tiers (NPFMC 1999).

- Tier 1 (data poor): Stocks that are not surveyed and some catch and effort data are available. MSY catch is estimated from a proxy of total mature biomass (TMB) and utilization rate; and F_{OFL} is set to F_{MSY}.

- Tier 2 (data moderate): Crab stocks have limited years of survey information and well-documented catch and effort data. A similar estimation procedure to tier 1 stocks is used and F_{OFL} is set to F_{MSY}.
- Tier 3 (data rich): Annual survey, catch and effort, and stock assessment information are available. The B_{MSY} is estimated as mean TMB from 1983 to 1997 trawl survey data; MSY catch is determined by $B_{MSY} \times F_{MSY}$; and F_{OFL} is set to F_{MSY}.

For all tiers, M is used as a proxy of F_{MSY}. The M value for king crabs (*Lithodes* and *Paralithodes*) is set to 0.2 and for Tanner and snow crabs (*Chionoecetes*) is set to 0.3. The M estimations are based on assumed maximum ages of 22-24 years for king and 15 years for Tanner and snow crabs, and using Hoenig's (1983) formula (NPFMC 1999).

Implementation of the old limit control rule (prior to 2008)

For tier 3 stocks (six stocks), which have a history of annual trawl survey data, NMFS determined the overfishing and overfished levels using the MSY control rule as follows:

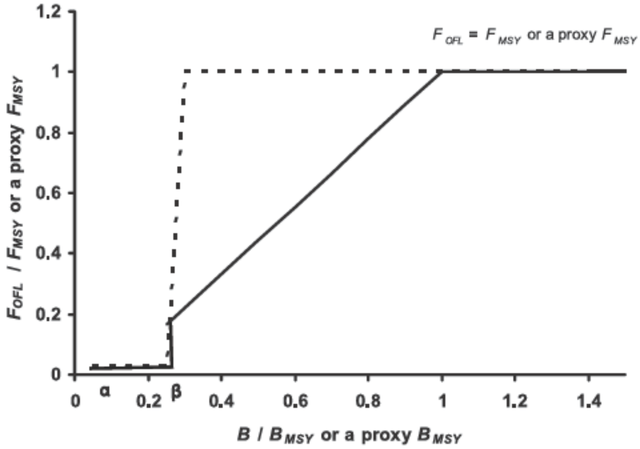

Figure 1. Limit control rules under the old Fishery Management Plan (FMP) (dashed line) and under the new FMP (solid line). The vertical dotted line showing directed fishery closure biomass level under old FMP is created from the snow crab rebuilding plan prescription, not documented in the old FMP.

1. The overfishing level (OFL) for the upcoming year was determined by an OFL retained catch threshold using the formula, $SY = TMB \times M$, where TMB was estimated from annual trawl survey data. If total allowable (retained) catch (TAC) > SY, then overfishing occurred.
2. The overfished status determination criteria were determined by comparing TMB with MSST (= $\frac{1}{2} B_{MSY}$) where B_{MSY} is the average 1983 to 1997 TMB. If $TMB < MSST$, then the stock was overfished.
3. MSY estimates were used as OFL for tier 1 and tier 2 stocks (remaining 16 stocks) that did not have trawl survey abundance estimates to determine sustainable yield.

The stock status determinations and total allowable catch (TAC) settings for tier 3 stocks occurred in the fall of the year after completion of the NMFS summer trawl survey and prior to the start of the crab fishery during the fall and winter. The North Pacific Fishery Management Council (NPFMC) reviewed the results and recommended remedial actions if overfishing or overfished status occurred or was expected to approach those conditions.

Old target control rule and its implementation

The Alaska Department of Fish and Game (ADFG) sets the target retained TAC for all crab stocks in accordance with Alaska Board of Fisheries and federal FMP regulations. The target control rule implementation procedures are discussed below in relation to two information-rich crab stocks, Bristol Bay red king crab and eastern Bering Sea snow crab, belonging to tier 3, but with contrasting life history characteristics. Both sexes of snow crab cease to molt when they attain maturity, but this does not occur in red king crab. Furthermore female snow crab can store sperm and self-fertilize, but female red king crab cannot store sperm.

Bristol Bay red king crab

The ADFG harvest strategy has the following criteria:

Threshold levels are 8.4 million mature female crabs and 6,577 t of effective spawning biomass (ESB) for ensuring adequate stock productivity, and a minimum TAC of 2,016 t for fishery viability. Following Zheng et al. (1995), ESB is defined as the biomass of mature females (≥90 mm carapace length, CL) that can be successfully mated by available mature males (≥120 mm CL). If the estimated abundance of mature males is insufficient for all females to be successfully mated, ESB will be less than mature female biomass. When the threshold levels are met, the harvest rate on mature male abundance at the time of the survey is determined as follows:

a. Harvest rate = 10%, if $6{,}577 < \mathrm{ESB} < 15{,}762$ t

b. Harvest rate = 12.5%, if $15{,}762 \le \mathrm{ESB} \le 24{,}948$ t

c. Harvest rate = 15%, if $\mathrm{ESB} \ge 24{,}948$ t

In addition, the TAC is capped at 50% of available legal male (≥ 135 mm CL) abundance. Male and female abundances are estimated at the time of the survey using survey selectivity, and harvest rates are applied to mature male (≥ 120 mm CL) abundance. The TAC is constrained to less than sustainable yield to avoid overfishing.

