

RESILIENCY OF GADID STOCKS TO FISHING AND CLIMATE CHANGE

24TH LOWELL WAKEFIELD FISHERIES SYMPOSIUM

EDITORS

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Symposium Dedication to Albert V. Tyler

This 24th Lowell Wakefield Fisheries Symposium on *Resiliency of Gadid Stocks to Fishing and Climate Change* is dedicated to the memory of Albert V. Tyler, who passed away unexpectedly in his sleep in September 2005. He had been enjoying his retirement on Salt Spring Island, British Columbia, with his wife, Nancy, since 2002.

After receiving his Ph.D. from the University of Toronto under F.E.J. Fry, Al's career extended from St. Andrew's Biological Station in New Brunswick, Canada, to Oregon State University in Newport and Corvallis, the Pacific Biological Station in Nanaimo, British Columbia, and the University of Alaska Fairbanks. His career focused primarily on groundfish, particularly Pacific cod and flatfishes, but also included Alaska crab species. His work on Pacific cod research addressed various aspects of reproductive biology, recruitment, stock dynamics, fishery oceanography, and interactions between cod and other species. While a member of the Scientific and Statistical Committee of the North Pacific Fishery Management Council, Al always took special interest in reviewing and commenting on the annual assessments for Pacific cod in the Gulf of Alaska and Bering Sea and Aleutian Islands regions. His insights, creative thinking, and research are well cited and highly relevant to current fisheries investigations.

Al was admired for his mentorship of graduate and undergraduate students. He received much joy from teaching and it showed. He always had time for thoughtful discussions, constructive critiques, and sound advice concerning student learning in the classroom, as well as graduate thesis research. While teaching popular and innovative fisheries courses, Al took a personal interest in the progress of all of his students. Certainly, I owe my fisheries career to the guidance and support of Al Tyler.

Throughout his successful career, "Big Al" maintained a balance between work, family, and personal pursuits. He was an excellent chef, specializing in Indian curries, an amateur painter, musician, and an all-around enjoyer of life.

It is fitting to dedicate this symposium and its proceedings to the career of Al Tyler. Al was a real champion of the Lowell Wakefield Symposium series. The goal of this symposium was to bring together scientists and managers from the Atlantic and Pacific oceans to synthesize the knowledge on the resiliency of gadid stocks to fishing and climate change. Al would have been right at home at this meeting, reveling in new scientific findings, stimulating discussions, and social camaraderie. Indeed, he was at home at this meeting in our hearts.

Gordon H. Kruse
President's Professor of Fisheries
University of Alaska Fairbanks

About the Proceedings Book and the Symposium

This proceedings includes eighteen peer-reviewed research and review papers on gadids that were presented at the symposium *Resiliency of Gadid Stocks to Fishing and Climate Change*, held October 31–November 3, 2006, in Anchorage, Alaska. The family Gadidae (and gadid-like fish) includes about 30 species, nearly all marine. This group includes the cods, haddocks, pollocks, lings, whittings, and hakes that inhabit cold-water seas of the North Atlantic, North Pacific, and Arctic oceans.

The symposium was motivated by the high commercial importance of gadids, the long and colorful history of research and management of this group of fishes, and the remarkable disparities in their stock and fishery dynamics exhibited in different regions of the world. The intent was to develop a better understanding of the underlying causative mechanisms, by drawing contrasts between gadid stocks and fishery dynamics from different marine ecosystems. For instance, a large biomass of pollock sustains the world's largest commercial fishery in the Bering Sea, and a Pacific hake stock supports a large fishery off the U.S. West Coast, both of which appear to remain healthy after decades of exploitation. In contrast, many cod stocks in both the northeast and northwest Atlantic Ocean experienced dramatic fishery collapses in the 1980s and 1990s, causing severe economic dislocation. Some of these fisheries have remained closed following stock collapse with no signs of stock recovery, whereas others have rebounded. Why do such differences exist?

Papers in this proceedings focus on gadid population and fishery dynamics and explore potential biological, ecological, and environmental mechanisms underlying these changes. Several key conclusions emerged from the symposium. First, conservative fishing restrictions help. For example, participants agreed that conservative catch limits and excellent catch monitoring programs are largely responsible for the generally healthy status of gadid stocks in the northeast Pacific Ocean. On the other hand, in the northeast and northwest Atlantic there are many clear cases of overfishing where the continuing inability to effectively control fishing mortality remains a major resource conservation issue to this day. In some of these areas, catch limits are consistently set above scientific advice and realized catches are higher still. Instances of illegal and unreported catches exacerbate these problems. Second, evidence has emerged that selective fishing practices are associated with shifts in biological attributes, such as growth and maturity schedules, which, in turn, affect stock productivity and the ability to recover, even if fishing mortality is later reduced to conservative levels. That is, the inherent ability of the stock to recover to previous levels has been compromised. Third, gadids are themselves members of dynamic

marine ecosystems, which are driven by complex changes in climate and oceanography, as well as changes in the abundance, distribution, and ecological relationships among species at all trophic levels. Periodic large climate regime shifts have major impacts on the productivity and ecosystem function of component species, including gadids. Even after many decades of research, it is clear that much more remains to be understood about gadids and their marine ecosystems. The convenors of this symposium believe that papers in the proceedings make a significant contribution toward this needed progress.

The symposium was coordinated by Sherri Pristash, University of Alaska Fairbanks, Alaska Sea Grant College Program, Fairbanks, Alaska. Organizing committee members are Gordon H. Kruse (chair), University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Juneau, Alaska; Ken Drinkwater, Institute of Marine Research, Bergen, Norway; Jim Ianelli, NOAA Fisheries, Alaska Fisheries Science Center, Seattle, Washington; George Lilly, Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, Newfoundland, Canada; Jason Link, NOAA Fisheries, Northeast Fisheries Science Center, Woods Hole, Massachusetts; Mikhail Stepanenko, Pacific Fisheries Research Center (TINRO-Center), Vladivostok, Russia; Diana Stram, North Pacific Fishery Management Council, Anchorage, Alaska; Vidar Wespestad, Resource Analysts International, Lynnwood, Washington; and Doug Woodby, Alaska Department of Fish and Game, Division of Commercial Fisheries, Juneau, Alaska.

Symposium sponsors were Alaska Sea Grant College Program; Alaska Department of Fish and Game; NOAA Fisheries; NOAA Research; North Pacific Fishery Management Council; and Wakefield Endowment, University of Alaska Foundation.

Proceedings Acknowledgments

This publication presents sixteen symposium papers. Each paper was reviewed by two peers, and was revised according to recommendations by associate editors who generously donated their time and expertise: Gordon Kruse, Ken Drinkwater, James Ianelli, Jason Link, Diana Stram, Vidar Wespestad, and Douglas Woodby.

Many thanks to the following people who reviewed one or more manuscripts for this book: Kerim Aydin, Keith Brander, Jon Brodziak, Steve Cadrin, Dave Carlile, Dan Cooper, Martin Dorn, Hilaire Drouineau, Tim Essington, Susan Fudge, Kurt Gamperl, Sylvie Guenette, Owen Hamel, Ray Hilborn, Nicola Hillgruber, Anne Hollowed, Laurie Kell, James Kieffer, Dan Kimura, Neil Klaer, George Lilly, Brian MacKenzie, Steve Martell, Erlend Moksness, Franz Mueter, Janet Nye, Steve Ralston, Hajo Rätz, George Rose, David Sampson, Paul Spencer, Jennifer Stahl, Rick Stanley, Michelle Staudinger, Dick Thorne, Mark Willette, Chris Wilson, and David Witherell.

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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.

Classification of Ovarian Stages of Walleye Pollock (*Theragra chalcogramma*)

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Abstract

Walleye pollock, *Theragra chalcogramma*, is the most commercially important species in the eastern Bering Sea. Estimates of maturity are critical for setting an appropriate harvest rate for pollock spawning biomass, and correct classification of ovaries into a maturity condition is necessary for accurate estimation of maturity. Data on length, weight, and ovary weight and condition were collected from 4,996 pollock in 2002 and 5,201 in 2003 aboard pollock trawlers across the eastern Bering Sea. In 2003, 173 pollock ovaries were collected and prepared for histological analysis. Maturity condition was assessed by macroscopic inspection of gonads, a gonado-somatic index (GSI), and histological methods. Macroscopic inspection was based on alterations in ovary size and appearance, whereas histological methods evaluated changes in oocyte stages. The GSI was calculated as the proportion of ovary to body weight. The GSI was a good indicator of pollock that had spawned or were about to spawn. Histological analysis confirmed the overall general appropriateness of macroscopic staging for mature versus immature fish, but it also indicated relatively high misclassification rates for particular maturity stages when using macroscopic staging methods alone. Among ovaries macroscopically classified as developing, 16% were at immature oocyte stages and 84% were at primary yolk to more advanced oocyte stages. This indicates that pollock classified macroscopically as “developing” may mature in either the current or subsequent spawning season. Macroscopic inspection and

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GSI in combination may be useful to determine maturity condition for some maturity stages; however, histological examination of ovaries is the most accurate method for all stages.

Introduction

Correct classification of ovaries into developmental stages is necessary to determine maturity status, a prerequisite for setting annual catch quotas using a harvest rate strategy based on spawning biomass estimates. Maturity condition during the spawning period may be identified by macroscopic inspection of gonads, a gonado-somatic index (GSI), histological methods, and/or oocyte (egg) size. Macroscopic inspection is based on alterations in ovary size and appearance, whereas histological methods evaluate changes in oocyte stages at the cellular level. The GSI is calculated as the proportion of ovary to body weight (Gunderson and Dygert 1988); female ovary and body weight increase in advance of spawning due to absorption of ambient water (Sakurai 1989). However, some loss in ovary weight occurs as each batch of eggs is spawned (Teshima et al. 1989).

Classification of pollock ovaries is confounded, because oocytes are found at several different developmental stages within an individual ovary. By convention, the most advanced stage is used for classification (Hinckley 1987). The proportions of oocytes at each stage do not vary with location in the ovary (Teshima et al. 1989), but the proportions of oocytes at particular stages change with the progression of the reproductive cycle (Hinckley 1987).

In the recovery or transitional state of the reproductive cycle, oocytes are found only in a yolckless condition (Sakurai 1989). However, throughout the reproductive cycle, a reserve of yolckless oocytes exists in early and late peri-nucleus stages, called the "reserve fund" (Hinckley 1987). A group of oocytes advance asynchronously from the "reserves" and begin yolk formation (vitellogenesis). Once the entire group has reached the tertiary yolk stage, vitellogenesis is complete, and no more "reserves" will be recruited for development in the approaching spawning season (Hinckley 1987). At this stage the fully yolcked oocytes and "reserves" are separated by a bimodal size distribution (Sakurai 1989). Batches of fully yolcked oocytes further develop synchronously into mature hydrated oocytes, first undergoing yolk coalescence and then hydration (Sakurai 1989). Oocytes become enlarged and transparent with the uptake of water during hydration causing the size and weight of the ovary to greatly expand. Oocytes are then discharged from their follicles and become ova during ovulation (Bowden et al. 1990). Finally, the batch of oocytes is spawned. Subsequently, additional groups of ova may undergo this process in the same spawning season, a repetitive process called batch spawning (Hinckley 1987). Atresia, or the

resorption of oocytes, may occur at low frequencies to remove residual oocytes that are abnormal or damaged or to adjust the number eggs spawned in a batch (Bromley et al. 2000). In Atlantic cod (*Gadus morhua*) high frequencies of atresia may result from poor nutrition associated with prey type and cessation of feeding (Rideout and Rose 2006) or water temperatures too cold for gamete development (Rideout et al. 2000). Mass atresia has also been attributed to low water temperature for Greenland halibut (*Reinhardtius hippoglossoides*; Federov 1971) and haddock (*Melanogrammus aeglefinus*; Hodder 1965).

Spent ovaries are identified by the combined presence of postovulatory follicles and oocytes in only early and late peri-nucleus stages (Hinckley 1987). Follicles are composed of an inner layer of cube-shaped granulosa cells and an outer layer of elongate thecal cells containing blood capillaries. The follicle surrounds the oocyte and serves to transport nutrients, wastes, and yolk proteins between the oocyte and the maternal bloodstream. After ovulation, the postovulatory follicle may appear as a convoluted structure (Hunter and Macewicz 1985).

Our objectives were to (1) confirm the appropriateness of macroscopic staging of ovaries with histological examination, (2) produce an accurate and understandable descriptive guide for future macroscopically staging of ovaries based on histology, and (3) investigate the usefulness of GSI for predicting maturity condition for walleye pollock in the eastern Bering Sea. Successful completion of these objectives allows subsequent evaluation of current estimation methods for pollock spawning biomass from which annual catch quotas are set for the eastern Bering Sea.

Methods

Maturity stage samples

Maturity data were collected by Pollock Conservation Cooperative (PCC) member vessels during the "A" roe season of 2002 and 2003 from late January to early April over the full geographic area fished by the participating PCC fishing vessels (Fig. 1). Vessels were highly concentrated north of Unimak Island and followed the 100 m depth contour beyond the Pribilof Islands. Ten female pollock from one haul per day per vessel were sampled from a range of lengths, and if possible, no more than 10 fish were taken from one 10 cm length category per week. This procedure assures an adequate size range of fish for estimation of maturity schedules. Each female fish was sampled for fork length, body weight, ovary weight, and maturity stage, based on macroscopic visual observation with criteria from NMFS five-stage scale (Table 1).

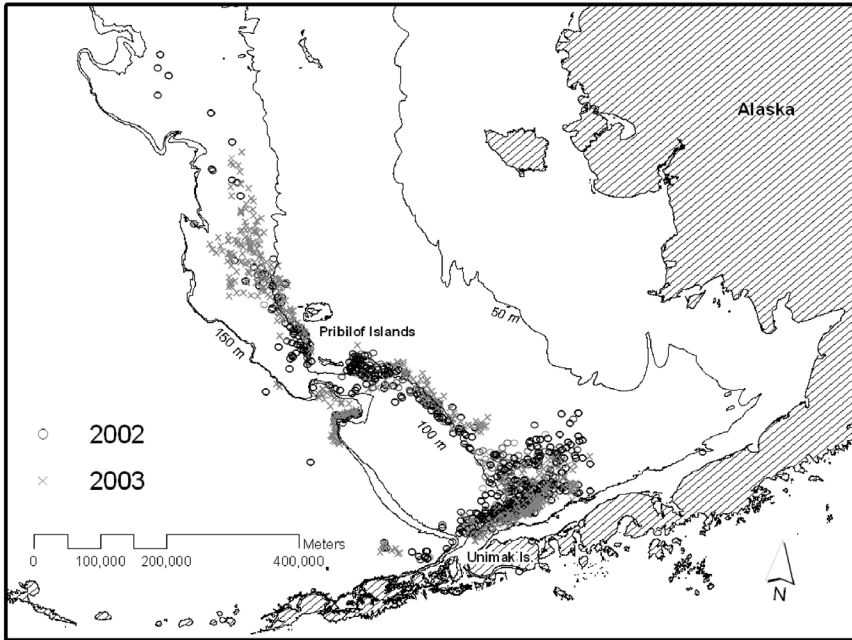


Figure 1. Distribution of Pollock Conservation Cooperative member pollock trawling vessels in 2002 and 2003 “A” fishing season (January 20-March 30 in 2002 and January 21-April 2 in 2003). Each symbol (X or O) represents a location where one or more net hauls occurred and pollock maturity data were collected.

Ovary tissue samples

We collected ovaries and maturity data from 173 female pollock aboard the 115 m midwater trawler *F/V Alaska Ocean* during normal fishing operations during February 22-28, 2003. Ovaries were sampled at all available developmental stages, with an emphasis on small, less-developed ovaries to reconcile uncertainty of macroscopic classification at early developmental stages. Because the proportion of hydrated oocytes increases toward the center of the ovary (Teshima et al. 1989), tissue was cut from one location at the midsection of each ovary (Bowden et al. 1990) to obtain the most advanced oocyte stage present. Tissues were placed in slotted microcassettes of approximate size 2.5 cm × 3.8 cm and stored in a solution of 1 part formalin and 9 parts water buffered with 20 g per L sodium acetate. In addition, fork length (nearest cm), ovary weight (nearest g), body weight (g) without stomach contents but

Table 1. Pollock maturity condition based on macroscopic examination. A five-stage scale was used by Pollock Conservation Cooperative member vessels to macroscopically stage female pollock ovaries; criteria were based on NMFS five-stage scale.

| Maturity code | Condition | Macroscopic examination |
|---------------|--------------|---|
| 1 | Immature | Ovary transparent with no eggs visible. Gonad small and tucked inside body cavity. |
| 2 | Developing | Ovaries translucent to opaque, and about half the length of body cavity. Spawn within following year. |
| 3 | Pre-spawning | Ovaries orange, reddish, and occupy about 2/3 of body cavity. Eggs are discernible and opaque. |
| 4 | Spawning | Roe runs with slight pressure. Most eggs are hydrated (translucent) with few opaque eggs. |
| 5 | Spent | Ovaries empty and flaccid. |

with ovaries and liver were measured, and for each fish maturity stage was estimated visually based on the five-point scale (Table 1). Ovary samples were embedded in paraffin, thin sectioned to a thickness of about 4 μm , and stained and counterstained with H&E at Phoenix Labs, Inc., Everett, Washington.

Laboratory and data analyses

Histological analysis was performed to confirm the accuracy of macroscopic determinations of maturity. The entire slide of each tissue sample was scanned with a compound microscope. Oocytes were photographed at each developmental stage (Figs. 2-10) and were classified into developmental stages according to criteria and published photographs (Hinckley 1987, Sakurai 1989). In addition, pollock ovary tissue was examined for atretic oocytes and the presence of postovulatory follicles (Fig. 10).

Pollock ovaries were classified to maturity stage based on the most advanced oocyte stage present (West 1990) and on the presence or absence of postovulatory follicles (Hinckley 1987). Criteria are shown in Table 2 with corresponding reference photographs (Figs. 2-10). Ovaries were categorized as pre-spawning if their most advanced oocytes were at primary yolk or more advanced stages with no empty follicles present. This classification is based on the presumption that walleye pollock oocytes develop from the primary yolk stage to spawning in four months (Y. Sakurai, Hokkaido University, pers. comm.). Ovaries were categorized as spawning if postovulatory follicles were present.

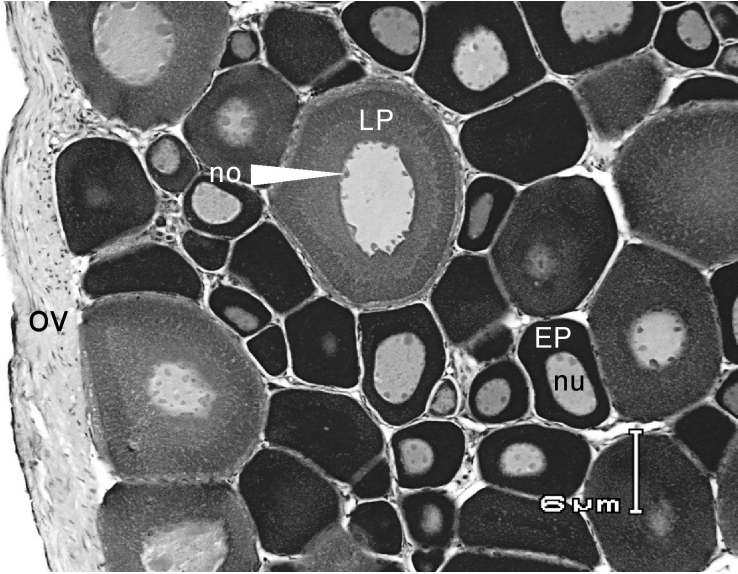


Figure 2. Immature pollock ovary showing the ovarian wall (ov) and containing both early (EP) and late (LP) peri-nucleus oocytes pictured with their nucleus (nu) and nucleolus (no).

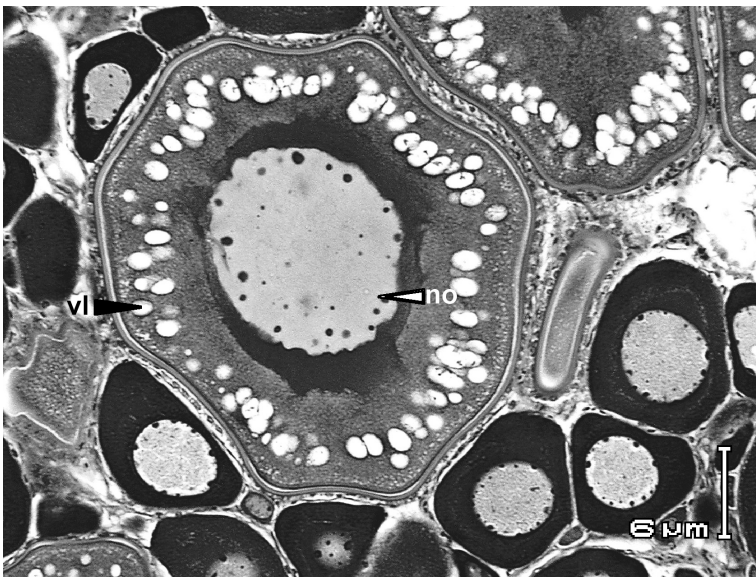


Figure 3. A yolk vesicle oocyte is pictured with its nucleoli (no), and vacuoles (vl).

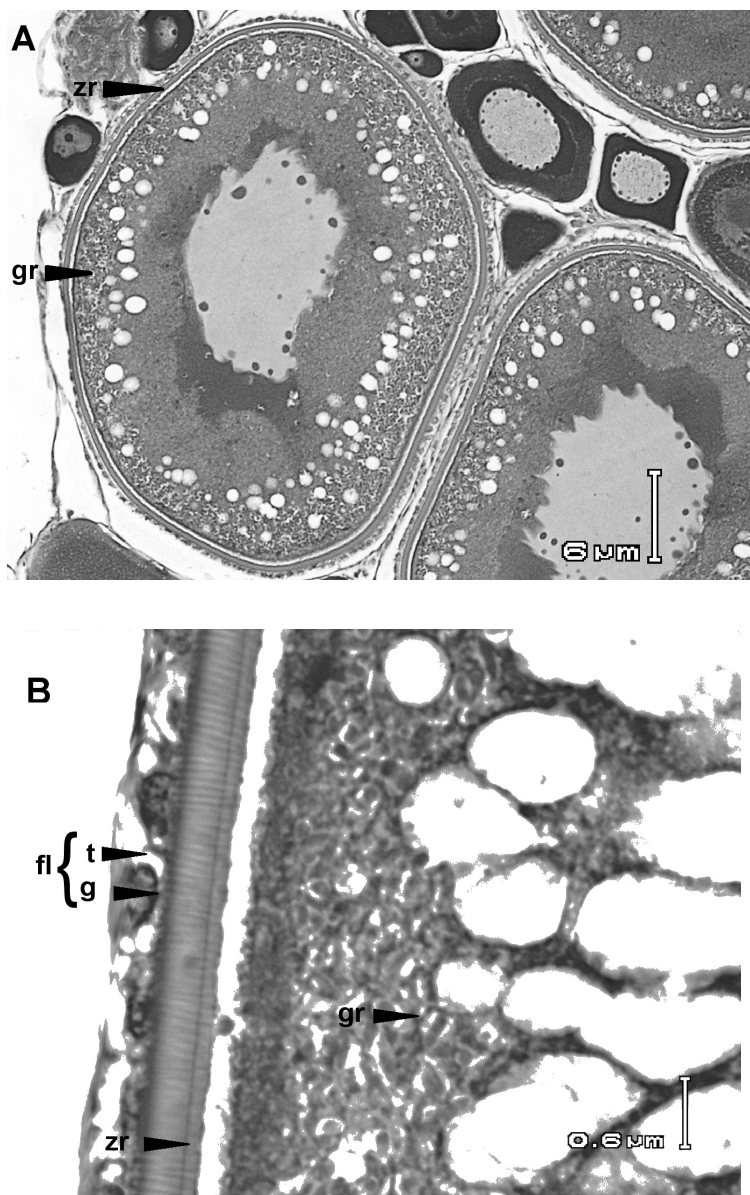


Figure 4. Primary yolk oocyte. The yolk granules (gr) and zona radiata (zr) are pictured for a primary yolk oocyte at (A) 100X and (B) 1,000X. The follicle (fl) and its parts, the granulosa (g) and theca (t), are also shown at 1,000X magnification.

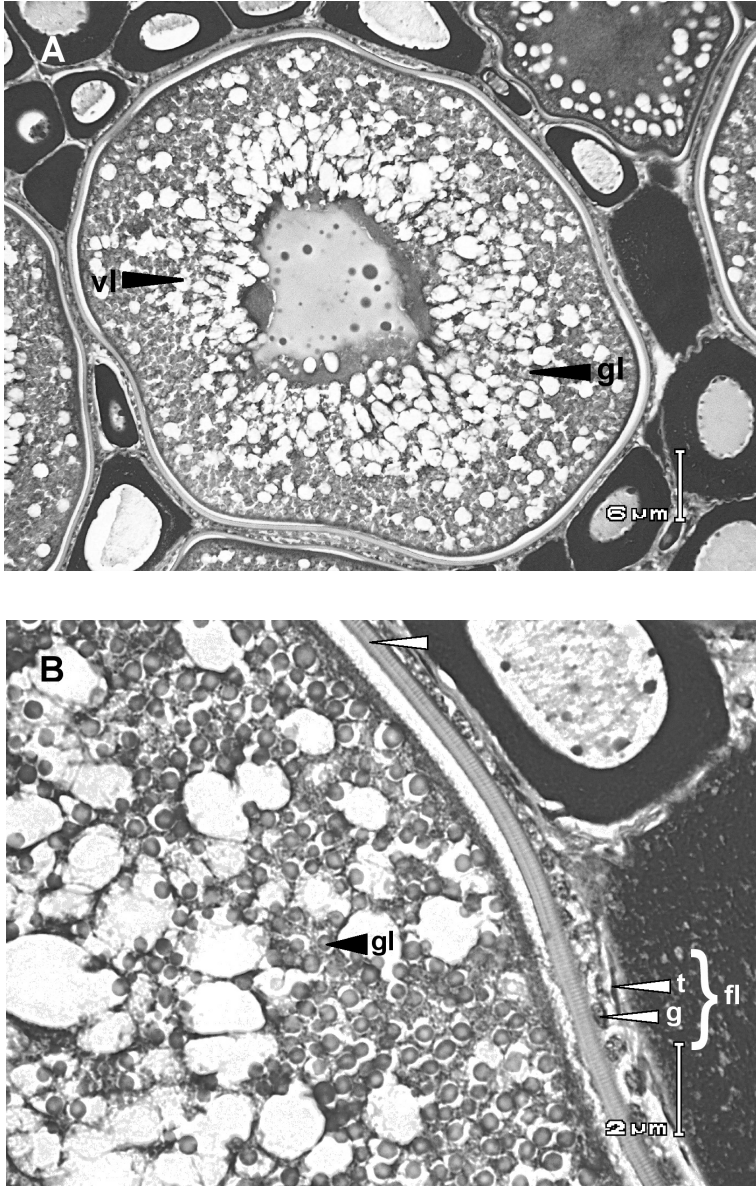


Figure 5. Secondary yolk oocyte. The vacuole (vl), and yolk globules (gl) are shown for a secondary yolk oocyte under (A) 100X and (B) 400X. In addition, the zona radiata (zr) and follicle (fl), including its parts of granulosa (g) and theca cells (t) are labeled for 400X.

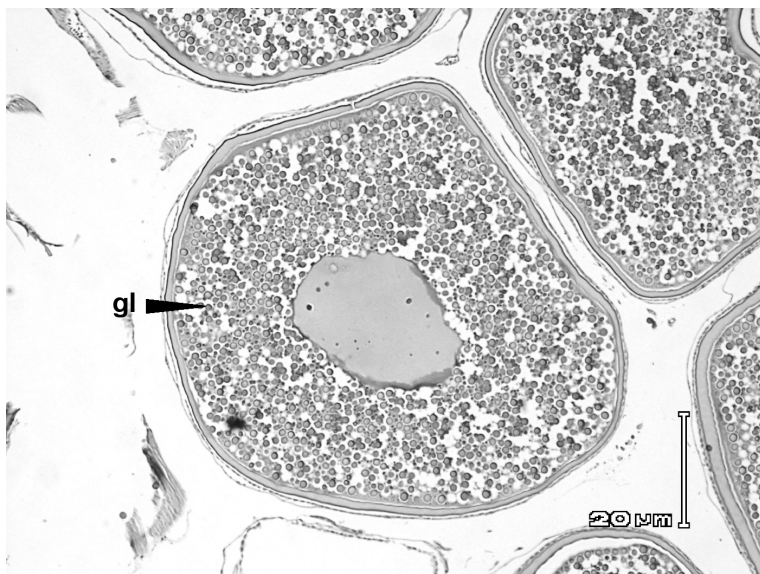


Figure 6. Tertiary yolk oocyte. A tertiary yolk stage oocyte is pictured with its yolk globules (gl).

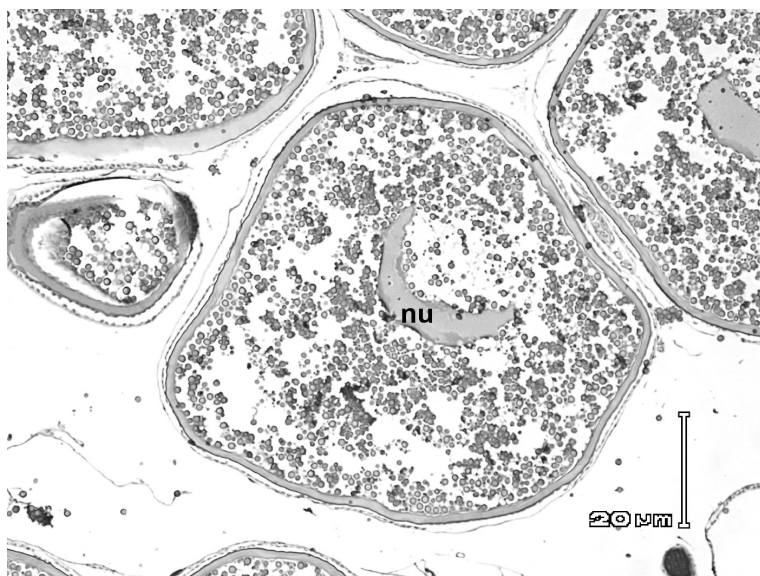


Figure 7. Nuclear migration. An oocyte is pictured at the nuclear migration stage with a crescent-shaped nucleus (nu).

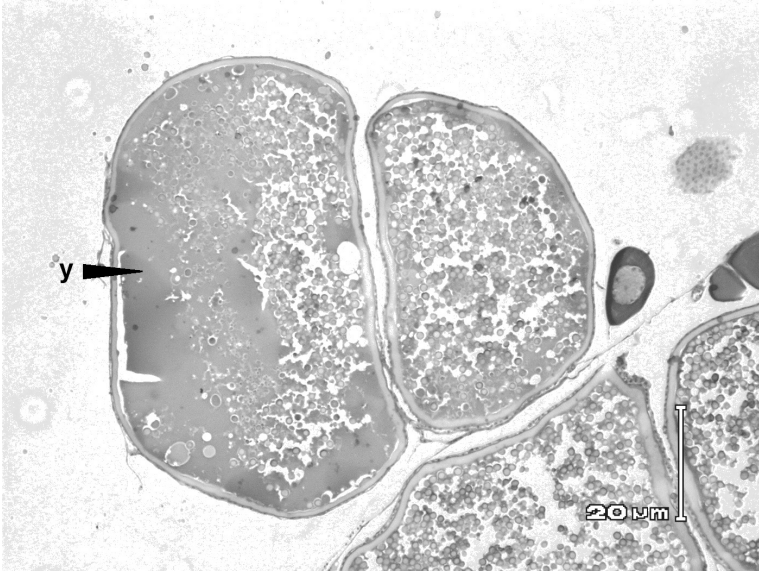


Figure 8. Prematuration. At the prematuration oocyte stage, fused yolk globules (y) are shown.

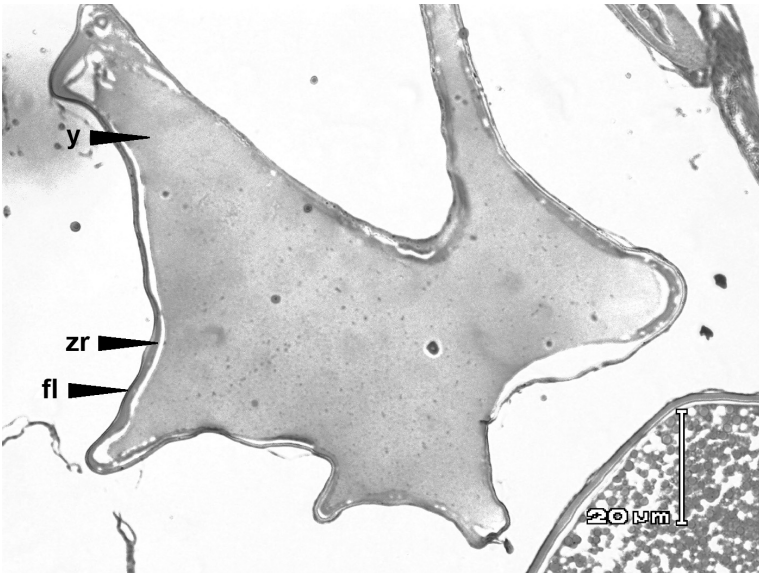


Figure 9. Maturation. The maturation stage is shown with its follicle (fl), fused yolk (y), and zona radiata (zr).



Figure 10. Postovulatory follicle. The nuclei (n), granulosa (g), and theca (t) cells of the degrading follicle are pictured along with blood capillaries (bc).

Results

A GSI was calculated for 158 histological samples of ovaries for which no evidence of atresia was found. When plotted against length, a break in GSI values occurred across all length classes; no GSI values were found between 3.8-6.9 (Fig. 11A, B). All ovaries that contained empty follicles were above this GSI break and their most advanced oocytes were at stages of nuclear migration to ovulation (Fig. 11A). Sixty percent of ovaries above the break did not have empty follicles, but had their most advanced oocytes in the nuclear migration, prematuration, or maturation stages. Below the break, no ovaries had oocytes advanced to the prematuration or maturation stages (Fig. 11A). All ovaries classified by histological analysis as immature, i.e., fish that will not spawn in the approaching season, were below the break and had a GSI value ≤ 1.0 (Fig. 11B). Altogether 74% of ovaries classified as mature were above the break. Ovaries that were below the break and classified as mature were primarily at early yolked stages. The mean ± 1 SD of the GSI for immature fish (0.482 ± 0.190 , $N = 49$) was statistically significantly lower than the mean for mature fish (9.22 ± 4.97 , $N = 109$) using a two-sample *t*-test for unequal variances, $t = -18.2$, $p < 0.001$.

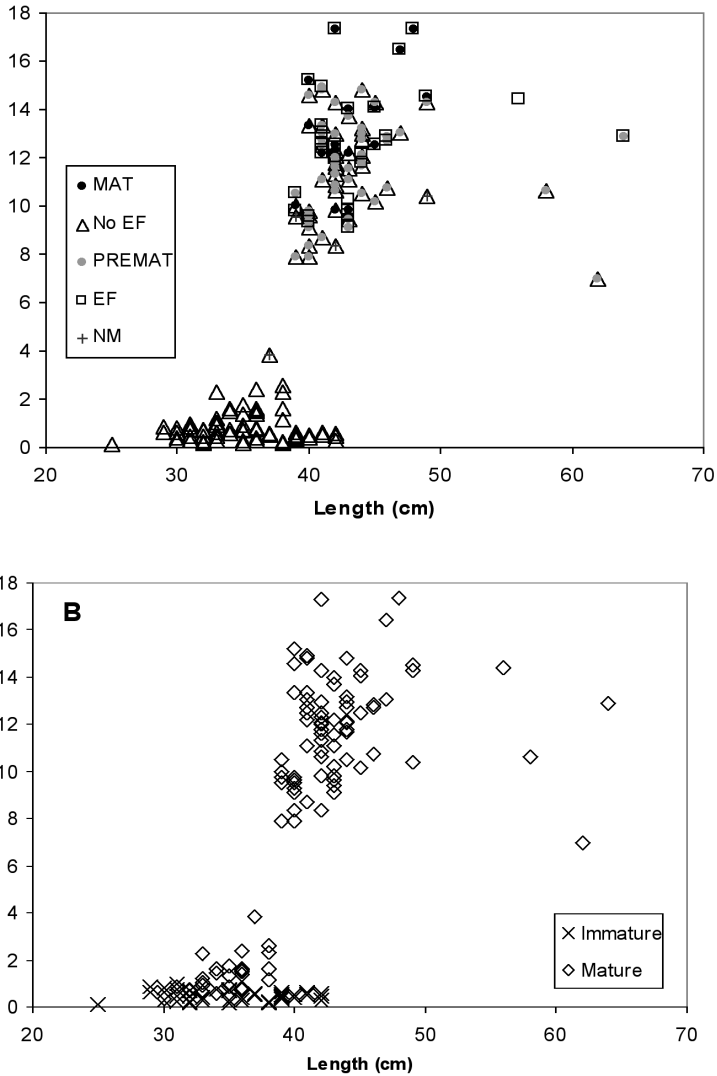


Figure 11. A plot of GSI versus fork length for histological samples collected in 2003 show a break in GSI values at about 6.9 for which ovaries: (A) contain empty follicles (EF) and/or have oocytes at the nuclear migration (NM), prematuration (PREMAT), or maturation (MAT) stages as their most advanced oocytes present; and (B) are classified as immature or mature based on histological examination. No ovaries with atresia were included.

Using macroscopic visual inspection criteria (Table 1), PCC personnel staged 4,865 pollock in 2002 and 5,095 in 2003. The GSI values were calculated and plotted against length for maturity stages 2 through 5. The GSI values were not calculated for immature (maturity stage 1) fish due to inaccuracy of small ovary weights measured by vessels' scales. Developing fish (maturity stage 2) had fork lengths of 24-78 cm and GSI values of 0.16-20 with an average of 4.36. Pre-spawning fish (maturity stage 3) were 28-78 cm fork length with GSI values from 1.32 to 34.43 with an average of 10.89. Spawning fish were 32-80 cm fork length with GSI values of 1.38 to 35.25 with an average of 13.49. Spent fish were 33-73 cm fork length with GSI values from 0.14 to 38.27 with an average at 7.12. Due to the high degree of overlap in GSI values among maturity stages, it was unnecessary to apply ANOVA to show the lack of statistical significance.

Of the 173 pollock ovaries collected for histological analysis, 64 (37%) were macroscopically classified as immature. Of these, the most advanced oocytes of 22% of the ovaries were at early yolked stages and 78% were at less developed stages (peri-nucleus or yolk vesicle). Twenty pollock (12%) were classified as developing; of these, 20% were at early developmental stages of peri-nucleus or yolk vesicle, 70% were early yolked, and 10% were late yolked to nuclear migration stages as their most advanced oocytes present. Eighty-nine pollock (51%) were staged as pre-spawning; 98% of these were at advanced oocyte stages from tertiary yolk to ovulation. No postovulatory follicles were found in ovaries macroscopically staged as immature or developing. Postovulatory follicles were found in 36 ovaries staged as pre-spawning. None of the sampled ovaries were categorized as spawning or spent by macroscopic inspection according to the five-stage scale utilized (Table 1).

The assessed maturity condition of ovaries staged histologically was not always in agreement with the macroscopically determined maturity condition (Table 3). The misclassification rate for fish macroscopically identified as immature was 41%, for developing 95%, and for pre-spawning 44%. After histological examination, maturity condition was concluded to be 59% immature, 19% developing, and 22% pre-spawning for ovaries macroscopically staged as immature; 15% immature, 5% developing, and 80% pre-spawning, for ovaries macroscopically staged as developing; and 56% pre-spawning, 38% spawning, and 6% not staged for ovaries macroscopically staged as pre-spawning. Ovaries were not staged if more than 50% of their oocytes were atretic. If ovaries macroscopically staged as developing are presumed not to spawn in the current year (i.e., immature), then 26% of mature ovaries were misclassified by macroscopic examination as immature and 0% of immature ovaries were misclassified as mature.

Ovary coloration varied with developmental stage. Ovaries with their most advanced oocytes at peri-nucleus or yolk vesicle stages

were transparent or translucent with a highly variable coloration, from colorless to maroon. Those with the primary yolk stage as their most advanced oocytes were translucent and orange or maroon, or opaque and orange. Ovaries with their most advanced oocytes at secondary, tertiary, or nuclear migration stages were opaque and orange and at pre-maturation, maturation, or ovulation stages were flesh or tan-orange.

Discussion

Our results indicate that GSI may be a good predictor of fish that are about to spawn or have already begun spawning. A break in GSI values separates most mature and immature fish based on histological determinations (Fig. 11). Mature fish above the break had their most advanced oocytes at the nuclear migration to ovulation stages and many had empty follicles (an indication that spawning had begun) (Fig. 11A). At the maturation stage, oocytes take up water during the hydration process and ovary weights may increase two to four fold above those other maturity stages (Hunter and Macewicz 1985). Thus, GSI is useful in identification of hydrated ovaries (Hunter and Macewicz 1985). Ovaries with their most advanced oocytes at nuclear migration or pre-maturation stages may have occurred above the break, because hydrated oocytes were in the ovary but not observed in the particular ovary sample examined histologically. The hydration stage is very short in duration and may not be commonly observed (Sorokin 1961, Hunter and Goldberg 1980).

Although Sakurai (1989) suggested that pollock that will spawn in the approaching season may be identified by $GSI \geq 2.5$, we found some pollock with their most advanced oocyte stages at early yolked, late yolked, or nuclear migration stages with $GSI < 2.5$; fish with oocytes at these stages are expected to spawn in the approaching season. Moreover, fish classified as developing, pre-spawning, and spawning based on macroscopic examination had average $GSI > 2.5$, but some individuals had $GSI < 2.5$. In addition, some immature and mature fish examined histologically had overlapping GSI values below the break (Fig. 11B). For these reasons, GSI cannot be used as the sole predictor of fish that will spawn in the approaching season in the eastern Bering Sea.

The GSI values for spent fish were intermediate between developing and pre-spawning/spawning pollock, consistent with findings of Merati (1993). Sakurai (1989) observed GSI values > 1.0 for post-spawning pollock but this criterion does not conform well to our observations. Although, the average GSI for spent fish in our study was 7.12, some GSI values were below 1.0. In addition, the position of some spent fish above the GSI break (Fig. 11) wrongly suggests post-spawners were either close to spawning or spawning. Consequently, GSI may not be

useful to identify post-spawners, which agrees with findings of Hunter and Macewicz (1985).