Eastern Bering Sea snow crab

This stock was declared overfished in 1999 and has been under a rebuilding plan since then (NPFMC 2000). In conjunction with the rebuilding plan prescriptions, the ADFG harvest strategy is modified as follows to allow for greater probability of rebuilding this depleted stock (Zheng et al. 2002, NPFMC 2007):

The threshold level is a minimum TAC of 11,340 t for fishery viability. When the threshold level is met, the harvest rate on mature male abundance at the time of the survey is determined using a control rule formula similar to that of the new control rule as follows with a maximum fishing mortality = 0.75 M.

a. Harvest rate = $0.77 \times M$ ($M = 0.3$), when $TMB \ge TMB_{MSY}$

b. Harvest rate = $\dfrac{0.75 \times M \times (\frac{TMB}{TMB_{MSY}} - \alpha')}{(1 - \alpha')}$, when $0.25 \times TMB_{MSY} \le TMB < TMB_{MSY}$

c. Harvest rate = 0, when $TMB < 0.25 \times TMB_{MSY}$ where $\alpha' = -0.35$.

The harvest rate is applied to mature male biomass, MMB (≥ 65 mm CW) at the time of the survey. In addition, a 58% maximum harvest rate on exploited (100% new-shell plus a percentage [25% for this paper] of the old-shell) legal male (≥ 102 mm CW) abundance is considered when estimating TAC to ensure stock productivity. TAC is constrained to less than sustainable yield to avoid overfishing.

New limit control rule

National Standard 1 of the Magnuson-Stevens Act is implemented using a management control rule that relates fishing mortality (F) to biomass (B) through a mathematical function. Management has control over F through catch limits and B is related to the stock. Thus, optimum yield is obtained by adjusting F in accordance with the level of current B scaled to B_{MSY}. The parameterization of the control rule (CR) in the face of uncertainty is done through Monte Carlo simulations using length-based projection models with stock assessment estimated parameter values (NPFMC 2007). Monte Carlo simulations did not provide definitive answers to some CR parameters, α and β (equations 1 to 4 below), and those parameters were set at fixed levels by the Crab Plan Team as representing best informed judgment. The fixed levels of α and β were those that produced short-term (first 10-year rebuilding of an overfished stock) higher mean yields and modest increases in the last year (30^{th} year) MMB/MMB_{MSY} ratio compared to either lower or higher values of α and β (NPFMC 2007). The F_{OFL} and B_{MSY} parameter definitions differ for different stocks depending on data and assessment richness. The estimates of those parameters also vary with different population dynamics and fishery selectivity characteristics of stocks and are determined through Monte Carlo simulations (NPFMC 2007).

Following the groundfish FMP model (NPFMC 1998), a five-tier system was proposed for 10 BSAI crab stocks. Twelve crab stocks formerly part of the old FMP were removed from the new FMP with management deferred to ADFG. Crab stocks fall into different tier levels depending on data and assessment richness. The tiers with CR formulas are listed below in descending order of information availability:

Tier 1:

a. $\dfrac{B}{B_{MSY}} > 1$

$F_{OFL} = \mu = \textit{arithmetic mean of the probability density function of} F_{MSY}$

b. $\beta < \dfrac{B}{B_{MSY}} \le 1 \qquad F_{OFL} = \mu\left(\dfrac{B / B_{MSY} - \alpha}{1 - \alpha}\right) \qquad (1)$

c. $\dfrac{B}{B_{MSY}} \le \beta$ directed fishery $F = 0$ and $F_{OFL} \le \mu$

Tier 2:

a. $\dfrac{B}{B_{MSY}} > 1 \qquad F_{OFL} = F_{MSY}$

b. $\beta < \dfrac{B}{B_{MSY}} \le 1 \qquad F_{OFL} = F_{MSY}\left(\dfrac{B / B_{MSY} - \alpha}{1 - \alpha}\right) \qquad (2)$

c. $\dfrac{B}{B_{MSY}} \le \beta$ directed fishery and $F = 0$ and $F_{OFL} \le F_{MSY}$

Tier 3:

a. $\dfrac{B}{B_{35\%}} > 1 \qquad F_{OFL} = F_{35\%}$

b. $\beta < \frac{B}{B_{35\%}} \leq 1$ $\quad F_{OFL} = F_{35\%}\left(\frac{B/B_{35\%} - \alpha}{1-\alpha}\right)$ (3)

c. $\frac{B}{B_{35\%}} \leq \beta$ $\quad$ directed fishery $F = 0$ and $F_{OFL} = F_{35\%}$

Tier 4:

a. $\frac{B}{meanB} > 1$ $\quad F_{OFL} = \gamma M$

b. $\beta < \frac{B}{meanB} \leq 1$ $\quad F_{OFL} = \gamma M\left(\frac{B/meanB - \alpha}{1-\alpha}\right)$ (4)

c. $\frac{B}{meanB} \leq \beta$ $\quad$ directed fishery $F = 0$ and $F_{OFL} \leq \gamma M$

Tier 5:

$OFL = average\ catch$

where

OFL = overfishing level,

B = a measure of the productive capacity of the stock such as spawning biomass or fertilized egg production. A proxy of B, mature male biomass (MMB) estimated at the time of primiparous female mating (February 15) is used as a default in the development of control rule (CR).

F_{MSY} = full selection instantaneous F that will produce MSY at the MSY producing biomass,

B_{MSY} = the value of biomass yielding MSY, if fished at F_{MSY},

$F_{35\%}$ = fishing mortality that will maintain the spawning biomass-per-recruit at 35% of the virgin spawning biomass-per-recruit level,

$B_{35\%}$ = 35% of the virgin B,

β = a parameter with restriction that $0 \leq \beta < 1$. A default value of 0.25 is used in the simulations,

α = a parameter with restriction that $0 \leq \alpha < 1$. A default value of 0.1 is used in the simulations, and

γ = a scalar value.

Tiers 1 and 2 are for stocks with a reliable estimate of the spawner-recruit (S-R) relationship, thereby enabling the estimation of F_{MSY} and

B_{MSY}. Tier 1 stocks have estimates of the probability density function of F_{MSY} from which a mean F_{MSY} can be estimated as F_{OFL}. Tier 2 stocks have point estimates of F_{MSY} used as the F_{OFL}. Currently, no BSAI crab stocks qualify for either tier 1 or tier 2 of the new FMP. Tier 3 is for stocks where reliable estimates of S-R data are not available, but proxies for F_{MSY} and B_{MSY} can be estimated. Two stocks, Bristol Bay red king crab and eastern Bering Sea snow crab, are assigned to tier 3. The proxies of F_{MSY} and B_{MSY} for these two stocks are determined as $F_{35\%}$ and $B_{35\%}$ respectively using Clark's (1991) method and stochastic simulations (see NPFMC 2007 for details of the Clark's method). Deterministic and stochastic simulations indicated that these MSY proxies maintained the stocks at healthy levels similar to that of MSY reference points under short-term (30-year) and long-term (100-year) fishery scenarios (Siddeek and Zheng 2007, NPFMC 2007). Tier 4 is for stocks where maturity, other essential life-history, and recruitment information are lacking. Therefore, it is not possible to estimate $F_{x\%}$ and $B_{x\%}$. Five stocks fall into tier 4. Required for tier 4 are reliable estimates of current B and M. The proxy for F_{MSY} is estimated as γM, where γ is a scalar allowed to be less than or greater than unity resulting in overfishing limits more or less biologically conservative than at M. Use of γ is intended to allow adjustments in the overfishing definitions to account for differences in biomass measures used in the new FMP. However, since tier 4 stocks are information-poor by definition, the environmental assessment associated with amendment 24 (NPFMC 2007) states that γ should not be set to a value that would provide less biological conservation and more risk-prone overfishing definitions without defendable evidence that the stock could support fishing at levels in excess of M. In the absence of reliable estimate of γ or of evidence that the stock biomass is sustainable at levels of exploitation in excess of M, a default value of unity is recommended. This default γ value assumes $F_{MSY} = M$, which had been used under the old FMP. The proxy for B_{MSY} is determined as the average biomass over a time period in which stock biomass was considered to be in dynamic equilibrium and capable of yielding MSY. Tier 5 is for stocks where essential life history, reliable estimates of B and M are lacking, but historical retained catch data are available. Three crab stocks fall into tier 5. The overfishing level (OFL) is estimated as average retained catch for a specified time period.

Implementation of the new limit control rule

For stocks in tiers 1 to 4, the sloping control rule in which F_{OFL} is scaled to B (Fig. 1) is used for stock status determination. If F exceeds F_{OFL} estimated at B, then overfishing occurs. The F and F_{OFL} are measured by corresponding realized and OFL total catches. If B declines below $\frac{1}{2}B_{MSY}$ (i.e., MSST), the stock is overfished. If B equals or declines below

$\beta \times B_{MSY}$, then the stock productivity is severely depleted and the fishery is closed.

The NPFMC reviews model structures and procedures for determining OFLs and MSSTs in June each year based on the previous year's data. In the fall, after the NMFS summer trawl survey data are incorporated, the Crab Plan Team estimates OFLs and MSSTs for the upcoming fishing season. At that time, the Crab Plan Team also determines if overfishing occurred in the previous year by comparing the OFLs with the total directed and non-directed catch removals of crab biomasses in the previous year, as well as the status of the stock relative to the overfished threshold in the current year. The Crab Plan Team recommends its findings to the NPFMC who in October adopts the OFLs and MSSTs for the upcoming fisheries. If thresholds are breached or approached, then the NPFMC recommends remedial measures in the form of a reduction in F or rebuilding plans (for overfished stocks) to reverse the situation.

New target control rules and their implementation

There is no specific target control rule (CR) prescribed in the new FMP. In this study, we examine $F_{40\%}$ CR as a candidate target CR for purposes of comparison. Currently, ADFG follows the same procedures as followed under the old FMP to set TACs after the NMFS summer trawl survey and before the start of most crab fisheries (15 October). The retained catch TACs are recommended for the fishery after total expected removals, including discard and bycatch losses, have been computed and verified that they do not exceed OFLs.