Differences or similarities among pollock GSI values between Funka Bay, Japan (Sakurai 1989); Shelikof Strait, Alaska (Merati 1993); and the eastern Bering Sea (this study) must be interpreted cautiously. It is inappropriate to compare GSI values across populations (deVlaming et al. 1982). Relationships between ovary weight and body size may change with development (deVlaming et al. 1982, Hunter and Macewicz 1985, West 1990), therefore samples may be biased when comparing GSI values for fish of different sizes. Larger fish may have larger GSI values than smaller fish at the same maturity stage (Hunter and Macewicz 1985, West 1990), and this effect is augmented during late maturation stages (Hunter and Macewicz 1985). In this regard, Sakurai (1989) calculated GSI values from a smaller range of pollock lengths and a smaller sample size than in our study.

The high rate of misclassification using macroscopic maturity staging is likely to be largely due to the subjectivity of the procedure; determinations are dependent on interpretations of color, size of the ovary and visibility of eggs. Some spent pollock, particularly large fish, may have been misclassified as immature. Instead, some of these large immature fish may have been in a non-reproductive state, as observed in Atlantic cod (Shirokova 1969 as cited by Morrison 1990, Rideout et al. 2000). Fish that skip spawning in a season because they do not commence vitellogenesis or they resorb yolked oocytes may be difficult to distinguish macroscopically from those that are immature (Rideout et al. 2005). Alternatively, because large fish may spawn first as with Atlantic cod (Morrison 1990), they may be more likely to be spent and misclassified as immature during data collection. Pre-spawning pollock will spawn in the current season and developing pollock will spawn in the following season; however, the distinction between the two stages is difficult to make based solely on macroscopic examination. In addition, significant numbers of pre-spawning (maturity stage 3) pollock may be misidentified as developing. Hence, histological analysis is superior, albeit more time consuming, than macroscopic examination, because stages of oocyte development are observed directly.

Additional misclassification errors based on macroscopic maturity staging may be due to errors in the classification scheme itself. For instance, according to criteria of the five-stage scale (Table 1), a spawning pollock has an ovary in which “most” eggs are hydrated. However, presence of hydrated oocytes indicates that spawning either will begin soon or has already begun (Hinckley 1986) because hydration is a brief stage (Sorokin 1961, Hunter and Goldberg 1980). Thus, applying this scale will lead to some fish defined biologically as spawning to be misclassified as pre-spawning. Spawning may be better described macroscopically by the presence of “any” hydrated oocytes. Likewise,

Table 2. Pollock maturity condition based on histological examination. Pollock were classified into a maturity condition based on histological examination of their ovaries (Hinckley 1986; Morrison 1990; Y. Sakurai, Hokkaido University, pers. comm.).

| Maturity condition | Histological examination |
|--------------------|---|
| I. Immature | Late peri-nucleus (Fig. 2) most advanced oocyte stage present. No postovulatory follicles. |
| II. Developing | Yolk vesicle stage (Fig. 3) most advanced oocyte stage present. Early and late peri-nucleus stages may also be present. No yolk formation. No postovulatory follicles. |
| III. Pre-spawning | Peri-nucleus, primary (Fig. 4), secondary (Fig. 5), and tertiary yolked (Fig. 6), nuclear migration (Fig. 7), and prematuration stages (Fig. 8) may be present, but maturation most advanced oocyte stage present (Fig. 9). No postovulatory follicles. |
| IV. Spawning | Ovulation has occurred. Peri-nucleus, yolked, nuclear migration, prematuration, and maturation stages may be present. Postovulatory follicles present (Fig. 10). |
| V. Spent | No oocytes beyond peri-nucleus stage. Atresia of unspawned maturation stage oocytes may be present. Postovulatory follicles present. |

coloration of pollock ovaries may be indicative of not only developmental stage, but also diet (J.F. Morado, NMFS, Seattle, pers. comm.) and perhaps other factors. Yolk begins to form as granules in the primary yolk stage (Hinckley 1986). Pollock ovaries with their most advanced oocytes at the primary yolk to nuclear migration stages, exhibited an orange coloration, indicating enough yolk had formed to affect the color of the ovary. We observed high color variation in ovaries that had their most advanced oocyte stages at the peri-nucleus, yolk vesicle, and primary yolk stages. Pollock ovaries at the immature, developing, and pre-spawning I stages may be more subject to color variability due to diet, because not enough yolk has formed to mask the influence of diet on coloration.

Classification of ovary development based on histology (Table 2) is not without other caveats. For instance, criteria to classify fish into the pre-spawning stage based on histology (Table 2) was based on the assumption that development from the primary yolk stage to spawning occurs in four months as in Funka Bay, Japan (Y. Sakurai, Hokkaido University, pers. comm.). However, development time in the eastern Bering Sea is unknown and may differ due to differences in temperatures or genotypes. Spawning in the eastern Bering Sea has been recorded from March to June (Hinckley 1986). Based on the assumption about ovarian development and given the spawning schedule, females

Table 3. Ovary classification matrix based on macroscopic and histological examination. Ovaries collected in 2003 were placed into a maturity condition based only on macroscopic inspection and then reclassified after histological examination. The rate of misclassification for macroscopic staging by developmental stage is illustrated. An ovary was not staged if more than 50% of its oocytes were atretic.

| Histological determinations | Macroscopic determinations | | |
|-----------------------------|----------------------------|------------|--------------|
| | Immature | Developing | Pre-spawning |
| Immature | 38 | 3 | 0 |
| Developing | 12 | 1 | 0 |
| Pre-spawning | 14 | 15 | 13 |
| Spawning | 0 | 1 | 71 |
| Not staged | 0 | 0 | 5 |

collected in the winter (late January to early April) with their most advanced oocytes at stages of primary yolk or beyond should spawn the same calendar year in the eastern Bering Sea or elsewhere in the Bering Sea. Thus, pollock categorized as immature or developing are not expected to spawn until the following season. Therefore, 22% of the pollock macroscopically classified as immature using criteria in Table 1 and the 80% classified as developing would spawn in the year of our data collection, but after the “A” fishing season. In addition, the time of development from peri-nucleus or yolk vesicle stages to spawning and the duration of each oocyte stage is unknown.

Sample size may have affected our results, as well. The sample size of ovaries used for histological examination was relatively small and was limited both temporally and spatially collected from only a few haul locations near the Pribilof Islands. The schedule of ovary development may vary by region due to temperature differences, by age class due to differences in thermal histories (T.W. Buckley, NOAA, Seattle, pers. comm.), and by populations owing to genetic variation in life history characteristics (Olsen et al. 2004). Interannual differences in development rates of Atlantic cod gonads are correlated with temperature and oxygen content of seawater (Uzars et al. 2001).

A new descriptive guide, including photographs and descriptions of ovaries at each stage was produced for more accurate macroscopic staging of pollock ovaries (Appendix). The descriptions of each maturity condition were based on macroscopic observation, histological analysis,

and previously developed guides (Hinckley 1986; Bowden et al. 1990; and N.J. Williamson, NMFS, Seattle, pers. comm.).

Difficulties in applying macroscopic determinations of maturity stages of pollock suggest the need for additional research. Histological examination should be performed for ovaries collected from locations across the eastern Bering Sea over several years to determine if the relationship between macroscopic and histological staging varies temporally or spatially. Laboratory studies should be performed to determine the time from development of various oocyte stages, such as from primary yolk to spawning, to determine potential differences among regions and over different thermal regimes experienced by pollock. Such a study is necessary to verify which fish will spawn in the approaching season and which will spawn in the subsequent season and to validate descriptive guides, such as ours. Fieldwork, such as tagging and sampling of fish in late spring or early summer, might determine if some pollock caught on the eastern Bering Sea shelf during the "A" fishing season spawn after the suggested spawning season and/or if they spawn elsewhere in the Bering Sea. More accurate classifications of mature or immature pollock are necessary for accurate estimation of size of maturity and spawning stock biomass for fishery management. We will address this last issue in a forthcoming paper.

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Appendix: Descriptive guide to macroscopic staging of pollock ovaries

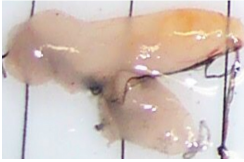
The following guide is intended to aid in the classification of pollock ovaries into accurate maturity stages based on visual macroscopic inspection. Photographs of ovaries and descriptions of ovary coloration and size are provided for each maturity stage. Additional information is provided on the topics of ovary coloration, ovary size, and atresia. Macroscopic staging criteria were developed based on personal observation and criteria from previously developed guides (Hinckley 1986; Bowden et al. 1990; N.J. Williamson, NMFS, Seattle, pers. comm.).

Assumptions

This guide is based on the assumption that pollock with ovaries classified in the “A” fishing season as pre-spawning will spawn within the current year and those with developing ovaries will spawn the following year. Ovaries were placed into the pre-spawning macroscopic maturity stage if they had oocytes of primary yolk or more advanced oocyte stages, because time of development from primary yolk stage to spawning occurs in four months in Funka Bay, Japan (Y. Sakurai, Hokkaido University, pers. comm.). However, the time of development from each histological stage to spawning is unknown in the eastern Bering Sea. Laboratory studies are needed to verify consistency with the time frame of development in Funka Bay or to determine an alternative. This guide would change if an alternative time frame were found for development.

The duration of each oocyte stage is unknown; therefore, an assumption of a short time interval is made. Otherwise, an ovary with oocytes at the beginning of the primary yolk stage may be classified differently from an ovary with oocytes at the end of this stage. Laboratory work is needed to verify the duration of each oocyte stage.

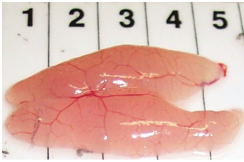
The photographed ovaries were not matched one to one with a histology classification, so some uncertainty exists in correct placement of each ovary into a macroscopic visual maturity category.



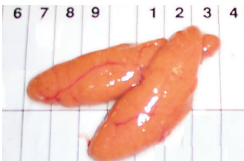
1. Immature: Ovaries transparent or translucent, colorless, gray, yellow, orange, orange-yellow, pink, maroon, reddish-orange, tan, or tan-orange. No eggs visible. Ovary small and tucked inside body cavity.

2. Developing: Picture is unavailable. Ovary translucent, orange, pink, maroon, reddish-orange, or tan-orange. No eggs visible. Ovary small. Likely to spawn the following year.

3. Pre-spawning:



I. (presumptive) Ovary translucent, orange, pink-orange, maroon, or tan-orange. No eggs visible to the eye. Ovary less than $\frac{1}{2}$ length of the body cavity. Well-developed red blood vessels. Likely to spawn later this year.



II. Ovary opaque, orange, bright orange, or dark orange. Visible eggs. Ovary occupies about $\frac{1}{2}$ of ventral cavity.



III. Ovary opaque, tan-orange or flesh colored. Visible eggs. Ovary occupies about $\frac{2}{3}$ of the body cavity.



4. Spawning: Some to most eggs are translucent from hydration. Ovary occupies whole body cavity. Other eggs are opaque and tan-orange or flesh colored. Ovary must be cut through center, where spawning begins, to check for hydrated eggs. Ova may run with pressure. Thin, stretched ovarian wall.



5. Spent: Ovaries empty and flaccid. Thick ovarian wall. (Photograph by Sarah Hinckley, NMFS.)

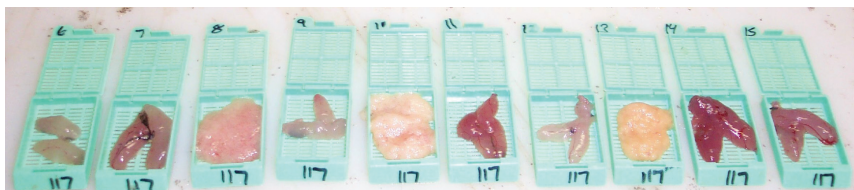


Figure A1. Color variation observed in visual stage 1 and stage 3 ovaries is pictured. Microcassette dimensions are approximately 2.5 cm x 3.8 cm.

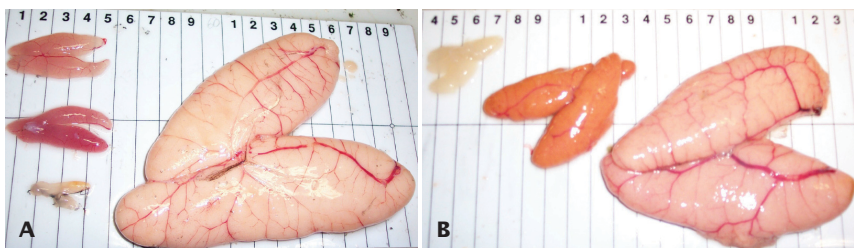


Figure A2. Ovary sizes: (A) Pre-spawning I ovaries are pictured on the top left and center left, immature on the bottom left, and pre-spawning III on the right. (B) Immature ovaries are shown on the left, pre-spawning II in the center, and pre-spawning III on the right.

Coloration

The described coloration of the ovaries at each developmental stage in this guide was observed, but other colors may occur. Color may be affected not only by the amount of yolk within the oocytes, but also by diet. Immature, developing, and early pre-spawning ovaries may be subject to more variability due to diet, because not enough yolk has formed to mask the influence of diet on coloration (Fig. A1).

Size

Ovaries become larger with yolk formation and development and very large with absorption of water with hydration (Fig. A2. A, B).

Atresia

Ovaries with atretic oocytes may appear at advanced developmental stages under macroscopic inspection; however, they may only contain early developmental stages or atretic oocytes.

Fluctuations of Northeast Arctic Cod Catches: A Review of Possible Sources

Odd Nakken

Straumsgrend, Norway

Introduction

Fisheries science was established to provide answers to the question of why fish catches fluctuate. The first explanation our previous colleagues came up with was that spatial displacements and migrations of fish related to changes in the environment (often temperature) were responsible for the experienced failures or successes of fishing. The discovery that year-class variations caused large fluctuations in stock abundance of cod and herring added considerably to our understanding and our ability to provide answers (Hjort 1914). Hjort and his coworkers established a sampling program of catches in the main Norwegian fisheries for cod and herring (length, age, sex, maturity stage) and these data enabled Toresen and Østvedt (2000) and Hysten (2002) to estimate annual stock abundances and fishing mortality rates for respectively herring and cod for the entire twentieth century.

This paper provides a brief review of the impact of changes in climate and environment as well as the effect of fisheries on the stock of northeast arctic cod. A far more comprehensive review of the subject for all Atlantic cod stocks is given in ICES (2006a).

Distribution and migration

Fig. 1 shows the distribution of cod stocks in the Northeast Atlantic and in Fig. 2 the habitat area of northeast arctic cod is given in more detail. In Fig. 3 are shown the development of temperature in the Barents Sea throughout the twentieth century and the catches and stock biomasses of northeast arctic cod.

The stock has shown large long-term shifts in distribution area. In the 1870s a rich fishery occurred for several years off the western

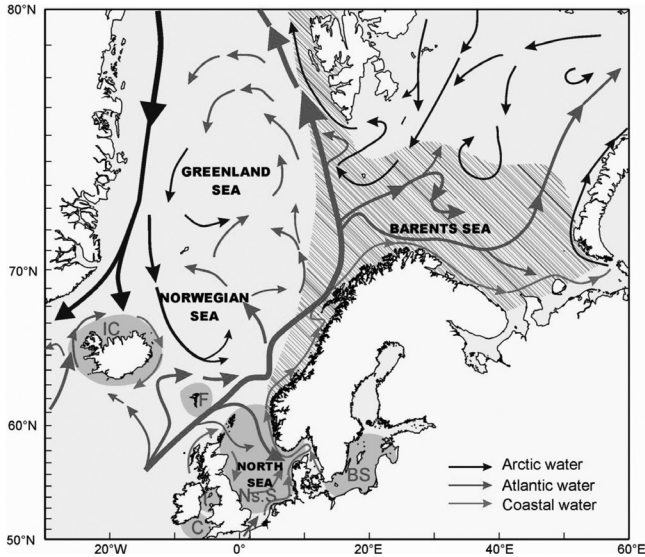


Figure 1. Currents and cod stocks in the Northeast Atlantic. IC = Icelandic stock, F = Faeroes stock, C = Celtic Sea stock, I = Irish Sea stock, Ns.S = North Sea stock, BS = Baltic Sea stock, Hatched area = Northeast Arctic stock.

part of Svalbard during summer. From the early 1880s until about 1910-1912 no fishable concentrations were located on the banks in the Bear Island–Svalbard region. During the warming of the North Atlantic in the 1920s and 1930s the distribution area of cod widened considerably (Drinkwater 2006). Large short-term shifts in distribution lasting for some years and closely related to changes in temperature have also been observed (Nakken and Raknes 1987, Ottersen et al. 1998). More recent studies have indicated temperature-related shifts in spawning areas. In cold periods a greater portion of the spawners went to the southern districts than in warm years when spawning in the areas north of Lofoten (the main spawning area) increased (Sundby and Nakken 2005, Godø 2003).

Stock size and temperature

In spite of rapidly increasing annual catches due to the development of international trawl fisheries in the Barents Sea in the 1920s-1930s the stock increased considerably in these years along with the warming of the waters. The same feature was seen in Icelandic and West Greenland waters, and explained by Täning (1949) as follows: “The rise of tem-

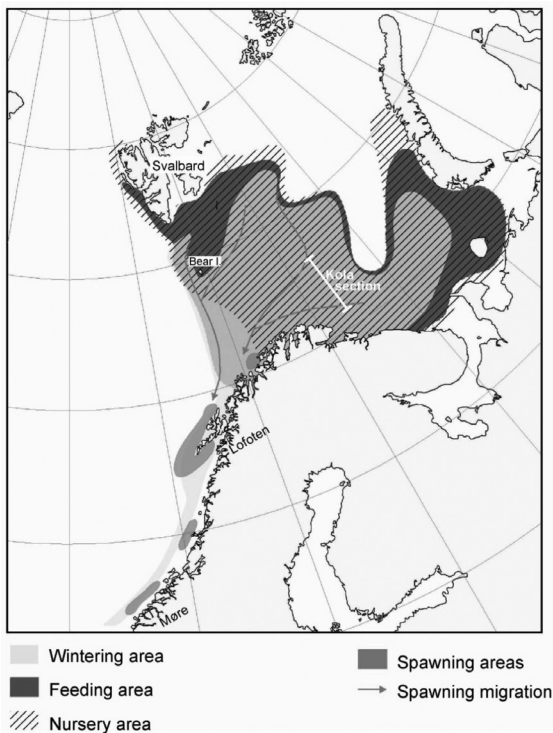


Figure 2. Northeast arctic cod. Distribution and migrations.

perature in the sea, especially in the far north, has not only been met with in the surface layers but down even to depths of about 600 to 800 meters. This rise in temperature was especially observed after 1925 when the arctic water began to retire. Owing to this rise in temperature, immense stretches of banks in northern seas previously covered with arctic water, have been made habitable for many species of animals including several species of food fishes normally avoiding arctic water. By the rise of temperature food fishes, such as the cod, for instance, have obtained an addition to their original area of distribution of thousands and thousands of square kilometres and with this an enormous augmentation of food; i.e. food competition has decreased, enabling an increase in individuals far beyond the normal."

It should be noted that the scientists at the time considered the warming of the sea and the growth of the cod stock in the 1920s-1930s as a deviation from the normal (Rollefsen and Täning 1948). Rollefsen (1946) expressed concern about the future of the Norwegian coastal

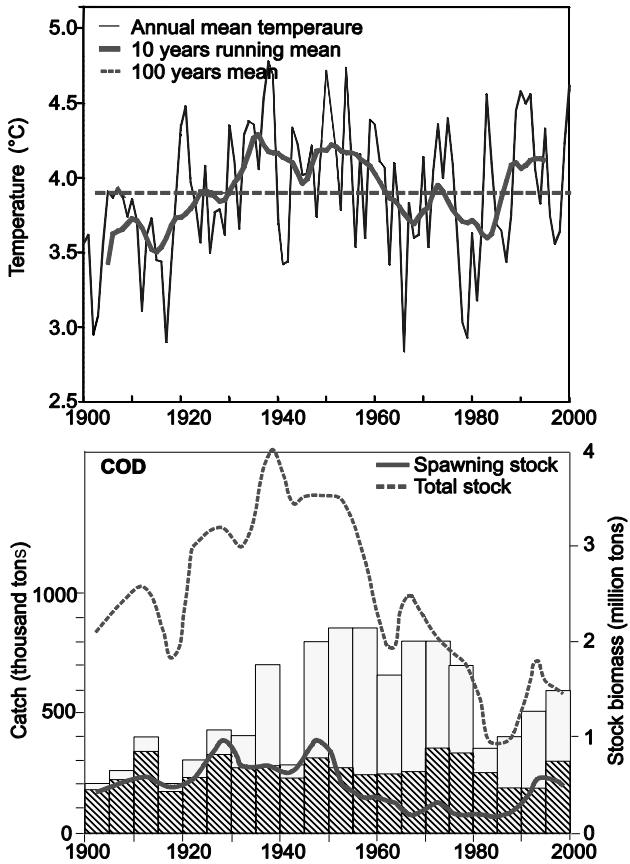


Figure 3. Upper: Temperature (average 0-200 m depth) at the Kola section in the Barents Sea. Lower: Catches and stock biomasses of Northeast Arctic cod. Columns are mean values of annual catches in 5 year periods. Norwegian catches are hatched (source: Hylen 2002).

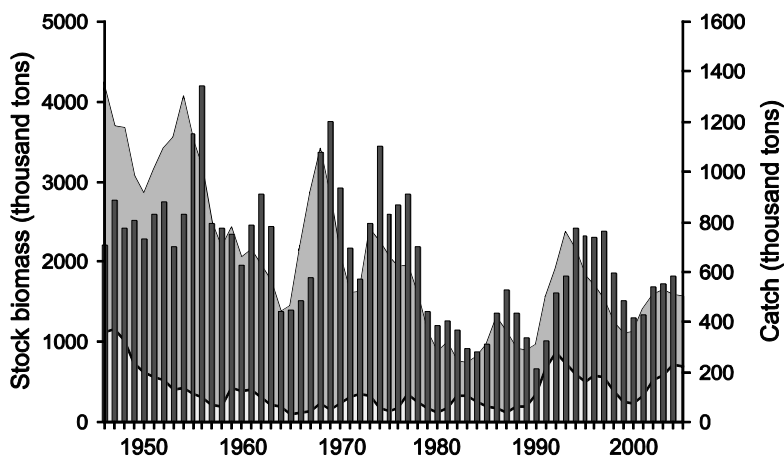


Figure 4. Northeast arctic cod. Total annual catches (columns), total stock biomass and spawning stock biomass, 1946-2005 (ICES 2006b).

fisheries for spawning cod. He feared that if offshore trawl fisheries continued to increase as they had before the war (1940-1945) and temperatures normalized then the cod stock would be overexploited and yields, particularly in the Norwegian coastal fisheries, would decline.

Catches and stock size

During World War II the Barents Sea was a war zone too dangerous for fishing vessels. No offshore fishing took place and catches were exclusively from Norwegian coastal fisheries. When the foreign trawlers returned to the area after the war, catches increased. In 1956 landings of cod exceeded 1.3 million t (Fig. 4). An analysis of the Norwegian data, carried out in 1956-1957, showed that yields from the spawning ground fisheries and the abundance of spawning fish had been substantially reduced during the 1950s. That work initiated creation of the Arctic Fisheries Working Group under ICES, a milestone in fish stock monitoring and management advice for the area. Since about 1960 ICES has, on the basis of existing knowledge, provided advice annually on how fisheries ought to be managed in order to obtain the best possible yields from the stock. However, actual fishing mortality rates have with few exceptions (1990 and 1991) been substantially higher than the recommended ones. The declining trend in stock biomass from 1955 to the late 1980s was caused mainly by fishing (Nakken 1994). Fishing mortal-

ity rates had been too high and fisheries might have had an adverse effect on recruitment by reducing the spawning stock to low levels and along with that the abundance of established (large old fish) spawners.

Since the mid 1970s, the main fishery management measure has been annual total allowable catches (TACs). The TACs as advised by ICES have quite frequently been too high due to overestimation of stock size in the annual assessments of the stock (Nakken 1998). In addition, the TACs agreed on by the management authorities (Norway and Russia) have as a rule exceeded the advised ones and the actual catches have quite often been higher than the agreed TACs. Fig. 5 shows a situation from about 1980 when the stock was overestimated in the annual assessments. The cooling of the Barents Sea in 1977-1982 caused the cod to concentrate in southwestern areas so that the CPUE-values used in the assessments were maintained although the stock was declining rapidly.

Recruitment—Environment and/or parent stock?

In Fig. 6 is shown recruitment at age 3 years for the year classes 1946-2004. Year classes of high and medium abundance occur more frequently in warm climate periods than in cold periods, and the recruitment is positively related to inflows of Atlantic waters to the area. These inflows transport copepods, the most important food source for cod larvae and fry, from the core area of copepod overwintering in the Norwegian Sea, to the drift routes of cod eggs and larvae, and create favorable conditions for growth and survival of cod juveniles during the first 5-6 months of life (Sundby 2000, Helle and Pennington 1999).

The importance of parent stock size and age structure for recruitment is well known. At an ICES meeting in 1970, Ponomarenko (1973) hypothesized the spawning stock-recruitment relationship for the stock as follows: "A large spawning stock including many age groups spawns over a larger area and a longer period of time than a small spawning stock. Hence the probability that some of the spawning products will encounter favourable conditions for survival increases with the biomass and the size range of spawners. Established spawners are shown to produce more viable eggs than first time spawners."

Capelin is the most important food source for cod and periods of low capelin abundance can seriously affect both growth and recruitment in cod. Fig. 7 shows mean length at age of first time spawners. Note the decline in size of all age groups in the early 1940s. These were cold years in the Barents Sea and coincided with a complete disappearance of spawning capelin at the northern coast of Norway in the years 1939-1942 (Olsen 1968). During the collapse of the capelin stock in the latter half of the 1980s the weights at age of young cod decreased sub-

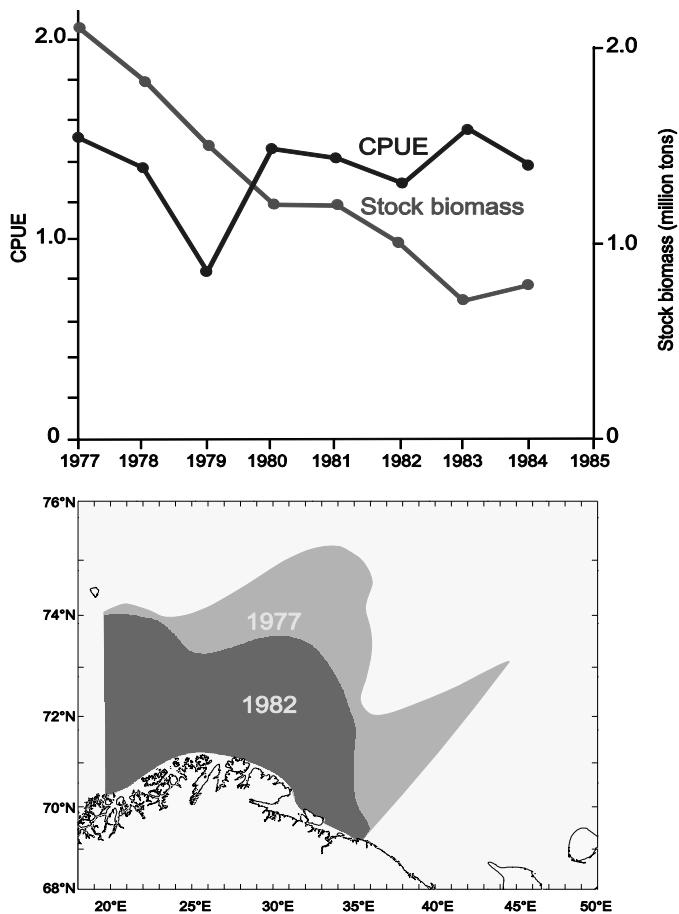


Figure 5. Northeast arctic cod and temperature. Implications for stock assessment. Upper: The development of catch per unit of effort and stock biomass during a cooling period in the Barents Sea (1977-1982). Lower: Fish distribution at the beginning and end of the period (Nakken 2002).

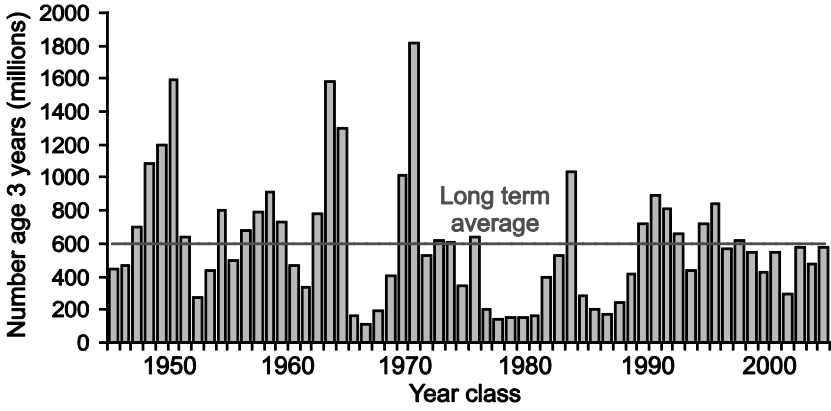


Figure 6. Northeast arctic cod. Recruitment at age 3 years (ICES 2006b).

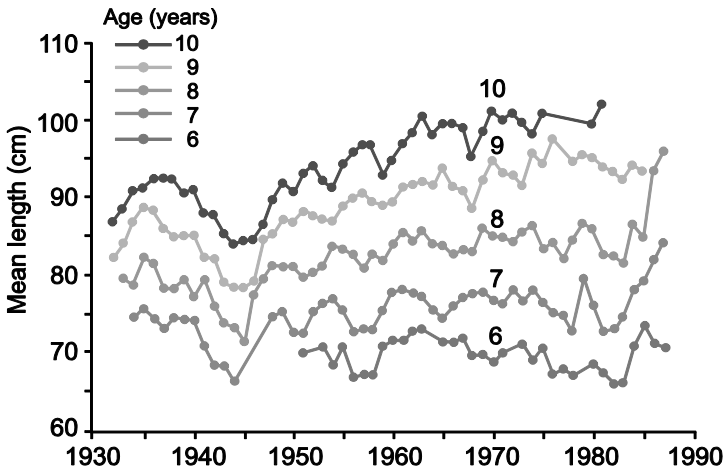


Figure 7. Northeast arctic cod. Mean length at age of first time spawners (Jørgensen 1990).

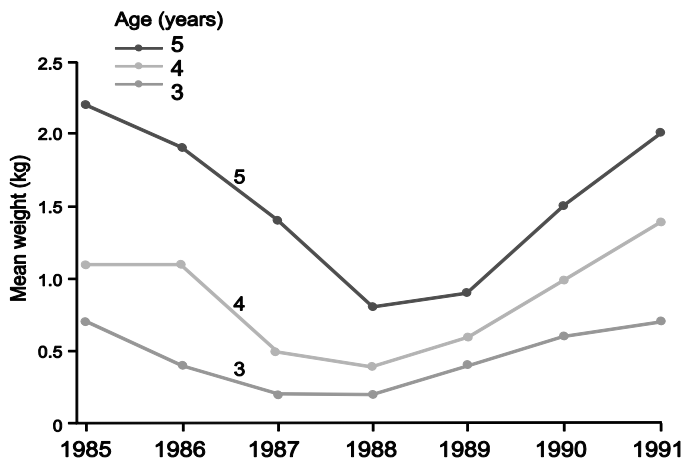


Figure 8. Northeast arctic cod. Weight at age during the collapse of the capelin stock in 1986-1989 (Nakken 1994).

stantially as seen in Fig. 8. Cannibalism increased in those years, and the combined effect of unexpected low weights and low recruitment due to cannibalism of 1-3 year olds was a stock in a much poorer state in 1987-1988 than predicted.

Fig. 9 shows the development of mean age at maturation. A similar tendency is shown for other stocks. As to the cause of the decline in age of mortality, two different mechanisms have been suggested (Heino et al. 2004). The first is density-dependent growth enhancement. When fishing removes fish from the stock the competition among the remaining specimens is reduced so that they experience better availability of food, better growth, and earlier maturation. The second is a genetic change. When fisheries remove the late maturing specimens before they reach maturity the “maturation at old age genes” gradually are removed from the stock. If this is so, we may wonder which other properties in the stock fishing have altered. A better understanding of the mechanisms involved in the development in Fig. 9 and of the consequences of such a development is strongly needed. Since eggs spawned by older cod are more viable than those from younger specimens the reproduction potential of the stock has been negatively affected by the development (see Sundby 2000 for references). Recruitment has become more dependent on environmental factors in recent decades when the age and age range of spawners have been low as compared with previous times when age at maturation was high and more age groups of older fish participated in the spawning (Ottersen et al. 2006).

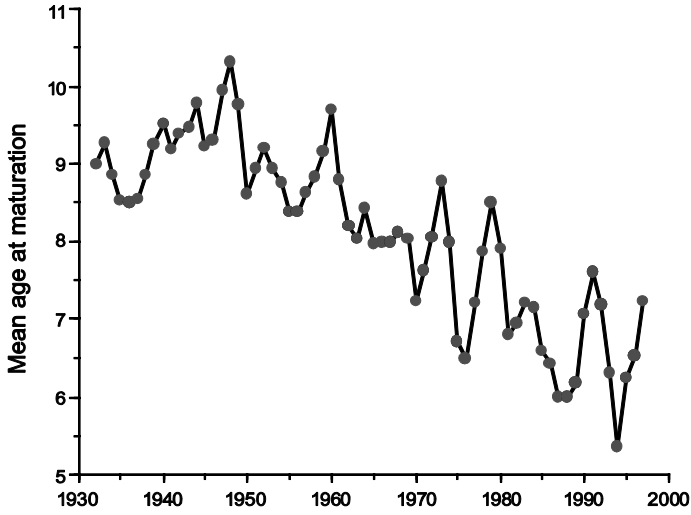


Figure 9. Northeast arctic cod. Age at maturation (Heino et al. 2004).

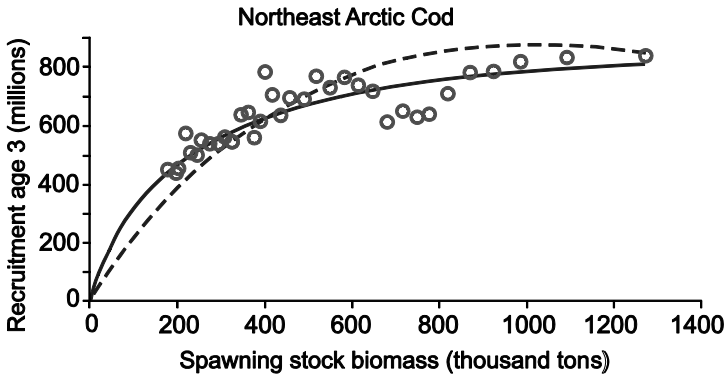


Figure 10. Northeast arctic cod. Spawning stock and recruitment at age 3 years (Jakobsen 1993).

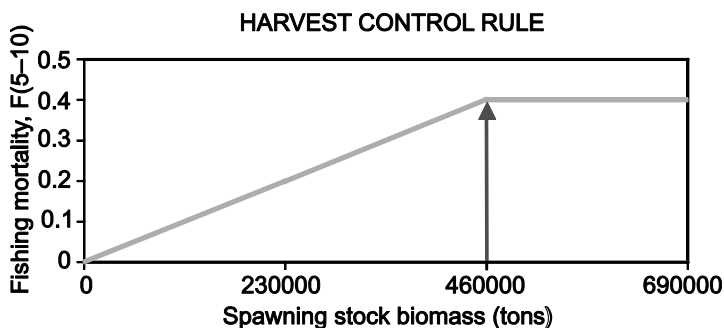


Figure 11. Northeast arctic cod. The harvest control rule.

Fig. 10 shows the spawning stock-recruitment relationship when environmental factors are “removed” by arranging the data set according to the number of recruits, starting with the lowest figure in the series, and calculate running mean values (Jakobsen 1996). When spawning stocks fall below 500,000 t recruitment is directly dependent on the biomass of spawners. Reference points established by ICES for spawning stock biomass and fishing mortality rate in accordance with the precautionary approach resulted in a precautionary biomass of spawners of 460,000 t. The precautionary fishing mortality rate was estimated at $F = 0.4$. Norway and Russia agreed some years ago to establish (and enforce) a harvest control rule based on the ICES findings. The main elements of the rule are shown in Fig. 11. The fishing mortality rate should be kept at or below $F = 0.4$ as long as the spawning stock biomass is higher than 460,000 t. If the biomass of spawners falls below that figure, the fishing mortality rate is to be reduced. It should be borne in mind that this is a rule to prevent stock declines and collapses and not a rule to obtain optimal yield from the stock. Assessments show that the better yields are obtained at lower fishing mortality rates ($F = 0.3$).

Can we rely on catch statistics?

Our perception of how fish stocks have fluctuated is, for most exploited stocks, based on catch data. Time series of stock numbers estimated from catch at age analyses form the basis for most results and our understanding of such dynamics. During recent decades catch statistics have deteriorated for many stocks in the Northeast Atlantic, including northeast arctic cod (Fig. 12). Since 1990, there have been two periods when the unreported annual catch was estimated from observations made by Norwegian fishing authorities. For the years between, no

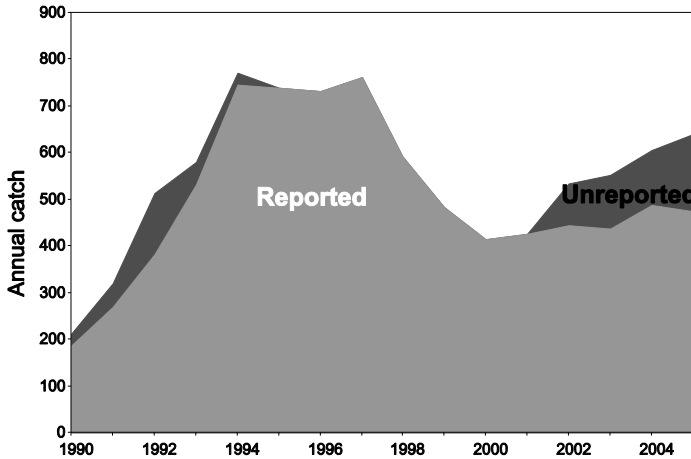


Figure 12. Northeast arctic cod. Annual catches (thousand metric tons) since 1990 (source: ICES, 2006b).

observations exist so that no estimates can be made. It is likely that also in those years considerable amounts of cod were taken in addition to the ones appearing in the catch statistics. One must thus question the usefulness of the various time series—spawning stock, recruits, and weight at age in catches etc.—for studies aiming at a better understanding of how climate, environment, and fisheries are interacting in causing the apparent fluctuations. The recruitment series (Fig. 6) for northeast arctic cod shows that no really outstanding year classes have appeared in recent decades although

- the spawning stock biomass recovered in 1990 to the levels observed in the early 1950s,
- the temperature increased in 1989-1990 to levels experienced in the 1950s, and
- our 0-group surveys resulted in record high abundance indices for many years throughout the 1990s.

Why did the stock produce six outstanding year classes from 1950 to 1970 and only one between 1983 and 2003? Is it only because of older parents in 1950s?

Acknowledgment

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Decline and Recovery of Atlantic Cod (*Gadus morhua*) Stocks throughout the North Atlantic

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Abstract

Many stocks of Atlantic cod (*Gadus morhua*) on both sides of the North Atlantic are currently at much reduced levels of biomass, but this situation is not in all instances the result of long, continuous decline. Most Northwest Atlantic stocks declined to low levels during the 1970s, but increased during the 1980s before declining even more severely during the late 1980s and early 1990s. Several of these stocks have shown little recovery despite severe restrictions on directed fishing. Many stocks in the Northeast Atlantic have experienced sustained increases and sustained decreases, but generally not in concert. Among-stock comparisons illustrate that fishing has played a dominant role in the dynamics of all cod stocks, but variability in climate has contributed to variability in recruitment, individual growth, and natural mortality. A cooling event during the last three decades of the twentieth century contributed to the rapid decline of several stocks in the Northwest Atlantic, and changes in life-history traits (growth rate, age and size at maturity) and in the biotic environment (predators and prey) may be contributing to recovery being slow.

Introduction

The Atlantic cod (*Gadus morhua*) is distributed in an arc across the North Atlantic. Stocks are recognized for management purposes from Georges Bank northward to Labrador, then northeastward to West and East Greenland, Iceland, and the Barents Sea (arcto-Norwegian or north-

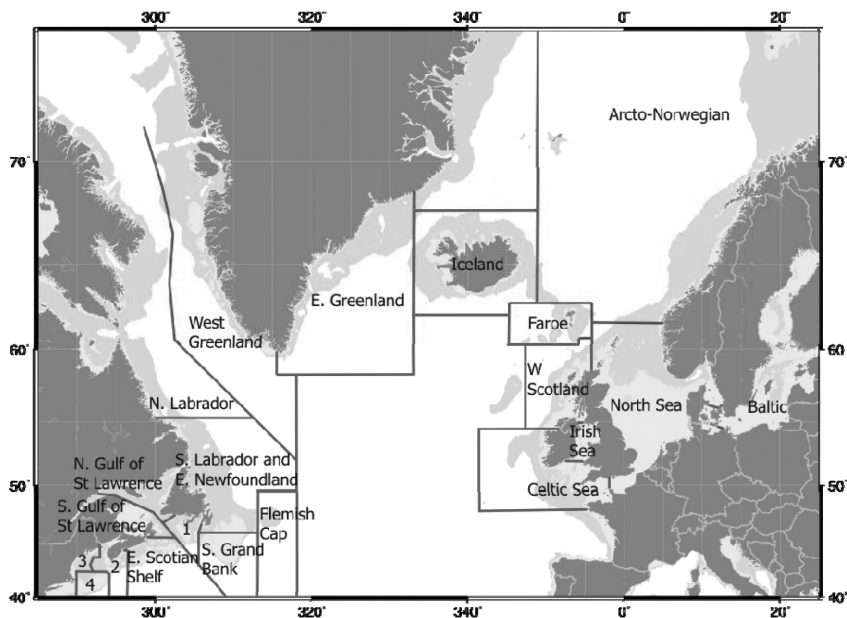


Figure 1. Map of the North Atlantic, showing the location of cod stocks. The stocks represented by numbers are 1 = S. Newfoundland, 2 = W. Scotian Shelf, 3 = Gulf of Maine, and 4 = Georges Bank. The map does not extend sufficiently to the southwest to include the whole of the Georges Bank stock area, nor does it extend sufficiently to the northeast to encompass the full range of the arcto-Norwegian stock in the Barents Sea. The boundaries of the Kattegat, West Baltic, and East Baltic stocks are not illustrated.

east arctic cod), and then southward to the Celtic Sea and eastward to the Baltic Sea (Fig. 1). All stocks are currently below the maximum biomass experienced during the past few decades, and most are at much lower levels (Brander 2007). However, these low levels are generally not the result of a long, steady decline. Most stocks in the Northwest Atlantic share a common pattern of a marked decline during the 1970s, an increase during the 1980s, and a severe decline during the late 1980s and early 1990s. Several of these stocks have shown little or no recovery during the past decade despite severe reduction or even cessation of directed fishing (Shelton et al. 2006). In contrast to the Northwest Atlantic stocks, the prolonged increases and decreases experienced by many stocks in the Northeast Atlantic tend not to be temporally correlated, and the declines have been less severe (Brander 2007). Many cod

stocks on both sides of the Atlantic have also experienced changes in demographic properties, such as age/size composition and geographic substructure, and changes in life-history traits, such as age and size at maturity and growth rate. While fishing has played a dominant role in the dynamics of most of these stocks, it is clear that changes in the environment have contributed to changes in recruitment, growth, and natural mortality. Comparisons among stocks may help clarify the relative roles of changes in fishing pressure, the physical environment, and the biotic environment in terms of both predators and prey. We report some of the findings of a workshop (ICES 2006b) that reviewed and synthesized knowledge regarding factors influencing the decline and recovery of cod stocks. Particular attention is given to reasons for non-recovery of several of the Northwest Atlantic stocks.