Environmental considerations in developing old and new control rules

The climate regime shifts that occurred in 1976-77, 1988-89, and 1998-99 in the North Pacific have been investigated in relation to marine fish and shellfish production in the BSAI and Gulf of Alaska (Loher et al. 1998, Hare and Mantua 2000, Benson and Trites 2002, Litzow 2006). The 1976-77 regime shift, characterized by warming sea surface temperatures, altered circulation patterns, and changes in the productivity patterns, appears to have the greatest impact on the marine fish and shellfish community reorganization in the BSAI and Gulf of Alaska (Loher et al. 1998, Hare and Mantua 2000, Litzow 2006). Recruitment of major crab predators, such as Pacific cod (*Gadus macrocephalus*), increased for a few years immediately after this regime shift (Hare and Mantua 2000). Snow crab abundance in their southern range decreased from 1990 to 2002 (Overland and Stabeno 2004). Indeed, population sizes of a number of eastern Bering Sea crab stocks, including Bristol Bay red king crab and eastern Bering Sea snow crab, have fluctuated during the last three decades, attributed to highly variable recruitment as a result of fishery and environmental causes (Zheng and Kruse 2006). There is evidence that the ecosystem of the Bering Sea is shifting in response to a northward retreat of cold waters (Overland and Stabeno 2004).

The old and new FMP drafting teams considered the effect of the 1976-77 regime shift on crab stock abundances when defining biological reference points. The old FMP drafting team considered a 15-year period from 1983 to 1997 as a stable environmental period to determine mean TMB as a proxy of B_{MSY}. The primary reasons given for this assumption were that a number of crab stocks had stabilized by 1983 after decreasing in the late 1970s and early 1980s and the finfish populations that increased sharply immediately after the regime shift had stabilized by 1983 (NPFMC 1999). The new FMP drafting team considered stock assessment parameter estimates from the 1985-2006 time series data as input values in the projection models to investigate CR parameters for the Bristol Bay red king crab (NPFMC 2007). Assuming that it takes approximately eight years for recruits to enter the modeled size range (65-200 mm CL), selection of data from 1985 is appropriate to avoid the effect of the 1976-77 regime shift on recruitment (Zheng 2006). The data series considered for snow crab base parameter estimates for projections started from 1978, and recruitment age to the model in the size range 25-45 mm CW is approximately four to five years (Turnock and Rugolo 2006). The effects, if any, from the 1976-77 regime shift on recruits to the model and model performance should be nominal. If productivity of the stock categorically changed as a result of the regime shift, the recruitment rate from mature biomass in 1973-1975 might differ relative to that from post-1976 mature biomass. Recruitments estimated in the model are averaged over 1978-2006 to estimate the $B_{x\%}$ proxy for B_{MSY}. Therefore, the majority of years in this average would be unaffected by potentially varying rates of recruitment.

Rebuilding

According to the implementation guidelines for National Standard 1, the maximum allowable time to rebuild an overfished stock to the B_{MSY} level is 10 years, unless rebuilding in this time frame cannot be achieved without directed fishing. In such cases, the maximum allowable time to rebuild would be given by the expected time to rebuild under $F = 0$, plus one mean generation time (Restrepo and Powers 1999).

The old FMP CR does not directly provide a means to rebuild an overfished stock. In comparison, the new FMP sloping control rule has built-in rebuilding features since, as the stock biomass declines, the F_{OFL} is adjusted accordingly (NPFMC 2007). Indeed, the rebuilding plan implemented for the overfished snow crab stock uses a sloping F_{OFL} CR not found in the old FMP CR definition (NPFMC 2000), but consistent with the new CR.

Illustration

Performance of old and new management control rules

Bristol Bay red king and eastern Bering Sea snow crabs are considered here for comparing the performance of the two control rules (CRs). A standard set of base parameter values (described below) are used in the simulations of a hypothetical overfished (50% B_{MSY}) stock for comparing performance measures for the CRs for the two stocks.

The simulations are initiated with a fixed number of immature new-shell recruits to the modeled population, divided equally between males and females, and distributed between length bins by a probability function. Full age structure is established by deterministically projecting the initial recruits through their entire life span up to a maximum age with a set of mortality and growth parameters. The deterministic projection process is continued for some years as a burn-in period and then extended stochastically with recruits generated by a stochastic S-R model with lognormal random errors (variance and autocorrelation estimated from S-R data) for a short-term (30 year) or a long-term (100 year) fishing period for estimating various performance statistics. The performance measures considered are: number of recruits, total and retained yields, mature male and female biomasses, rebuilding time, percent of time overfished and fishery closed, and percent of final year B relative to B_{MSY}.

The base parameters (molt probability; size transition matrix; maturity probability; size-specific fishing, handling, and trawl bycatch mortality; time series of spawner-recruit abundances; and recruit distribution) for the projection models are estimated from stock assessment results based on historical fisheries and survey data, 1985-2006 for red king crab (Zheng 2006, NPFMC 2007) and 1978-2006 for snow crab (Turnock and Rugolo 2006). The projection models assume

a. constant M values of 0.18 for red king crab and 0.23 for male and 0.29 for female snow crab,

b. terminal molt at maturity for both sexes of snow crab,

c. 80% discarded crab handling mortality in the non-directed (e.g., trawl and scallop) fisheries,

d. directed pot fishery discarded crab handling mortalities of 20% for red king crab and 50% for snow crab,

e. the Ricker S-R model with a steepness parameter (h) value of 1.67, a maximum R value of 29 million crabs, an overall recruitment variation (σ^2) of 1.64, and an autocorrelation (ρ) of 0 for red king crab, and

f. the Beverton-Holt S-R model with an h value of 0.68, a maximum R value of 2 billion crabs, a σ^2 value of 0.74, and a ρ value of 0.6 for snow crab.

The conceptual formulation of the length-based projection models are described in NPFMC (2007) for both stocks and in Siddeek and Zheng (2007) for the red king crab stock.

Under the old FMP, the two crab stocks considered in this study belong to tier 3 irrespective of the biomass levels. However, under the new FMP, once tier levels are selected, the stocks are assigned to a, b, or c levels in the selected tiers based on the relation of current mature male biomass (MMB) levels to B_{MSY} or proxy B_{MSY} benchmarks specified for each stock. The 2006 MMB estimates resulted in the assignment of red king and snow crab stocks to tier 3b. In tier 3b, the F_{OFL} for red king and snow crab stocks are determined by the CR equation (3) in which the proxy for F_{MSY} is $F_{35\%}$.

The CRs under the old and new management plans provided different status determination criteria (overfished and overfishing reference points), which, in turn, could have led to different conclusions regarding stock status for a given year's stock assessment. For example, the 2006 total mature biomass (TMB) for red king crab exceeds the TMB_{MSY} level under old CR, but the 2006 MMB is below the MMB_{MSY} level under new CR. While both biomass metrics were above their respective overfished thresholds, overfishing limits and management controls resulting from the old and new CRs differ. The 2006-07 total allowable catches (TAC) in terms of retained catches are well below the 2006 sustainable yields (overfishing limits) for the two stocks under the old CR, but the snow

Table 1. Comparison of the application of the old and new control rules using 2006 data for Bristol Bay red king and eastern Bering Sea snow crab stocks.

Reference points and catches	Bristol Bay red king crab (t)		Eastern Bering Sea snow crab (t)	
	Old FMP	New FMP	Old FMP	New FMP
B_{MSY}	40,642	35,311	418,035	160,900
MSST	20,321	17,656	209,017	80,450
B_{2006}	71,305	29,728	248,390	95,709
F_{OFL}	0.2	0.297	0.3	0.511
Total catch OFL_{2006}	14,261	8,065	74,517	13,599
Realized total catch $OFL_{2006\text{-}07}$	7,810	7,810	19,101	19,101
$TAC_{2006\text{-}07}$	7,031	7,031	16,602	16,602
Realized retained catch $TAC_{2006\text{-}07}$	7,143	7,143	16,493	16,493

The old control rule overfishing level (OFL) catches are determined from 2006 total mature abundances at the time of the survey, whereas the new control rule OFL catches are estimated from 2006 legal male abundances at the time of the fishery.

Old FMP is the 1999 amendment to the crab Fishery Management Plan.

New FMP is the 2007 amendment to the crab Fishery Management Plan.

MSST is minimum spawning stock threshold.

Table 2. Short-term rebuilding simulations under the old and new control rules for Bristol Bay red king and eastern Bering Sea snow crabs.

	Bristol Bay red king crab				Eastern Bering Sea snow crab			
	Limit FMSY CR (tier 2)	Old target CR (tier 2)	New limit F35% CR (tier 3)	New F40% CR (tier 3)	Limit FMSY CR (tier 2)	Old target CR (tier 2)	New limit F35% CR (tier 3)	New F40% CR (tier 3)
Mean recruit number	24.6	1.00	1.01	1.02	1,433.4	0.98	0.98	1.02
Mean total yield	8,500	0.91	0.97	0.88	52,768.5	1.00	1.02	0.97
Mean retained yield	7,237	0.90	0.97	0.88	43,181.9	1.00	1.01	0.97
Mean mature male biomass	31,317	1.04	1.06	1.15	179,733.5	0.95	0.93	1.08
Mean mature female biomass	38,316	0.99	1.01	1.02	121,670.6	0.98	0.98	1.02
Rebuilding time[a]	11	1.0	0.91	0.91	13	1.15	1.15	0.92
Overfished[b]	18.4	1.04	0.84	0.67	2.41	2.69	2.05	0.63
Fishery closure[c]	1.0	1.4	0.80	0.70	0	0.14	0	0
30th year biomass ratio[d]	108	1.14	1.06	1.18	109	0.97	0.92	1.1

[a] Median number of years taken for mature male biomass to reach maximum sustainable yield (MSY) mature male biomass for the first time.

[b] Mean percent of years in a 30 year fishery the mature male biomass <50% MSY mature male biomass.