Atlantic cod stocks

Cod stocks differ in many respects. Some (e.g., southern Grand Bank, Flemish Cap) are associated with shelf areas far from land, but most stocks inhabit areas adjacent to a land mass. Some of the latter stocks have components associated with the coast, and these may be relatively distinct and sedentary, especially if they inhabit fjord systems such as at West Greenland (Hovgård and Wieland 2008) and Norway (Løken et al. 1994). Many such “unit stocks” are considered to represent stock complexes or metapopulations (Smedbol and Wroblewski 2002, Horwood et al. 2006).

The ecosystems in which the stocks are embedded differ in many aspects. For example, temperature decreases from south to north on both sides of the North Atlantic, but the difference in temperature between east and west at a given latitude can be substantial because of the pattern of ocean circulation. The Labrador Current and local winter cooling produce low temperatures off Labrador and eastern Newfoundland, in the Gulf of St. Lawrence, and on the eastern Scotian Shelf, whereas the North Atlantic Drift warms the coasts of Europe and provides suitable temperature conditions for cod far into the Barents Sea. Average bottom temperatures, as reported by Brander (2007), vary from 0°C off Labrador to 11°C in the Celtic Sea.

The ecosystems also vary with respect to finfish diversity. The arcto-boreal ecosystems (Labrador-Newfoundland, Iceland, Barents Sea) have historically been dominated by one piscivorous fish species (cod) and one forage species (capelin, *Mallotus villosus*) (Livingston and Tjelmeland 2000). In contrast, ecosystems toward the southern limit of the cod’s distribution, such as Georges Bank in the west and the North Sea in the east, have a broader array of piscivores and potential prey. The Baltic Sea fauna is depauperate compared to the adjacent North Sea because of its low salinity, and has historically been dominated by cod and two species of clupeoids serving as forage fish.

The stocks have historically differed considerably in size (Table 1; Fig. 2). During the period for which data are available, the maximum biomass of both the West Greenland and arcto-Norwegian cod has been estimated at about 4 million t immediately after the Second World War, whereas another four (S. Labrador–E. Newfoundland in the northwest and Iceland, North Sea, and eastern Baltic Sea in the northeast) have exceeded 1 million t. In contrast, the Gulf of Maine stock in the northwest and the west Scotland, Irish Sea, and Celtic Sea stocks in the northeast have not exceeded 60,000 t.

Changes in total biomass

Information on population dynamics is available for most stocks from mathematical reconstruction models (sequential population analysis, SPA) that are based on commercial catch data and biological sampling of size and age distributions as well as on fishery-independent indices of abundance (ICES 2005, Shelton et al. 2006, Brander 2007). (We use SPA as a generic term for such models, which include virtual population analysis, VPA.) It is common in inter-stock comparisons to focus on trends in spawning stock biomass (SSB) (e.g., Myers et al. 1996) because of the implicit, though flawed (Marteinsdottir and Begg 2002), assumption of proportionality between SSB and reproductive potential. However, trends in SSB may not reflect the extent of stock decline if the computation of SSB incorporates the decline in age-at-maturity documented for many stocks (Bratney et al. 2005). Therefore, we will focus on trends in total biomass (Table 1; Fig. 2).

Although the output of reconstruction models is a valuable source of information on the dynamics of individual stocks, models may differ greatly among stocks with respect to structure, assumptions, and the inclusion of data such as unreported catch, recreational catch, discards, and estimates of removals by conspecifics and other predators. The extent to which such differences influence the results of inter-stock comparisons is generally not documented. In addition, the time periods covered may differ considerably, which hampers the comparison of long-term trends. Some models go back to the 1940s and even beyond, but many go back only to the 1970s or even just the 1980s. In addition, SPA has been discontinued for formal assessment of some stocks (Table 1), viz. West Greenland (Hovgård and Wieland 2008), S. Labrador–E. Newfoundland (Lilly 2008), Flemish Cap (Vázquez and Cerviño 2005), eastern Scotian Shelf (Fanning et al. 2003), western Scotian Shelf (Clark and Hinze 2004) and, most recently, southern Newfoundland (DFO 2006). In most of these cases, the stock trajectories continue to be monitored by bottom-trawl surveys. For example, the survey of the S. Labrador–E. Newfoundland stock indicates that biomass in the offshore continued to decline after the decision that SPA models were no longer reflective

Table 1. Stock names, management areas, the period covered by recent population models and the maximum total biomass within that period.

| Stock | NAFO or ICES management area | SPA period | Maximum total bio-mass (1,000 t) (year) | Data sources and ICES assessment working group codes |
|------------------------------------|------------------------------|------------|---|---|
| West Greenland (WGR) | I | 1946-1989 | 4,129 (1949) | Buch et al. 1994; updated by Hovgård and Wieland 2008 |
| N. Labrador (NLAB) | 2GH | — | — | Lilly and Murphy 2004 |
| S. Labrador–E. Newfoundland (SLEN) | 2J3KL | 1962-1992 | 2,982 (1962) | Bishop et al. 1993 |
| Flemish Cap (FLEM) | 3M | 1972-2001 | 113 (1976) | Vázquez and Cerviño 2002 |
| S. Grand Bank (SGBK) | 3NO | 1959-2004 | 395 (1967) | Power et al. 2005 |
| S. Newfoundland (SNF) | 3Ps | 1977-2004 | 200 (1985) | Bratley et al. 2005 |
| N. Gulf of St. Lawrence (NGSL) | 3Pn4RS | 1974-2005 | 603 (1983) | Fréchet et al. 2005 |
| S. Gulf of St. Lawrence (SGSL) | 4TVn | 1971-2004 | 474 (1986) | Chouinard et al. 2006 |
| E. Scotian Shelf (ESS) | 4Vsw | 1970-1997 | 320 (1985) | Mohn et al. 1998; Fanning et al. 2003 |
| W. Scotian Shelf (WSS) | 4X | 1983-2002 | 77 (1983) | Clark et al. 2002; Clark and Hinze 2004 |
| Gulf of Maine (GOM) | 5Y | 1982-2004 | 41 (1982) | Mayo and Col 2005 |
| Georges Bank (GEOB) | 5Z, 6 | 1978-2004 | 141 (1981) | O'Brien et al. 2005 |
| Arcto-Norwegian (ARNO) | I, II | 1946-2004 | 4,169 (1946) | ICES 2005: AFWG |
| Kattegat (KAT) | IIIc | 1971-2004 | 45 (1973) | ICES 2005: WGBFAS |
| W. Baltic (WBAK) | IIIId, 22-24 | 1970-2004 | 116 (1972) | ICES 2005: WGBFAS |
| E. Baltic (EBAL) | IIIId, 25-32 | 1966-2004 | 1,057 (1982) | ICES 2005: WGBFAS |
| North Sea (NSEA) | IIIa, IV, VIIId | 1963-2004 | 1,146 (1980) | ICES 2005: WGNSSK |
| Iceland (ICE) | Va | 1955-2004 | 2,282 (1955) | ICES 2005: NWWG |
| Faroe Plateau (FAR) | Vb1 | 1961-2004 | 155 (1976) | ICES 2005: NWWG |
| W. Scotland (WSCT) | V1a | 1978-2004 | 54 (1980) | ICES 2005: WGNSDS |
| Irish Sea (ISEA) | V1a | 1968-2003 | 30 (1973) | ICES 2005: WGNSDS |
| Celtic Sea (CSEA) | VIIe-k | 1971-2003 | 34 (1988) | ICES 2005: WGSDDS |

NAFO is Northwest Atlantic Fisheries Organization. ICES is the International Commission for the Exploration of the Sea. The ICES assessment reports are at <http://www.ices.dk/iceswork/workinggroups.asp>.

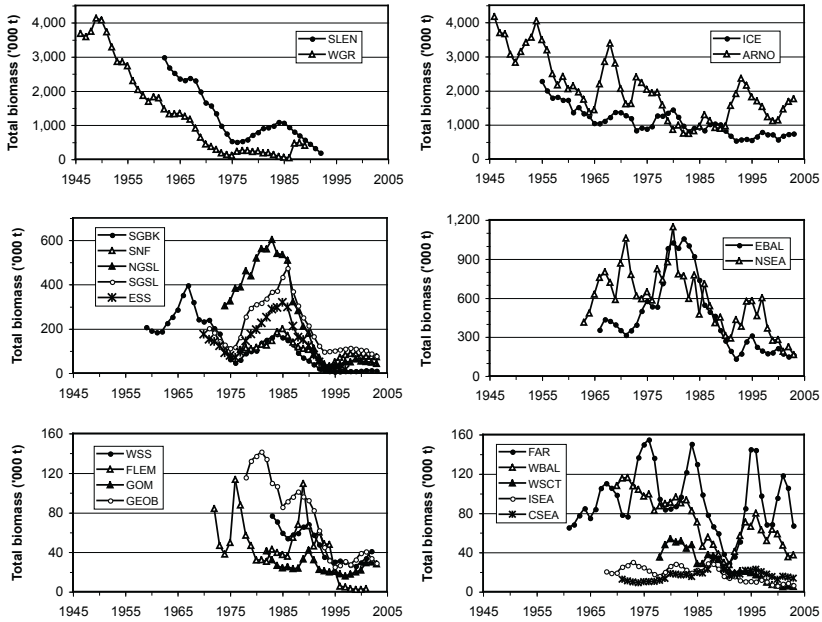


Figure 2. Total biomass (thousand t), as estimated by sequential population analysis (SPA), for cod stocks in the Northwest Atlantic (left panels) and Northeast Atlantic (right panels). The stocks are arranged from large (top panels) to small (bottom panels). Note differing scales on ordinate axes. Data sources as in Table 1.

of stock dynamics (Lilly 2008). The extent of decline in this stock, as deduced from research vessel catches, is considerably greater than indicated by SPAs of the early 1990s (Bishop et al. 1993), but somewhat less than indicated by the SPA used by Smedbol et al. (2002) and reported by Shelton et al. (2006).

If 1970 is used as a point of reference (Brander 2007), then all stocks except the Celtic Sea stock have declined (Fig. 2). However, there have been periods of increase and of decrease in almost all stocks, and even the Celtic Sea stock is now below its peak in the late 1980s. In addition, the longer term views available for some stocks, especially those of West Greenland and the Barents Sea, suggest that the extent of decline during the latter half of the twentieth century may actually be greater than indicated by the short-term view afforded by current assessment models.

As noted above, the declines have been more pronounced in the Northwest Atlantic than in the Northeast (Fig. 2). The West Greenland stock declined to a low level by the mid-1970s and collapsed in the early 1990s (Fig. 2; Hovgård and Wieland 2008). The Northern Labrador stock (not shown because no SPA is available) had collapsed by the late 1970s and had virtually disappeared by the late 1980s (Smedbol et al. 2002, Lilly and Murphy 2004). Stocks farther south off Atlantic Canada, from Southern Labrador–Eastern Newfoundland to the eastern Scotian Shelf, continued to be productive into the 1980s, but collapsed in the late 1980s and early 1990s (Fig. 2). In contrast, stocks in the Northeast Atlantic are currently in a variety of states, from moderately good (arcto-Norwegian, Iceland) to depressed (west of Scotland, North Sea, Baltic Sea), but none are considered to have collapsed.

Major hypotheses for changes in stock biomass

Stock biomass is influenced by the effects of fishing and climate on recruitment, individual growth, and mortality. The various factors interact, and it is often difficult to disentangle them.

Fisheries

The effect of fisheries on stock biomass

It is generally accepted that excessive fishing pressure has been the major reason for the declines in cod stocks (Myers et al. 1996, Sinclair and Murawski 1997). However, there are many reasons why fishing may have been excessive, and their relative importance may differ considerably among stocks. The reasons for overfishing include management goals that may not have been precautionary, especially in earlier years (Sinclair and Murawski 1997, Garcia and Moreno 2005), scientific overestimation of population size (Sinclair et al. 1991, Mohn 1999), the establishment of management plans that include landings in excess of scientific advice (Horwood et al. 2006, Shelton et al. 2006), and the killing of fish in excess of the amount specified in management plans. The latter includes reported overruns and non-reported catches, which may include both landings (Horwood et al. 2006) and discards (Hutchings and Ferguson 2000). A full inquiry into causes of declines and recoveries should include and distinguish among the above components. We can mention only a few examples.

The importance of unrestrained fishing is clearly demonstrated in the Northwest Atlantic, where distant-water trawling fleets caused a substantial increase in landings during the late 1950s and 1960s (Fig. 3) and contributed to a rapid decline in the biomass of several stocks during the 1960s and 1970s (Fig. 2). The declaration of 200 nautical mile fisher-

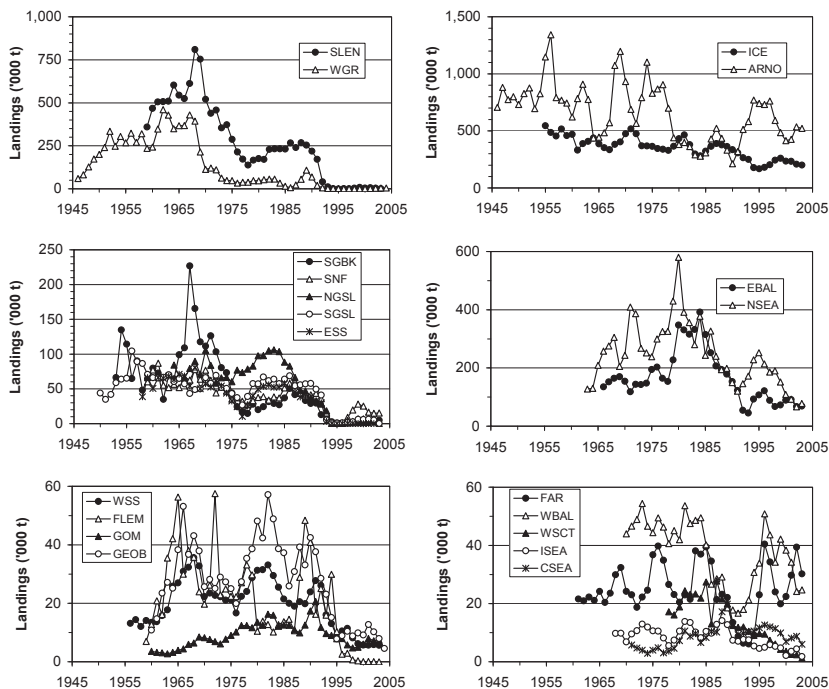


Figure 3. Landings (thousand t) from cod stocks in the Northwest Atlantic (left panels) and Northeast Atlantic (right panels). The stocks are arranged from large (top panels) to small (bottom panels). Note different scales on ordinate axes. Data sources as in Table 1. For Gulf of Maine (GOM), landings from 1981 are commercial only, and commercial plus recreational thereafter. For Flemish Cap (FLEM), landings from 1988 to the late 1990s include estimates that represent a large proportion of the total.

ies zones in 1977 reduced fishing mortality temporarily and contributed to recovery of many stocks, especially S. Labrador–E. Newfoundland, southern Grand Bank, southern Newfoundland, and eastern Scotian Shelf. However, most Canadian stocks declined once again, and to a greater extent, during the late 1980s and early 1990s. Some investigators (Hutchings and Myers 1994, Hutchings 1996, Myers et al. 1996) have stated that these declines during the late 1980s and early 1990s were caused entirely by fishing, and indeed SPA modeling indicates a sharp increase in fishing mortality for many of these stocks, most notably those from the eastern Scotian Shelf northward to S. Labrador–E. Newfoundland (Fig. 4). Fishing mortality tended to be chronically higher

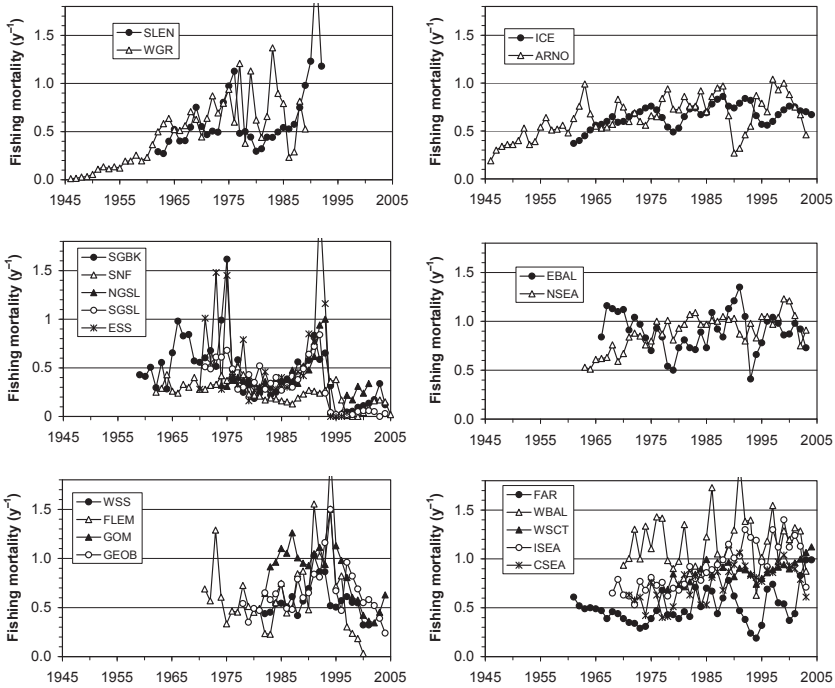


Figure 4. Fishing mortality, as estimated by sequential population analysis (SPA), for cod stocks in the Northwest Atlantic (left panels) and Northeast Atlantic (right panels). The stocks are arranged from large (top panels) to small (bottom panels). Data sources as in Table 1.

than intended (the retrospective problem as described in Sinclair et al. 1991), but the cause of the sharp rise in fishing mortality is not entirely clear. In the case of the S. Labrador–E. Newfoundland stock, there was a large and sudden downward re-evaluation of the population estimate in 1988–1989 (Baird et al. 1991) and, for socioeconomic reasons, the total allowable catch (TAC) was not adjusted downward to the full extent implied by the revised estimate, causing fishing mortality to rise rapidly (Shelton 1998). It is unclear whether this by itself can explain the collapse of the stock because reported landings have been insufficient to account for the large and rapid decline in indices of abundance from research surveys (Shelton and Lilly 2000, Lilly 2008). Additional factors that might have contributed to the collapse are discussed below.

If fishing were the only, or major, cause of the declines, then cessation of fishing might be expected to halt and then reverse the declines

(Myers et al. 1995). Moratoria on directed fishing were indeed instituted for S. Labrador–E. Newfoundland cod in 1992, for all other stocks adjacent to Canada as far south as the eastern Scotian Shelf in 1993, for southern Grand Bank cod in 1994, and for Flemish Cap cod in 1999. The effects of these moratoria were variable but generally much less positive than had been hoped (Rice et al. 2003). The S. Labrador–E. Newfoundland and eastern Scotian Shelf stocks continued to decline after imposition of the moratoria, and have shown no signs of recovery even though directed fisheries have remained closed (except for coastal fisheries that targeted inshore populations of the S. Labrador–E. Newfoundland stock during some years). The fishery on the southern Grand Bank cod stock has also remained closed, but there is evidence that recovery has been impeded by bycatch in fisheries directed at other species (Shelton and Morgan 2005). The Flemish Cap stock has shown no sign of recovery. The two stocks in the Gulf of St. Lawrence recovered slightly, but small directed fisheries during most years since 1998 have reversed most of the gains. Local inshore populations off eastern Newfoundland (the coastal region of the S. Labrador–E. Newfoundland stock) also increased, but directed fisheries during 1998–2002 contributed to a substantial decline (Lilly et al. 2005). Only the southern Newfoundland stock has experienced substantial recovery and has remained open to directed fishing since being reopened in 1997. However, even that stock has been declining recently. The reopening of directed fisheries on the two Gulf of St. Lawrence stocks and the inshore area of the S. Labrador–E. Newfoundland stock are examples of instances wherein short-term socioeconomic concerns and statements by fish harvesters regarding stock status have taken precedence over the information provided by a formal scientific stock assessment process.

The contrast between the rapid rebuilding of Canadian stocks in the 1970s and early 1980s and the virtual absence of recoveries during the late 1990s and early 2000s remains only partly explained (Rice et al. 2003). The directed and bycatch fisheries of the 1990s and 2000s are certainly part of the reason (Shelton et al. 2006), but other factors appear to have contributed to lower productivity.

Other consequences of fishing

Fishing may affect populations in several additional ways. Mean age and age diversity of spawners has declined in many stocks (Marteinsdottir et al. 2005), and this has been found to affect recruitment in some stocks. For example, decline in age diversity has been associated with low recruitment in Icelandic cod (Marteinsdottir and Thorarinsson 1998). However, such an effect was not found in southern Gulf of St. Lawrence cod (Swain and Chouinard 2000). The decline in mean age and age diversity of spawners in arcto-Norwegian cod has resulted in recruitment becoming more strongly influenced by climate variability

(Ottersen et al. 2006). Fishing may cause changes in life-history traits, such as growth rate and age and size at maturation (see below). Fishing stocks down to low levels may also affect their viability because of behavioral problems, such as increased difficulty in finding a mate and breakdown of migration patterns or social structures (Allee effects; Frank and Brickman 2000). There could also be depensation associated with predation, as discussed below.

Climate variability and change

Cod stocks may respond to decadal-scale climate changes. For example, the warming of much of the northern North Atlantic during the 1920s and 1930s resulted in a general northward expansion of many fish species, including cod (Rose 2005, Drinkwater 2006). The most conspicuous change was the increased abundance and northward expansion of cod at West Greenland (Hovgård and Wieland 2008), but there was also expansion of cod farther to the north and east in the Barents Sea and increased use of northern spawning areas at both Iceland and the Norwegian coast.

Important changes were also associated with the increasingly positive (high) phase of the North Atlantic Oscillation (NAO) from the 1960s to the 1990s. During this period, the positive phase tended to result in decreased air and sea temperatures and increased ice cover in the Northwest Atlantic from the Labrador coast to the eastern Scotian Shelf, and contributed in several ways to a reduction in productivity of cod stocks in that region (Drinkwater 2002). In contrast, the intensification of the positive phase of the NAO led to increased inflow of warm Atlantic water into the Barents Sea, promoting recruitment to the arcto-Norwegian cod stock (Ottersen and Stenseth 2001). North-south differences in the impact of the NAO on cod recruitment have also been found. During a positive NAO phase, recruitment tends to be lower than normal in the southernmost stocks on both sides of the Atlantic and higher in the northernmost stocks (and vice versa for negative phase) (Brander and Mohn 2004, Stige et al. 2006).

Finally, the North Atlantic has been warming during the past decade (ICES 2006c). Although higher temperatures are generally expected to be beneficial for cod toward the northern limits of cod distribution (Planque and Frédoou 1999, Drinkwater 2005), there has been little response to date off eastern Canada (Shelton et al. 2006). For cod populations toward the southern limit of cod distribution, the warming may prove to have negative effects (Planque and Frédoou 1999, Drinkwater 2005).

Stock demographics and life-history traits

Recruitment

Much of the variability in heavily exploited cod populations is due to changes in recruitment. This is particularly evident when populations increase. For example, the abundance of cod at Greenland has been strongly dependent on the arrival of larval cod from Iceland (Drinkwater 2006, Hovgård and Wieland 2008). The increase in abundance of North Sea cod during the “gadoid outburst” of the 1960s and 1970s was due to an increase in average recruitment (Hislop 1996, Heath and Brander 2001).

Many hypotheses have been proposed to explain variability in recruitment to specific cod stocks (ICES 2005). The spawning potential of the parent population is generally assumed to be of major importance, but many factors affect the survival of progeny, such that there may be considerable among-year variability in the number of recruits per unit of spawning biomass. A high survival of progeny (recruits per unit of spawning biomass) contributed to the increase in several Canadian cod stocks in the late 1970s and early 1980s (Sinclair 1996, Chouinard et al. 2003), whereas a low (or lower) survival contributed to the decline of some of the same stocks in the late 1980s and early 1990s and their weak recovery during the late 1990s and 2000s (Shelton et al. 2006). The mechanisms by which pre-recruit survival is affected involve many aspects of the physical and biotic environment. Physical mechanisms include annual variability in the transport of the zooplanktonic food for cod larvae into the Barents Sea and North Sea (Sundby 2000) and the replenishment of salinity and oxygen in the Baltic Sea by episodic inflow of water from the Kattegat and the North Sea (Köster et al. 2005). Some examples involving feeding and predation are discussed below.

Growth

Changes in recruitment and fishing mortality have received most of the attention regarding changes in stock size, but variability in individual growth may also be important. Sinclair (1996) noted that the gradual reduction in weight-at-age from the late 1970s to the early 1990s has had a notable effect on the biomass of several stocks off Canada (particularly S. Labrador–E. Newfoundland, northern and southern Gulf of St. Lawrence, and eastern Scotian Shelf). Brander (2007) examined changes in total biomass in 15 stocks from across the Atlantic, and found that 14 have declined since 1970. In 10 of these, the periods of decline were preceded by or coincided with declines in mean weight-at-age. For the ten stocks experiencing periods of increasing total biomass, all increases were accompanied by increasing weight-at-age.

Changes in growth affect productivity and thus the biomass that can be harvested sustainably for a given fishing mortality. In addition,

Drinkwater (2002) and Brander (2007) suggested that, because TACs are in terms of weights, declines in weights-at-age should have resulted in increased numbers of fish caught per unit of quota. It is not clear whether this mechanism has played a role in Canadian stocks, because the catch predictions have generally been based on the average weight-at-age during recent years, and should therefore be close to the actual value (unless weight-at-age dropped suddenly and substantially from one year to the next). It might be of interest to investigate whether such a mechanism has contributed to the rise in fishing mortality in several Canadian stocks during the late 1980s and early 1990s.

Changes in size-at-age within a stock may result from several factors, including changes in temperature, stock size, prey abundance (see below), and size-selective fishing (Sinclair et al. 2002a,b). With respect to temperature, among-stock comparisons have shown that growth rate (Brander 1995), condition (Rätz and Lloret 2003), and overall productivity (Dutil and Brander 2003) are higher in stocks that live at higher temperatures. In addition, evidence from experiments and in the field shows that the effect of temperature change is progressively greater at lower temperatures (Brander 2007). Thus, the cooling of the 1980s and early 1990s off eastern Canada from the eastern Scotian Shelf northward may have had a particularly strong influence on cod in that area because they were already living in a relatively cold environment. Nevertheless, the large changes in size-at-age of cod in the southern Gulf of St. Lawrence from 1971 to 1998 appear to be most strongly related to changes in size-selective mortality, followed by effects of density-dependent growth, with only relatively minor variation attributed to changes in the temperature of the water occupied by the cod (Sinclair et al. 2002b).

A persistently low growth rate has been an important contributor to the continuing low productivity of several stocks off Canada (Shelton et al. 2006). This is particularly the case for the stock in the southern Gulf of St. Lawrence (Chouinard et al. 2003), and Swain et al. (2007) provide evidence that this may have been caused by genetic change in response to size-selective fishing.

Maturity

Age- and size-at-maturity have declined in many stocks (Martensdottir and Begg 2002). An examination of probabilistic maturation reaction norms (Heino et al. 2002) provides evidence for a genetic change, most likely in response to fishing, in all stocks investigated, viz. Georges Bank and Gulf of Maine (Barot et al. 2004), S. Labrador–E. Newfoundland, southern Newfoundland and southern Grand Bank (Olsen et al. 2005), and arcto-Norwegian (Heino et al. 2002). Maturing early gives a selective advantage under most high mortality regimes, because only fish that mature and reproduce before being caught will pass their genes to the

next generation. Reversion to older age-at-maturity and larger size-at-maturity when mortality is reduced may be slow if late maturation does not offer a strong selective advantage (Law 2000).

In the context of recovery from low population size, Hutchings (2005) conducted simulations to explore the consequences of a reduction in age-at-maturity, coupled with additional factors such as reduced reproductive success in first-time spawners and increased mortality upon attainment of maturity. He found that a reduction in age-at-maturity might reduce annual population growth, and concluded that fishing-induced changes in life-history traits might in themselves impede recovery.

Natural mortality

The importance of changes in natural mortality to the dynamics of cod stocks has received increased emphasis with the recognition that mortality remained high in several depressed stocks off eastern Canada after directed fishing was stopped, and that increased natural mortality slowed stock recovery (Shelton et al. 2006). Several analyses (e.g., Sinclair 2001) demonstrated that natural mortality started to increase well before the fisheries were closed. For the cod stock in the southern Gulf of St. Lawrence, analyses suggest that the increase in natural mortality played a role in the collapse of the stock (Chouinard et al. 2005), and this may be true for several other stocks as well.

A series of publications during the mid-1990s (Hutchings and Myers 1994, Myers and Cadigan 1995, Hutchings 1996, Myers et al. 1996) stated that there was no evidence of an increase in natural mortality in the S. Labrador–E. Newfoundland stock and other Canadian cod stocks during the period of collapse. It was only after data had accumulated for several additional years that analyses started to provide evidence that natural mortality had indeed increased, and such an increase was then incorporated into SPA models for the stocks in the northern (Fréchet et al. 2005) and southern (Chouinard et al. 2006) Gulf of St. Lawrence and the stock on the eastern Scotian Shelf (Mohn et al. 1998). The use of SPAs for the S. Labrador–E. Newfoundland stock as a whole was discontinued during the early 1990s, but exploration of these models demonstrated that reported landings were insufficient to account for the large and rapid decline in indices of abundance from research surveys (Shelton and Lilly 2000, Lilly 2008). The “missing fish” could be attributed to increased levels of unreported landings or discards, but might also be the result of increased natural mortality. More recently, tagging studies have provided evidence of elevated natural mortality in inshore populations along the east coast of Newfoundland (Lilly et al. 2005).

Biotic factors affecting stock biomass

Prey

Changes in the abundance or availability of prey may have consequences for growth (and condition), recruitment, and mortality of the predators. Such influences are more commonly detected in ecosystems that have relatively few prey species, such as the Baltic Sea and the arcto-boreal areas.

Capelin abundance has been positively correlated with growth rate in Icelandic cod (Stefánsson et al. 1998) and arcto-Norwegian cod (Mehl and Sunnanå 1991), and with somatic condition and liver reserves of arcto-Norwegian cod (Yaragina and Marshall 2000). For S. Labrador–E. Newfoundland cod, Krohn et al. (1997) reported that capelin biomass explained some of the variability in cod growth and condition, but other studies did not find a significant relationship (ICES 2006b, p. 89). In contrast to the positive association often seen elsewhere, the condition of cod and other groundfish species on the eastern Scotian Shelf declined significantly (Choi et al. 2004) at the same time as the biomass of pelagics increased. Bundy and Fanning (2005) hypothesized that the poor condition observed in small cod is due to competition with increased populations of planktivorous fish, and proposed that cod that are in poor condition when small may remain that way when they become larger.

A decline in condition (or liver index) might affect spawning potential of cod stocks by decreasing the likelihood of maturing (Marteinsdottir and Begg 2002), increasing the incidence of skipped spawning (Rideout et al. 2005, Jørgensen et al. 2006) and reducing the reproductive output of those fish that do spawn (Lambert and Dutil 2000).

In the absence of findings of dead or moribund fish, the question of whether a decline in cod condition has contributed to an increase in natural mortality (other than predation) is difficult to address. Nevertheless, fish exhibiting critically low condition for survival (according to the value determined to be critical in a laboratory setting) were found in the northern and southern Gulf of St. Lawrence (Lambert and Dutil 1997, Schwalme and Chouinard 1999) during the early to mid-1990s. Dutil and Lambert (2000) concluded that natural mortality from poor condition contributed to lower production of the northern Gulf of St. Lawrence cod. It is not clear whether the poor condition was related to a decline in abundance of prey, but it has been hypothesized that cooling caused a shortening of the feeding season (Castonguay et al. 1999). The decline in condition of eastern Scotian Shelf cod is not related to the abundance of pelagic prey, because the historically important prey species increased following the cod collapse (see above). For S. Labrador–E. Newfoundland cod, it was hypothesized that the collapse might be due in part to an increase in stress associated with a change

in abundance and availability of capelin (Atkinson and Bennett 1994), but data from the appropriate times and locations may be insufficient to test this hypothesis (Lilly 2001). With respect to the lack of recovery in the offshore portion of the S. Labrador–E. Newfoundland stock, Rose and O’Driscoll (2002) stated that the high mortality experienced by cod since the collapse is due to poor condition, which in turn is due to low capelin availability (but see Lilly et al. 2005).

The abundance of forage species might also affect cod through secondary links in food webs. For example, it has been hypothesized that when forage species such as capelin are in low abundance, then predators such as harp seals (Nilssen et al. 2000) may feed to a greater extent on cod. Also, cannibalism might increase within a cod population when prey abundance is low, and this might reduce year-class strength. For example, the incidence of cannibalism in arcto-Norwegian cod appears to increase when capelin biomass is low (Hamre 2003, ICES 2006a).

Planktivorous forage fish might affect cod by preying on, or competing with, its early life-history stages (eggs, larvae and perhaps pelagic juveniles). A negative relationship between the biomass of pelagic fish (herring and mackerel) and the number of recruits per unit of spawning biomass of cod has been shown for the southern Gulf of St. Lawrence (Swain and Sinclair 2000). High values of recruits per unit of spawning biomass from the mid-1970s to the early 1980s coincided with a period during which pelagic biomass had been reduced by overfishing. A variant of this mechanism is the “cultivator effect”: a large predator may protect its offspring by preying on species that are their potential predators and competitors. If the predator becomes less abundant, its prey becomes more abundant, through released predation, and then keeps the predator under control at a low level by preying on or competing with its early life-history stages. Such a mechanism has been hypothesized for cod and its planktivorous fish prey in the Baltic Sea (Köster and Möllmann 2000) and on the eastern Scotian Shelf (Bundy and Fanning 2005).

Predators

Predation is an important component of natural mortality, especially for smaller cod, as has been illustrated by numerous diet studies and multispecies models. An important question is whether natural mortality varies over time, and whether such variability contributes to large changes in stock abundance.

As noted above, natural mortality evidently increased in several Canadian stocks during the 1980s and has remained high. The causes remain unclear and contentious. Numerous studies have discussed the possibility that predation by (gray and/or harp) seals is an important component of the high mortality in the eastern Scotian Shelf stock (Fu et al. 2001, Bundy and Fanning 2005), in the southern and northern Gulf

of St. Lawrence stocks (Chouinard et al. 2005, Fréchet et al. 2005) and in the S. Labrador–E. Newfoundland stock (Lilly et al. 2005). Formal cod stock assessment meetings within Canada have concluded that predation by seals has contributed to recovery of these stocks being slow or nonexistent (Rice et al. 2003).

One of the paradoxes associated with these analyses is that elevated mortality appears in not only juvenile cod but also adult cod, whereas diet data generally reveal seal feeding only on small cod (Hammill and Stenson 2000). It has been suggested by some (e.g., Chouinard et al. 2005) that the high mortality of adult cod might be a consequence of belly-feeding (a manner of feeding whereby the seal takes a bite from the cod's belly, leaving the head and muscle mass). Such feeding by seals is difficult to detect by visual examination of stomach contents or scats because there are no hard parts involved. However, belly-feeding by harp seals on cod has been observed in eastern Newfoundland (Lilly and Murphy 2004).

The heightened attention to the role of seals and other marine mammals in the dynamics of cod stocks off Canada is partly due to opposing population trends. Many species of marine mammals were heavily exploited for centuries and consequently declined to low numbers, but some have increased during the recent 2-3 decades under more restrictive management measures. In the Northwest Atlantic, this is particularly the case for harp seals (Hammill and Stenson 2005) and gray seals (Trzcinski et al. 2005). In contrast, exploitation of cod has increased in recent decades, and many stocks are at all-time lows. Seals (and other marine mammals) do not have a strong dependency on cod, their major prey usually being pelagic species of fish and squid. However, if these predators continue to eat some cod even if cod abundance is low, then they may contribute toward keeping the cod in a "predator pit" (Shelton and Healey 1999). Marine mammals may also compete with cod for prey resources such as capelin and sand lance, thus affecting cod growth and condition.

Loss and re-establishment of spawning populations

It has long been recognized that Atlantic cod has a rich population structure, with many of the unit stocks identified for management purposes (Fig. 1; Table 1) consisting of several substocks or metapopulations (Templeman 1962). Ames (2004) provides evidence that some of this substock structure may have disappeared, or have been reduced, even before the initiation of scientific study of the Atlantic cod resources. The existence of metapopulation structure has been supported and amplified by recent studies using advanced techniques in fields such as genetics (Ruzzante et al. 1999), otolith chemistry (Jónsdóttir et al.

2006), and tagging (Wright et al. 2006). The view of stock dynamics afforded by SPA (Fig. 2) provides considerable reason for concern about the viability of “unit stocks,” but there are additional concerns related to maintaining population diversity within the stocks (Frank and Brickman 2000, Smedbol and Stephenson 2001). Some components may be more susceptible than others to overexploitation because they are smaller, less productive, or more accessible for harvesting. The extent to which among-component differences in recruitment, growth, and mortality have contributed to the overall decline in unit stocks is by no means clear. However, there are examples of different population trajectories within the established unit stocks. The S. Labrador–E. Newfoundland stock declined first in the north (deYoung and Rose 1993, Lilly 1994) and the recent decline in North Sea cod has been more pronounced in the south (Horwood et al. 2006).

An important question for management is whether areas where stocks or stock components have been depleted can be repopulated by cod from adjacent areas. Obviously, colonization of suitable areas has happened over the scale of millennia, but evidence of recolonization of vacated areas or supplementation of depleted areas during recent times is less clear. Much of the increase in the cod at West Greenland during the 1920s and 1930s was due to eggs and larvae imported by currents from Iceland (Buch et al. 1994), but it remains uncertain whether the fish from Iceland established self-supporting spawning populations at West Greenland, as stated by Anisimov et al. (2007), or depended on the inflow of new recruits from Iceland. Along the eastern Skagerrak coast, where local spawning aggregations have been depleted, juvenile cod may still occur in high numbers in some years, but most are recruited from offshore spawning areas, mainly in the North Sea, and they return to offshore areas instead of spawning locally along the coast (Svedäng and Svenson 2006). For the S. Labrador–E. Newfoundland stock, there is concern that fishing on inshore populations will lessen the likelihood that those populations will expand to offshore waters and establish spawning groups there (Lilly et al. 2005). However, Beacham et al. (2002) contend that the population substructure that has been demonstrated between most inshore and offshore areas indicates a low likelihood that inshore-spawning cod will contribute to offshore recovery. In addition, Ruzzante et al. (2001) found that the geographic pattern of genetic differentiation in the offshore remained stable from the mid-1960s (pre-collapse) to the mid-1990s (post-collapse), from which they inferred that if recovery eventually occurs, it will likely be through in situ population re-growth rather than by immigration.

Concluding remarks

We provide examples of the insight that may be derived from among-stock comparisons. However, there is much opportunity for additional study. For example, the stocks off eastern Canada differ with respect to the extent of collapse, degree of recovery, and relative importance of the various factors contributing to low productivity since the collapse. These differences exist over short distances, and could provide the contrast required for more detailed investigation. Another example of strong contrast is the divergent histories of arcto-boreal stocks on either side of the North Atlantic. What have been the relative roles of fisheries and climate variability (especially with reference to the North Atlantic Oscillation) in the collapse of the S. Labrador–E. Newfoundland stock and the persistence of the arcto-Norwegian stock?

A general conclusion from the experience off eastern Canada is that fisheries scientists and managers may have limited ability to “rebuild” to previous levels any cod stocks that might decline to very low levels. Simply turning off directed fishing may be insufficient to promote recovery. Bycatch in fisheries directed at other species in conjunction with various natural phenomena, including depensation due to predation and altered life-history traits, may constrain such stocks at low abundance for considerable periods.

The effects of fishing and climate variability interact. Stocks may become more sensitive to the effects of fishing when adverse climate conditions reduce productivity (reduced recruitment and growth; increased natural mortality) and more sensitive to climate when fishing has caused changes in population processes (growth, maturation) and demographic properties (age structure and geographic sub-structure). Some life-history traits, especially growth and maturation, can be monitored by sampling commercial and research catches and may give timely indications of changes in productivity. In order to develop their routine use in assessing risk of collapse under different fisheries management strategies, indicators of possible change in productivity, such as weight-at-age, somatic condition, liver index and maturation reaction norm, should be investigated using tropho-dynamic, life-history, and risk-assessment models.

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The Decline, Recovery, and Collapse of Atlantic Cod (*Gadus morhua*) off Labrador and Eastern Newfoundland

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Abstract

The stock of Atlantic cod (*Gadus morhua*) off Labrador and eastern Newfoundland, in Northwest Atlantic Fisheries Organization (NAFO) divisions 2J3KL, declined severely in the 1960s and 1970s, recovered partially during the 1980s, and then collapsed to a very low level during the early 1990s. The stock was closed to directed fishing in 1992, and has remained closed in the offshore, but there have been no sustained signs of recovery of offshore populations. The first decline was caused by overfishing, notably by non-Canadian trawler fleets. Recovery was promoted by a reduction in landings attending the 1977 declaration by Canada of a 200 mile fishery limit and good growth of young year classes that were already in the population. The collapse in the late 1980s and early 1990s was caused by a confluence of negative factors, including fishing mortality that was higher than intended because of overestimation of stock size during the 1980s, a decision not to reduce fishing mortality dramatically when a sudden and severe downward reevaluation of stock status was announced (1988-1989), and the arrival of severe oceanographic conditions during the early 1990s. The lack of recovery is due largely to extremely high mortality. There is insufficient information to determine whether this mortality is caused by ongoing fishing for other species or by natural factors. The latter include the possibilities that the quantity or quality of prey is limiting and that the stock is being held in a predator-prey pit by seals and other predators.