[c] Mean percent of years in a 30 year fishery the mature male biomass <25% MSY mature male biomass.

[d] Mean percent of 30th year mature male biomass relative to MSY mature male biomass.

The mean and median are estimated from 1,000 simulations of a 30-year fishery with an initial mature male biomass of 50%BMSY with stochastic stock-recruitment curves (Ricker for red king crab and Beverton-Holt for snow crab), biomass observation error, and harvest implementation error. All estimates are given as proportions relative to respective limit FMSY CR (tier 2) values in columns 2 and 6. F40% values are treated as the new target CR for comparison purpose only even though they are not implemented as the new target CR. In columns 2 and 6, the number of recruits is expressed in millions of crabs, and yields and biomasses are expressed in t.

crab TAC is above the total catch overfishing level (OFL) determined at tier 3(b) under the new CR (Table 1). The old and new CRs were not simultaneously in effect and, under each plan, the overfishing and overfished status determination were made by comparing total catch removals and stock biomass to their respective reference points.

Short-term (30-year) rebuilding simulations of overfished stocks, in which initial biomass is arbitrarily set to the overfished level of 0.5 MMB_{MSY}, indicate similar performance by the old target CR (i.e., ADFG harvest strategy) and the new limit CR ($F_{35\%}$) on mean number of recruits, yields, and biomasses (Table 2). However, the median rebuilding time, overfished percent, and fishery closure percent are lower under the $F_{35\%}$ CR than the ADFG harvest strategy for both stocks. The $F_{40\%}$ CR (lower fishing mortality than $F_{35\%}$) under the new FMP performed better than all other control rules with the exception of lower realized yields (Table 2). The F_{MSY} CR (tier 2) uses F_{MSY} as the overfishing limit fishing mortality (F_{OFL}) in the CR formula (equation 2). The F_{MSY} is determined using a Ricker stock-recruitment (S-R) model for the Bristol Bay red king crab and a Beverton-Holt S-R model for the eastern Bering Sea snow crab. However, the S-R model fits on the historical stock recruitment data are not convincing and hence the F_{MSY} estimates are approximates and used only for comparing the performance of tier 3 CRs for the two stocks with the hypothetical F_{MSY} CR (NPFMC 2007).

A short-term (six-year) projection of 2006 abundance of Bristol Bay red king crab stock indicates an increasing trend in total catch and similar fluctuations in MMB over the years under the $F_{40\%}$ CR compared to that of the old target CR with and without the $F_{35\%}$ constraint (Table 3). The six-year projection of 2007 abundance for eastern Bering Sea snow crab indicates a decline in total catch, but an increase in MMB over the years under the $F_{40\%}$ CR compared to that of the old target CR with and without the $F_{35\%}$ constraint. The $F_{35\%}$ constraint on the ADFG harvest strategy slightly improved the total catches and MMB over the unconstrained harvest strategy for both stocks (Table 3). If the ADFG harvest strategy is the choice in the absence of explicit guidance for a target CR in the new FMP, then the $F_{35\%}$ constraint on the ADFG harvest strategy seems a good option for setting TACs for both stocks given that it results in improved stock status (e.g., MMB) and yield to the fisheries relative to the unconstrained ADFG strategy. New CRs consider only the relationship between F and MMB. On the other hand, ADFG harvest strategy considers not only mature and legal male abundances but also mature female abundance (for red king crab) and new- and old-shell crab composition (for snow crab) to set the harvest strategy. Hence combining the two would be a good strategy to manage the stocks.

Table 3. Short-term projections of total catch and mature male biomass (MMB) on 15 February, 2007-2012, using the old target control rule (CR) (ADFG harvest strategy), the old target CR constrained by the new limit ($F_{35\%}$) CR, the new limit CR, and the new $F_{40\%}$ CR for Bristol Bay red king and eastern Bering Sea snow crabs.

	Bristol Bay red king crab				Eastern Bering Sea snow crab			
	Old target CR (tier 2)		Old target CR (tier 2) constrained by the new limit $F_{35\%}$ CR (tier 3)		Old target CR (tier 2)		Old target CR (tier 2) constrained by the new limit $F_{35\%}$ CR (tier 3)	
Year	Total Catch	15 Feb MMB	Total catch	15 Feb MMB	Total catch	15 Feb MMB	Total catch	15 Feb MMB
2006	8.76	33.62	8.76	33.62				
2007	10.10	37.90	10.02	37.94	22.3	95.7	22.3	95.7
2008	13.09	48.50	12.13	49.39	34.7	120.3	32.9	121.6
2009	14.35	57.46	13.98	58.60	43.7	144.4	44.3	145.6
2010	13.61	60.41	13.56	61.49	42.2	141.9	42.3	142.6
2011	11.63	54.04	11.75	54.86	33.7	134.0	33.5	134.8
2012	11.44	57.07	11.56	57.71	40.1	135.7	39.2	137.1
	New limit $F_{35\%}$ CR (tier 3)		New $F_{40\%}$ CR (tier 3)		New limit $F_{35\%}$ CR (tier 3)		New $F_{40\%}$ CR (tier 3)	
2006	8.76	33.62	8.76	33.62				
2007	10.20	37.82	8.42	39.33	22.3	95.7	22.3	95.7
2008	11.97	49.40	10.22	52.35	34.8	120.2	26.2	126.4
2009	14.77	57.90	12.85	62.34	53.3	136.8	45.1	150.8
2010	16.83	57.87	14.89	63.65	41.8	133.8	38.0	150.9
2011	15.71	48.04	14.25	54.41	32.6	128.2	30.2	144.8
2012	15.26	47.99	14.16	54.83	38.4	132.4	34.8	149.2

$F_{40\%}$ values are treated as the new target CR for comparison purpose only even though they are not implemented as the new target CR. The catch and population numbers in 2006 for red king crab and in 2007 for snow crab are used for projections. All estimates are mean values from 1,000 simulations under the stochastic stock-recruitment curves (Ricker for red king and Beverton-Holt for snow crabs). Catch and biomass values are expressed in 1,000 t.

Discussion and conclusion

The principal differences between the old and new management control rules are (1) the definition of control rule (CR), the former considers a constant F_{OFL} whereas the latter prescribes a sliding scale (in relation to B) CR; (2) biomass currency unit, the former considers total mature biomass (TMB) whereas the latter considers mature male biomass (MMB) as the spawning biomass unit; and (3) the definition of overfishing level (OFL), the former considers retained catch whereas the latter considers total removal, whenever data are available, which is the sum of directed fishery retained catch and discard losses, and non-directed fishery discard losses.

The constant F_{OFL} strategy does not consider rebuilding of a stock when the biomass is low, but the sliding CR strategy does. Management of the overfished snow crab stock under the Alaska Department of Fish and Game (ADFG) rebuilding harvest strategy since 1999, with a sliding CR, provides support for this type of formulation in the new CRs as the stock rose above minimum spawning stock threshold (MSST) although did not exceed B_{MSY} at the end of 10-year rebuilding period (Turnock and Rugolo 2009). Because the current CR parameters were determined under prevailing stock productivity, an improvement in stock productivity might provide desired or better than desired results. If a climate regime shift similar to 1976-77 would occur in the near future and if productivity categorically altered, then the CR parameters would need to be re-evaluated under those conditions. The management control rule and tier system implemented for Bering Sea and Aleutian Islands (BSAI) crab stocks by the new FMP amendments is similar to the North Pacific Fishery Management Council's groundfish tier system (NPFMC 1998). In the groundfish system, the F_{ABC} (ABC is acceptable biological catch) is the maximum target F to ensure a buffer between F_{OFL} and the target F. For crab, the FMP defers the specification of the allowable harvest level to the State of Alaska with federal oversight. The annual total allowable catch (TAC) can be set at levels equal to or below the OFL. The provisions of the new National Standard 1 will require the NPFMC to determine the buffer between the TAC and OFL considering management and scientific uncertainty to insure overfishing does not occur.

Mating ratio based on laboratory studies has been used to modify female spawning biomass as a proxy for egg production (Zheng 2006). However, mating ratios in the natural environment are unknown and females of the *Chionoecetes* species may mate with more than one male in the same season, which contravenes the mating ratio calculation (NPFMC 2007). Thus MMB at the time of mating is used as a proxy for egg production instead of effective spawning biomass (ESB).

The new CR appears to be more conservative than the old CR in managing the crab fisheries largely due to the fact that biological reference points are based on male abundance only, which is directly affected by the male-only fishery, and total removal of crabs from the population is accounted for in the yield optimization process. On the other hand, the old CR considers the total abundance comprising mature males and mature females to determine overfishing limits and biomass reference points. Under the old OFL definition, since the sustainable yield threshold includes non-retained stock biomass components, it is possible to remove almost all adult male crabs from the population without reaching OFL. However, existing ADFG harvest strategies do not provide an opportunity to reach that condition and the overfishing definitions in the new FMP completely remove that possibility.

The default parameter values, $\alpha = 0.1$, $\beta = 0.25$, $\gamma = 1$, $F_{x\%} = F_{35\%}$, and the spawning stock biomass index of MMB, are currently used in the new CRs with the understanding that the NPFMC may recommend different values for a specific stock or stock complex as merited by the best available scientific information. The above default parameter values were estimated using data from Bristol Bay red king and eastern Bering Sea snow crabs. If the productivities of any king or Tanner crab stocks differ substantially from these representative stocks, then the new FMP allows for changing the default values for the stocks.

It is to be noted that bycatch limits are established in BSAI groundfish fisheries and the statewide scallop fishery for red king, Tanner, and snow crabs. If bycatch limits are exceeded, specified area closures are triggered for the offending fishery. With the implementation of the more precautionary management approach via the new CR, crab stock biomass is expected to increase and equilibrate around B_{MSY} as a result of enhanced reproductive output. Under this management strategy, the annual overfishing limit is a total catch OFL that includes all stock losses from directed and non-directed fisheries. To the extent that bycatch losses represent deferred economic value to the fisheries or comprise potentially significant losses in terms of the overfishing definitions, bycatch limits need to be re-evaluated, which has not been explicitly specified in the new FMP.