Introduction

The stock of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, often referred to as the “northern cod,” experienced a severe decline during the 1960s and 1970s, a partial recovery during the 1980s, and a collapse during the late 1980s and early 1990s. Despite a moratorium that was imposed on directed fishing in 1992, and has continued to the present (2006) in the offshore, there have been no sustained signs of recovery of the offshore populations.

The literature on the biology and dynamics of northern cod is voluminous and often contradictory; see overviews by Lilly and Murphy (2004), Vilhjálmsson et al. (2005), and Lilly et al. (2006). The present paper provides a brief description of the fishery, population dynamics, and environmental trends, and presents a simple comparison of the two declines, with particular attention to the manner in which science, management, and climate variability may have contributed to the lack of success in arresting the collapse. Difficulties associated with determining the extent, timing, and causes of mortality are emphasized. Although much recent attention has been directed to inshore populations (see below), the present paper focuses on the offshore populations that at one time constituted the bulk of the stock.

The stock

The northern cod stock occupies Northwest Atlantic Fisheries Organization (NAFO) divisions 2J3KL, which extend from the southern Labrador Shelf at 55°20'N to the northern half of Grand Bank at 46°00'N. Within this area, cod occur from the coast to 600 m, and occasionally to at least 800 m, on the upper continental slope.

The stock has long been considered a stock complex (Templeman 1962, Lear 1986, Smedbol and Wroblewski 2002), although individual populations are poorly identified and distinguished. Historically, much of the cod overwintered in deep water on the outer slopes of the continental shelf. During spring most of these fish moved onto the shelf, and many migrated during late spring and summer to coastal waters where they fed on capelin (*Mallotus villosus*) that had approached the coast to spawn (Templeman 1966). The return migration occurred during autumn. The extent to which this inshore-offshore migration has persisted since the collapse of the stock is unclear (Lilly et al. 2006). There are also inshore populations that appear to be genetically and functionally distinct from populations in the offshore (Ruzzante et al. 1999, 2001; Beacham et al. 2002; Lilly et al. 2006). It is thought that these inshore populations have historically been very small relative to the populations that overwintered and spawned in the offshore. The biology and dynamics of the inshore populations have been studied

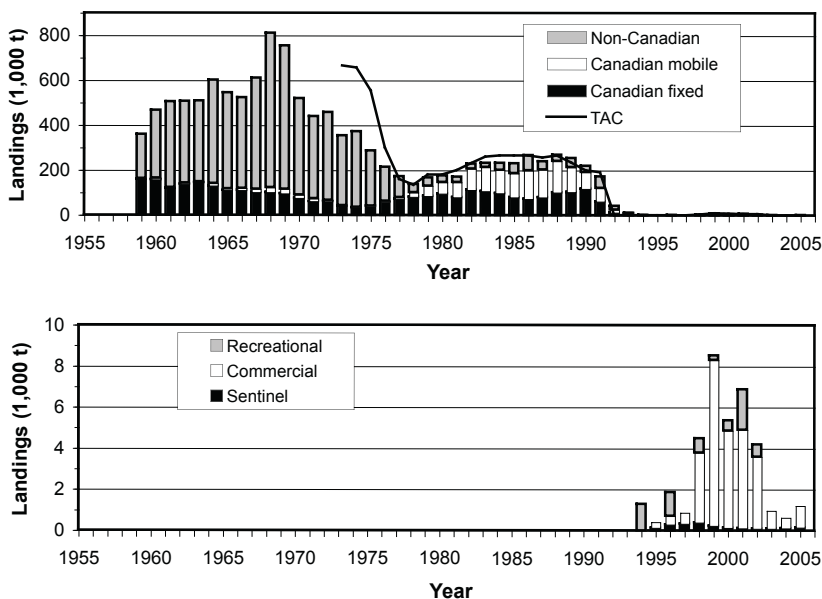


Figure 1. Total allowable catches (TACs) and landings (thousands of tons) of cod in NAFO divisions 2J3KL during 1959-2005. The upper panel shows landings by non-Canadian and Canadian fleets, with the latter divided into mobile gear (offshore) and fixed gear (mainly inshore). The lower panel shows fixed gear landings by sector during 1994-2005. Commercial landings include bycatch (from Lilly et al. 2006).

intensively during the past decade (Rose 2003, Lilly and Murphy 2004, Lilly et al. 2006).

The fishery

For centuries, harvesters caught the cod during its summer feeding migrations into shallow water near the coast and on the plateau of Grand Bank (Templeman 1966, Lear 1998). Deep waters ceased to be refugia in the 1950s and 1960s, when distant-water trawlers from Europe located and exploited the dense aggregations of cod overwintering along the shelf break and longliners with powered gurdies located and fished the deep nearshore waters off the headlands and in the bays. The longliners were introduced in the 1950s and switched to highly effective monofilament gillnets in the 1960s (Templeman 1966).

Reported landings escalated from 360,000 t in 1959 to 810,000 t in 1968 (Fig. 1). Management by total allowable catch (TAC) was intro-

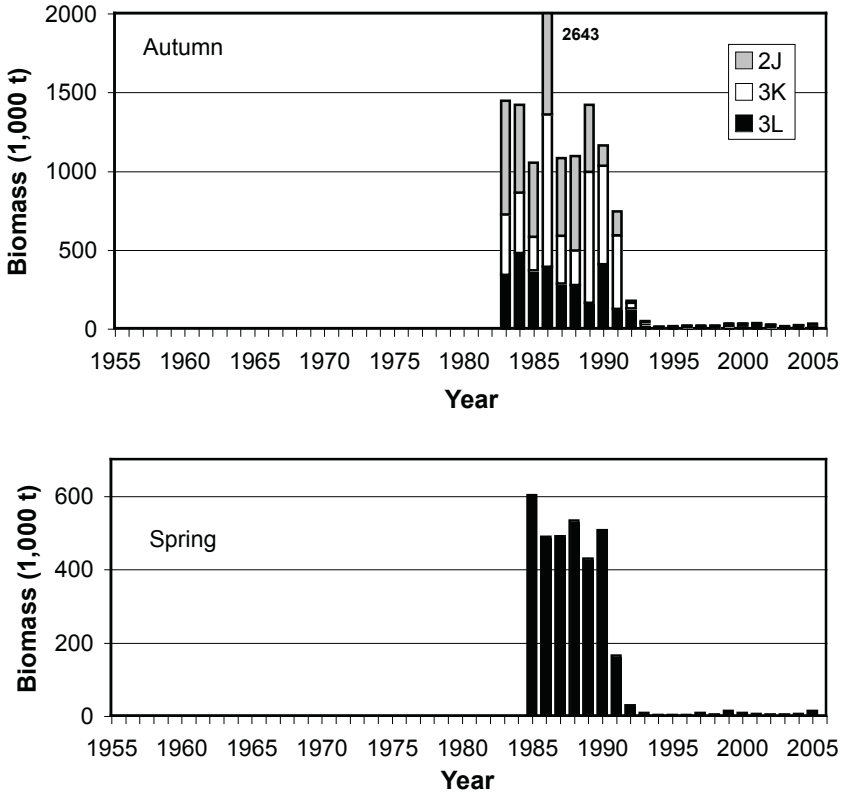


Figure 2. Biomass indices from bottom-trawl surveys in divisions 2J3KL during autumn (top panel) and division 3L during spring (bottom panel) (from Lilly et al. 2006). The total in autumn 1986 was 2,643,000 t.

duced in 1973, but the early TACs were ineffective at controlling fishing mortality, since they proved to have been set much too high. Landings plummeted to 214,000 t in 1976. Canada declared a 200 nautical mile zone of Extended Fishery Jurisdiction in 1977 and landings were further reduced to 139,000 t in 1978. Landings rose to about 250,000 t during the 1980s as the inshore fishery experienced greater success and Canadian trawlers replaced the non-Canadian trawlers on the offshore grounds. However, landings declined in the early 1990s as quotas were reduced and cod became increasingly difficult to find. A moratorium on directed commercial fishing was declared in July 1992.

Research surveys showed that the stock continued to decline for at least two years after the start of the moratorium (Fig. 2). By the

mid-1990s, it was apparent that the offshore populations were barely detectable; the cod were small and broadly distributed at low density. However, some inshore populations in the southern half of the stock area appeared to be more productive. They included cod that were older and larger than those in the offshore, and they occurred at densities that supported catch rates in sentinel surveys (small inshore test fisheries conducted by commercial fish harvesters) that were surprisingly high when such monitoring started in 1995. Catch rates in these sentinel surveys increased during the next few years.

Although the moratorium on directed commercial fishing was declared in 1992 and unrestricted recreational fishing was terminated at the end of 1993, small bycatch and directed fisheries were permitted in the inshore in subsequent years (Lilly et al. 2003, 2006). These fisheries (Fig. 1) included the sentinel surveys, which occurred every year starting in 1995, and limited recreational fisheries, which were permitted in some years. They also included directed commercial fisheries that were reintroduced to the inshore alone in 1998 but closed in 2003. Bycatches in fisheries directed at other species occurred in every year. The peak landings from all sectors combined was about 8,500 t in 1999.

Population dynamics

Prior to the collapse of the stock, mathematical reconstruction of the population based on the reported landings (sequential population analysis or SPA) was the main tool used to estimate the size of the stock as a whole and to provide a basis for projections (Bishop and Shelton 1997). The use of SPA was discontinued during the early 1990s because of poor fit between model output and the index of abundance derived from the autumn bottom-trawl surveys (Shelton and Lilly 2000). The poor fit could have resulted from several causes. (1) The survey indices may have been positively biased for a few consecutive years, suggesting that the decline started before the early 1990s. For support of this idea, see critiques by Hutchings (1996) and Hutchings and Ferguson (2000). If, however, the survey indices were a good reflection of the trend in abundance, then the stock declined rapidly in the early 1990s and a large number of fish are unaccounted for in the landings. This leads to two other classes of possibilities. (2) The fish were caught by either Canadian or non-Canadian fleets and either discarded or landed without reporting, or (3) a large number of cod died through natural causes, such as predation or poor condition attending low availability of suitable prey. Several “illustrative” SPA models were attempted in the late 1990s and 2000s. One was based on the studies of Shelton and Lilly (2000), who computed the number and age of fish that would have to be added to the reported catch during several years in the early 1990s to make the catch fit the survey index, without relaxing standard

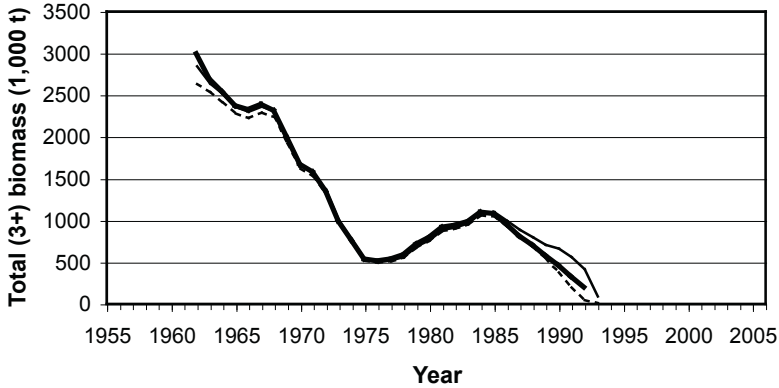


Figure 3. Trend in total (3+) biomass (thousands of tons) as estimated by sequential population analysis (SPA). The solid bold line shows the biomass from the 1993 assessment (Bishop et al. 1993, reconstructed by Peter Shelton, DFO, St. John's, NL, Canada, 2003, pers. comm.); the dashed line shows an “illustrative” model with no alteration of catch (Lilly et al. 1998); and the thin solid line shows a model with sufficient unreported catch added to allow the model to fit the pattern in the survey index (Smedbol et al. 2002, Shelton et al. 2006).

assumptions regarding natural mortality and catchability. This “missing fish” SPA was described by Smedbol et al. (2002). Some of the output is provided by Shelton et al. (2006).

The models indicated that the 3+ biomass declined from almost 3,000,000 t in the early 1960s to about 500,000 t in 1975-1977 (Fig. 3). The stock recovered partially to just over 1,000,000 t by the mid-1980s, but declined again during the late 1980s and reached an extremely low level by about 1994. The actual time course from the mid-1980s onward is somewhat uncertain, but is very important, because one must know when events occurred before one can investigate cause. At what time during the second decline did the stock reach the nadir of the first decline? SPA models based on reported catch indicate that total biomass dropped below 500,000 t during 1989 (Bishop et al. 1993), whereas the comparable date from the SPA model in which an estimate of unreported catch was added (the missing fish model; Smedbol et al. 2002) would be 1991. Although the time course of the collapse remains uncertain, the stock clearly dropped quickly through the floor established in the late 1970s and continued to decline. This uncertainty about the actual time course of the collapse means that the biomass at the time that

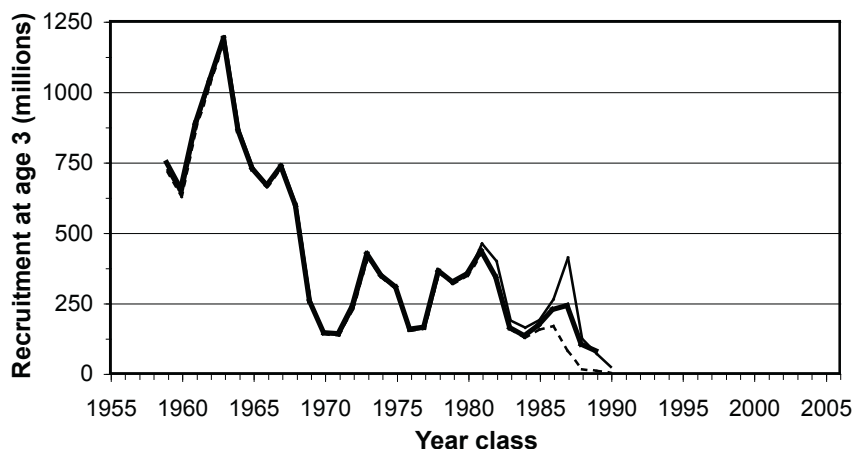


Figure 4. Recruitment at age 3 (in millions) as estimated by various SPAs. Lines as in Fig. 3.

the moratorium was imposed (July 1992) is uncertain, but both models discussed above indicate that the stock was already below its lowest level of the late 1970s.

Recruitment, as estimated by SPA (Fig. 4), peaked in the early 1960s and then declined to a low level by 1970-1971. There followed three periods of moderately good recruitment. The last of these (the 1986 and 1987 year classes) is of great interest. These year classes seemed moderately strong at ages 2 and 3 in research vessel surveys (Fig. 5) and were caught in large numbers in the inshore fishery in 3L during the early 1990s, but they seemed to disappear rapidly (Shelton and Lilly 2000). Perception of the strength of these year classes, especially the 1987 year class, varies considerably depending on the data and models that are chosen (Fig. 4, 5). All year classes since the early 1990s have been very weak.

Fishing mortality, as estimated by SPA (Fig. 6), increased during the 1960s and 1970s to a peak exceeding 1.0 y^{-1} in 1976, decreased after Canada's declaration of a 200 mile limit, and then increased gradually through the 1980s, with an apparent rapid escalation to extremely high values in the late 1980s and early 1990s. Total mortality as estimated from surveys also increased to extremely high levels in the early 1990s (Fig. 7), and remained high subsequent to the collapse.

There have also been important changes in life-history characteristics (Lilly et al. 2006). The sampling of commercial landings has shown that mean weight-at-age increased during the late 1970s and early 1980s

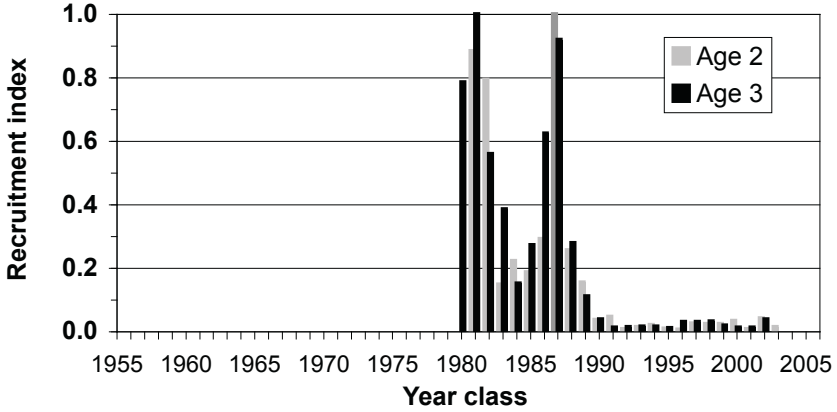


Figure 5. Relative sizes of the 1980-2003 year classes in the offshore of divisions 2J3KL, as measured by the mean catch per tow at ages 2 and 3 during the autumn bottom-trawl surveys. Number per tow has been scaled to a maximum of 1 within the time-series for each age (from Lilly et al. 2006).

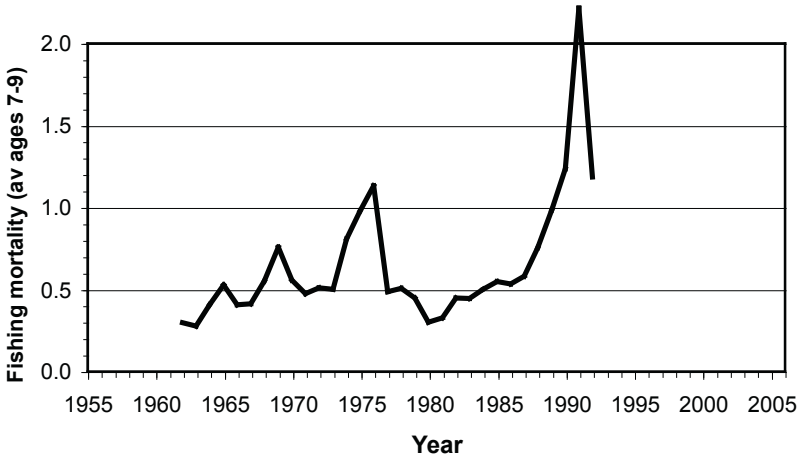


Figure 6. Fishing mortality, averaged over ages 7-9, as estimated by SPA during the 1993 assessment (Bishop et al. 1993).

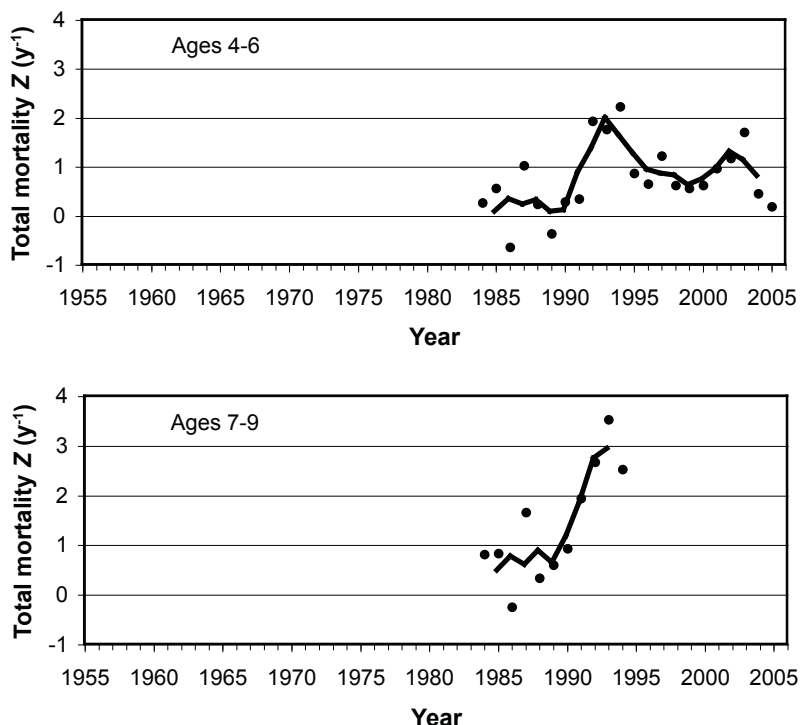


Figure 7. Annual instantaneous total mortality (Z ; y^{-1}) calculated from catch per tow at age during the autumn bottom-trawl surveys in 2J3KL combined, for ages (i) 4-6 combined (top panel) and 7-9 combined (lower panel) and computed for year t as follows: $Z = -\ln(C_{i,t}/C_{i-1,t-1})$. For example, in the top panel the value of 0.27 in 1984 is the total mortality experienced by the 1980-1978 year classes from ages 3-5 in 1983 to ages 4-6 in 1984. The line is a 3-year moving average. (Modified from Lilly et al. 2006.)

and then declined during the remainder of the 1980s and early 1990s. Sampling of catches from the autumn bottom-trawl surveys indicates that the extent of the decline varied among divisions; there was a strong decline in 2J, a lesser decline in 3K, and little or no decline in 3L. Size-at-age has improved since the early to mid-1990s, but remains below values observed in the late 1970s. Body condition and liver index also declined during the early 1990s, especially in 2J. Since the mid-1990s, condition levels have been similar to those measured in the mid-1980s. Age at maturity has declined. Olsen et al. (2005) demonstrated that maturation reaction norms shifted toward earlier ages and smaller sizes

during the 1980s and particularly the early 1990s, providing evidence of rapid evolutionary change that they interpreted to be the consequence of strong selection by the fishery.

Physical and biotic environment

The physical environment off Labrador and eastern Newfoundland has experienced considerable variability since the start of standardized measurements in the mid-1940s (Colbourne and Anderson 2003, Colbourne et al. 2005). A general warming phase reached its maximum by the mid-1960s. Beginning in the early 1970s there was a general downward trend associated with intensification of the positive phase of the North Atlantic Oscillation (NAO). Very cold periods occurred in the early 1970s, early to mid-1980s, and early to mid-1990s (Fig. 8). The annual depth-averaged temperature at station 27 (in the inner branch of the Labrador Current off St. John's) reflects annual variability in the temperature of the near-surface waters much more than does the cross-sectional area of the cold intermediate layer (CIL), and in this respect 1991 stands out as a particularly cold year. Ocean temperatures started to warm in 1995 and have generally been above normal for a decade, with some indices reaching record or near-record levels in recent years.

The collapse of the 2J3KL cod stock in the early 1990s was the most prominent in a series of profound changes within the Newfoundland-Labrador ecosystem. Among these were severe declines in most other demersal fish, including species that were not targeted by commercial fishing (Atkinson 1994, Gomes et al. 1995). There was also a surge in snow crab (*Chionoecetes opilio*) and especially northern shrimp (*Pandalus borealis*) (Lilly et al. 2000) and an increase in the abundance of harp seals (*Pagophilus groenlandicus*) from fewer than 2 million individuals in the early 1970s to almost 6 million by the late 1990s (Hammill and Stenson 2005). Capelin, the dominant forage fish in the area, experienced dramatic changes in many aspects of its abundance/biomass, distribution, well-being, and phenology in the early 1990s, with most changes being especially pronounced in 1991 (Carscadden et al. 2001).

The first decline and partial recovery

It has generally been assumed that the decline of the 2J3KL cod stock in the 1960s and 1970s was due entirely to overfishing, but there was so little fishery-independent information at the time that it would be difficult to test other hypotheses. The increase in landings was due primarily to the intensive offshore fishing by non-Canadian fleets, although there was undoubtedly a contribution from technological changes in the inshore fishery during the 1950s and 1960s. The number of participants

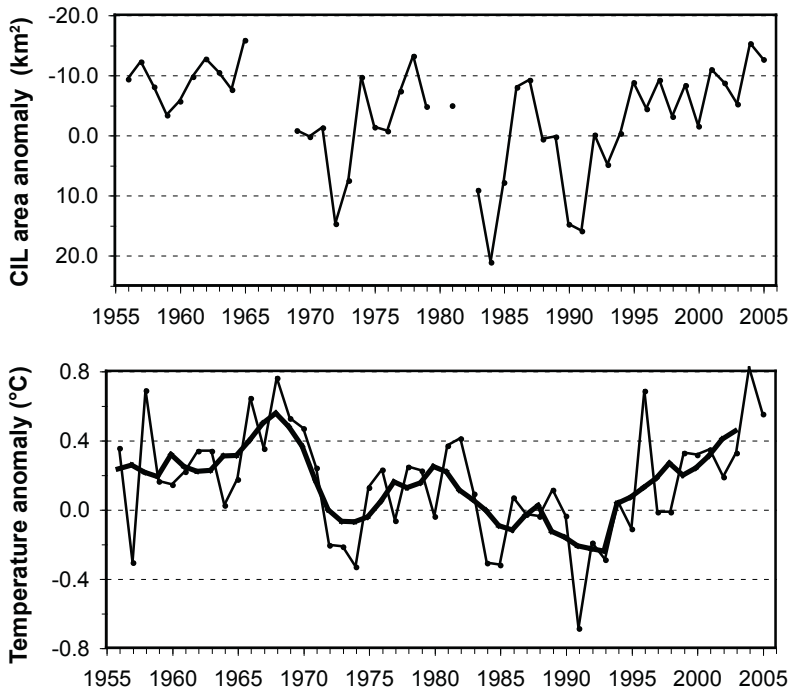


Figure 8. Two indices of temperature from the Newfoundland Shelf. The upper panel shows anomalies from the cross-sectional area of the cold intermediate layer (CIL) during summer occupations of a transect off Cape Bonavista on the east coast of Newfoundland. The CIL is defined by the upper and lower 0°C isotherms. The larger the area, the more cold water on the shelf. Note that the ordinate axis is reversed. The light line in the lower panel is the temperature anomaly of the annual depth-averaged temperature at station 27 off St. John's. The heavy line is a 5-year moving average. (Modified and updated from Colbourne et al. 2005; additional data provided by Eugene Colbourne, DFO, St. John's, NL, Canada, 2006, pers. comm.)

in the inshore fishery had declined during the 1970s (Schrank 2005). Inshore landings declined to a minimum in 1974 but started to increase even before declaration of Canada's 200 mile fisheries zone in 1977. Nevertheless, the declaration of the zone displaced the non-Canadian fleets, and a low in offshore landings occurred in 1978. The stock started to increase (Fig. 3) and fishing mortality declined for a few years (Fig. 6), even though total landings were increasing (Fig. 1).

The recovery following declaration of the 200 mile limit was built largely on the moderately strong 1973-1974 (and 1975) year classes. These year classes had been spawned prior to the declaration of the 200 mile limit, were subjected to reduced fishing mortality compared to year classes that had preceded them, experienced good growth at the normal or above normal temperatures at that time, and contributed to an increase in stock size.

The second decline (collapse) and non-recovery

There is considerable controversy regarding the cause(s) of the second decline (the collapse). Many studies (e.g., Hutchings and Myers 1994, Hutchings 1996, Myers et al. 1996) have concluded that the collapse was caused entirely by fishing activity, which would include reported landings (Fig. 1), unreported landings, and discards. There has, however, been much attention to the role of the physical environment. Several authors have pointed to various ways in which the decline in water temperature might have contributed to the collapse, either directly by reducing productivity (Parsons and Lear 2001; Drinkwater 2002, 2005) or indirectly by affecting distribution (Rose et al. 2000). The relative importance of fishing and environment is difficult to determine. Certainly, fishing played a very large role. This paper discusses the role of science and management in the setting of TACs that were too high. It does not attempt to discuss the possible effects of unreported landings and unquantified dumping and discarding.

After the extension of fisheries jurisdiction, the intent was to fish conservatively so as to promote stock growth, but in retrospect it is clear that fishing mortality was consistently underestimated and stock size consistently overestimated during the 1980s (Sinclair et al. 1991, Shelton 2005). A major change in scientific perception of stock size occurred in 1988-1989 (Baird et al. 1991b, Bishop and Shelton 1997). This change in perception was due to several factors, including the employment of improved assessment methodology and mounting evidence that the influential 1986 survey estimate (Fig. 2) was anomalously high. Although the estimate of stock size was reduced dramatically in a single step, assessments by DFO (Baird et al. 1991a, Bishop and Shelton 1997) and an independent review committee (Harris 1989, 1990) indi-

cated that there was still a considerable quantity of cod in the sea in 1989. Harris (1990) wrote, "The rather stable level in the biomass since 1984 . . . is supported by the commercial catch index and the (research vessel) data. It also accords reasonably well with the trends in inshore catches during this same period. All this brings us to the view that the state of the stock measured by the biomass trends does not support a conclusion that anything drastic or threatening has occurred to the northern cod stock to date."

The reduction in the estimate of stock size implied a large reduction in TAC. The Harris review panel in its interim report recommended that the quota be reduced, but not to the extent implied by the new estimate. This was because "the sudden reduction in catch levels designed to reduce the F value to the $F_{0.1}$ level of approximately 0.20 would be altogether too drastic a measure in view of the social and economic repercussions of such action. A not unreasonable compromise position, we believe, would be reduce the fishing mortality from its current level to a point approximately half-way to the $F_{0.1}$ level " (Harris 1989).

TACs were reduced during the next few years, but not to the $F_{0.1}$ level (Shelton 1998). Fishing mortality was allowed to escalate (Fig. 6). Simulations have indicated that the stock would have declined even if TACs had been set at the $F_{0.1}$ level, but the change in the control rule turned "what might have been a severe stock decline under a fixed fishing mortality rate into a collapse" (Shelton 1998). The actual extent to which fishing mortality increased remains uncertain (see below).

Subsequent to publication of the Harris report in 1990 there was a rapid disappearance of cod from all research vessel surveys. These included the autumn and spring bottom-trawl surveys (Fig. 2) and spatially limited hydroacoustic studies off southern Labrador (Anderson and Rose 2001) and eastern Newfoundland (Rose and Kulka 1999).

The extent to which scientific assessment contributed to the collapse remains in debate. If stock size had not been overestimated through the 1980s, then TACs would presumably have been lower, the stock presumably would have grown more than it did, and the stock might have been less susceptible to adverse environmental conditions (assuming, of course, that the environment did play a role in the collapse). In addition, the change in scientific perception of stock status in 1988-1989 was so large and sudden that politicians were concerned about the socio-economic costs of reducing the quota severely. Quotas were reduced, but not sufficiently to keep fishing mortality from escalating.

The big question, as noted above, is the extent to which fishing mortality escalated. If fishing was the sole cause of the disappearance of the fish, then fishing mortality must have risen rapidly to levels exceeding 2.0 y^{-1} (Shelton 1998) and there must have been a tremendous increase in the quantity of fish discarded or landed without reporting (Shelton and Lilly 2000).

Is there evidence that some of the increase in mortality was due to natural causes? The stock of American plaice (*Hippoglossoides platessoides*) off Labrador and northeastern Newfoundland declined to a very low level through the 1980s and early 1990s, a period during which reported catches were low (Morgan et al. 2002). Most other species of demersal fish, including many of no commercial value, declined dramatically through the same period (Atkinson 1994, Gomes et al. 1995).

Note as well that the total mortality rate of cod, as estimated from catch rate at age in the autumn bottom-trawl surveys, remained very high after directed fishing was stopped (Fig. 7). If part of this high mortality is due to unusually high natural mortality, then at what time did natural mortality increase? Did it increase only after the stock became greatly reduced in abundance (about 1993-1994), or did it increase during the early 1990s, or even before? In this context, it may be noted that the level of natural mortality input into SPA modeling has been increased above the commonly accepted value of 0.2 y^{-1} , for a series of years starting in the late 1980s and extending into the 1990s and even later, during assessments of several other groundfish stocks in Atlantic Canada, notably American plaice on Grand Bank (Morgan and Brodie 2001) and cod in the northern and southern Gulf of St. Lawrence and on the eastern Scotian Shelf (Shelton et al. 2006).

The possible role of the physical environment is of considerable interest because of an apparent coincidence between the rapid disappearance of cod from research surveys (Fig. 2, 7) and the low temperature (Fig. 8) and extensive ice cover of the early 1990s. While it seems unlikely that significant numbers of fish died as a direct consequence of exposure to cold water, there is still insufficient evidence to reject the possibility that the cold water and extensive ice cover led to a reduced duration of feeding opportunity, which then led to poor body condition and death (Atkinson and Bennett 1994, Dutil and Lambert 2000).

The reason for the continuing high total mortality in the offshore (Fig. 7) remains unclear. It could be that the fishing that has continued for other species is causing sufficient removals (landings and discards) to keep the cod populations from rebounding. However, recorded landings of cod from offshore Canadian fisheries have been less, and generally much less, than 130 t each year since the mid-1990s (Lilly and Murphy 2004). The level of landings from non-Canadian fisheries is more uncertain, but is understood to be less than 80 t each year (Lilly et al. 2006). Discards from shrimp fisheries were estimated to have been as high as 13 t in 1996 (Kulka 1998) but less than 5 t each year during 1997-2003 (Lilly and Murphy 2004). Bycatches of cod in shrimp fisheries are low because of the use of restrictor grates (Kulka 1998) and the relatively low density of small cod in the offshore (Anderson and Gregory 2000). These estimates of landings and discards in the various fisheries appear to be very small relative to survey indices of offshore

biomass, which averaged about 22,600 t during 1995-2005 (Lilly et al. 2006). The information on landings and discards has not been used to compute fishing mortality in the offshore because there is no information on catchability of cod at length for the survey trawl that has been used since 1995, and hence the survey indices of numbers at length have not been converted to estimates of abundance at length. In the absence of an estimate of fishing mortality, it is difficult to assess the level of natural mortality. Nevertheless, the apparent low level of catch has led to the suspicion that natural mortality is high.

High natural mortality could be caused by inadequate quantity or availability of suitable prey or by intensive predation. The dominant prey of cod in this ecosystem has historically been capelin (Lilly 1987, 1991), but capelin biomass as measured during offshore hydroacoustic surveys declined dramatically during the early 1990s and has remained very low (Carscadden et al. 2001). Rose and O'Driscoll (2002) concluded from studies of cod condition and feeding in specific areas and seasons, that cod was not faring well in certain offshore areas, and that this was due to low availability of capelin. In contrast, the routine monitoring of cod during autumn research surveys has not identified any problems with cod growth or condition (Lilly et al. 2006). The role of predation is also difficult to quantify. Although cod has many predators, the one that has attracted most attention is the harp seal, which consumes small cod whole and large cod by taking bites from their bellies to extract the liver (Lilly and Murphy 2004). The harp seal population has increased considerably during recent decades and, together with other predators, could be maintaining cod in a predator pit (Shelton and Healey 1999, McLaren et al. 2001, Rice et al. 2003). It must be emphasized, however, that there are many uncertainties associated with the estimation of the quantity of cod consumed by seals (Stenson and Perry 2001, McLaren et al. 2001, Lilly and Murphy 2004), and the incorporation of such estimates into cod mortality rates. Of particular concern in the present context is the small number of stomach samples taken from seals in the offshore.

There is also a possibility that the cause of the high mortality of cod in the offshore lies not in the offshore, but in the adjacent inshore. Fixed-gear landings, almost all of which came from the inshore, ranged from 400 t to 8,500 t during 1995-2005 (Fig. 1). If some of the cod in the offshore have continued the historic pattern of spring-summer migration to coastal waters, then a portion of them may have been caught by the inshore fisheries. If this were an important source of mortality for offshore populations, one would expect a positive correlation between offshore mortality and total landings, almost all of which came from the inshore. However, a positive correlation was not found between offshore mortality at ages 4-6 and the total landings (by number) of cod of ages 4-6 (Fig. 9).

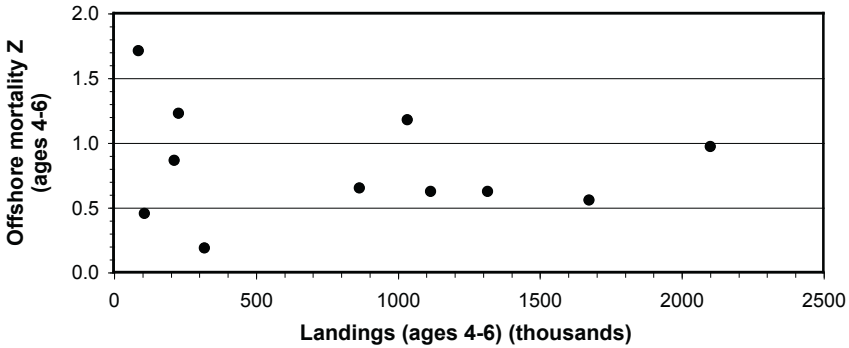


Figure 9. Relationship between offshore total mortality (Z) of cod of ages 4-6 (as shown in Fig. 7) and total landings of cod of ages 4-6, for the years 1995-2005. Landings at age are from Lilly et al. (2006), ($r = -0.15$).

The cause of the high total mortality of cod in the offshore since at least the mid-1990s remains unclear. It has not been possible to distinguish the relative contributions of fishing (both offshore and inshore) and natural mortality, nor to decompose natural mortality into that caused by predation and that related to other factors, such as insufficient prey.

Summary of differences between the two declines

Many factors may have contributed to the sharp contrast between the partial recovery of the northern cod stock following its first decline and the lack of recovery following the second. Among these is the difference in management circumstances. During the late 1970s, a substantial reduction in offshore effort and landings was accomplished with no social or economic repercussions to Canada, whereas in the late 1980s a substantial reduction in landings, as implied by the change in scientific perception of stock status, would have entailed substantial socioeconomic consequences. The TAC reductions that were implemented in 1989 and 1990 did have important consequences, but these were minor compared to the consequences of the moratorium imposed just a few years later.

There were also important differences in the environment, both physical and biotic. The period immediately following declaration of the 200 mile limit was characterized by normal or above-normal temperatures, whereas the late 1980s were normal or below normal and were

followed by the cold years of the early 1990s, with the winter and spring of 1991 being particularly severe. The cold temperatures and extensive ice cover of the early 1990s may have influenced the cod directly, such as by a direct effect of temperature on growth, but may also have influenced the cod indirectly, such as by diminishing the abundance or availability of prey, especially capelin, and thereby adversely affecting cod growth, condition and survival.

The major difference between the two periods was the difference in total mortality. When fishing mortality was reduced in the late 1970s, there were two moderately strong year classes (those of 1974 and 1975) that were already in the population, were subjected to diminished fishing pressure, and contributed to good population growth. In contrast, the two moderately strong year classes (those of 1986 and 1987), that had just entered the population when the large overestimation of population size was recognized in 1988-1989, disappeared quickly during the next few years, as did all older and younger year classes in the population at the time. The relative contribution of fishing and natural mortality to the increase in total mortality remains unclear. It is notable that the discontinuation of directed fishing failed to halt the decline.

Concluding remarks

A confluence of negative factors contributed to failure to prevent or even arrest the second decline (the collapse) of northern cod. The Canadian research vessel survey index did not start until after declaration of the 200 mile limit (1978 in 2J3K and 1981 in 3L). Therefore, the only fishery-independent index of abundance was still of short duration by the mid-1980s. In addition, the index was plagued by what in retrospect are clearly year-effects, the most significant being the strong positive year-effect in 1986 (Baird et al. 1991b). When the overestimation of stock size was recognized in 1988-1989, there followed in rapid succession a decision not to reduce the TAC to the extent implied by the revised estimate, and then a major cooling of the environment.

The role of the environment may be further inferred from the contrasting fates of the cod off Labrador-Newfoundland and the cod in the Barents Sea. The intensification of the positive phase of the North Atlantic Oscillation that produced the cold conditions off Labrador-Newfoundland during the 1980s and especially the early 1990s contributed to warmer waters and increased inflow of water rich in zooplankton in the Barents Sea. The northern cod off Labrador-Newfoundland collapsed while the Arcto-Norwegian cod in the Barents Sea thrived, despite high fishing mortality (Ottersen et al. 2006).

The absence of any sustained sign of recovery in the offshore populations of northern cod by 2005, 13 years after declaration of the moratorium, further supports the contention that fishing has not been the only factor governing stock dynamics. It is possible that factors

other than fishing contributed to the collapse, and that at least some of those factors are still operating. It is also possible that once the stock had declined to a very low level, for whatever reason, then factors other than fishing may have assumed greater importance. Of considerable interest are the possibilities that the quantity or quality of prey is limiting and that the stock is being held in a predator-prey pit by harp seals and other predators.

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Fishery and Environmental Aspects Relevant for the Emergence and Decline of Atlantic Cod (*Gadus morhua*) in West Greenland Waters

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Abstract

Historical information dating back from the seventeenth century indicates that the occurrence of Atlantic cod in Greenland waters was episodic and varied as a result of changes in the marine environment. The general warming in the beginning of the twentieth century led to the establishment of a self-sustaining and very abundant stock at West Greenland, which through the 1930s and 1960s frequently produced rich year classes. However, even in this period the productivity of the West Greenland cod stock appeared to be substantially lower than other North Atlantic stocks. A prolonged period of decline in stock biomass was observed in 1950-1975, which can be attributed to excessive fishing. The stock collapsed completely in the beginning of the 1990s, and in 2005 the first clear sign of new recruitment was seen. These recruits originated from spawning in Icelandic waters and, if protected from fishing, may start a rebuilding of the spawning stock in Greenland waters, which may then allow a sustainable exploitation as long as the recent favorable environmental conditions prevail in the future.

Introduction

Fluctuations and collapses of Atlantic cod stocks have been seen in several areas of the North Atlantic, and the effects of the environment and the fishery have been difficult to disentangle in almost all of these cases (ICES 2006a).

The occurrence of Atlantic cod at Greenland has been episodic in historical times. A more permanent presence of Atlantic cod in West Greenland waters was recorded first in the beginning of the twentieth century, which was accompanied by a rapid development of an international offshore fishery after World War II. From a maximum of about 4 million t in 1949, stock biomass declined to 110,000 t in 1975. Since then biomass has fluctuated at low levels being largely dependent on two large year classes (1973 and 1984) that led to temporary increases to about 250,000 t in 1978 and 640,000 t in 1987. The offshore commercial fishery collapsed completely in the early 1990s.

At Greenland, periods of low recruitment of Atlantic cod have historically been associated with relatively cold conditions (Buch et al. 1994). Air and ocean temperatures at West Greenland increased again in the mid-1990s, but an indication for a potential recovery of the cod stock was first detected in 2005 (ICES 2006b).

The present study characterizes periods of decline and recovery of Atlantic cod at West Greenland in terms of stock biomass, fishing mortality, spawning stock biomass, and recruitment. It further investigates the role of the fishery and environmental factors with respect to a delayed recovery of the Atlantic cod stock and the potential for a sustainable exploitation in Greenland waters in the future.

Material and methods

The present paper relies on different information sources that are of relevance for relating climate and fisheries. Of particular importance is the tracking of the development in the stock that, for the period when cod were fished commercially, is covered by an analytical stock assessment (1924 to 1989) and later by the designated groundfish survey conducted by Germany (1982-2005).

Analytical assessment and catch data

Results from a VPA (virtual population analysis) presented by Buch et al. (1994) have been re-evaluated using revised catch statistics. Catch (in numbers of fish) since 1956 were taken from Schumacher (1971) and Horsted et al. (1983). For the years previous to that, catch at age information was read from figures in Hansen (1949) for the period 1924-1947 and from unpublished figures (also from Hansen) for the period 1948-1955, scaled up to match the reported landings. Weights at age in the catch were taken from Horsted et al. (1983). Weights prior

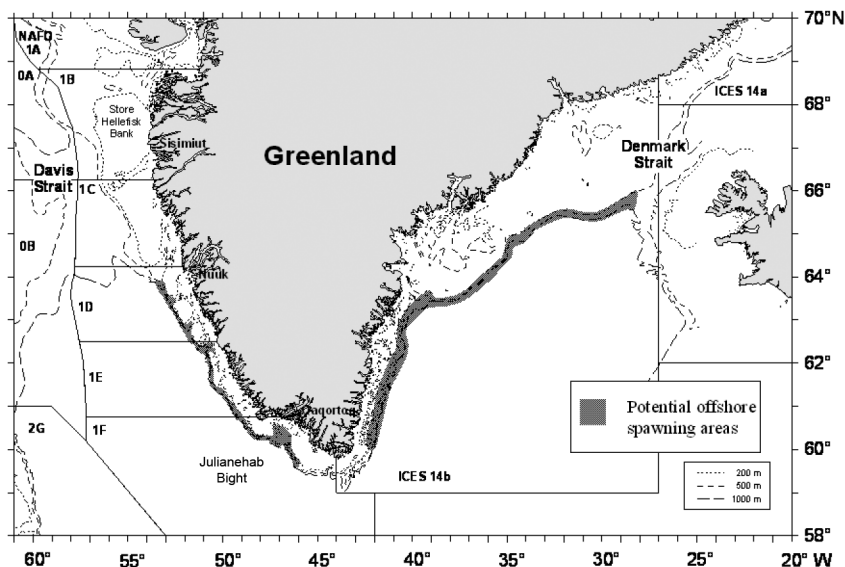


Figure 1. Study area and spawning grounds of Atlantic cod in East and West Greenland offshore waters. Redrawn after Wieland and Hovgård 2002.

to 1974 were assumed at the level provided for 1965-1973. Weight in the stock was assumed to be similar to that of the catch. Maturity data given in Horsted et al. (1983) were averaged and applied as a common maturity for the entire period. Fishing mortality was below 0.1 for many years before the 1950s. To avoid an overestimate of stock size, the terminal F values were not allowed to drop below 0.08, which is a value derived from catch curves for age 9-14 from the period 1930-1939, when catch, and presumably effort, were relatively stable. The present run has been updated with the significant Portuguese catch revisions for the World War II years provided by Horsted (2000). This implies that for the period before 1945 the present VPA estimates differ from those of Buch et al. (1994).

Survey data

The Institute for Sea Fisheries in Hamburg, Germany, has conducted a stratified random groundfish survey annually since 1982 in Greenland offshore waters. The survey covers the shelf area outside the 3 nautical mile limit and the continental slope down to a depth of 400 m off East and West Greenland between 67°00'N and 59°00'N (ICES area 14 and NAFO Div. 1B-1F, Fig. 1). The primary target of the survey is Atlantic

cod, and the fishing gear used is a groundfish trawl rigged with a heavy ground gear. Towing speed is 4 knots. The survey provides swept area estimates of abundance (by age) and biomass (all ages pooled) for the East and West Greenland offshore area. In addition, geo-reference data of age-disaggregated numerical densities by tow have been available for the present analysis and were used to calculate centers of gravity by age for different year classes.

Results and Discussion

Climate setting

Air temperatures measured in Nuuk were generally low until the early 1920s, followed by a clear positive trend until 1930, and remained relative high until the mid-1960s (Fig. 2). After an intermediate cold period around 1970, air temperature increased again during the 1970s. Thereafter, two very cold periods occurred in the mid-1980s and the early 1990s, which was followed by a continuous rise to the highest value in the time series recorded in 2005.

Since 1950 sea temperature in the surface layer has routinely been measured at Fylla Bank just outside the fjord area of Nuuk (64°N) (Fig. 2). Temperature was relatively high ($\approx 2^{\circ}\text{C}$) in the late 1960s, during most years in the 1970s, and in the second half of the 1980s. These warm periods were interrupted by years of very low temperatures ($< 1^{\circ}\text{C}$). Since the beginning of the 1990s, the time series show an increasing trend toward a record high value observed in 2005 (3.8°C). Air and surface layer temperature in general reveal a high degree of correspondence.

The climatic conditions are influenced by the ocean current system that transports warmer water to the West Greenland areas. Off East Greenland polar water is transported southward by the East Greenland Current that meets the warmer Atlantic water from the Irminger Current off Southeast Greenland. These water masses gradually mix and turn northward at Cape Farewell, on the southern tip of Greenland, forming the West Greenland Current. The amount of cold polar and warmer Atlantic water varies between years and together with the air-sea heat fluxes determines the water temperature off West Greenland (Buch et al. 1994, Ribergaard 2006). The currents concurrently transport fish eggs and larvae in a clockwise direction, around southern Greenland, i.e., from Iceland to South Greenland and from East and South Greenland to northern West Greenland areas. Annual changes in the current pattern may be of importance for the establishment of later year-class strength.

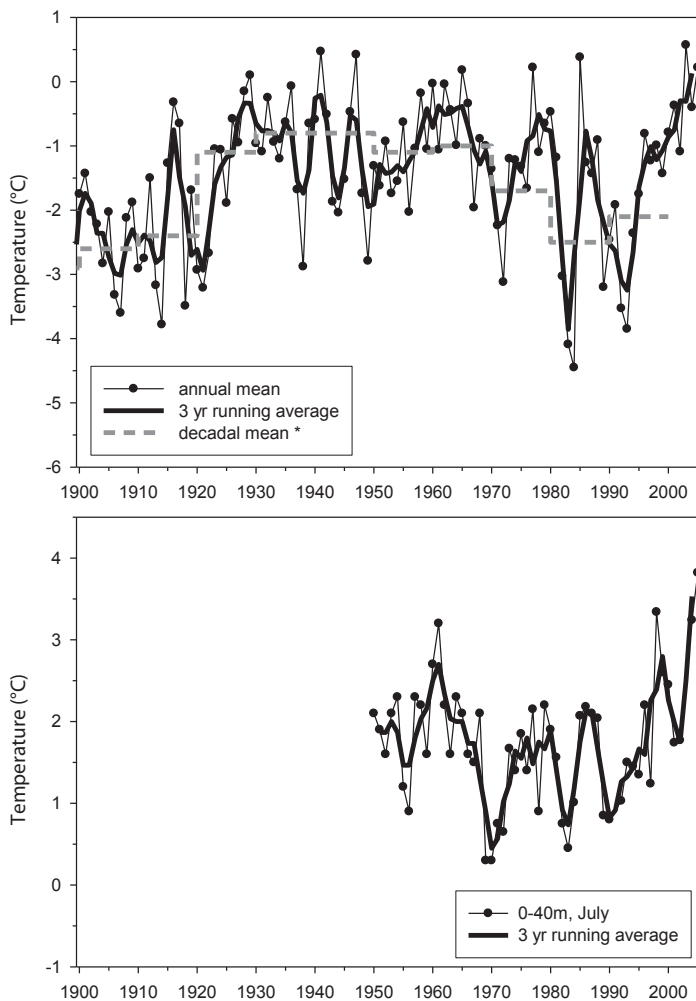


Figure 2. Air temperature measured in Nuuk and ocean surface layer temperature recorded at Fylla Bank (Ribergaard 2006). * indicates decadal annual air temperatures merged from 12 locations at West Greenland (Vinther et al. 2006).

Stock structure

Three different “stocks” of Atlantic cod occur in Greenland waters that are conveniently labelled by their spawning areas:

Inshore spawning populations are found in various fjords in West Greenland, predominately in the area between 62° and 66°N. The best-studied population is that found in the bottom of the Nuuk Fjord, where massive densities of cod eggs indicate a major spawning site close to the settlement of Kapisillit (Smidt 1979, Storr-Paulsen et al. 2004). Tag and recapture information indicate that the fjord populations remain in the fjord and coastal areas (Hansen 1949, Hovgård and Christensen 1990) and that limited mixing occurs between different fjord populations (Storr-Paulsen et al. 2004).

Offshore spawning populations that spawn at the shelf off Southeast and Southwest Greenland. Information on spawning areas was reviewed by Wieland and Hovgård (2002) who also worked up the historical ichthyoplankton information from Greenland waters. Highest average cod larvae densities were found off West Greenland in June/July between 62° and 66°N, indicating that the main nursery areas of the offspring spawned off Southeast and Southwest Greenland were shelf areas north of about 64°N. In addition, a considerable proportion of the larvae was found far offshore in the Davis Strait, and these larvae were definitely lost from the Greenland population but may have contributed to the development of the Labrador cod (Dickson and Brander 1993).

Icelandic cod. Spawning takes place off Southwest Iceland and most of the eggs and larvae drift to the north of Iceland where they settle, but some are carried into the Greenland area. In some years the larval drift has been extensive, i.e., in 1973, 1984, and 1985 (Astthorsson et al. 1994).

The stock definitions, including both spawning areas and larval dispersion mechanisms, have been broadly understood since the 1940s (e.g., Hansen 1949) but there are few possibilities to separate the historical catches into separate stock components. For more recent years there is, however, considerable information available that allows at least some year classes to be assigned to a dominating stock origin. For instance, the year classes of 1973 and 1984 were observed drifting in significant numbers from Iceland (Astthorsson et al. 1994) and they were recognized by surveys and later fished in eastern and southern areas of Greenland. The “homing” of these year classes to Iceland are indicated by a high proportion of tag-recaptures in Icelandic waters (Riget and Hovgård 1989, Storr-Paulsen et al. 2004) and the year classes are estimated to have contributed substantially to Icelandic cod catches after emigration back from Greenland waters (Schopka 1993, Shepherd and Pope 1993).

In the earlier years, tagging studies that commenced in the 1920s and were particularly extensive in the period 1950-1965, have docu-

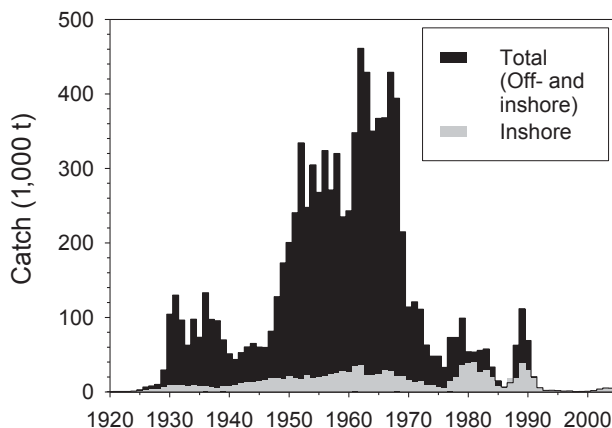


Figure 3. Catches of Atlantic cod in West Greenland inshore and offshore waters.

mented a clear north-south pattern in the spatial distribution of tag-returns from the commercial fisheries where southerly tagged cod clearly dominate the recoveries from Iceland (Hansen 1949, Hovgård 1993, Buch et al. 1994). Riget and Hovgård (1989) evaluated the tag return pattern by year classes, noting a high proportion of Icelandic recoveries of cod tagged south of $62^{\circ}30'N$ for almost any year class tagged. In contrast, recapture rates off Iceland of cod tagged in areas north of $62^{\circ}30'N$ were generally low except for particular year classes, e.g., the 1945, 1962, and notably the 1973 year class.

Fisheries and catches

For the seventeenth to nineteenth centuries, two short periods of fishing for Atlantic cod are documented (see Buch et al. 1994 and Dickson et al. 1994 for reviews) but in 1851 the fishery came to an abrupt end. Indications for a return of Atlantic cod to West Greenland was first seen in autumn 1909, and from 1917 onward Atlantic cod spread gradually northward along the coast and extended as far north as the Upernavik area at $73^{\circ}N$ in the late 1930s (Jensen 1939).

The fishery for Atlantic cod gradually developed during the 1920s and in its early days was dominated by a foreign offshore hook and line fishery (Horsted 2000). In the 1930s catches rose to annual levels between 60,000 and 130,000 t (Fig. 3). Foreign fishing, except by Portugal, stopped during World War II but expanded rapidly thereafter and culminated in the early 1960s when the total international catch was about 460,000 t. A dramatic decline started after 1968 when catches

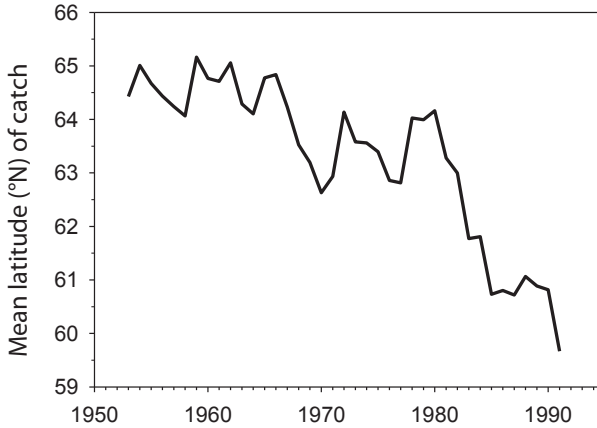


Figure 4. Changes in mean latitude of the offshore catch of Atlantic cod at West Greenland. Based on Horsted 2000.

in 1969 and 1970 halved compared to the preceding year's level. A further decline took place in the beginning of the 1970s and catches dropped below 7,000 t in 1986. After an intermediate rise to 110,000 t in 1989, almost solely caused by the very strong 1984 year class, the directed offshore fishery for cod collapsed completely in the beginning of the 1990s with no signs for a recovery since then.

The inshore catches of Atlantic cod, defined as the catches taken by artisan Greenland fisheries that operate in coastal and fjord areas, generally followed the overall trend indicating that to a large extent the fishermen were harvesting the same stock components as found offshore. Inshore catches remained below 10,000 t per year until 1942, and fluctuated between 20,000 and 35,000 t during the 1950s and 1960s as well as in some periods in the late 1970s and early 1980s (Fig. 3). Approximately 40,000 t were landed in 1989, almost all belonging to the 1984 year class. Since then, the inshore catches declined dramatically to a historic low of less than 400 t in the mid-1990s. Catches have increased considerably in the most recent five years to a level of about 10,000 t in 2006.

Changes in catch distribution

Throughout the 1950s and 1960s Atlantic cod was commonly caught in all West Greenland offshore areas but with catches concentrated between of 62 and 69°N. From the late 1960s catches almost disappeared from the area north of 66°N, resulting in an overall southward displacement of the fisheries that remained until 1980 (Fig. 4). Thereafter, cod catches

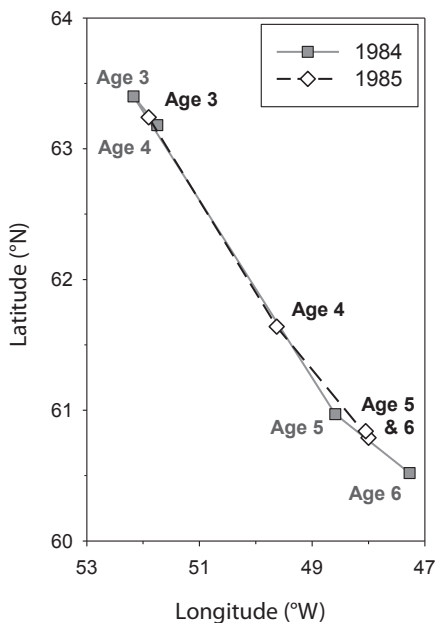


Figure 5. Changes in center of gravity of the 1984 and 1985 year classes of Atlantic cod off West Greenland at age 3-6. Text next to the symbols denotes age groups of the year classes; based on data from the German groundfish survey.

declined drastically in the areas north of Nuuk at 64°N, and by the end of the 1980s cod catches were exclusively taken in the southernmost areas of West Greenland. The latter displacement was primarily caused by a southward migration of the 1984 and 1985 year classes at the ages when maturation began (Fig. 5). It may be reasonable to assume that the pronounced decrease in temperature in the late 1980s (Fig. 2) may have accelerated the “homing” to Iceland of the 1984 and the 1985 year classes.

Changes in stock biomass, spawning stock size, and fishing mortality

According to virtual population analysis, stock biomass for cod at age 3 and older as well as spawning stock biomass (SSB) peaked in 1950 at about 4.1 and 3.3 million t, respectively (Fig. 6). Subsequently, both age 3+ biomass and SSB declined almost continuously until the mid-1970s to values of about 100,000 and 25,000 t, respectively. SSB remained

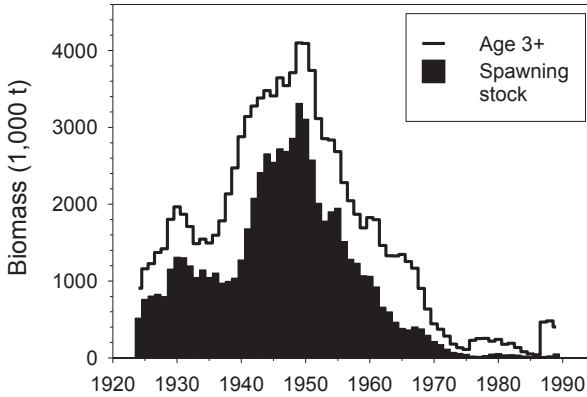


Figure 6. Estimates of stock biomass (age 3+) and spawning stock biomass of Atlantic cod at West Greenland.

at very low levels in the following decades, whereas age 3+ biomass showed some intermediate increases at the end of the 1970s and during the late 1980s due to recruitment of the 1973 as well as the 1984 and the 1985 year classes, all three year classes being predominantly of Icelandic origin.

The fishing mortalities rose continuously until 1939 but remained throughout that period at or below a level of 0.1 per year (Fig. 7). Fishing mortality declined during the war years to increase to the pre-war levels around 1950. These low mortalities are consistent with the observation that large year classes remained for a long time in the fisheries, e.g., the 1934 and 1936 year classes were significant in the catches until the early 1950s (Hansen and Herman 1953). The fishing mortality increased significantly during the 1960s to values of about 0.8 per year, a level that was generally maintained until the collapse of the offshore cod fishery in the early 1990s.

Changes in recruitment

Average recruitment at age 3 in the period 1924 to 1935 was about 123 million fish with the year classes 1922, 1924, 1926, and 1932 all being at or above 200 million fish (Fig. 8). In the following four decades recruitment was exceptionally high with averages of 256 and 203 million fish in the years 1936-1950 and 1951-1965, respectively. The year classes 1934, 1936, 1947, 1957, and 1961 were all estimated above 400 million fish at age 3 and in no year was the recruitment below 70 million fish. Since 1966, recruitment was much lower with an average of 53 million fish in the period until 1985.

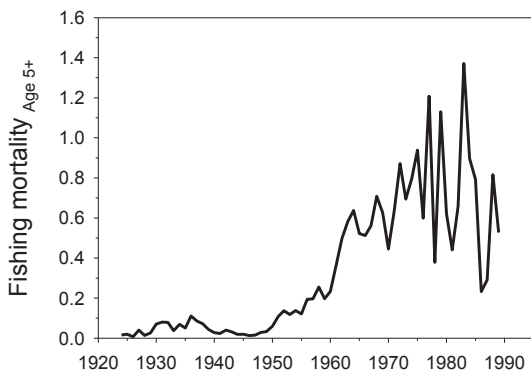


Figure 7. Estimates of mean fishing mortality (1924-1981 = age 5-12; 1982-1989 = age 5-7) for Atlantic cod at West Greenland.

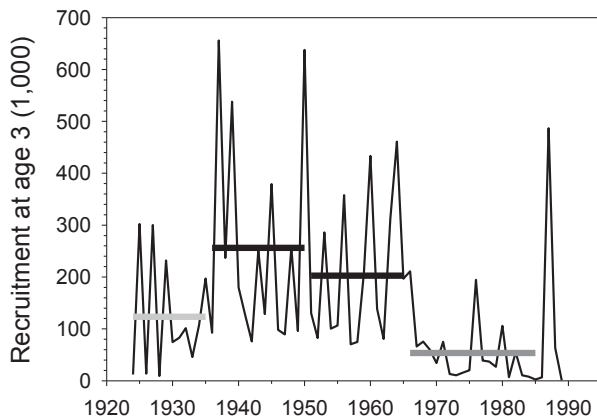


Figure 8. Recruitment at age 3 of Atlantic cod at West Greenland in the years 1924 to 1989. Horizontal lines represent mean values.

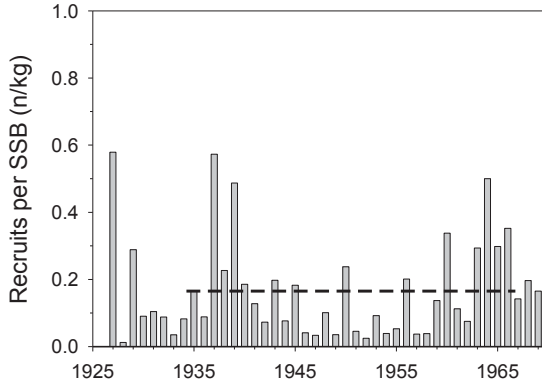


Figure 9. Number of age 3 recruits per unit of spawning biomass for Atlantic cod at West Greenland prior to the 1970s. Dashed line represents mean value for the years 1935-1966.

The changes in the mean levels of recruitment coincided with changes in the temperature regime (Fig. 2) suggesting that above average recruitment is restricted to warm periods and that the frequency and richness of strong year classes drastically declines when temperature is low. This conclusion is, however, confounded by the decrease in stock size and the recent poor recruitment may alternatively be explained by the decline in SSB; i.e., when exempting year classes of Icelandic origin no year classes stronger than 75 million fish emerged after the spawning stock biomass fell below 500,000 t in 1970 (Fig. 6). Both factors may of course affect recruitment simultaneously, i.e., leading to a lower resilience of the stock toward adverse climate conditions when the SSB is low.

The ratio of recruitment to SSB (both available from the West Greenland VPA) provides a simple index of stock productivity. For recent years where recruitment is thought to be dominated by cod of Icelandic origin, this index is very high and considered rather useless for drawing meaningful conclusions. For the period prior to the appearance of the 1973 year class the index is, in contrast, surprisingly low (Fig. 9). The average R/SSB ratio for the period prior to 1973 is estimated at 0.16 recruits per kg of spawner biomass, which implies that about 6.2 kg of SSB is needed to produce a single recruit. This value is very low when compared to other North Atlantic cod stocks where recent stock assessment provides R/SSB values of 0.94 for Icelandic cod (ICES 2006c: year classes 1955-2002; actually estimated at 0.77 for age 4 cod and is discounted to age 3 by applying an instantaneous mortality of 0.2 per

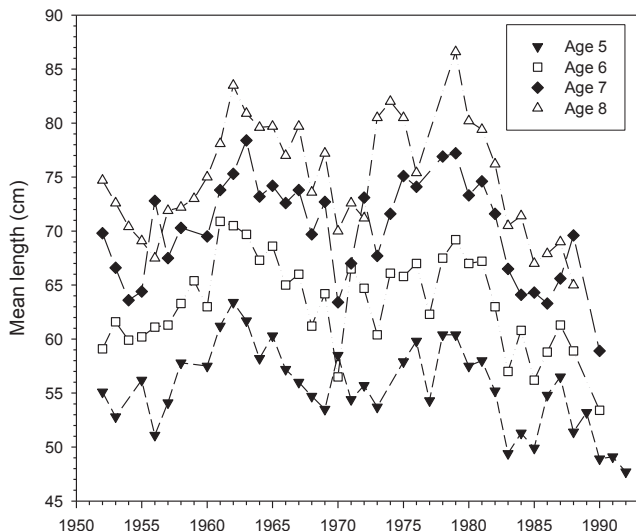


Figure 10. Mean length at ages 5-8 of Atlantic cod at West Greenland. Data from Riget and Engelstoft 1998.

year) and of 2.01 for the arcto-Norwegian cod (ICES 2006d: year classes 1946-2003), respectively.

A potential explanation for the poor recruitment productivity may be that the cod in Greenland remains in the pelagic phase for more than four months, being highly dependent on experiencing adequate current conditions for reaching suitable settling areas (Wieland and Storr-Paulsen 2005). The oceanographic conditions around Greenland are variable depending on annual changes in the important current systems (ICES 2002). For the Greenland offshore stock component the ichthyoplankton information suggests that in many years the majority of larvae are carried out in the Davis Strait, hence being lost from the Greenland population (Dickson and Brander 1993, Wieland and Hovgård 2002).

Changes in growth and condition

Large variations in length-at-age have been observed for cod in Greenland waters, and Brander (2007) demonstrated that periods of decline in total biomass were preceded or coincided with declines in mean weight-at-age for several other cod stocks in the North Atlantic. At Greenland, two periods of considerable decline in mean length-at-age can be identified since 1952, i.e., from 1962-1970 and from 1979-1983

Table 1. Correlation between length-at-age of Atlantic cod at West Greenland and ocean surface layer temperature recorded at Fylla Bank.

| Age | 1962-1970 and 1979-1983 | | | 1962-1983 | | | 1952-1992 (all years) | | |
|-----|-------------------------|------------|------------|-----------|------------|------------|-----------------------|------------|------------|
| | <i>R</i> | <i>N</i> * | <i>P</i> * | <i>r</i> | <i>N</i> * | <i>P</i> * | <i>r</i> | <i>N</i> * | <i>P</i> * |
| 5 | 0.613 | 19 | <0.01 | 0.488 | 16 | <0.05 | 0.382 | 23 | n.s. |
| 6 | 0.736 | 21 | <0.001 | 0.545 | 16 | <0.05 | 0.274 | 22 | n.s. |
| 7 | 0.591 | 22 | <0.01 | 0.494 | 15 | <0.05 | 0.137 | 21 | n.s. |
| 8 | 0.693 | 20 | <0.001 | 0.726 | 15 | <0.001 | 0.184 | 19 | n.s. |

r = Pearson product moment correlation coefficient; *N** and *P** = effective number of degrees of freedom and associated error probability adjusted for autocorrelation according to Pyper and Peterman (1998); n.s. = not significant at 5% level.

(Fig. 10) and were apparent in both Greenland and German commercial catch data (Hansen 1987, Riget and Engelstoft 1998, Rätz et al. 1999). The observed declines in mean length are quite substantial and correspond to a reduction in weight of more than 40%. Hansen (1949) noted a similar large decrease in length-at-age between 1934 and 1945 corresponding to decreases in weight between 30% and 50% for Northern Greenland and the Nuuk Fjord, respectively.

Correlations between the available length-at-age information since 1952 and the Fylla Bank surface layer temperature were found to be relatively poor by both Riget and Engelstoft (1998) and Rätz et al. (1999). However, it is striking that both of the two recent periods, as well as Hansen's early period, coincide with declining temperature. When restricting the analysis to the two periods for which the most prominent changes were observed, i.e., the years 1962-1970 and 1979-1983, highly significant ($P < 0.01$) correlations between the decrease in surface layer temperature and the mean length-at-age are found for all of the four age groups considered here. The correlations remain significant with the intermittent period of 1971-1978 included but break down for the entire time series (Table 1).

Water temperatures are definitely colder north of the Fylla Bank section and warmer south of it (e.g., Ribergaard 2006). The Fylla Bank records may therefore not adequately represent the temperatures experienced by the fish when the stock distribution area retracts southward as observed during the late 1960s and the 1980s (Fig. 4).

A positive correlation between temperature and the Fulton condition factor is observed from German fourth quarter survey catches since 1982 (Lloret and Rätz 2000). They find the annual average condition factor in the range 0.83 to 0.95 and note that these levels are low compared to other North Atlantic cod stocks. Greenland information on condition factor changes from commercial catches in the first quarter

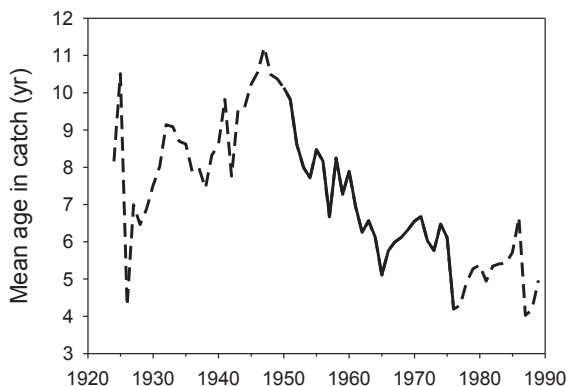


Figure 11. Mean age of Atlantic cod in the catch off West Greenland.

of 1979-1984 indicates somewhat higher condition factors, about 1.0 during 1979-1982 and 0.9 during 1983-1984 (Hansen 1987).

Effect of the fisheries

The effect of the fisheries is mirrored in the age structure in the catches. The period prior to 1950 is characterized by a steady increase in the mean age in the catch which approximates that of a virgin stock—the stock should probably by any standards here be labeled as “underfished” (Fig. 11). With the increase in fishing mortality following World War II, the age structure declined considerable to stabilize at average levels of around 6 in the early 1970s. Since then the age composition has been dominated by younger fish while at the same time showing greater fluctuations reflecting the more or less “monoculture” harvesting of single available year classes.

Fifty percent maturity is estimated by about age 6-7 (Horsted et al. 1983) and the drop of the mean age since the 1950s indicates that the majority of repeated spawners had been removed from the stock by the mid-1960s. The capability of the stock for frequently producing rich year classes and hence the resilience of the stock to changing temperature conditions may thereby have declined. Such an effect, i.e., a decrease in resilience to climate change with a decline in the mean age of the spawning stock, has been demonstrated by Ottersen et al. (2006) for the arcto-Norwegian cod stock.

Even in the period of consistently good recruitment, the productivity of the cod stock at West Greenland appears low (0.16 recruit per kg SSB), and high levels of SSB are only achievable at low fishing mortalities. A recruitment per SSB analysis based on the 1961-1963 fishing pattern

Table 2. Input and result of a yield/SSB per recruit analysis based on the weight, maturity, and fishing mortality at age as used in the VPA. Natural mortality is set at 0.2. The VPA fishing mortalities are the average of the 1961-1963 F -values. The equilibrium F vector defines the fishing mortalities that are needed to derive an SSB per recruit of 6.19 and corresponds to an $F_{(5-12)}$ of 0.14.

| Age (yr) | F from VPA | Equilibrium F | z | Weight (kg) | Maturity ogive | Stock (n) | Catch (n) | Yield (kg) | SSB (kg) |
|----------|--------------|-----------------|------|-------------|----------------|-----------|-----------|------------|----------|
| 3 | 0.02 | 0.01 | 0.21 | 0.58 | 0.01 | 1.00 | 0.01 | 0.00 | 0.01 |
| 4 | 0.10 | 0.03 | 0.23 | 1.28 | 0.03 | 0.81 | 0.02 | 0.03 | 0.03 |
| 5 | 0.27 | 0.08 | 0.28 | 1.72 | 0.11 | 0.65 | 0.04 | 0.08 | 0.12 |
| 6 | 0.38 | 0.11 | 0.31 | 2.51 | 0.32 | 0.49 | 0.05 | 0.12 | 0.39 |
| 7 | 0.56 | 0.16 | 0.36 | 3.52 | 0.61 | 0.36 | 0.05 | 0.17 | 0.77 |
| 8 | 0.55 | 0.16 | 0.36 | 4.66 | 0.83 | 0.25 | 0.03 | 0.15 | 0.97 |
| 9 | 0.48 | 0.14 | 0.34 | 5.07 | 0.94 | 0.18 | 0.02 | 0.10 | 0.84 |
| 10 | 0.48 | 0.14 | 0.34 | 5.68 | 0.98 | 0.13 | 0.01 | 0.08 | 0.70 |
| 11 | 0.52 | 0.15 | 0.35 | 5.37 | 0.99 | 0.09 | 0.01 | 0.06 | 0.48 |
| 12 | 0.62 | 0.18 | 0.38 | 8.65 | 1.00 | 0.06 | 0.01 | 0.08 | 0.55 |
| 13 | 0.60 | 0.17 | 0.37 | 9.58 | 1.00 | 0.04 | 0.01 | 0.06 | 0.42 |
| 14 | 0.48 | 0.14 | 0.34 | 9.60 | 1.00 | 0.03 | 0.00 | 0.03 | 0.29 |
| 15+ | 0.48 | 0.14 | 0.34 | 9.60 | 1.00 | 0.06 | 0.01 | 0.08 | 0.62 |
| | $F(5-12)$: | 0.14 | | | | | Sum: | 1.05 | 6.19 |

and the weight-at-age and maturity used in the VPA (Table 2) indicates that to maintain an SSB level of 6.2 kg per recruit requires a mean fishing mortality (age 5-12) of not more than 0.14. This estimate was found to be rather insensitive to reasonable changes in weight-at-age, e.g., using weights matching the high (1960) or low (1970) size at age observations in Riget and Engelstoft (1998) provided mean F_{5-12} estimates of 0.14 and 0.12, respectively. Within this framework the estimated fishing mortality provides an equilibrium measure of the sustainable harvesting rate, i.e., when F is above that equilibrium level the stock decreases and vice versa. Scaling the R/SSB analysis to population levels indicates that a SSB of about 1.6 million t is needed to produce the average of 256 million recruits that was observed in the 1935-1966 period. Fished at the equilibrium level ($F = 0.14$), this stock size would yield annual catches of about 270,000 t. However, this level of fishing mortality has been considerably exceeded in all years after 1960 (Fig. 7), which may have led to a vicious cycle that resulted in a lowering of SSB and subsequently further reductions in recruitment.

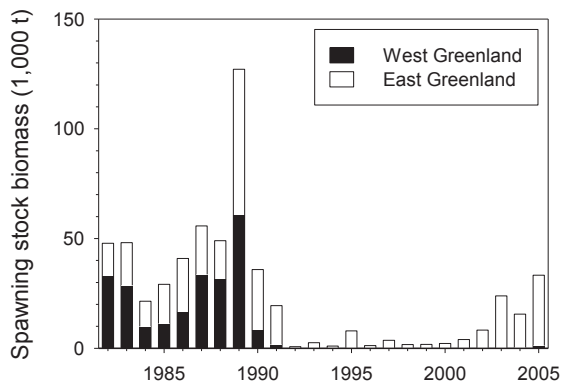


Figure 12. Spawning stock biomass of Atlantic cod in East and West Greenland offshore waters in the years 1982 to 2005. Data from German groundfish survey (ICES 2006b).

Effect of management

The major stock decline took place while the fisheries were still an international “free” fishery only restricted by modest access limitations (foreign vessels were not permitted to fish inside the 3 nautical mile limit), mesh-size, and minimum landing size regulations, introduced in the late 1960s (Horsted 1991). TAC (total allowable catch) regulations were introduced in 1974. This, however, did not provide an effective stock protection because the TACs were typically set above the level recommended in the biological advice. Furthermore, the TACs were inefficiently enforced considering the substantial amount of non-reported and mis-reported landings as noted by Horsted (2000).

Stock development in recent decades

Spawning concentrations in the offshore Greenland area

The offshore fisheries have been very limited in the last 15 years and surveys and exploratory fisheries now suggest that dense concentrations of large spawning cod again occur in the East Greenland area north of 63°N (ICES 2007). The present spawning area is, however, rather small compared to the extension of the spawning areas known historically.

Recruitment pulses from “foreign” spawning areas and actual distribution

Recruitment became largely dependent on larval drift from Iceland during the 1970s and 1980s, and the importance of this stock for the recruitment of cod in Greenland is particularly evident since the begin-

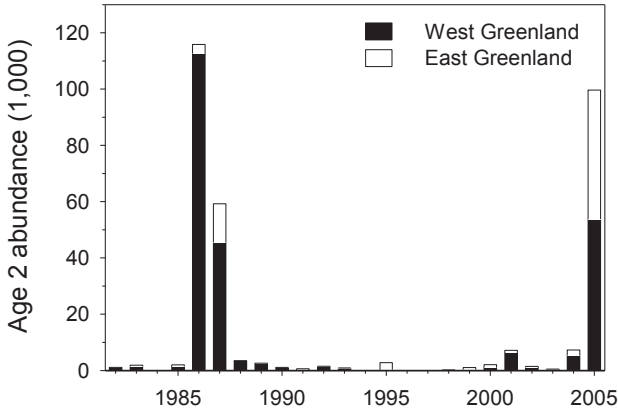


Figure 13. Recruitment at age 2 of Atlantic cod in East and West Greenland offshore waters in the years 1982 to 2005. Data from German groundfish survey (ICES 2006b).

ning of the 1990s when virtually no spawning stock was observed in Greenland waters (Fig. 12). After 18 years with almost no recruitment survey indices of abundance at age 2, 2005 indicated the appearance of a strong 2003 year class (Fig. 13). At age 3 this year class has been estimated to be about one third the strength of the large 1984 year class (ICES 2007). The 2003 year class is found predominantly at East and South Greenland, which makes it rather unlikely that spawning in Greenland waters has contributed to its formation.

Other factors relevant for a potential recovery

The mean bottom temperatures recorded by the German groundfish survey have increased more or less continuously since the late 1980s at both West and East Greenland, and the temperatures observed in the past 5 years are considerably higher than in the earlier years covered by the survey time series (Fig. 14). The abundance survey indicates that the stock has not yet responded to the increase in temperature suggesting that a spawning stock biomass beyond the present level may be needed before the stock can take advantage of a more favorable environment.

However, the relevance of factors other than temperature and the size of the spawning stock for a potential recovery in Greenland have been discussed in the past years. These included an increase in mortality of juvenile Atlantic cod due to bycatch in the expanding shrimp fishery and increased predation by seals. The fishery for northern shrimp has expanded considerably since the late 1980s, in particular at

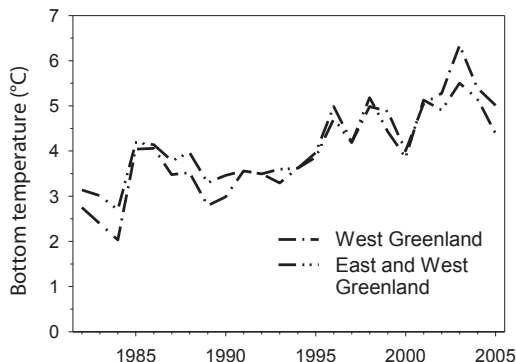


Figure 14. Mean bottom temperatures off West Greenland and for East and West Greenland combined, weighted by stratum areas in the German groundfish survey.

West Greenland. Before a sorting grid became mandatory in the shrimp fishery in 2002, age 1 and 2 cod may have been caught at higher rates in that fishery but bycatches are at present estimated as insignificant (ICES 2007). A recent census suggests that the population of seals has increased to a relatively high level. There is, however, no evidence that predation by seals has an ultimate effect on the cod stock dynamics considering that high cod stock sizes have also been observed in previous periods of high seal abundance (ICES 2006a).

Conclusions

The emergence of the Greenland cod stock is generally assumed to be related to the change in climatic conditions inter alia by the emergence of a very warm period in the northern Atlantic from about 1920 to 1965 (Hansen 1949, Drinkwater 2006). Cod were first observed in abundances in southern West Greenland and it is assumed that it originated from Iceland either as staying adult fish or by a larval drift within the Irminger Current. The stock increase during the 1920s was associated with a significant northward extension of the distribution areas. As northern nursery and feeding areas can be linked to spawning from East and Southwest Greenland this pattern suggest that the Greenland spawning stock was established during the initial years of the warm period. The SSB increased gradually over a 30-year period to reach about 3 million tons in 1950. This increase can be attributed to the combined effects of good recruitment and very low exploitation rates. The stock declined when fishing pressure increased after 1950 and recruitment

dropped significantly after the mid-1960s where all later strong year classes are assessed as being of primarily Icelandic origin. The stock concurrently retracted from the historically important northern areas indicating that the decline in recruitment was particularly affecting the spawning stocks off Greenland. Since 1980 no appreciable recruitment can be associated with any Greenland spawning as high densities of cod have been seen only for year classes of presumably Icelandic origin and restricted to the areas off East and South Greenland.

The decline of the stock can primarily be attributed to inappropriate intensive fishing considering the low productivity in terms of recruit per unit of spawning stock biomass. The decline in the spawning stock biomass and the associated decrease in the mean age in the stock may further have made the stock less resilient to the changes in the environment. The fishing mortality remained high although the climatic conditions had become unfavorable and the spawning stock fell below a level that was previously needed to produce sufficient recruitment at regular intervals. As a consequence of the high exploitation level, the stock completely collapsed within a few years, i.e., by the end of the 1980s. However, a reduction in fishing pressure at that time would probably have come too late to prevent the collapse of the stock considering the adverse temperature conditions in the late 1980s and the fact that the spawning stock in Greenland waters was already so low that recruitment depended largely on larval drift from Iceland.

The presence of an offshore spawning stock at East and Southwest Greenland appears to be essential for a positive response in stock size should the present favorable temperature conditions continue. A rebuilding of the stock at East and Southwest Greenland may possibly be initiated by recruitment from Iceland. To facilitate recovery, no directed cod fishing should be allowed in the Greenland offshore areas until a significant increase in spawning stock biomass has been observed.

Acknowledgments

Jörg Appel (Institute for Sea Fisheries in Hamburg) provided the georeferenced data for Atlantic cod and bottom temperatures from the German groundfish survey, and we would like to thank him and his colleagues, Dr. Manfred Stein and Dr. Hans-Joachim Rätz, involved in the German groundfish survey for their cooperation.

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Size-at-Age in Haddock (*Melanogrammus aeglefinus*): Application of the Growing Degree-Day (GDD) Metric

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Abstract

While growth variation in fishes is the result of a number of different factors (temperature, food consumption, genetic composition, etc.), temperature has been identified as one controlling factor on fish size-at-age. Thus, variation in size-at-age due to variation in temperature should be explained before the other factors are explored. We argue that the relevant metric for explaining temperature-dependent size-at-age variation in most fishes is physiologically relevant temperature; i.e., the thermal integral parameterized as the growing degree-day (GDD, $^{\circ}\text{C} \times \text{d}$) metric. Accordingly, we employ GDD to examine the change in size-at-age (length-at-day, LaD) among eastern Scotian Shelf (Northwest Atlantic Fisheries Organization statistical divisions 4VW) haddock (*Melanogrammus aeglefinus*) from 1970 through 2003. Significant variation in length-at-day (LaD) among year classes (decline in slopes and intercepts of LaD-at-GDD relations) remains after LaD variation due to GDD (temperature) is explained. The unexplained variation is postulated to be a result of temperature-independent factors such as condition or size-selective fishing or both.