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References

Benson, A.J., and A.W. Trites. 2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. Fish Fish. 3:95-113. doi:10.1046/j.1467-2979.2002.00078.x

Clark, W.G. 1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish. Aquat. Sci. 48:734-750. doi:10.1139/f91-088

Hare, S.R., and N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. 47(2-4):103-146. doi:10.1016/S0079-6611(00)00033-1

Hoenig, J.M. 1983. Empirical use of longevity to estimate mortality rates. Fish. Bull. U.S. 81:898-903.

Litzow, M.A. 2006. Climate regime shifts and community reorganization in the Gulf of Alaska: How do recent shifts compare with 1976/77? ICES J. Mar. Sci. 63:1386-1396. doi:10.1016/j.icesjms.2006.06.003

Loher, T., P.S. Hill, G. Harrington, and E. Cassano. 1998. Management of Bristol Bay red king crab: A critical intersections approach to fisheries management. Rev. Fish. Sci. 6(3):169-251. doi:10.1080/10641269891314285

NPFMC. 1998. Amendment 56 to the Fishery Management Plan for the groundfish fishery of the Bering Sea and Aleutian Islands area and Amendment 56 to the Fishery Management Plan for the groundfish fishery of the Gulf of Alaska to redefine acceptable biological catch and overfishing. North Pacific Fishery Management Council, 605 West 4th Ave, Anchorage, AK 99501. 24 pp.

NPFMC. 1999. Amendment 7 to the Fishery Management Plan for the commercial king and Tanner crab fisheries in the Bering Sea/Aleutian Islands to 1. Revise definitions of overfishing, MSY, and OY. 2. Update the BSAI crab FMP. North Pacific Fishery Management Council, 605 West 4th Ave, Anchorage, AK 99501. 48 pp.

NPFMC. 2000. Amendment 14 to the Fishery Management Plan for the king and Tanner crab fisheries in the Bering Sea/Aleutian Islands and a regulatory amendment to the Fishery Management Plan for the groundfish fishery of the Bering Sea and Aleutian Islands area. A rebuilding plan for the Bering Sea *C. opilio* stock. North Pacific Fishery Management Council, 605 West 4th Ave, Anchorage, AK 99501. 145 pp.

NPFMC. 2007. Amendment 24 to the Fishery Management Plan for Bering Sea and Aleutian Islands king and Tanner crabs to revise overfishing definitions. North Pacific Fishery Management Council, 605 West 4th Ave, Anchorage, AK 99501. 191 pp.

Overland, J.E., and P.J. Stabeno. 2004. Is the climate of the Bering Sea warming and affecting the ecosystem? Eos 85(33):309-312. doi:10.1029/2004EO330001

Restrepo, V.R., and J.E. Powers. 1999. Precautionary control rules in US fisheries management: Specification and performance. ICES J. Mar. Sci. 56:846-852. doi:10.1006/jmsc.1999.0546

Siddeek, M.S.M. 2002, Review of biological reference points used in Bering Sea and Aleutian Islands (king and Tanner) crab management. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report No. 5J02-06, Juneau, Alaska. 94 pp.

Siddeek, M.S.M., and J. Zheng. 2007. Evaluating the parameters of a MSY control rule for the Bristol Bay, Alaska, stock of red king crabs. ICES J. Mar. Sci. 64:995-1005. doi:10.1093/icesjms/fsm069

Turnock, B., and L.J. Rugolo. 2006. Stock assessment of eastern Bering Sea snow crab. In: BSAI Crab Plan Team (compilers), Stock assessment and fishery evaluation report for the Bering Sea and Aleutian Islands king and Tanner crab fisheries. North Pacific Fishery Management Council, 605 West 4th Ave, Anchorage, AK 99501. Appendix A, pp. 1-73.

Turnock, B., and L.J. Rugolo. 2009. Stock assessment of eastern Bering Sea snow crab. In: BSAI Crab Plan Team (compilers), Stock assessment and fishery evaluation report for the Bering Sea and Aleutian Islands king and Tanner crab fisheries. North Pacific Fishery Management Council, 605 West 4th Ave, Anchorage, AK 99501, pp. 29-130.

Zheng, J. 2006. Bristol Bay red king crab stock assessment in 2006. In: BSAI Crab Plan Team (compilers), Stock assessment and fishery evaluation report for the Bering Sea and Aleutian Islands king and Tanner crab Fisheries. North Pacific Fishery Management Council, 605 West 4th Ave, Anchorage, AK 99501. Appendix B, pp. 1-68.

Zheng, J., and G.H. Kruse. 2006. Recruitment variation of eastern Bering Sea crabs: Climate-forcing or top-down effects? Prog. Oceanogr. 68:184-204.

Zheng, J., M.C. Murphy, and G.H. Kruse. 1995. A length-based population model and stock-recruitment relationships for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. Can. J. Fish. Aquat. Sci. 52:1229-1246. doi:10.1139/f95-120

Zheng, J., S. Siddeek, D. Pengilly, and D. Woodby. 2002. Overview of recommended harvest strategy for snow crabs in the eastern Bering Sea. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 5J02-03, Juneau, Alaska. 28 pp.

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