Introduction

Variation in fish size-at-age has a direct effect on vulnerability to fisheries, predator-prey interactions, and reproductive potential (Francis 1994). Thus, explaining or predicting growth variation through size-at-age is essential to population and ecosystem studies as well as in determining fishing targets (e.g., size) and pressures suitable for sustainable fisheries. Variation in size-at-age may result from variation in a number of contributing factors—primarily temperature, food consumption, and genetic composition. Of these, temperature is a controlling factor governing metabolic reaction rates at the cellular level (Fry 1971) and affecting growth processes directly and indirectly (e.g., food consumption). Accordingly, time-dependent variations in temperature are reflected in time-dependent variations in development and in size-at-age where the latter is frequently used to infer growth rate. To properly examine the effect of variation in temperature on size-at-age among ectotherms one must use the correct time-scale (Gilbert et al. 1976). Instantaneous or average temperature estimates (e.g., daily or annual average) do not necessarily reflect the phenotypic expression of the time-based growth integral (size-at-age) in a complementary time-dependent manner; e.g., any point in a temperature time-series is instantaneous and thus aliased with respect to the size-at-age series. Instead, the growth integral is best examined using the time-based integral of the heat available for growth. For up to 270 years in some areas of ectotherm research (e.g., agriculture and entomology; Seamster 1950, Atkinson 1994, Bonhomme 2000) and recently in fish research (Neuheimer and Taggart 2007), the approximation of the thermal integral employed to describe size-at-age is the growing degree-day (GDD, $^{\circ}\text{C} \times \text{d}$). The GDD metric is a simple measure of daily temperature above a given threshold temperature. Among fishes it has been shown to explain between 92 and 99% of variation in size-at-age over a range of species among environments, temperature regimes, and laboratory and field studies represented by 41 data sets (Neuheimer and Taggart 2007). Moreover, the same authors show that among data sets the GDD metric explains most of the size-at-age variation that results from variation in the thermal history (the integral) of a given fish species. Thus, the GDD metric compares fish size-at-age variation on a physiologically relevant time-scale, thereby disentangling size-at-age variation due to physiologically relevant variation in temperature from that which may be attributable to other factors such as food availability and genetic composition. While other factors will influence size-at-age, temperature should be investigated foremost and before much effort is invested in the alternatives (Brander 1995).

In this paper, we employ the GDD metric to examine variation in length-at-age (mm) of the eastern Scotian Shelf (Northwest Atlantic Fisheries Organization, NAFO statistical division 4VW) haddock

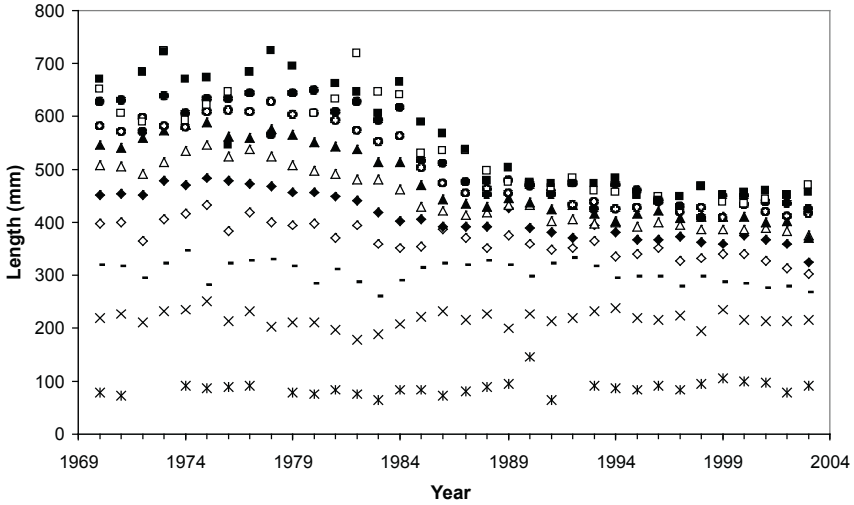


Figure 1. Variation in length (mm) at age (year) for 4VW haddock from 1970 through 2003 (Frank et al. 2001) for ages 0+ (star), 1 (cross), 2 (horizontal line), 3 (open diamond), 4 (filled diamond), 5 (open triangle), 6 (filled triangle), 7 (open circle), 8 (filled circle), 9 (open square), and 10 (filled square).

(*Melanogrammus aeglefinus*) for the mature ages 5-10 over the period 1970-2003. This stock is considered to be a challenge for the utility of the GDD metric in explaining size-at-age variation given the profound reduction in size-at-ages 3+ that has occurred over the past 30 years (Frank et al. 2001).

Methods

Haddock length-at-age (i.e., length-at-day, LaD, mm, Fig. 1) data for the NAFO division 4VW (Fig. 2) from 1970 through 2003 were obtained from the summer groundfish-trawl research vessel (RV) survey conducted annually by Fisheries and Oceans Canada. We restrict most analyses to mature haddock (ages 5-10; Mohn and Simon 2002) to avoid the allometry and discontinuities in LaD as a function of GDD that occur when life-history transformations such as maturation are marked by a change in energy allocation from growth to other physiological demands.

Monthly mean temperature data were extracted from the Bedford Institute of Oceanography hydrographic database for 1960-2006 and the 75±25 m depth stratum over the area on the Scotian Shelf that encompasses the majority of trawl locations and depths in the summer RV

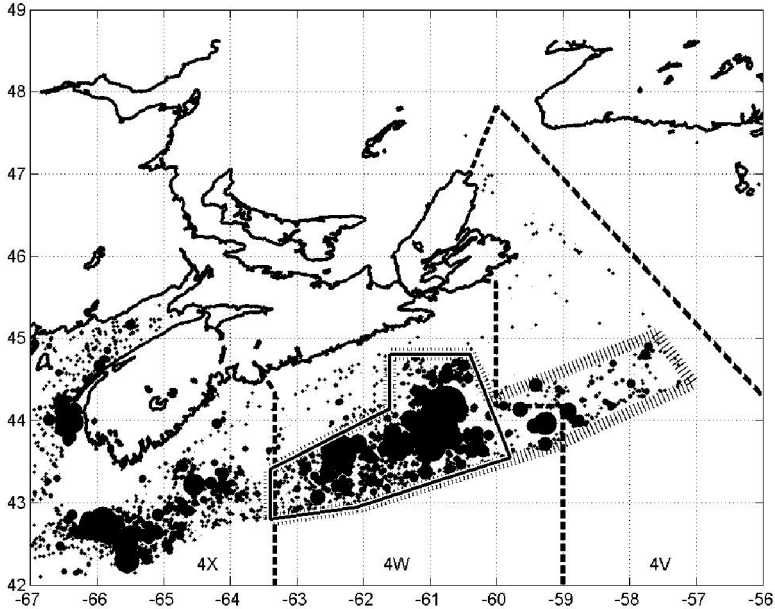


Figure 2. Chart showing the Northwest Atlantic Fisheries Organization (NAFO) statistical divisions 4V, 4W, and 4X (dashed lines) on the Scotian Shelf off Nova Scotia, Canada, with locations of research vessel survey sampling stations associated with highest catch per unit effort of haddock (i.e., upper 3 quartiles of log-transformed effort-adjusted abundance, expanding filled circles) and polygons outlining the area wherein temperature was extracted from the Bedford Institute of Oceanography hydrographic database (polygon 1, hatched line, preliminary evaluation including divisions 4V and 4W; polygon 2, solid black line, subsequent evaluation including only division 4W; see Discussion).

survey area associated with the highest haddock catch per unit effort; i.e., upper 3 quartiles of log-transformed effort-adjusted abundance (Fig. 2, polygon 1). The mean monthly temperature estimates were linearly interpolated (month to month) where necessary (Fig. 3). The interpolated temperature series was then smoothed using a uniformly weighted, centered 25-month moving average to provide the daily estimates. Analysis performed with 13-month, 37-month, and 61-month moving averages (to examine the influence of moving average extent) led to similar results in all cases. The GDD at day n ($^{\circ}\text{C} \times \text{d}$) is calculated as

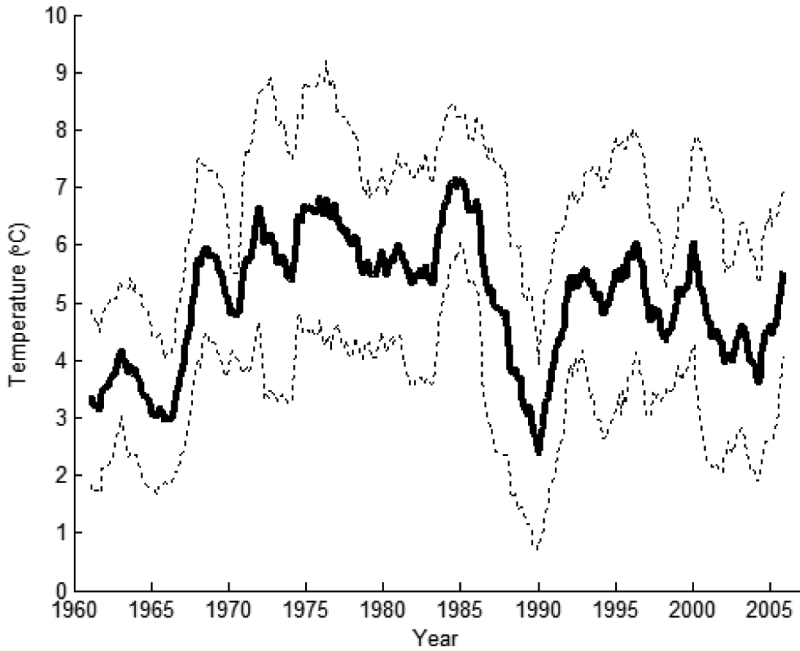


Figure 3. Smoothed (25-month centered moving average) interpolated monthly average temperature (°C, solid line) \pm one standard deviation (°C, dotted lines) for polygon 1 in Fig. 2. Data from the Bedford Institute of Oceanography hydrographic database.

$$GDD(n) = \sum_{i=1}^n (T_i - T_{Th}) \times \Delta d, \quad T_i \geq T_{Th} \quad (1)$$

where T_i is the temperature estimate at day i , T_{Th} is the predetermined threshold temperature ($T_{Th} = 0^\circ\text{C}$, see Neuheimer and Taggart 2007) and Δd is the time step (sampling frequency, i.e., 1 d). Variation in LaD and GDD for each year class was compared and quantified through linear regression according to

$$LaD = \beta \times GDD + \alpha \quad (2)$$

where β is the slope, $\text{mm} \times (\text{°C} \times \text{d})^{-1}$, and α is the intercept, mm, of the LaD-at-GDD relation. Neuheimer and Taggart (2007) demonstrated that in most cases LaD-at-GDD exhibits a strong linear relation.

Table 1. Parameters for age-dependent linear regression of length-at-age (mm) on year (1970-2003) for NAFO division 4VW haddock.

| Age | Slope (mm per year) | Intercept (mm) $\times 10^3$ | r^2 | P -value | Sample size (n) |
|-----|------------------------|---------------------------------|-------|------------|--------------------|
| 0 | | | | 0.09 | 30 |
| 1 | | | | 0.80 | 34 |
| 2 | -1.0 | 2.3 | 0.22 | 0.005 | 34 |
| 3 | -2.8 | 5.9 | 0.76 | <0.001 | 34 |
| 4 | -4.2 | 8.7 | 0.87 | <0.001 | 34 |
| 5 | -5.3 | 11.0 | 0.87 | <0.001 | 34 |
| 6 | -6.7 | 13.7 | 0.87 | <0.001 | 34 |
| 7 | -7.2 | 14.9 | 0.84 | <0.001 | 34 |
| 8 | -7.8 | 16.0 | 0.80 | <0.001 | 34 |
| 9 | -7.7 | 15.8 | 0.73 | <0.001 | 31 |
| 10 | -9.3 | 19.1 | 0.81 | <0.001 | 32 |

Results

NAFO-4VW haddock show a significant decline in length-at-age for ages 3+ from the mid-1970s through to the early 1990s with the highest rate of decline occurring over the 1982-1989 period (Fig. 1, Table 1). Length-at-age for ages 0+ and -1 show no trend over time and for age 2 the relation is marginal as time (year) explains 22% of the length-at-age variation relative to >73% for ages-3+ and older (Table 1).

Bathypelagic (75 \pm 25 m) water temperature within the domain of high haddock abundance on the eastern Scotian Shelf exhibited rapid cooling during the mid to late 1980s followed by rapid warming in the early 1990s (Fig. 3). Contrary to expectations, variation in GDD within the stock, at shelf scales, did not explain the majority of variation in length-at-day among haddock year classes as it does, for example, among 17 cod stocks at ocean basin scales (Neuheimer and Taggart 2007). There is nearly as much variation in LaD as a function of physiological time (GDD) across year classes as there is LaD as a function of calendar time (Fig. 4). There was significant variation among LaD-at-GDD relations for the 1965-1996 year classes (Fig. 4b, ANCOVA, different slopes $P < 0.0001$). By inspection (Fig. 4), the year classes were aggregated into two periods, prior to 1979 and 1979 and later, to compare the LaD-at-GDD relations (i.e., slope and intercept; Fig. 5). The LaD as a function of GDD relations among the <1979 year classes demonstrate similar slopes ($P = 0.43$) and differing intercepts ($P = 0.0018$) and there is no time-dependent trend in the intercepts (Fig. 5b, linear regression, $P = 0.71$). The LaD as a function of GDD relations among the ≥ 1979 year

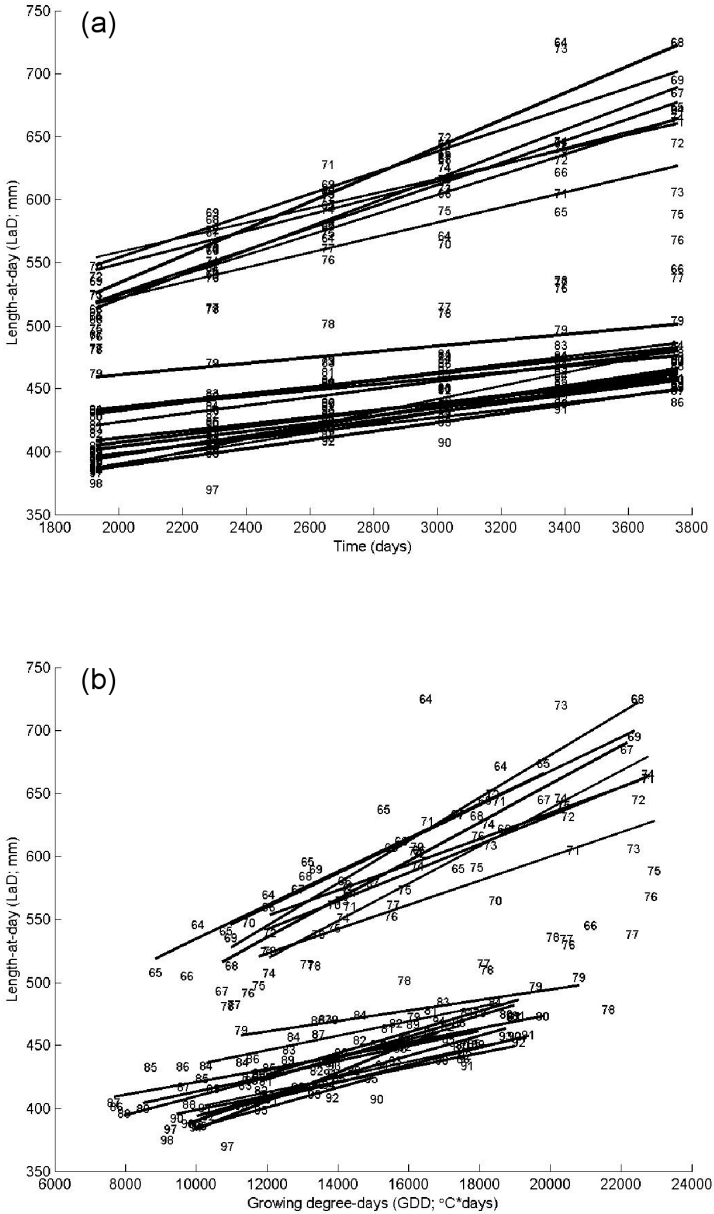


Figure 4. Length-at-day (mm) for 4VW haddock ages 5-10 as a function of (a) calendar time (days, significant variation among year class relations, ANCOVA, different slopes $P < 0.0001$); and as a function of (b) GDD ($^{\circ}\text{C} \times \text{d}$, significant variation among year class relations, ANCOVA, different slopes $P < 0.0001$). Data-labels denote year-class decade and year in the 1900s.

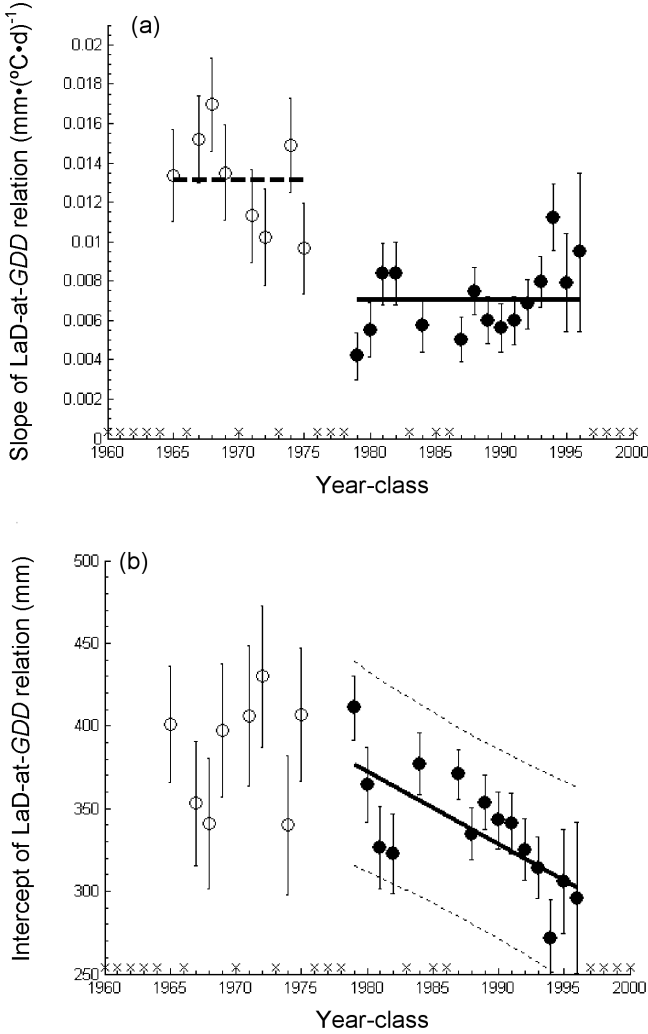


Figure 5. Parameters of the LaD-at-GDD relation for early (<1979, open circles) and late (≥1979, filled circles) year classes. (a) Slopes, $\text{mm} \times (\text{°C} \times \text{d})^{-1}$, and associated standard error of the LaD-at-GDD relations are similar within early (open circles, dashed horizontal line) and late (filled circles, solid horizontal line) year classes. (b) Intercepts, mm, and associated standard error of the LaD-at-GDD relations are different within early (open circles) and late (filled circles) year classes. There was a significant decline in the intercept among late year classes (solid line, linear regression dashed lines indicate 95% confidence intervals around the prediction). Crosses denote year classes with non-significant ($P > 0.05$) LaD-at-GDD relations.

classes also demonstrate similar slopes ($P = 0.17$) but unlike the earlier year classes there is a near-systematic year-class-dependent decay in the intercepts of the LaD-at-GDD relations (Fig. 5b. linear regression, $r^2 = 0.50$, $P = 0.003$). Further, the mean slope of the LaD-at-GDD relation for the <1979 year classes is $0.013 \pm 0.0009 \text{ mm} \times (\text{°C} \times \text{d})^{-1}$ and is nearly twice that (Fig. 5a, Shapiro-Wilk normality test: $P > 0.62$; two-sample t -test: $P < 0.0001$) estimated for the ≥ 1979 year classes at $0.007 \pm 0.0004 \text{ mm} \times (\text{°C} \times \text{d})^{-1}$.

Discussion

The NAFO-4VW haddock stock experienced a decline in LaD in the 1980s that was coincident with changes in a number of factors affecting fish growth, as inferred through population size-at-age; factors that included a doubling of the fishing effort and a decrease in water temperature (Zwanenburg 2000). As a first step toward disentangling the various factors that could potentially explain the variation in haddock length-at-age, we turned to temperature as Brander (1995) suggests we must, and examined variation in LaD (mm) with GDD ($\text{°C} \times \text{d}$) as a function of variation in year-class thermal history; i.e., the physiologically relevant measure of temperature. In doing so we find the thermal integral explains only a small portion of the variation in LaD among the 4VW haddock year classes.

A major requirement for employing the GDD metric is that the temperature measure used is representative of that experienced by the organism over the growth period of interest (Neuheimer and Taggart 2007). Over the period we examine here, the distribution of the 4VW haddock generally shifted from an area restricted primarily to division 4W (polygon 2, Fig. 2) for the 1965-1974 year classes to an area generally including divisions 4V and 4W (polygon 1, Fig. 2) for the 1975-1984 year classes, and then back to division 4W for the 1985-1994 year classes. Bathypelagic water temperatures for polygons 1 and 2 demonstrate similar cooling in the mid to late 1980s and warming in the early 1990s, and though the uncertainties (standard deviations) are large in either case (Fig. 6a), the temperature in polygon 2 was warmer than that in polygon 1 (Fig. 6b) for most of the time. During both the early (<1979) and late (≥ 1979) periods of year-class groupings, the majority of the stock was restricted to division 4W (polygon 2, Fig. 2). Consequently, we ask, if we limit our temperature analyses to the polygon 2 temperature estimates, do we find that GDD is better able to explain the variation in LaD among the early and late groupings of year classes? The answer was unequivocally no, as we resolved similar relations among year classes as were resolved using the polygon 1 temperature data. The only difference was a slightly lower slope in the mean LaD-at-GDD relation for the late year classes using the polygon 2 temperature data, $0.006 \pm$

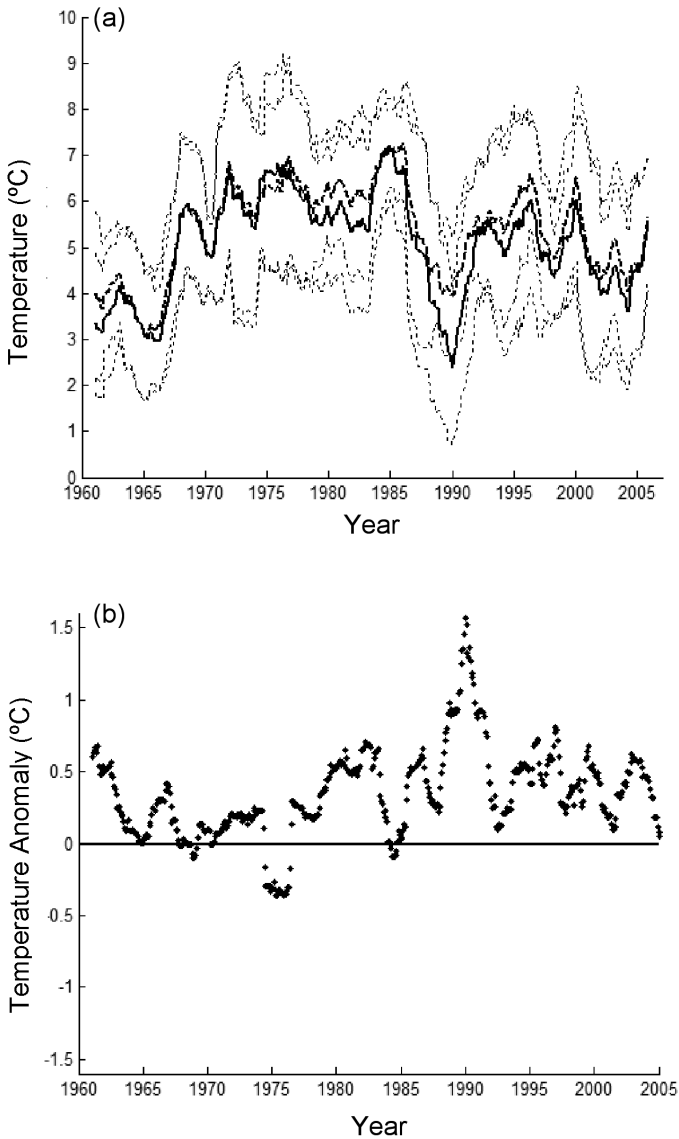


Figure 6. (a) Smoothed (25-month centered moving average) interpolated monthly average temperature (°C) \pm one standard deviation (°C, dotted lines) for polygon 1 (solid line) and polygon 2 (dashed line) illustrated in Fig. 2 and (b) temperature anomaly calculated using the polygon 1 and polygon 2 smoothed temperature series. Data from the Bedford Institute of Oceanography hydrographic database.

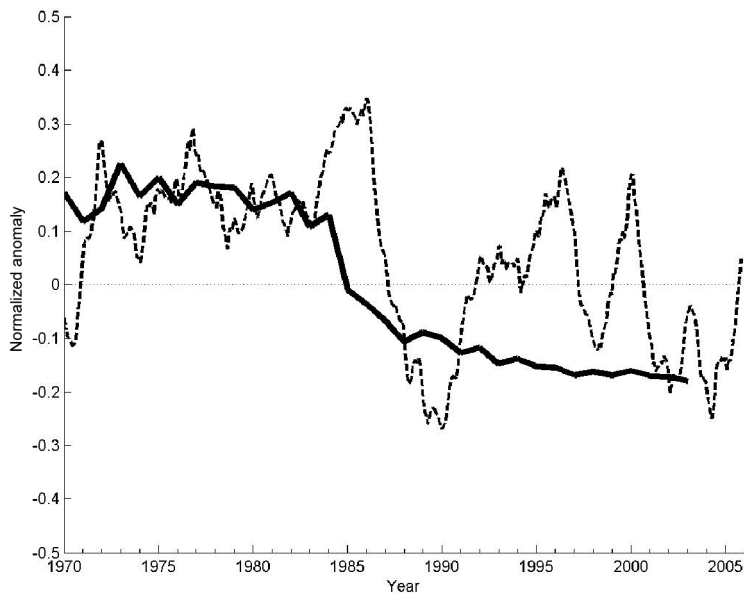


Figure 7. Normalized anomalies of mean length for ages 5-10 (solid line) and smoothed (25-month moving average) interpolated monthly mean temperature (dashed line, from polygon 1, see Fig. 3).

$0.0004 \text{ mm} \times (\text{°C} \times \text{d})^{-1}$, relative to that of polygon 1, $0.007 \pm 0.0004 \text{ mm} \times (\text{°C} \times \text{d})^{-1}$; each nearly half that exhibited for the earlier year classes (see above). Therefore, when distributional changes and the associated temperatures are incorporated into the analyses the majority of variation in LaD among year classes remains unexplained.

In summary, the above analyses show that variation in thermal history (GDD) is unable to explain the majority of variation in LaD among 4VW haddock year classes on the Scotian Shelf despite the fact that cooler water is often cited as a primary source of the size-at-age decline in this stock (e.g., Trippel 1995). The cold water argument is most easily attributed to observations of the decline in temperature on the shelf appearing to occur concurrently with the decline in LaD for this stock. However, the decline in size-at-age precedes that of temperature by approximately 3 years as illustrated by calculating the normalized anomalies for mean length-at-ages 5-10 and temperature (Fig. 7). Furthermore, when temperatures returned to near-normal in the 1990s, the size-at-age did not return to near-normal but continued to decline (see also Zwanenburg 2000, Drinkwater and Frank 2001). These conclusions remain when we employ time to examine LaD and when we use the

integrated temperature measure (GDD); the preferred metric particularly when various year classes with different growth (and thermal) histories are involved and when spatially different thermal histories related to distributional changes in the stock are considered. Further, perhaps the most compelling argument is based on the evidence that LaD for 4VW haddock ages 0, 1, and marginally so for 2, remain unchanged regardless of the thermal environment (integrated or not). Age-0 haddock occupy pelagic waters for approximately four months before becoming bathypelagic along with older age-classes (DFO 2001). If temperature was the major source of variation in LaD, one would expect the youngest ages to be equally affected (Drinkwater and Frank 2001) and this is not the case (Fig. 1, Table 1).

It is clear that temperature variation, as parameterized through the thermal integral, does not explain the decline in 4VW haddock size-at-age over the study period. However, it has been shown elsewhere that temperature can explain LaD among fish, within species, in many environments if the comparisons are made using the same physiological timescale (i.e., GDD), and where it does not, it is an indication that the residual variation in LaD can be attributed to other factors (Neuheimer and Taggart 2007). Here we employed the GDD metric to identify the portion of variation in size-at-age that is attributable to variation in thermal history. The question becomes: what other factors may explain the remaining size-at-age variation in the 4VW haddock; i.e., the variation in slopes and intercepts of LaD-at-GDD relations among year classes shown in Fig. 5? We postulate that the unexplained variation may be attributable to changes in fishing pressure (e.g., Olsen et al. 2004). Most fishing gear is size-selective (Sinclair et al. 2002). If a portion of the phenotypic variation in size-at-age is rooted in genetic variation, it is possible that fishing mortality (often exceeding natural mortality by a factor of 2 or 3) may represent a strong genetic selection on a population (Engelhard and Heino 2004, Hutchings 2005) resulting in evolutionary changes in growth and maturation (Law 2000, Stokes and Law 2000). Evidence for these impacts of size-selective fishing is noted elsewhere in the North Atlantic; greater reductions in size-at-age are found in target than non-target species (Zwanenburg 2000).

Management strategies differ depending on the sources of the variation in size-at-age, requiring the causal mechanisms to be identified before management can be successful (Sinclair et al. 2002). Indeed, “failure to simultaneously consider alternative mechanisms, especially size-selective mortality, can lead to incorrect conclusions about the role of environmental factors in determining growth of fishes” (Sinclair et al. 2002). Thus the ability to assess the effects of fishing pressure on the variation in size-at-age of a population lies in the ability to disentangle those effects from other possible sources of size-at-age variation (e.g., temperature, etc.). Here we have extricated the influence of temperature

variation on LaD in 4VW haddock. The next phase of our work is focused on examining the influence of size-selective fishing on the systematic decline in size-at-age found in this stock.

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Using Acoustics to Evaluate the Effect of Fishing on School Characteristics of Walleye Pollock

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Abstract

Walleye pollock (*Theragra chalcogramma*) is the target of one of the world's largest fisheries and is an important prey species in the eastern Bering Sea (EBS) ecosystem. Little is known about the potential effects of fishing on the school characteristics and spatial distribution of walleye pollock. Few dedicated research surveys have been conducted during pollock fishing seasons, so analysis of fishery data is the only feasible approach to study these potential effects. We used acoustic data collected continuously by one fishing vessel in January-February 2003, which operated north of Unimak Island. Results from comparisons between two fishing periods showed significant changes of pollock distribution at different scales. The schools were smaller and denser during the second period. Furthermore, the spatial distribution of schools became sparser, as evidenced by the lower frequency of schools per elementary distance sampling unit and the increase in average

next-neighbor distances (NNDs). However, the average NND between schools within a cluster and the average abundance of clusters did not change significantly. Variography was used to investigate the changes at scales larger than 1 nm. The increased range, nugget effect, and sill in the second period indicated changes of pollock spatial distribution; however, it is unclear whether these changes are attributable to fishing or ecological processes.

Introduction

Pelagic species usually form dense aggregations, or schools, during daytime and disperse at night. Walleye pollock (*Theragra chalcogramma*), which is semi-pelagic, forms persistent mid-water and near-bottom schools during the spawning season. For schooling species, the pattern of aggregation may have a large effect on fishery catchability (Castillo and Robotham 2004). Harvesters are skilled at finding fish aggregations using search strategies aided by technology (echosounders, oceanographic sensors, satellite imagery, etc.). Consequently, strong interactions would be expected between the distribution and behavior of both fish and harvesters (Potier et al. 1997, Wilson et al. 2003, Bertrand et al. 2004). Wilson et al. (2003) studied how fishing activities affected the pollock distribution in Barnabas Trough in 2002, but did not find strong impacts. This paper focuses on changes in pollock schooling during a one-month fishing season in the eastern Bering Sea (EBS) using acoustic data collected aboard a commercial fishing vessel.

The commercial fishery for walleye pollock in the EBS is one of the largest fisheries in the world. This species is also an important component of the EBS ecosystem as a major prey species. Recently there has been great interest in the potential biological interaction between Steller sea lions (*Eumetopias jubatus*) and commercial fishing, following the classification in 1997 of the western population of Steller sea lions as endangered under the Endangered Species Act. It remains unknown whether fishing causes significant decreases in pollock abundance or changes in their spatial distribution that in turn adversely affect the foraging success of sea lions (Zeppelin et al. 2004).

Acoustic survey methods have been widely used for assessment because of their high temporal and spatial resolution (Simmonds and MacLennan 2005). Commercial vessels can be good platforms for collecting scientific acoustic data (Melvin et al. 1998, 2002; Wyeth et al. 2000; Mackinson and Kooij 2006), and are particularly useful for in-season monitoring of stock trends (Stephenson et al. 1999, Melvin et al. 2001). Pollock is the main sound scatterer at 38 kHz during the winter spawning season in the EBS (Dorn et al. 2002). Since 1979, acoustics have been used to estimate pollock abundance in mid-water during the echo-integration trawl (EIT) surveys of the EBS (Barbeaux and Dorn 2003).

However, these surveys are mainly conducted in the summer, except for several winter surveys conducted in 2001 and 2002 (Honkalehto et al. 2002). The first major fishing season (called the "A" season opening on January 20) occurs in winter. Consequently, surveys do not provide adequate information about interactions between fishing and pollock aggregations (Barbeaux and Dorn 2003).

Scientists from the Alaska Fisheries Science Center (AFSC) and University of Alaska Fairbanks developed a prototype data logger to interface with 38 kHz echosounders onboard fishing vessels and capture the acoustic backscatter returns in 2001 (Dorn et al. 2002). Since 2002, the joint opportunistic acoustic data (OAD) program has been collecting, processing, and storing acoustic data from selected factory trawlers participating in the eastern Bering Sea pollock fishery (Dorn et al. 2002). Seven fishing vessels collected acoustic data during normal fishing operations in the "A" season when the fish form pre-spawning aggregations. These data make it possible to study the relationship between pollock aggregations and fishing activities. However, due to difficult weather conditions and equipment breakdowns, much of the opportunistic data cannot be utilized. Here, only the acoustic data collected by one vessel in 2003, which had fewer missing pings and was generally of higher quality than data from other vessels, were used to examine pollock aggregation patterns in the area north of Unimak Island.

Materials and methods

Data collection and study area

The vessel is a large factory trawler that mainly operated north of Unimak Island (near 54°46'N, 164°08'W) in the eastern Bering Sea from January to February 2003 (Fig. 1). The vessel operated in the same area during the early and late periods of the fishing season. Acoustic data were logged with an uncalibrated 38 kHz Simrad ES60 split-beam echosounder with 1 ms nominal pulse length and 7.1° beam width. Uncalibrated acoustic data are of course not suitable for absolute fish density estimation; however, the purpose of this study was the analysis of school morphology characteristics, spatial patterns, and relative changes in school density, which should be robust to the lack of calibration.

Data analysis

Echoview 3.30 software (SonarData 2005) was used to process raw data and classify the echo trace from 15 m below the surface to 0.5 m above the bottom. Walleye pollock schools were detected and characterized using the school module in Echoview. We used only data collected dur-

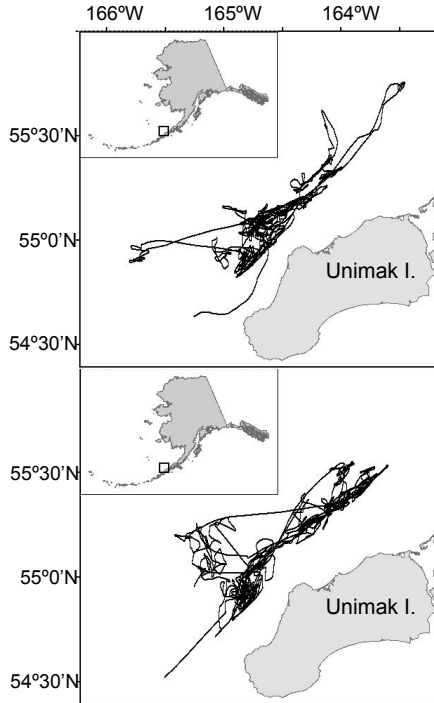


Figure 1. Area of operation of the fishing vessel in January-February 2003. The upper and lower panels display the fishing tracks from Jan. 22 to Feb. 5, and from Feb. 14 to Feb. 24, respectively.

ing daylight hours, when pollock show schooling behavior. Criteria from Wilson et al. (2003) were used to classify the pollock aggregations as follows. The threshold for detecting schools was set to -70 dB at 1 m. The other six input parameters for the school algorithm were minimum school length (40 m); minimum school height (5 m); minimum candidate length, i.e., minimum length allowed for a single school candidate (5 m); minimum candidate height, i.e., minimum height allowed for a single school candidate (2 m); maximum vertical linking distance, i.e., maximum vertical distance allowed between two school candidates being linked to form a school (5 m); and maximum horizontal linking distance (20 m) (SonarData 2005). A representative echogram showing walleye pollock schools is shown in Fig. 2.

School descriptors were generated by the Echoview software, including morphometric descriptors (length, thickness and area of schools, Fig. 2), positional descriptors (longitude, latitude, school depth, bottom

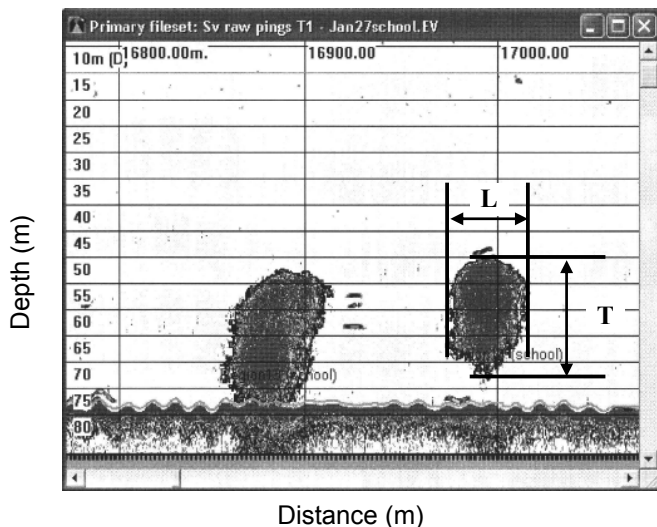


Figure 2. Representative echogram of walleye pollock schools. L is the length and T is the thickness of a school.

depth), and energetic descriptors (S_v , volume backscattering strength; $NASC$, nautical area scattering coefficient) (Simmonds and MacLennan 2005). Based on the above descriptors, some relational descriptors were also determined as follows. Fractal dimension of a school is an index of shape complexity and is a function of school perimeter related to school area (Nero and Magnuson 1989). The line backscattering coefficient, s_L , is a measure of a school's total backscatter and is calculated by integrating the volume backscattering coefficient (s_v) over the sectional area of aggregation (MacLennan et al. 2002). An abundance index, I_{abun} , was obtained by multiplying $NASC$ by school area. The vertical distribution of a school, V_D , is the distance between school depth and bottom depth.

To examine pollock schooling changes during fishing, two separate fishing periods were used to investigate the changes at the school scale and larger scales. Based on the available data and the track of the fishing vessel, the first period was set from January 22 to February 5, and the second period was set from February 14 to February 24. The vessel operated in roughly the same area in both periods, allowing comparisons to be made between periods (Fig. 1). For hypothesis testing, the detected schools during the two periods were pooled and the statistical significance was determined by Student t -tests (Zar 1999).

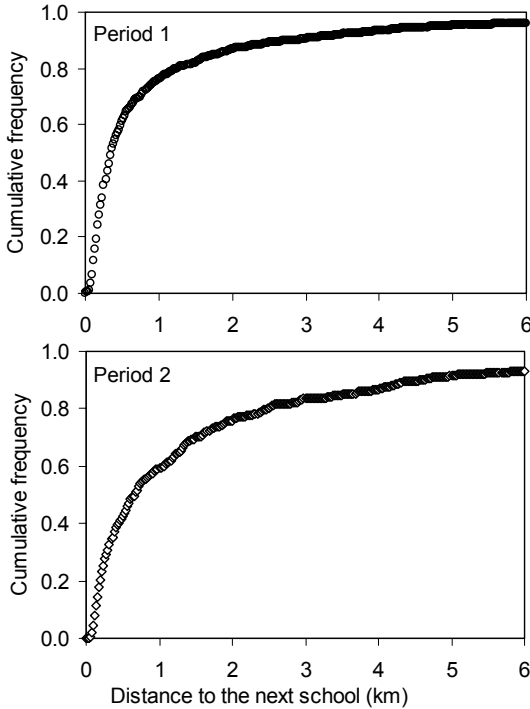


Figure 3. The cumulative distribution of the distance to the next school along the fishing track in the two periods.

It is common for schools of pelagic species to group together in larger scale aggregations, called clusters (Swartzman 1997, Petitgas 2003). To test if there was clustering of schools, the school data for each day were binned into 1 nm elementary distance sampling units (EDSUs) along the fishing track; this distance is commonly used in acoustic analysis (Reid 2000). Statistical significance was tested by the Pearson χ^2 criterion:

$$\chi^2 = \sum_{i=1}^m (n_i - \bar{n})^2 / \bar{n}$$

which has a χ^2 distribution with $m-1$ degree of freedom (Swartzman 1997), where m is the number of EDSUs, n_i is the number of schools of the i th EDSU, and \bar{n} is the average number of schools in an EDSU.

If there was evidence of clustering, the patterns in school clusters were studied. To define a cluster, the next-neighbor distance (NND) was computed for each school along the fishing track. A 1 km thresh-

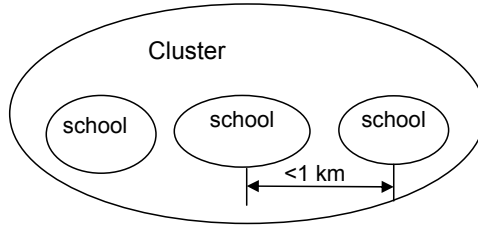


Figure 4. Schematic figure showing the relationship between cluster and schools.

old NND was used to group schools into different clusters because it is near the leveling-off point of most NND-cumulative distributions (Fig. 3) (Petitgas 2003). This point is used as the threshold because the curvature of the distribution curve is related to the repetition rate of the process and hence to the scale of the clustering. Fig. 4 shows the schematic relationship between a cluster and schools. After clustering, some additional variables were recorded: the number of clusters (N_{clus}), the length of each cluster (L_{clus}), the number of solitary schools (N_{sol}) (schools not in clusters), the number of schools per cluster (N_s), and the number of schools per unit cluster length (ρ_{clus}). The abundance index was also calculated for clusters (I_{clus}) and solitary schools (I_{sol}). To test if the threshold is appropriate, a linear regression was conducted for the number of schools in cluster versus the cluster length (Petitgas 2003).

Variography was used to examine changes in the spatial structure between the two fishing periods. Based on the detected schools, we calculated the arithmetic average of the school volume backscattering coefficient (s_v) within each 1 nm EDSU for constructing one-dimensional variograms. Acoustic survey data are characterized by a few large values with a majority of rather low values. This may cause severe problems in structural analysis based on the semi-variogram and its parameters. Consequently a robust version of the experimental semi-variogram (Cressie and Hawkins 1980) is used:

$$\gamma^*(h) = \frac{1}{2} \frac{\left\{ \frac{1}{|N(h)|} \sum_{i=1}^{N(h)} |z(s_i) - z(s_i + h)|^{1/2} \right\}^4}{0.457 + 0.494/|N(h)|}$$

where $z(s_i)$ is the value of the school descriptor s_v at location s_i , $z(s_i + h)$ is the value of s_v at a distance h from s_i , and $N(h)$ is the number of pairs with a distance h apart.

A spherical model was used to fit semi-variograms (Cressie 1993). The range, sill, and nugget characterize the spatial structure of pollock

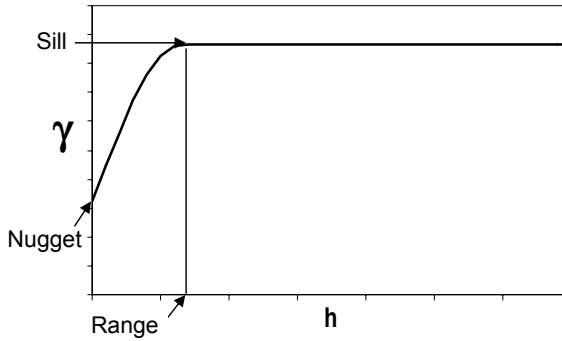


Figure 5. Parameters of the model variogram.

at a scale larger than 1 nm. The range is the distance where the semi-variogram levels off at the sill (Fig. 5). The discontinuity at the origin is the nugget effect caused by measurement error and variation at scales smaller than the lag size.

Results

Echo trace classification

There were 808 schools identified in the first period and 474 schools identified in the second period. Several school characteristics exhibited significant differences between the two periods (Table 1). School density was significantly higher in the second period, as evidenced by higher $NASC$ and s_L ($P < 0.001$). The density almost doubled but the school size became smaller in the second period, as evidenced by the decrease in all morphometric descriptors (school length, thickness, and area in Table 1, $P < 0.01$). Despite the smaller size in the second period, the abundance index was higher ($P < 0.05$). Fractal dimension was significantly different between the two periods ($P < 0.001$); the schools became smoother in the second period as indicated by their smaller fractal dimensions. Unlike the differences in morphometric and energetic descriptors, the vertical distribution of schools (approximately 7.5 m above bottom, Table 1) was similar for the two periods ($P = 0.74$).

NND-clustering

The average number of schools per EDSU for each day, \bar{n} , was higher in the first fishing period than in the second period (Table 2). A non-parametric test was used to test the difference of the daily \bar{n} in the two periods and the results demonstrated that they are statistically different (Wilcoxon rank test, $P < 0.05$). The clustering of schools was apparent for

Table 1. The school descriptors generated by Echoview and some relational descriptors.

| | Period 1 | | Period 2 | | P-value |
|--|----------|-------|----------|-------|---------|
| | Average | SE | Average | SE | |
| Length (m) | 114.46 | 7.80 | 80.75 | 6.31 | 0.003 |
| Thickness (m) | 15.26 | 0.26 | 11.27 | 0.28 | <0.001 |
| Area (m ²) | 899.39 | 73.50 | 580.77 | 85.21 | 0.006 |
| NASC (m ² /nmi ²) | 22630 | 2015 | 44569 | 3144 | <0.001 |
| Fractal | 1.478 | 0.004 | 1.429 | 0.004 | <0.001 |
| s_L (m) | 0.048 | 0.004 | 0.079 | 0.009 | <0.001 |
| I_{abun} | 5.80 | 0.65 | 8.91 | 1.46 | 0.03 |
| V_D (m) | 7.42 | 0.22 | 7.56 | 0.40 | 0.74 |

s_L = the line backscattering coefficient; I_{abun} = the abundance index of school; and V_D = the distance between the school depth and bottom depth. A Student *t*-test was used to test for significant differences between the two periods.

most days (Table 2). It is not surprising that the average NND increased in the second period ($P < 0.001$, Table 3), because the number of schools per EDSU was smaller (Table 2).

With a fixed 1 km threshold to identify clusters, 723 schools were grouped into 115 clusters with 85 solitary schools in the first period. In the second period, 349 schools were grouped into 80 clusters with 125 solitary schools. The coefficients of determination (R^2) from the linear regression of the number of schools in a cluster on cluster length are high in the two periods (0.92 and 0.88, respectively).

Although the average NND between schools increased in the second period, the distances between schools within the clusters did not differ in the two periods, because there was similar number of schools per unit cluster length (i.e., ρ_{clus} , Table 3). The larger NND is due to the larger distance between clusters ($P = 0.04$) and between solitary schools ($P = 0.10$). In contrast, there are more schools in each cluster in the first period ($P < 0.05$), which resulted in the cluster length being significantly higher in the first period ($P < 0.05$). Also, the number of schools per km significantly decreased and the ratio of solitary schools to total schools significantly increased in the second fishing period (Wilcoxon rank test, $P < 0.05$) (Fig. 6). However the decrease of the number of clusters per km was not significant (Wilcoxon rank test, $P = 0.098$) (Fig. 6). The Wilcoxon rank test was used here because these ratios were calculated for each day and sample sizes were small. Cluster abundance was similar for the two periods ($P = 0.96$) although on average clusters were of smaller size with fewer schools in the second period. Similarly, abundance of solitary schools did not differ between the two periods.

Table 2. Statistics of schools per elementary distance sampling units (EDSU).

| | | | | | | | | | | | | | |
|-----------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Date | 1/22 | 1/23 | 1/24 | 1/25 | 1/26 | 1/27 | 1/28 | 1/29 | 2/1 | 2/2 | 2/3 | 2/4 | 2/5 |
| \bar{n} | 3.18 | 3.67 | 4.05 | 2.21 | 0.52 | 1.03 | 1.76 | 2.36 | 2.71 | 0.56 | 1.78 | 1.69 | 3.39 |
| χ^2 | 364* | 220* | 168* | 174* | 89* | 258* | 280* | 402* | 259* | 64 | 136* | 79* | 412* |
| Date | 2/14 | 2/15 | 2/16 | 2/17 | 2/18 | 2/19 | 2/20 | 2/21 | 2/22 | 2/23 | 2/24 | | |
| \bar{n} | 1.69 | 2.14 | 1.38 | 2.24 | 2.48 | 0.50 | 1.17 | 1.65 | 1.20 | 0.35 | 0.35 | | |
| χ^2 | 107* | 248* | 183* | 169* | 319* | 102 | 157* | 378* | 185* | 101* | 131* | | |

\bar{n} is the average number of schools in the EDSU. The asterisk means the chi-square test is statistically significant at a $P < 0.05$ level.

Table 3. Parameters estimated by next neighbor distances (NND) clustering procedure.

| | Period 1 | | Period 2 | | P value |
|----------------------|----------|-------|----------|---------|---------|
| | Average | SE | Average | SE | |
| NND (m) | 1,232.2 | 104.8 | 2,399.7 | 251.5 | <0.001 |
| D_{sol} (m) | 4,149.4 | 368.7 | 5,225.5 | 538.3 | 0.10 |
| D_{clus} (m) | 6,467.3 | 886.4 | 10,298.7 | 1,832.1 | 0.04 |
| L_{clus} (m) | 1,724.7 | 200.9 | 1,203.0 | 148.6 | 0.04 |
| N_s | 6.28 | 0.64 | 4.36 | 0.47 | 0.02 |
| ρ_{clus} (#/km) | 5.65 | 0.42 | 5.43 | 0.47 | 0.74 |
| I_{clus} | 34.04 | 5.81 | 33.52 | 9.15 | 0.96 |
| I_{sol} | 8.93 | 3.27 | 12.09 | 3.53 | 0.53 |

NND = average next-neighbor distance among all schools; D_{sol} = average next-neighbor distance among solitary schools; D_{clus} = average distance to the next cluster; L_{clus} = average length of clusters; N_s = average number of schools per cluster; ρ_{clus} = average number of schools per unit cluster length; I_{clus} = average abundance index of clusters; I_{sol} = average abundance index of solitary schools. The Student t -test was used for the statistical significance.

Variography

Variograms for the average s_v showed significant structure in the two periods (Fig. 7). The nugget effect only contributed a small part of the variance (42% for the first period and 25% for the second period). The variograms for the two periods were different, indicating that the spatial structure of walleye pollock changed between the two periods. The estimated nugget, sill, and range (0.12, 0.29, 5.9, respectively) in the first period were smaller than those (0.66, 2.61, 16.8, respectively) in the second period, which indicates an increase in variability of pollock schools at all spatial scales and that the spatial structure of pollock schools was more extended after fishing.

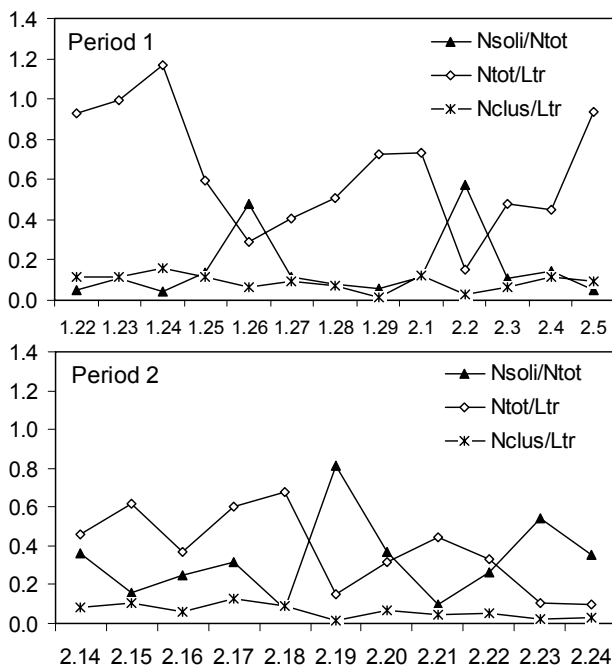


Figure 6. Results of the next neighbor distances (NND) clustering procedure for the two fishing periods: ratio of solitary schools (N_{soli}) to total number of schools (N_{tot}), ratio of N_{tot} to track length (L_{tr}), and ratio of number of clusters (N_{clus}) to L_{tr} .

Discussion

Walleye pollock is one of the main prey species of Steller sea lions. The decline in the sea lion abundance has caused concerns about potential competition between commercial fishing and sea lions. Wilson et al. (2003) described two kinds of fishing effects on pollock. First, fishing removal may cause the decline of the stock abundance in a local area. However, Battaile and Quinn (2006) found evidence pollock recover from this impact in about one week, so this effect may not be strong. Second, fishing may affect long-term pollock behavior that may cause changes in pollock spatial structure. The fish may dive deeper after fishing or form smaller but denser aggregations. The spatial coverage of fish may decrease after disturbance. Both of these effects may impact the foraging behavior of predators on pollock.

To study the effects of fishing on a fish population, one method is to observe the exploited population over a short period, such as the

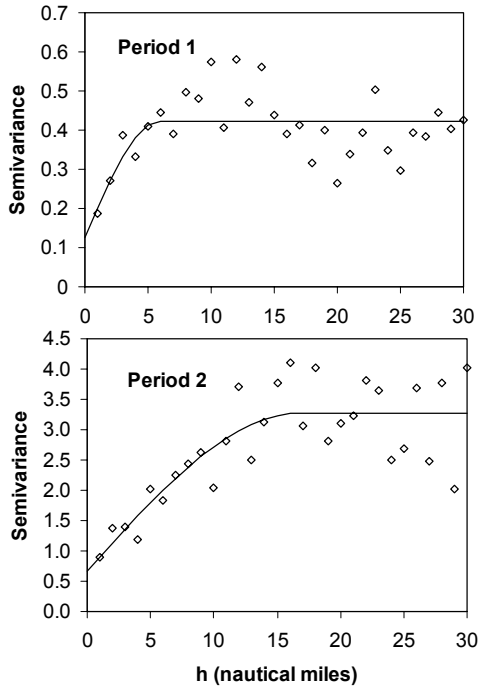


Figure 7. Variograms for two fishing periods. Lag interval was 1 nm and a total of 30 lags were used.

Wilson et al. (2003) study on the interaction between pollock and fishing in the Gulf of Alaska east of Kodiak Island. The study area was surveyed before, during, and after fishing activities. Pollock spatial distribution, biomass and vertical distribution were compared to investigate the effect of fishing. They were unable to detect significant links between fishing and pollock distribution and biomass.

We used two fishing periods because nearly the same areas were fished in both (Fig. 1). Although the fishing tracks were not exactly the same in the two periods as in a scientific survey, the fishing tracks were highly overlapped in the study area. Most of the areas traversed in the second period had been traversed during the first period. Therefore, we considered it reasonable to compare the pollock distribution during the two periods.

The study vessel headed northeast after February 6 and returned to the study area on February 14. The other fishing vessels exhibited similar fishing patterns based on our data. This exploitation pattern gave pollock in the study area about one week without fishing impacts.

The average abundance was similar in the two fishing periods, suggesting that any local depletion that may have occurred was apparently replenished by pollock moving in from other areas.

This paper mainly addressed the question of changes in pollock spatial distribution at different scales over a short time period (about one month). After some days of fishing, the pollock schools seemed to have significant changes at the small scale (school level). The schools became denser (increased $NASC$ and s_L), smaller (decreased morphometric descriptors), and smoother (decreased fractal dimension). Since total abundance did not change substantially between the two fishing periods, an increase in school density would be expected to result in a decrease in school frequency and an increase in the distance among schools. Unlike the significant changes in morphometric and energetic descriptors, the vertical distribution did not change significantly, suggesting that the fish did not dive deeper as has been hypothesized. The bottom depth is mostly less than 150 meters on the fishing grounds north of Unimak Island. Since most of the detected schools were just above the bottom, the ability of schools to dive deeper is restricted, so the vertical distribution of disturbed fish in deeper fishing areas cannot be inferred from our study.

Clustering of schools is a common phenomenon for schooling fish (Swartzman 1997, Petitgas 2003). Our study confirmed that there is clustering of eastern Bering Sea pollock schools. To identify the clusters, both fixed distance threshold (Swartzman 1997) and variable threshold (Petitgas 2003) methods have been used. For comparison of clusters in the two fishing periods, we chose the fixed threshold method, because of the short time period and small area covered in this study. The 1 km threshold value was chosen based on the cumulative frequency of NNDs. Our results established that this threshold worked well according to the criteria by Petitgas (2003). There are neither too many clusters nor solitary schools, and there is a high R^2 for the linear regression of the number of schools in a cluster on cluster length.

Similar to the results at the school level, there were also significant changes at the level of clusters of schools and 1 nm EDSU. A decrease of school numbers per EDSU and the increase in NNDs suggest that fishing may have had a short-term effect. One interesting result is that the NND between schools within clusters did not change. This suggests that there is some attraction/repulsion process that keeps NND within clusters the same while changing the number of schools in a cluster. The increased overall NND was caused by an increase in inter-cluster distance or perhaps distances between solitary schools (Table 3). In contrast, the cluster abundance was similar between the two periods despite the changes of school characteristics in clusters. Similarly, average abundance of solitary schools did not differ during the two periods. Pollock may find more places suitable for aggregation in the absence of fishing,

but then find fewer areas suitable after encountering fishing impacts. Once these preferred areas are chosen, pollock might form tighter and smaller schools or clusters of schools with high abundances.

Variograms display the spatial distribution pattern of pollock schools at a scale larger than 1 nm. The nuggets for the two periods contributed only a small portion of the variance, which suggests the presence of spatial correlation. From the increased sill and nugget, pollock schools became more variable in spatial distribution at all scales greater than 1 nm, which is also found at school level. In the second period, most of the school descriptors had higher variances (Table 1). The range in the second period is higher than that of the first period (Fig. 7), indicating that spatial correlation of pollock extends to greater distances.

In summary, our results suggest the following operative hypothesis of pollock schooling behavior during the A fishing season. Pollock aggregate into schools in the daytime and disperse at night during the spawning season. After about two weeks of fishing, the aggregation pattern changes both at the school scale and scales larger than 1 nm. Pollock aggregate in smaller but denser schools that have a patchier distribution in space. The changed aggregation pattern may be due to commercial fishing or to biological changes in behavior and movement. It is unknown whether the increased patchiness of pollock is a persistent feature of the A fishing season. This study is a first look at pollock schooling and the effects of fishing on pollock school distribution. The observations are somewhat limited, so it is difficult to draw strong conclusions. However, the results of this study suggest fishing may alter school distribution and density. We recommend further research be undertaken to better understand the relationship between fishing removals and the subsequent reduced spatial extent of the pollock and the possible effect on the foraging ability of Steller sea lions and other predator species dependent on pollock.

Acknowledgments

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The Incredible Shrinking Georges Bank Haddock (*Melanogrammus aeglefinus*)

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Abstract

The Georges Bank haddock stock began to recover from a state of near collapse (5% of B_{MSY}) in the mid-1990s after portions of the stock were protected by large-scale, year-round, closed areas. The stock produced an exceptionally abundant year class in 2003 and may provide the potential to rebuild the stock to B_{MSY} in the near future. Coincident with this exceptional recruitment event, consistent annual decreases in haddock mean lengths and weights at age have occurred across all age groups since 2001. We investigated how stock density, consumption, and temperature variations during 1968-2004 affected haddock growth by using assessment results and food habit data collected from research surveys. Time series of bottom-water temperature anomalies and cohort-specific growth data were used to investigate the effects of changes in stock density and temperature on growth. The Georges Bank haddock stock shows clear signs of density-dependent growth, an important consideration in stock recovery and assessment.

Introduction

The Georges Bank haddock (*Melanogrammus aeglefinus*) stock has been fished since at least the early 1900s, when reliable catch records were initiated. The Georges Bank haddock stock is currently managed as western and eastern Georges Bank stock units to reflect a harvest sharing agreement between the United States and Canada (Fig. 1). This important New England groundfish produced average annual yields of

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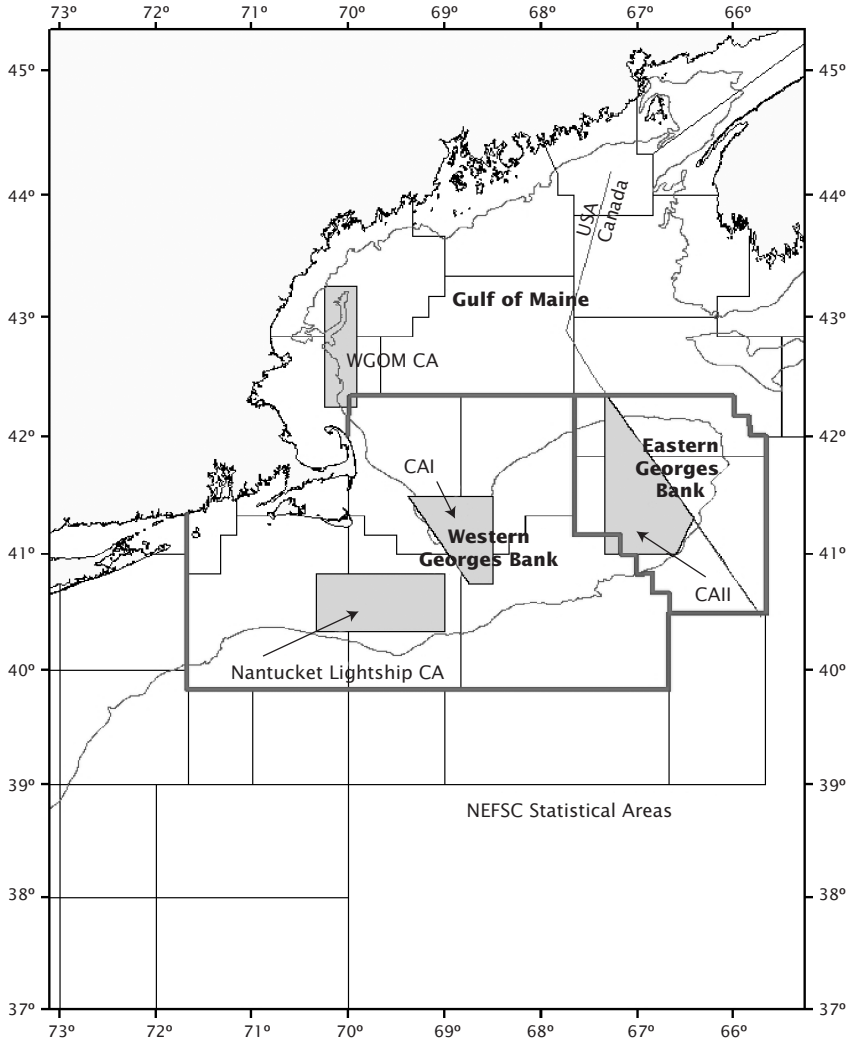


Figure 1. Distribution of Georges Bank and Gulf of Maine haddock stocks in relation to Northeast Fisheries Science Center (NEFSC) statistical areas along with western and eastern Georges Bank management units and four large-scale closed areas: Closed Area I (CAI), Closed Area (CAII), Nantucket Lightship CA, and western Gulf of Maine (WGOM) CA.

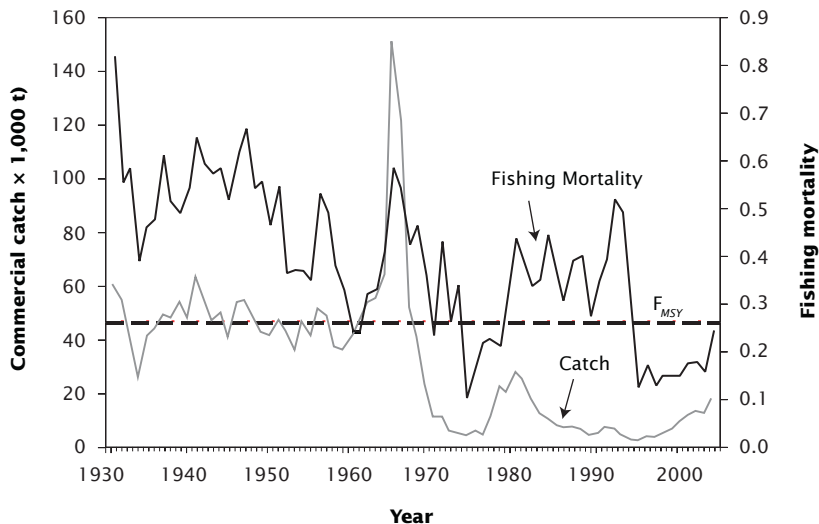


Figure 2. Nominal catches (shaded area) and fishing mortality (solid line) for Georges Bank haddock along with the current estimate of fishing mortality to produce maximum sustained yield (F_{MSY} , dashed line) during 1931-2004.

about 46,000 t during 1931-1960 (Brodziak et al. 2006) despite experiencing relatively high fishing mortality rates of roughly $F = 0.5$ (Fig. 2). The haddock stock was heavily fished by distant water fleets in the mid-1960s and was severely depleted by the early 1970s. Two strong year classes (Fig. 3, 1975 and 1978) bolstered the stock in the mid-1970s, but these year classes were rapidly fished out. The stock subsequently declined through the 1980s until it was declared to have “collapsed” in 1994 (Fig. 3).

Restrictive fishery management measures, including year-round closed areas, days-at-sea restrictions, and increased trawl mesh sizes, were implemented to rebuild New England groundfish stocks in the mid-1990s (Fogarty and Murawski 1998, Brodziak and Link 2002). These measures were effective at reducing fishing mortality on Georges Bank haddock, which experienced fishing mortalities lower than the overfishing threshold for the longest period on record during 1995-2004 (Fig. 2). The stock had a distinct positive response to reduced fishing mortality (Fig. 3). Spawning biomass increased from a record low of 15 kt in 1995 to 117 kt in 2004. The rapid turnaround of the Georges Bank haddock stock was incredible to some who believed there was little chance that this collapsed stock would ever recover.

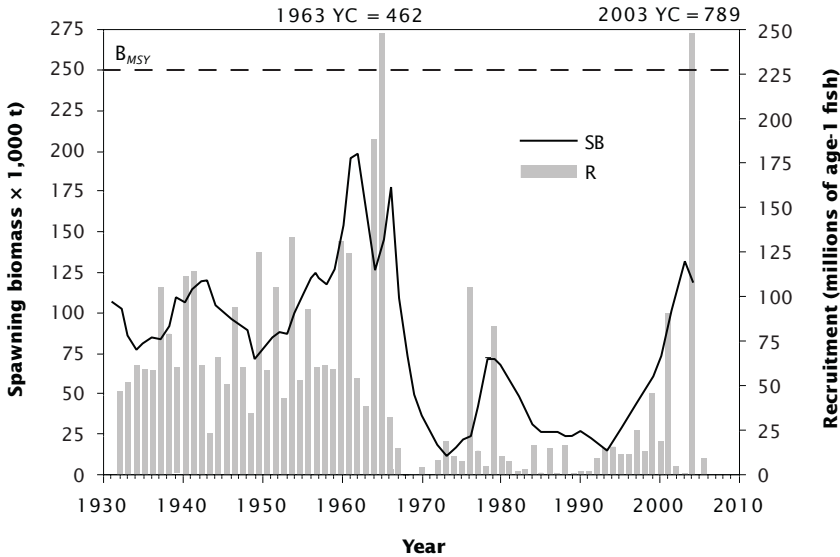


Figure 3. Spawning biomass (SB, solid line) and recruitment (R, vertical bars) of Georges Bank haddock along with the current estimate of spawning biomass to produce maximum sustained yield (B_{MSY} , dashed line) during 1931-2004.

As the stock has recovered, however, there has been a marked decline in mean lengths and weights at age. In particular, reductions in juvenile and adult mean lengths and weights at age have been substantial in both research survey and commercial fishery samples conducted in recent years (Van Eeckhaute and Brodziak 2005, Brodziak et al. 2006). Current juvenile and adult sizes at age, indexed by the Northeast Fisheries Science Center (NEFSC) spring survey mean length at age 2 and age 5, are well below their long-term average (Fig. 4). An age-5 haddock now is roughly the same size as an age-4 haddock during the 1980s and is roughly 5 cm smaller on average than an age-4 haddock during the 1970s. Overall, haddock size at age has been shrinking since the late 1990s.

The Georges Bank haddock stock produced an exceptionally abundant year class in 2003 (Van Eeckhaute and Brodziak 2005, Brodziak et al. 2006). This year class appears to be the largest ever recorded and has the potential to rebuild the stock to biomass well beyond B_{MSY} by 2007 (Fig. 3). The growth pattern of the 2003 year class appears to be slower than of the exceptional 1963 year class (Fig. 5), which grew very slowly in comparison to other year classes on average. The slow growth of the 2003 year class has meant that it will not recruit to the commer-

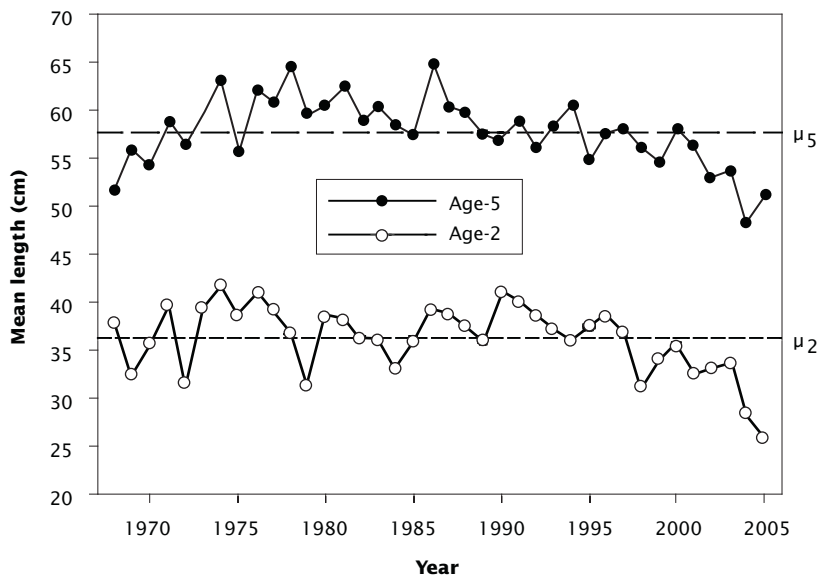


Figure 4. Mean length at age of juvenile (age 2, open circle) and adult (age 5, solid circle) Georges Bank haddock during NEFSC spring research surveys along with their mean values (μ_2 and μ_5), 1968-2005.

cial haddock fishery, which has a 48 cm minimum size limit, until it reaches age 4 or older. The delay of about one year in recruitment has been a surprise to the New England fishing industry, which expected to harvest this abundant year class in 2006 to help defray reduced yields from Georges Bank cod and other overfished groundfish.

In this study, we empirically address the question of why Georges Bank haddock are growing more slowly than during the 1970s to mid-1990s. We used stock assessment data along with oceanographic and food habit data collected from research surveys to investigate several factors that could affect growth: stock density, oceanographic conditions, and food consumption/prey availability. We particularly wanted to test for first-order effects of these factors on juvenile and adult size and on average growth increment. Using alternative regression models fit to both mean size at age within a cohort across years and across cohorts with an annual time step, we investigate the implications of changes to haddock growth for the assessment and management of the Georges Bank haddock stock.

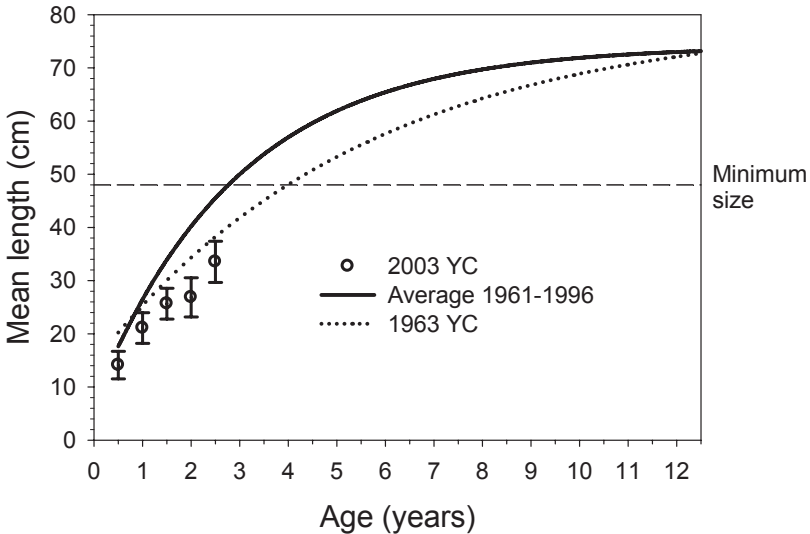


Figure 5. Comparison of observed mean length at age ($\pm \sigma$) of the 2003 Georges Bank haddock year class during Northeast Fisheries Science Center (NEFSC) research surveys conducted between autumn 2003 and autumn 2005 with von Bertalanffy growth curves for the exceptional 1963 year class (dotted line) and the average growth curve for the 1961 through 1996 year classes (solid line) estimated using the likelihood method described by Kimura (1980) as well as the minimum legal commercial size (dashed line) for the U.S. fishery.

Materials and methods

Response variables

Size-at-age data based on otolith ageing were used to characterize haddock growth during the past four decades. Research survey data collected during the NEFSC spring bottom trawl survey provided a consistent set of standardized information on haddock size at age during 1968-2005 (Brodziak et al. 2006). Typically, this survey samples Georges Bank for 2-3 weeks during late March to early April. Mean spring survey length at age 2 was used as an index of juvenile haddock growth (Fig. 4); this is roughly the current median age of sexual maturity for Georges Bank haddock (Brodziak et al. 2006). The mean survey length at age 5 was used as an index of adult growth (Fig. 4). The difference between realized size at age 5 and age 2 was also used to index the growth rate of individual cohorts and also to measure the realized difference in size at age within a year across cohorts.

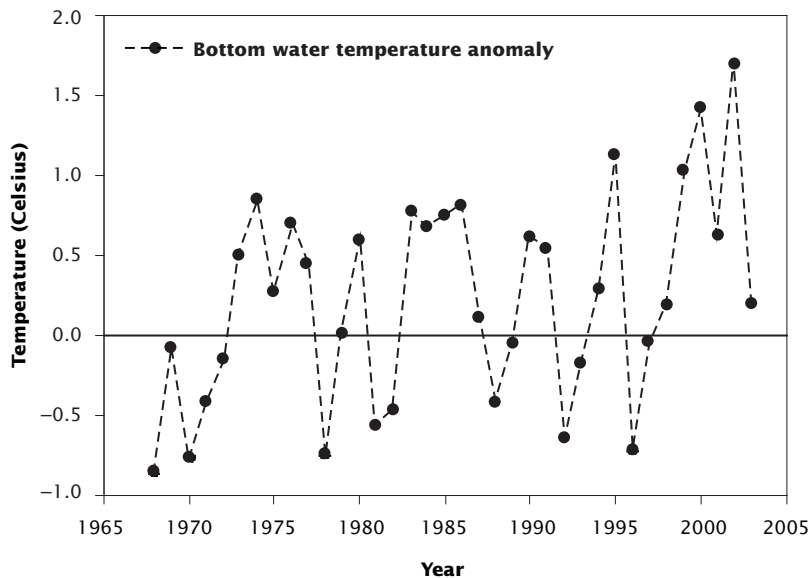


Figure 6. Annual bottom water temperature anomalies for Georges Bank based on research surveys during 1968-2003.

The growth indices provided three time series of growth response data for individual cohorts. These were size at age 2 by cohort, 1966-2003; size at age 5 by cohort, 1963-2001; and growth increment age 5 to age 2 by cohort, 1966-2001, where year indexes the cohort. Similarly, there were three time series for realized size at age within a year: observed size at age 2 by year, 1968-2005; observed size at age 5 by year, 1968-2005; and observed growth increment age 5 to age 2 by year, 1968-2005. Overall, the six growth series were used as response variables in analyses to evaluate the effects of stock density, temperature, and food availability on haddock growth.

Explanatory variables

Three explanatory variables were used to characterize the effects of changes in haddock stock density, environment, and feeding conditions on growth. For stock density, spawning biomass was used as a proxy for the relative magnitude of adult biomass (Fig. 3). These data were available for 1963-2004 from the most recent stock assessment (Brodziak et al. 2006). Changes in environmental conditions were indexed by a time series of bottom water temperature anomalies for Georges Bank, measured as annual deviations from the long-term average (Fig. 6). The bottom water temperature anomalies for Georges Bank were computed

Table 1. Length ranges (cm) of haddock age groups used to estimate total consumption by time period.

| Period | Age group | | | |
|-----------|-----------|-------|-------|-----|
| | I | II | III | IV |
| 1975-1984 | 1-47 | 48-61 | 62-71 | >71 |
| 1985-1994 | 1-47 | 48-57 | 58-72 | >72 |
| 1995-1999 | 1-46 | 47-57 | 58-67 | >67 |
| 2000-2005 | 1-42 | 43-52 | 53-60 | >60 |

using the methods of Mountain et al. (2004) and were available for 1968-2003 (D. Mountain, NEFSC, pers. comm.). However, there were no comparable estimates of haddock feeding condition on Georges Bank. As a result, we developed a proxy for feeding conditions based on an estimate of the amount of biomass (grams of wet weight) consumed by the haddock stock in each year.

Consumption estimates

We developed estimates of annual Georges Bank haddock consumption using food habit data collected from annual NEFSC spring and autumn survey data. To do this, all available haddock stomach data were compiled to compute mean per capita ration size for four age groups: age 0 to age 2 (group I), age 3 and age 4 (group II), age 5 through age 8 (group III), and age 9 and older (group IV). Length-specific stomach volume measurements were aggregated over 10-year periods to ensure adequate sample sizes, because few haddock stomachs were collected during periods of very low stock abundance in the 1980s to early 1990s and also because there was annual variability in food habit observations. The time periods chosen for aggregating the food habit data were 1975-1984, 1985-1994, 1995-1999, and 2000-2005. The last decade of data was split into two 5-year periods to account for the almost tenfold change in stock density during 1995-2004. The food habit data were also split out by length groups to approximate ontogenetic changes in diet. In this case, it was necessary to approximate the length ranges of age groups during each time period to account for changes in average length at age (Table 1). Given these size cutoffs, estimates of haddock per capita consumption by age group were computed using methods described in Link and Almeida (2000). Annual haddock consumption during 1963-2004 was then estimated as the product of mean per capita consumption per group times the stock size estimate of each group from the most recent assessment (Brodziak et al. 2006). No food habit data were available for Georges Bank haddock during 1963-1974, and

mean per capita consumption estimates for this period were imputed by assuming that per capita consumption during 1963-1974 was similar to that during 2000-2005, a period when stock density was similar. The importance of the effects of time period and age group on observed haddock stomach weights were tested using type III sums of squares for a two-way unbalanced ANOVA (Searle 1987). We also tested whether mean per capita consumption estimates differed at the $\alpha = 0.05$ confidence level between time periods and between age groups using Tukey's studentized range test.

Model selection and multimodel inference

There were several possible ways in which haddock growth might have changed in relation to stock density and oceanographic and feeding conditions since the 1960s. To address this, we used a multimodel inference approach to model selection and hypothesis evaluation (c.f., Burnham and Anderson 2002 and references therein). We evaluated three hypotheses using two ways of comparing size at age between years, both by cohort and across year classes. Under the first hypothesis, juvenile growth has been unaffected by stock density and oceanographic and feeding conditions. This was investigated by testing whether mean length at age 2 was influenced by each of the factors. Under the second hypothesis, adult growth was independent of the factors. This was also evaluated by testing whether mean length, in this case for age-5 haddock, was significantly altered by the three predictors. The third hypothesis was that growth rate from juvenile to adult was invariant with respect to the three factors; this was evaluated using the growth increment from mean size at age 2 to age 5. The three hypotheses were tested using two treatments of the growth data. These treatments represented growth effects on individual cohorts and across year classes by lagging the growth indices to match the time in which the explanatory factors influenced growth (Table 2). For the hypotheses by cohort, the potential effects were assumed to occur on age-0 haddock. In particular, the conditions experienced by haddock early life history stages consisting of eggs, larvae, and newly settled juveniles were tested for their impact on subsequent growth. To assess the hypotheses across year classes, the potential effects of prevailing conditions on realized growth of juveniles and adults from different year classes were compared within each year. In this case, the observed predictors were assumed to influence growth pattern of juvenile and adult haddock, as indexed by age-2 and age-5 mean length, within a given year (Table 2).

We used a model selection and multimodel inference approach (Buckland et al. 1997, Burnham and Anderson 2002) to approximate the first order effects of the predictors on growth indicator (G). This approach allowed us to characterize model selection uncertainty if alternative models with different predictors provided similar fits to the

Table 2. List of hypotheses about the potential effects of stock density (D), temperature (T), and consumption (C) by haddock on observed Georges Bank haddock juvenile and adult mean lengths at age (a) by year (k), denoted as $\mu_{a,k}$, and observed juvenile to adult growth increments to be tested using stepwise model selection.

| Hypothesis | Response variable | Explanatory variables |
|---|-----------------------------|-----------------------|
| Juvenile size is independent of D , T , and C experienced at age 0 by cohort (k) | $\mu_{2,k+2}$ | D_k, T_k, C_k |
| Adult size is independent of D , T , and C experienced at age 0 by cohort (k) | $\mu_{2,k+5}$ | D_k, T_k, C_k |
| Juvenile to adult growth increment is independent of D , T , and C experienced at age 0 by cohort (k) | $\mu_{5,k+5} - \mu_{2,k+2}$ | D_k, T_k, C_k |
| Juvenile size is independent of D , T , and C within a year (k) | $\mu_{2,k}$ | D_k, T_k, C_k |
| Adult size is independent of D , T , and C within a year (k) | $\mu_{5,k}$ | D_k, T_k, C_k |
| Juvenile to adult growth increment is independent of D , T , and C within a year (k) | $\mu_{5,k} - \mu_{2,k}$ | D_k, T_k, C_k |

growth data. The global linear model included each of the potential predictors, annual stock density, D , temperature anomaly, T , and total haddock consumption, C , as explanatory variables assuming independent and identically distributed errors (ϵ) with zero mean and a constant variance.

$$G = b_0 + b_D D + b_T T + b_C C + \epsilon$$

Subsets of predictors of the global model represented alternative hypotheses regarding which predictors had an important effect on growth. Model selection and multimodel inference techniques were applied to determine whether the global model or an alternative subset of predictors was most appropriate for each of the six hypotheses (Table 2).

The model selection criterion was the Akaike Information Criterion (AIC), which is an information-theoretic approach to judge the adequacy of alternative model fits to a fixed data set (Akaike 1983). In the linear regression case considered here, AIC produces identical model rankings as Mallows's C_p statistic for models with normal residuals and constant variance (Burnham and Anderson 2002). All single-predictor deletions from the global model were compared using AIC. When a simpler model had a superior fit with a lower AIC, then that model supplanted the

global model and the next set of possible single-term predictor deletions was again evaluated using AIC. This iterative model selection approach stopped at the best numerically-fitting model when no single-term deletion improved the AIC fit. If the AIC differences (Δ_{AIC}) between previous and subsequent best-fitting model were small, however, on the order of $\Delta_{\text{AIC}} < 2$ (c.f., Burnham and Anderson 2002), then both models provided similar fits to the data and, as a result, there was model selection uncertainty. In this case, we used model averaging based on the AIC differences of the two best-fitting models to evaluate the relative probability that each was true since the model selection criterion did not provide a clear choice. This was accomplished by computing the Akaike weight (W_k) for model k ($k = 1, 2$) as

$$W_k = \frac{\exp\left(-\frac{1}{2}\Delta_k\right)}{\sum_{j=1}^2 \exp\left(-\frac{1}{2}\Delta_j\right)}$$

where Δ_k is the difference between the AIC for model k and the best fitting model with the smallest AIC value and using the weights for averaging model coefficients and computing their model-averaged standard errors (Buckland et al. 1997, Burnham and Anderson 2002). The resulting model-averaged coefficients were then used to quantify the importance of each relevant predictor of growth, although in practice, averaging was applied for only one out of the six growth indicators examined.

Correlations and autocorrelations of the three explanatory variables were also used to assess whether they conformed to model assumptions of independence and uncorrelated errors. Last, nonparametric bootstrapping was applied to estimate parameter bias as well as standard errors of the regression coefficients of the best fitting or model-averaged result (Efron and Tibshirani 1993). In this case, 10,000 bootstrap replicates were used to assess whether parameter bias was important in comparison to parameter variability.

Results

Consumption estimates

Consumption estimates on a per capita basis showed differences among age groups by time period (Fig. 7). ANOVA results indicated that time period, age group, and their interaction were significant ($R^2 = 0.34$, $P < 0.0001$). Per capita consumption estimates were significantly different for each pair of time periods except 1995-1999 and 2000-2005. Similarly, per capita consumption estimates were significantly different between all age groups. Consumption by juvenile haddock (group I) appears to have been higher during the 1980s and 1990s than in recent years.

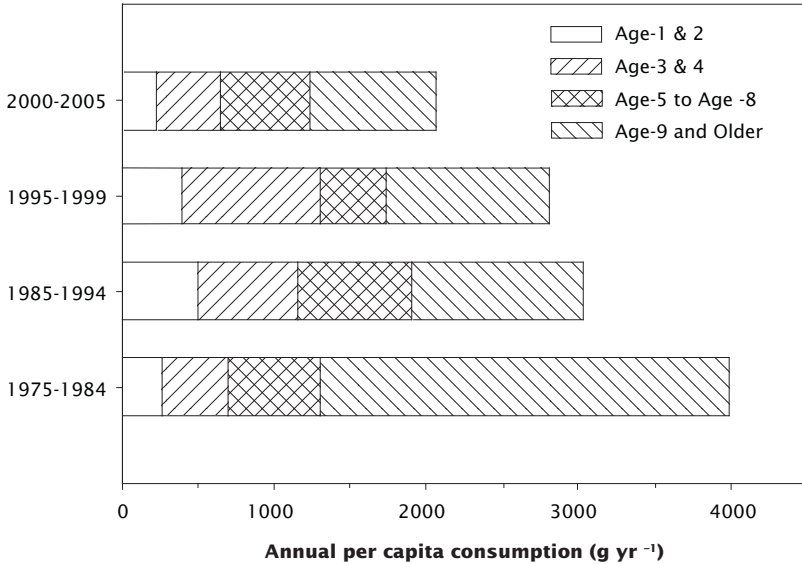


Figure 7. Research survey estimates of annual per capita prey consumed by Georges Bank haddock by age group during four time periods: 1975-1984, 1985-1994, 1995-1999, and 2000-2005.

Consumption by young adult haddock (group II) also appears to be higher during the same time period. In contrast, consumption by older haddock (groups III and IV) appears to have been higher per capita during the 1970s and 1980s. Overall, it appears that there has been a decrease in per capita consumption by older haddock since the 1970s, with a marked decrease for the oldest age group.

Estimates of total haddock consumption during 1963-2005 (Fig. 8) tend to track stock density as might be expected. Summed over the entire time series, consumption by juvenile haddock (group I) represents about 49% of total haddock consumption even though this group has the lowest per capita ration size. The nominal biomass consumption estimates derived from survey food habit data indicate that annual consumption peaked in the mid-1960s and subsequently declined as haddock abundance diminished under intensive fishing pressure. A moderate increase in haddock consumption occurred during the mid-1970s coincident with the production of the large 1975 and 1978 year classes. Consumption then declined and fluctuated about record low levels during the 1980s to early 1990s. Since the mid-1990s, haddock consumption has increased with stock size. Total haddock consumption in the early 2000s appears to have reached the peak levels experienced

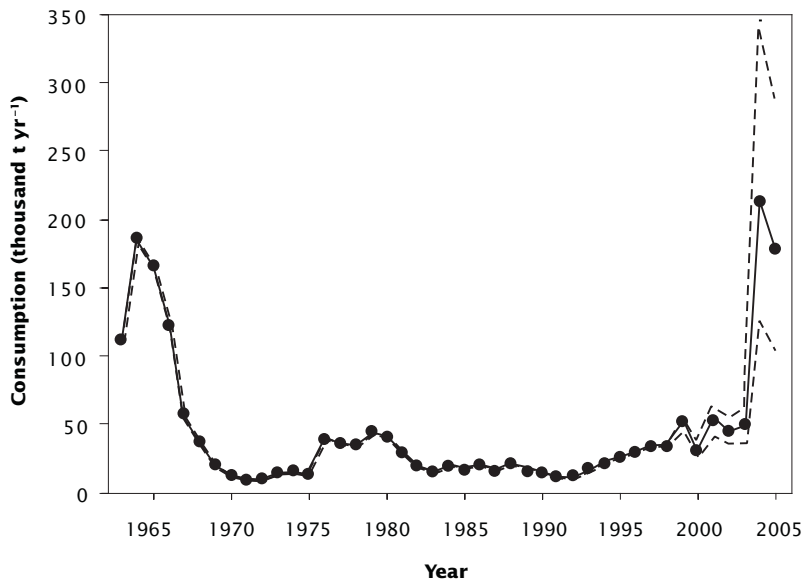


Figure 8. Estimates of annual prey consumption (wet weight, solid line) by Georges Bank haddock during 1963-2005 along with 80% confidence intervals (dashed lines) based on uncertainty in current stock size at age estimates taken from Brodziak et al. (2006).

in the 1960s. Current haddock consumption levels are among the highest ever observed on Georges Bank.

Model selection and multimodel inference

Some of the explanatory variables for the model selection analyses were correlated and also exhibited serial correlation, as might be expected. Total consumption and stock density exhibited a strong positive correlation, $\rho = 0.78$ ($P < 0.001$), primarily due to the dependence of the total consumption estimates on annual stock size estimates. In contrast, temperature was not significantly correlated with either stock density or consumption ($\rho < 0.25$). Among the three potential predictors of growth, both the stock density and consumption series exhibited significant autocorrelations. For spawning biomass, a significant positive autocorrelation occurred at lags 1 through 3 while total consumption had significant positive autocorrelations at lags 1 and 2. In contrast, the bottom temperature series did not exhibit autocorrelation. Overall, the significant serial correlation of the stock density and consumption

Table 3. Model selection results showing the best fitting linear model or model-averaged^a coefficients for the six hypotheses about the potential effects of stock density (*D*), temperature (*T*), and haddock consumption (*C*) on observed Georges Bank haddock juvenile and adult mean lengths at age (*a*) by year (*k*), denoted as $\mu_{a,k}$, and observed juvenile to adult growth increments by cohort or across year classes along with bootstrap *w* of standard error (SE) and bias.

| By cohort | | | | | | | | | |
|--|----------------|-------|-----------------|-----------|-------------------|----------------------------------|---------------------|-----------------------|--|
| Growth Indicator | Δ_{AIC} | R^2 | <i>P</i> -value | Intercept | SE _{int} | Slope | SE _{slope} | Bias _{slope} | |
| Juvenile size ($\mu_{2,k+2}$) | 13.2 | 0.48 | $P < 0.001$ | 40.112 | 0.725 | $b_D = -0.087$ | 0.016 | 0.002 | |
| Adult size ^a ($\mu_{2,k+5}$) | 0.4 | 0.18 | $P = 0.01$ | 61.263 | 1.528 | $b_T = -0.680$ $b_C = -0.140$ | 1.048 0.067 | 0.038 0.006 | |
| Growth increment ($\mu_{5,k+5} - \mu_{2,k+2}$) | 20.6 | 0.17 | $P = 0.02$ | 21.573 | 0.561 | $b_T = -2.377$ | 0.802 | 0.026 | |
| Across year classes | | | | | | | | | |
| Growth Indicator | Δ_{AIC} | R^2 | <i>P</i> -value | Intercept | SE _{int} | Slope | SE _{slope} | Bias _{slope} | |
| Juvenile size ($\mu_{2,k}$) | 13.2 | 0.24 | $P = 0.002$ | 38.878 | 0.767 | $b_D = -0.049$ | 0.014 | -0.001 | |
| Adult size ($\mu_{5,k}$) | 5.6 | 0.13 | $P = 0.03$ | 59.989 | 0.804 | $b_D = -0.038$ | 0.018 | 0.002 | |
| Growth increment ($\mu_{5,k} - \mu_{2,k}$) | 16.5 | 0.00 | ns | 21.826 | 0.513 | ns | ns | ns | |

series suggested that the least squares estimates of regression parameters could be biased due to a lack of independence. The magnitude of this potential parameter bias was evaluated in the bootstrap analyses of the best fitting regression coefficients.

The model selection analyses for growth impacts by cohort indicated that stock density, temperature, and haddock consumption experienced at age 0 each had a significant effect on haddock growth (Table 3). The juvenile size by cohort analysis indicated that the stock density experienced at age 0 had a significant negative impact on the realized mean size at age 2 of that year class (Table 3). The bias of the stock density slope coefficient was less than 3% of the estimated slope which indicated that parameter bias due to serial correlation was unimportant. The AIC difference of the best fitting model was substantial (Δ_{AIC}) in this case and model uncertainty was not apparent for the set of models examined. The regression model results also suggested that stock density explained about half of the observed variability in survey mean size at age 2, which is a substantial amount considering the variety of biotic and abiotic factors that could influence growth.

For the model selection analysis of adult size by cohort, there was substantial model uncertainty with an AIC difference of only $\Delta_{AIC} = 0.4$.

In this ambiguous case, results of the best fitting (total consumption only) and penultimate (total consumption and temperature) models were averaged using Akaike weights computed from the Δ_{AIC} . The associated probabilities for the best fitting and penultimate models were 0.55 and 0.45, respectively. The model-averaged results showed that both total consumption and temperature experienced at age 0 influenced the realized mean size at age 5 (Table 3). In this case, higher total consumption and higher temperatures were associated with smaller mean juvenile size. However, total consumption appeared to have a more pronounced effect given the high variability of the estimated temperature coefficient. The bias estimates for the consumption and temperature slope coefficients were roughly 4% and 6% of the regression coefficients suggesting that parameter bias was relatively low in comparison to the corresponding coefficients of variation, which were roughly 50% and 150%. Overall, the model-averaged results explained only about 18% of the variability in mean adult size and the majority of the variability in adult mean size was based on a combination of non-modeled factors.

The results for the growth increment index suggested that the temperature experienced by a year class at age 0 had an important influence on subsequent growth rate between age 2 and age 5 (Table 3). In this case, higher temperatures had a negative impact on growth increment, similar to that observed for adult size. Parameter bias of the temperature slope coefficient was also estimated to be relatively minor, about 1% of the estimated slope. Nonetheless, there was substantial unexplained variability.

The model selection analyses for growth indicators across year classes indicated that only stock density had a detectable effect on realized growth within a year (Table 3). The regression analysis of observed juvenile size within a year showed that stock density had a significant negative effect on mean length at age 2 when higher stock densities were associated with smaller juvenile sizes at age. In this case, the bias of the stock density slope coefficient was about 2% of the estimated slope, which was minor compared to its standard error. Overall the juvenile size-at-age model explained about one quarter of the variation in juvenile size at age 2.

The analysis of adult size within a year showed similar results (Table 3). Stock density within a year had a significant negative impact on realized mean length at age 5. The relative bias of the stock density slope coefficient was about 6%, much lower than its coefficient of variation of 47%. Nonetheless, the amount of variability explained was relatively low, roughly 13%, and most of the variation in adult size within a year was due to non-modeled factors. The model selection analysis of the observed size difference between age 2 and age 5 haddock within a year showed that none of the relevant factors had a significant effect on this growth indicator (Table 3). In this case, there was no apparent

signal in the growth differences among cohorts and the stock density, temperature or consumption indices by year.

Discussion

The model selection and multimodel inference analyses indicated that there was strong support for the hypotheses that juvenile haddock size was affected by stock density. Stock density experienced in early life history stages had a significant negative impact on juvenile size when analyzed by cohort. This suggests that cohorts that experience low stock densities at age 0 have an initial positive opportunity for rapid growth due to less intraspecific competition. Stock density also had a significant negative impact on observed juvenile size within a year although the estimated strength of this effect was about half that of the stock density experienced at age 0. In this case, higher stock density would likely be associated with reduced per capita ration consumption and reduced juvenile growth rate. Overall, high stock density has a negative impact on the size of juvenile haddock on Georges Bank.

Adult haddock size was similarly affected by stock density but was also influenced by total consumption and temperature. Total haddock consumption and temperature experienced by a cohort at age 0 both had a significant negative effect on realized adult size. This suggests that competition for food and metabolic costs experienced by early life history stages influence subsequent adult size. Lower temperatures and lower total consumption by haddock provide a positive growth opportunity for a cohort. In contrast, observed adult size was significantly negatively associated with stock density within a year. This suggested that competition for food within a year can also influence adult size at age. Overall, adult haddock size was larger when stock density was low or when a cohort experienced favorable growth conditions in its first year.

The model selection analyses showed that the growth increment from juvenile to adult was influenced by temperature when assessed for individual cohorts. There was a significant negative impact of temperature experienced at age 0 on growth increment. This suggests that haddock cohorts that experience unfavorable growth conditions early in life continue to grow slowly in subsequent years.

There is a strong linkage between spawning biomass and observed juvenile and adult sizes at age in the Georges Bank haddock stock. An increase in spawning biomass on the order of 100,000 t would be predicted to lead to a decrease in mean length on the order of 4 to 5 centimeters in juvenile and adult sizes at age. Increases in total consumption by haddock, which is significantly positively correlated with spawning biomass, would likely have similar effects. In this case, it would be simpler to use spawning biomass as an index of the possible effects of

density-dependent growth of haddock because it is a standard component of the haddock stock assessment. Overall, the significant negative impact of high stock density and total consumption on growth provide a clear answer to the question of why the 2003 year class of Georges Bank haddock did not recruit to the fishery in 2006.

Previous studies have also suggested that Georges Bank haddock exhibit a density-dependent growth pattern (Clark et al. 1982) although specific mechanistic factors such as the effect of increased consumption were not examined. The tight coupling between haddock stock density and consumption estimates developed in this study suggests that stock density can be a useful proxy for measuring aggregate intraspecific feeding effects. The fact that haddock feed on a wide variety of benthic organisms (Link and Almeida 2000, Brodziak 2005) suggests that interspecific feeding interactions with other benthivores may also be important. The diet of haddock on Georges Bank overlaps with that of several skate and flatfish species (Garrison 2000, Link and Almeida 2000, Link et al. 2002), yet it is unknown if the recent increases in overall haddock stock consumption affect these species. Furthermore, reduced weights at age have been reported for a number of New England groundfish in recent years (NEFSC 2005). The degree of dietary overlap between haddock and other demersal fishes is rather broad; an evaluation of the joint consumptive impacts of haddock, flatfish and elasmobranchs on Georges Bank would help elucidate whether the system can support several groups of species at or near biomasses that would maximize their individual surplus production. This is an important research topic given recent controversial increases in some groundfish biomass targets (Greene 2002) and the aforementioned decrease in size- or weight-at-age data for several groundfish species.

One of the important results of this study was that juvenile haddock consumption was roughly half of total consumption despite the fact that the per capita ration of adults is several-fold larger than for juveniles. This has potential importance in assessing the consumptive impacts of exceptional haddock year classes, such as the 1963 or 2003, on the growth of prior and subsequent year classes and possibly also with recruitment. Herrington proposed that haddock could exhibit a dome-shaped stock recruitment curve based on intraspecific competition between juvenile haddock and adults on winter feeding grounds (Herrington 1947). Given the empirical findings of this study, Herrington's hypothesis may have increased support. In particular, the theoretical basis of the dome-shaped Shepherd stock-recruitment curve depends on density-dependence in juvenile growth. Whether Georges Bank haddock exhibit a dome-shaped pattern or a flat-topped stock-recruitment relationship is important for the long-term management of this transboundary resource. The lack of stock-recruitment observations at high spawner abundance, in excess of 200,000 t, has certainly limited

the opportunities to detect a decrease in haddock recruitment at higher stock density. Nonetheless, given the size of the recent 2003 year class, the probability of gathering data at high spawner abundance has vastly increased and there will be a valuable opportunity to directly observe the demographic changes associated with high spawner abundance.

The implications of density-dependence in growth for the assessment and management of the Georges Bank haddock stock are substantial and important. A prerequisite for documenting and understanding this pattern has been the ongoing collection of annual haddock size-at-age data. This sampling has continued since the 1930s and it is highly recommended that this long-term monitoring be continued. The primary implication of density-dependent growth of Georges Bank haddock is that the biological reference points of threshold fishing mortality and target spawning biomass need to be revised to account for the observed pattern. The current reference points do not explicitly account for density-dependent changes in haddock growth as stock density increases. To this end, extending the methodology of Brodziak and Legault (2005) to account for density-dependent growth patterns would be a useful approach.

The impacts of the observed shrinkage in haddock size at age are important for this rapidly recovering stock. The recent slower pattern of growth implies that it will likely take more than three years for haddock to recruit to the minimum legal size of 48 cm. This delayed recruitment could lead to an increase in discards of sublegal haddock in coming years, especially from abundant cohorts such as the 2003 year class.

A related issue is whether the benthic production on Georges Bank is currently sufficiently similar to the historic pattern during the 1930s-1960s, when the haddock fishery was very productive. While the Georges Bank ecosystem has experienced strong anthropogenic impacts through intensive fishing over the past 50 years (Fogarty and Murawski 1998), there are few data to quantify changes in benthic production and the potential impacts on haddock growth. In the case of the incredible shrinking Georges Bank haddock, we will just have to be patient and see what nature reveals.

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Estimation of Age-Specific Migration in an Age-Structured Model

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Abstract

The standard Eastern Bering Sea (EBS) walleye pollock (*Theragra chalcogramma*) age-structured stock assessment model has no spatial dimension. To better understand its dynamics on finer spatial and temporal scales, an age-specific movement (ASM) model was developed. The ASM model stratifies the assessment data into two regions (northwest [NW] and southeast [SE] EBS), includes movement, and allows population parameters to be region-specific. The ASM model was used to evaluate hypotheses on age-specific movement between the NW and SE and covered years 1977 to 2005 and ages-3 to 10+. Estimates of biomass and population parameters from the ASM model were similar to those of the standard stock assessment model. The ASM model fitted the yearly observed catch numbers and yield, and catch-age composition data well, but some population parameters were highly uncertain or highly correlated. More in-depth information on finer spatial and temporal scales is needed from spatially explicit studies of EBS walleye pollock. Having additional information from a mark-recapture study would help to stabilize the ASM model and allow some assumptions to be relaxed.

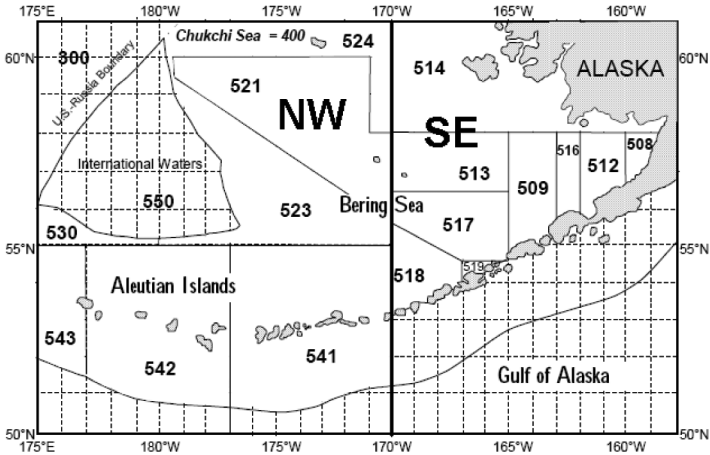


Figure 1. Fishery management areas and the hydroacoustic (EIT) survey are divided between the NW and SE Eastern Bering Sea by 170°W. Area 518 is the Bogoslof district and areas 541-543 encompass the Aleutian Islands region.

Introduction

Fish are mobile creatures so it seems natural to include movement and spatial structure in a model that estimates abundance and affects fisheries management policies. Yet, movement and spatial structure of fish populations are infrequently incorporated into stock assessment (Quinn and Deriso 1999, Chapter 10). Ignoring spatial structure can lead to misinterpretations of basic population-dynamic processes (Härkönen and Harding 2001), and ignoring movement can lead to errors in detecting potential stock declines (Nielsen 2004, Chapter 1).

Walleye pollock (*Theragra chalcogramma*) is the dominant species in the commercial groundfish catch off Alaska. In 2003, the eastern Bering Sea (EBS)–Aleutian Islands walleye pollock fishery accounted for 76% of the groundfish catch (1.49 million metric tons [t]) and 63% of the total ex-vessel value (\$302 million dollars) (Hiatt et al. 2004). Of this catch, 0.36 million t were caught in the northwest (NW) EBS, and 1.13 million t were caught in the southeast (SE) EBS (Ianelli et al. 2004) (Fig. 1).

The modern fishery (since the early 1990s) has had two seasonal components: a winter roe fishery on spawning aggregations (“A-season”) with an opening on January 20, and a summer/fall “B-season” opening in mid-late June (prior to 2000 the opening was later). Beginning in 2002, the A-season was allocated 40% of the catch and the B-season, 60%. Both seasons’ lengths depend on the catch rates (Ianelli et al. 2005). Juvenile

walleye pollock reach sexual maturity and recruit to the fishery at about age-4 at lengths of 40 to 45 cm (Wespestad 1993).

The stock structure of walleye pollock in the EBS is poorly understood (Ianelli 2005). Walleye pollock exhibit movements throughout their life history and during the year. During the spring and summer EBS walleye pollock migrate to feeding areas, and during the winter they migrate to spawning areas. Most walleye pollock populations spawn during the late winter and early spring (Mulligan et al. 1989, Bailey et al. 1999).

Interannual variations in walleye pollock recruitment are important because they drive the annual population size that affects higher and lower trophic levels and the harvest levels of the fishery. Walleye pollock recruitment is determined by both biological (egg production, cannibalism, predators, food sources, spawning biomass, larval mortality, year-class strength), and environmental-oceanographic (temperature, storms, ice cover and retreat, currents, cold-pool) factors (Wespestad et al. 2000, Mueter et al. 2006).

Studies have shown that there are differences in the biological and behavioral aspects of walleye pollock in the NW and SE EBS (Fig. 1). Walleye pollock in the NW EBS are slightly smaller and have lower average growth rates than walleye pollock in the SE EBS (Lynde et al. 1986, Ianelli et al. 2004). Differences in cannibalism rates, spawn timing, feeding rate, and reproductive output may also occur between the SE and NW EBS. Some of these observations can be explained by the hypothesis that as walleye pollock get older (ages 3+), there is a general ontogenetic movement from the NW to SE EBS (Bailey et al. 1999, Buckley et al. 2001).

The standard EBS walleye pollock stock assessment model is an age-structured population dynamics model (Quinn and Deriso 1999, Chapter 8; Ianelli et al. 2004). The main structure of the model is represented by "true" but unobservable population numbers-at-age that are based on an array of parameters for fishing and natural mortality, and recruitment, some of which are estimated within the model. Fishing mortality is parameterized to be semi-separable with both year and age (selectivity) components. Parameters such as mean weights-at-age and -year, maturity-at-age, and natural mortality are estimated independently of the model.

Currently there are no estimates of EBS walleye pollock movement rates. We determined if age-specific movement could be estimated from the current disaggregated assessment survey and fishery data. We tested the two following hypotheses: (1) The age-specific movement (ASM) model can estimate migration without movement (tagging) data, but with a great deal of uncertainty; and (2) The ASM model performs better than a non-movement version of the spatial, two-season ASM model.

Table 1. Thirteen disaggregated data sources showing available data years in parentheses and unavailable data years labeled missing. BTS stands for bottom-trawl survey and EIT stands for echo-integration trawl survey.

| Surveys | Fishery |
|---|---|
| 1. BTS_NW, | 5. NW_A catch-at-age, |
| 2. BTS_SE ('82-'04), | 6. NW_A yield ('77-'04), Missing: '88-'90,'97, |
| 3. EIT_NW, | 7-12. NW_B, SE_A, SE_B catch-at-age and yield ('77-'04), Missing: '88-'90, |
| 4. EIT_SE ('94, '96,'97, '99, '00, '02), | 13. Total yield ('77-'05) |

Methods

Data sources

Thirteen data sources were used to fit the model (Table 1). Stock assessment data from the bottom trawl survey (BTS), the echo-integration trawl (EIT) survey, and the fishery were stratified into two regions, the northwest (NW) and southeast (SE) EBS (scientist personnel, Alaska Fisheries Science Center, 2006). The fishery data were further stratified into two seasons ("A" and "B"). The fishery management areas and the EIT survey are divided into NW and SE by 170°W (Fig. 1). The bottom trawl survey data are defined by a slight angle from the 170°W dividing line. The division differences are a function of the sampling design. The Bogoslof district (area 518) fishery data could not be disaggregated from the EBS data when the data were split between the NW and SE and the A and B harvest seasons. The only significant catch from the Bogoslof district came from 1984 to 1991 (Ianelli et al. 2005) (Fig. 1).

Age-specific movement model

A discrete-time region specific age-structured model was specified as an operational population dynamics model (e.g., Fournier and Archibald 1982, Hilborn and Walters 1992, Schnute and Richards 1995) that was a simplified version of the 2005 stock assessment (Ianelli et al. 2005). This age-specific movement (ASM) model was divided into components throughout the year as follows: spawning and recruitment (starting at time A in the winter), the A fishing season (A to \bar{A}), walleye pollock movement after spawning to summer feeding areas along with half of the natural mortality (\bar{A} to B), the B fishing season (B to \bar{B}), and finally walleye pollock movement before spawning along with half of the natural mortality (\bar{B} to A) (Fig. 2). There were 185 total parameters estimated in the ASM model.

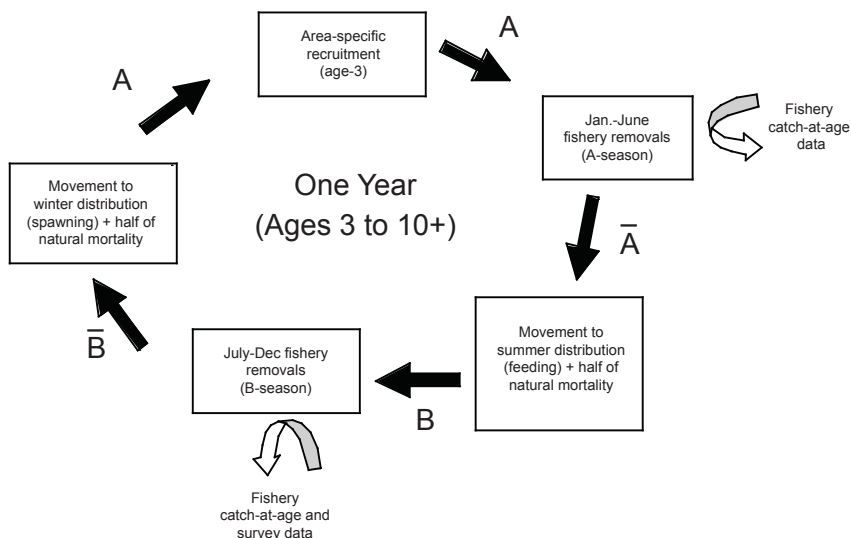


Figure 2. Depiction of the spatial model. Seasons (A, \bar{A} , B, \bar{B}) are denoted on the outer circle.

Subscripts on parameters were as follows:

- a age
- y year
- k season (A, \bar{A} , B, or \bar{B})

Superscripts on parameters were as follows:

- r region (NW or SE)
- l identifier; (stochastic component [ϵ]: R = recruitment, I

= initial numbers at age), (selectivity [v, β, δ]: F = fishery, BTS = bottom trawl survey, EIT = echo-integration trawl survey), (variance [σ]), (survey abundance [n]: EIT or BTS), (survey catchability coefficient [q]: BTS or EIT).

Recruitment by region was specified as a function of an estimated mean recruitment value \bar{R} (abundance at age-3 for the entire EBS), an estimated scalar allocating the fraction of recruitment to the SE region (hence $1-\phi$ is the fraction of recruitment in the NW), and estimated stochastic components ϵ for a total of 74 estimated recruitment parameters. Equations are only given for the NW. Analogous equations for the SE can be obtained by replacing the region-specific population parameters for the NW with those for the SE.

Recruitment to the NW region for age-3 was modeled as

$${}^{\text{NW}}N_{3,y,A} = (1 - \phi)\bar{R}e^{(\text{NW } \epsilon_y^R)}, 1977 \leq y \leq 2005. \quad (1)$$

The initial numbers at age for 1977 were modeled as

$${}^{\text{NW}}N_{a,1977,A} = (1 - \phi)\bar{R}e^{(\text{NW } \epsilon_a^I)}, 4 \leq a \leq 10+. \quad (2)$$

Next, abundance and fishing mortality were modeled as

$${}^{\text{NW}}N_{a,y,\bar{A}} = {}^{\text{NW}}N_{a,y,A} e^{-\text{NW } F_{a,y,A}} \quad (3)$$

where

$${}^{\text{NW}}F_{a,y,A} = v_a^F {}^{\text{NW}}F_{y,A}, \quad (4)$$

in which v_a^F is the estimated age-specific fishery selectivity and ${}^{\text{NW}}F_{y,A}$ is the estimated fishing mortality for fully available ages in the NW region during the A season in year y . Removals by the EIT and the bottom trawl survey, which occur in the middle of the year, were considered insignificant and not subtracted out as mortality. There were 99 total estimated fishing mortality rate parameters for fully available ages because some fishing mortalities were set equal to a close year from an analogous season and region (i.e., 1987 = 1988 = 1989, 1990 = 1991, 1997 = 1998, and 2004 = 2005) (Table 1).

Selectivity was modeled as a logistic function with two parameters β^l and δ^l ,

$$v_a^l = \frac{1}{1 + e^{\frac{-2.94(a - \beta^l)}{\delta^l}}}. \quad (5)$$

The superscript l on the selectivity parameters identifies the parameter's use for either the fishery selectivity or the survey selectivity. The parameter β^l is the age at which 50% of the fish are vulnerable to the fishery (or survey), whereas the parameter δ^l is the width (in years) between the age at 50% selection and the 5% and 95% selection values. For example, if $\beta^l = 5$ and $\delta^l = 2$, then age-3 selectivity is 5% and age-7 selectivity is 95%. This parameterization allows for interpretable scaling and can be useful for Bayesian analyses (where priors might be developed). A total of six selectivity parameters were estimated, two each for the fishery, the BTS, and the EIT survey.

Movement

After the A season, movement from region r to region r' (${}^{r,r'}P_{a,k}$) was assumed to occur, along with a half year of natural mortality, or

$${}^{\text{NW}}N_{a,y,B} = {}^{\text{NW,NW}}P_{a,\bar{A}} {}^{\text{NW}}N_{a,y,\bar{A}} e^{-M/2} + {}^{\text{SE,NW}}P_{a,\bar{A}} {}^{\text{SE}}N_{a,y,\bar{A}} e^{-M/2}. \quad (6)$$

Natural mortality was assumed constant and set at 0.3, the same value used in the standard stock assessment model. It was assumed that

natural and fishing mortality do not differ between males and females at any life stage. This is based on studies of relative age compositions between sexes that did not differ significantly in the EBS (Pereyra et al. 1976). Next, the B season fishery occurred, resulting in abundance

$${}^{NW}N_{a,y,\bar{B}} = {}^{NW}N_{a,y,\bar{B}} e^{-{}^{NW}F_{a,y,\bar{B}}}. \quad (7)$$

Following the B season, the remaining half-year of natural mortality and the end-of-year movement before spawning were assumed to occur, resulting in abundance at the start of the next year and next age as

$${}^{NW}N_{a+1,y+1,A} = {}^{NW,NW}P_{a,\bar{B}} {}^{NW}N_{a,y,\bar{B}} e^{-M/2} + {}^{SE,NW}P_{a,\bar{B}} {}^{SE}N_{a,y,\bar{B}} e^{-M/2}, \quad (8)$$

where $3 \leq a \leq 9$ and $1977 \leq y \leq 2004$. In this equation, the number in the NW region at the end of the previous season (\bar{B}) that stayed in the NW region is added to the number that moved to the NW region from the SE region at the end of the previous season (\bar{B}). The plus group, which combines abundances for adult fish ages-10+, was modeled as

$${}^{NW}N_{10+,y+1,A} = {}^{NW,NW}P_{9,\bar{B}} {}^{NW}N_{9,y,\bar{B}} e^{-M/2} + {}^{SE,NW}P_{9,\bar{B}} {}^{SE}N_{9,y,\bar{B}} e^{-M/2} + \quad (9)$$

$${}^{NW,NW}P_{10+,\bar{B}} {}^{NW}N_{10+,y,\bar{B}} e^{-M/2} + {}^{SE,NW}P_{10+,\bar{B}} {}^{SE}N_{10+,y,\bar{B}} e^{-M/2}$$

where $1977 \leq y \leq 2004$.

The movement probabilities for the ASM model were based on the hypothesis that as walleye pollock get older (ages-3+), there is a general ontogenetic movement from NW to SE EBS (Bailey et al. 1999, Buckley et al. 2001). Movement probabilities for the first age (age-3 fish) that stayed in the same region were logit-transformed as

$${}^{NW,NW}P_{3,k} = \frac{1}{e^{-({}^{NW}\omega_k)} + 1} \quad (10a)$$

and

$${}^{SE,SE}P_{3,k} = \frac{1}{e^{-({}^{SE}\omega_k)} + 1} \quad (10b)$$

for estimation stability, where ${}^r\omega_k$ varied by region and season for a total of four estimated movement parameters (${}^{NW}\omega_A$, ${}^{SE}\omega_A$, ${}^{NW}\omega_B$, ${}^{SE}\omega_B$). The initial model configuration was conditioned such that the movement probabilities were relative to the next youngest age group for the probabilities NW→NW,

$${}^{NW,NW}P_{a,k} = \gamma_k {}^{NW,NW}P_{a-1,k}, \quad 4 \leq a \leq 10+, \quad (11)$$

because the region- and age-specific movement rates were expected to be difficult to estimate.

Based on available knowledge, the scalar γ was set at 0.8 for the first set of movements (season \bar{A}) and at 0.9 for the second set (season \bar{B}). For the movement probabilities for the SE, we assumed that once fish were in the SE region, they would follow an adult movement pattern. So each subsequent age after age-3 was assumed equal to the value at age-3 for both seasons, or

$${}^{\text{SE,SE}}P_{3,k} = {}^{\text{SE,SE}}P_{a,k}, \quad 4 \leq a \leq 10+. \quad (12)$$

In a two region model, the probability of moving is 1 minus the probability of staying.

Estimation

A penalized joint negative log likelihood function (PL) (Maunder and Deriso 2003) or “errors in variables” (EV) method (Ludwig and Walters 1981, Collie and Sissenwine 1983, Ludwig et al. 1988) was developed to allow estimation of model parameters. This consisted of producing model estimates of catch in numbers, yield, and survey abundances to compare with data. The PL or EV was used as the objective function consisting of the addition of fourteen components (thirteen data sources and one penalty function) that each followed lognormal distributions. All the data sources were independent except for the catch in numbers, yield, and total yield. The total yield was included along with the yield by region and season, because the individual yields were estimated with more error, a few years of yield data were missing (Table 1), and it was important that the estimated total yield be close to the observed total yield for the entire EBS. The variance terms $\sigma^{2(l)}$ were either taken from the 2004 stock assessment report (Ianelli et al. 2004) or were given a value consistent with available knowledge.

The log likelihood component for the region- and season-specific catch-at-age data (NW_A, $\sigma = 0.3$; NW_B, SE_A, and SE_B, $\sigma = 0.2$ [J.N. Ianelli, unpubl. data, 2006]) was

$$L_1 = \sum_r \sum_a \sum_y \sum_k \frac{\ln \left(\frac{{}^r c_{a,y,k}}{{}^r \hat{c}_{a,y,k}} \right)^2}{2 ({}^r \sigma_k^{2(l)})} \quad (13)$$

where c and \hat{c} were the observed and predicted catch numbers, respectively. All subsequent likelihood components were of this form. The predicted catch was from the Baranov catch equation

$$C = \frac{F}{Z} N (1 - e^{-Z}), \quad (14)$$

where no natural mortality occurs during the catch period ($M = 0$). Therefore, the predicted catch-at-age was

$${}^r\hat{c}_{a,y,k} = {}^rN_{a,y,k}(1 - e^{-rF_{a,y,k}}). \quad (15)$$

The predicted survey numbers (NW_BTS, SE_BTS, NW_EIT, and SE_EIT, $\sigma = 0.2$ [Ianelli et al. 2004]) were

$${}^r\hat{n}_{a,y}^l = {}^rN_{a,y,B} v_a^l q^l \quad (16)$$

where q^l was the catchability coefficient by survey, for a total of two estimated catchability coefficient parameters. The superscript l designated the survey as the bottom trawl (BTS) or hydroacoustic (EIT). The age-specific selectivity for the bottom trawl and EIT survey was modeled as in eq. (5).

Predicted yield (NW_A, NW_B, SE_A, and SE_B, $\sigma = 0.05$ [Ianelli et al. 2004]) was

$${}^r\hat{y}_{y,k} = \sum_{a=3}^{10+} ({}^r w_{a,y,k} {}^r\hat{c}_{a,y,k}), \quad (17)$$

The sum of the product of the mean body weight (kg) of the catch (w) and the predicted catch in numbers across ages. Predicted total yield ($\sigma = 0.1$, J.N. Ianelli, unpubl. data, 2006) was then

$$\hat{Y}_y = \sum_r \sum_k ({}^r\hat{y}_{y,k}). \quad (18)$$

The penalty function, consisting of three components, was modeled as

$$L_5 = \left[\sum_y \ln \left(\frac{{}^{NW}\hat{N}_{3,y,A}}{{}^{SE}\hat{N}_{3,y,A}} \right)^2 \right] + \left[\sum ({}^{NW}\varepsilon_y^R)^2 + \sum ({}^{SE}\varepsilon_y^R)^2 \right] + \left[\sum ({}^{NW}\varepsilon_a^I)^2 + \sum ({}^{SE}\varepsilon_a^I)^2 \right]. \quad (19)$$

Because the recruitment numbers of EBS walleye pollock are highly variable and difficult to predict (Ianelli et al. 2004), the first part of the penalty function keeps the NW and SE age-3 abundances similar. The second and third parts of the penalty function conditioned the stochastic components to sum to zero.

The ASM model was implemented in AD model builder language (Fournier 1996, Otter Research Ltd.).

Analyses

To evaluate confounding of parameters, the correlation matrix, derived from the Hessian, was examined. Model outputs of the ASM model and the 2005 stock assessment were compared and any patterns in the residuals were identified.

Table 2. Fit of the ASM model in terms of its negative log likelihood components. Components for the SE region are shown in parentheses.

| Data sources | Likelihoods |
|---|-------------|
| NW (SE) BTS | 883 (1,402) |
| NW (SE) EIT | 4,061 (446) |
| NW (SE) A season fishery | 1,308 (810) |
| NW (SE) B season fishery | 982 (1,046) |
| NW (SE) A yield | 28 (34) |
| NW (SE) B yield | 54 (38) |
| Total fishery yield | 10 |
| Penalty Components (eq. 19): | |
| 1. Recruitment (NW, SE similar) | 65 |
| 2. Recruitment deviations | 312 |
| 3. Initial abundance (age-3) deviations | 11 |
| Total likelihood | 11,489 |

Results

The ASM's total and penalty likelihoods and fit to the thirteen data sources are listed in Table 2. The data sources with the greatest influence (largest component of the total likelihood) were the SE bottom trawl survey, the NW EIT survey, the NW catch-at-age data for the A season, and the SE catch-at-age data for the B season.

The estimated percentage of fish that stayed in the NW during the \bar{A} season decreased from 99% (age-3) to 21% (ages-10+), while the percentage of fish that stayed in the NW during the \bar{B} season decreased from 75% (age-3) to 36% (ages-10+). Thirty percent of the fish stayed in the SE during the \bar{A} season (ages-3 to 10+) and 70% stayed in the SE during the \bar{B} season (Fig. 3).

From the analysis of the ASM's Hessian correlation matrix, only a few important correlations were found. The only correlations between fishery and/or survey selectivity were negative correlations between the ${}^{NW}\omega_{\bar{B}}$ movement parameter and the fishery selectivity parameters β^F and δ^F of -0.51 and -0.51 , respectively. There was a positive correlation between the survey catchability coefficients for the EIT q^{EIT} and bottom trawl q^{BTS} surveys (0.45).

There were a few limitations associated with the ASM model. First, there were high variances for the stochastic components r_{2005}^R (NW and SE), and the ${}^{NW}\omega_{\bar{A}}$ movement parameter. Second, some parameter estimates did not vary much from their starting value, i.e., the fishery

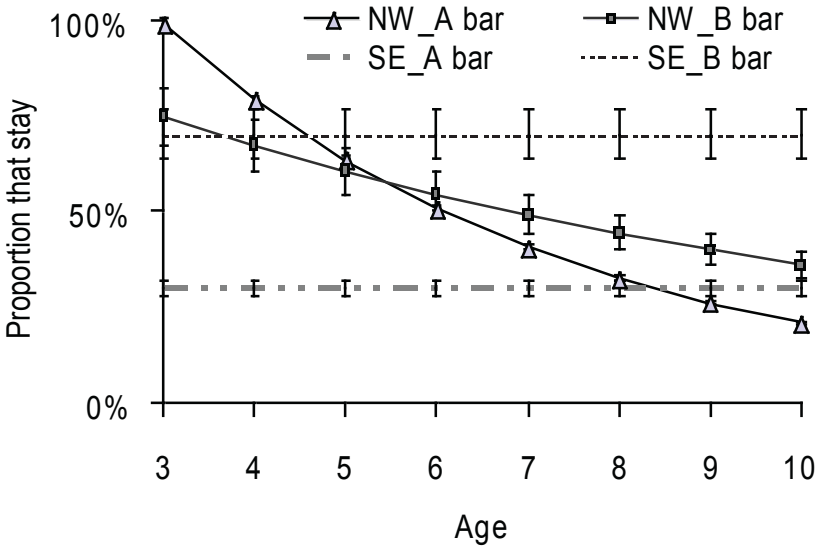


Figure 3. Estimated migration with 95% confidence intervals for the ASM model. The lines represent the proportion of fish that stay in each region and season for a particular age.

selectivity parameter, β^F (starting value = 4 and estimate = 3.98), and the scalar allocating the fraction of recruitment between regions, ϕ (starting value = 0.50 and estimate = 0.50).

Recruitment and beginning year biomass estimates from the 2005 standard stock assessment (Ianelli et al. 2005) were usually somewhat lower than the ASM model's estimates, though of the same order of magnitude (Fig. 4A and 4B). While the ASM model's estimates of age-3 abundance fluctuated between 533 million and 22 billion fish, the 2005 stock assessment's estimates fluctuated between 1.2 and 16 billion fish. The ASM model fitted the observed total yield well in most years, except it underestimated the yield in years 1988, 1989, 1991, and 2005 and overestimated the yield in 1990 (Fig. 5).

The ASM model fitted well the yearly observed yield data by region and season, the yearly observed catch data in numbers by region and season, and the catch-age composition data (results not shown). Except for years 1977 and 1981 to 1984, the ASM model closely fitted the yearly observed catch in numbers in the NW_A fishery. The ASM model fitted the yearly observed catch in numbers in the NW_B fishery well except for underestimates in years 1977, 1986, 1997, and 2004. The ASM model frequently underestimated the observed SE_B fishery catch numbers (1977 to 1979, 1981, 1982, 1993, and 1999). Although the ASM model

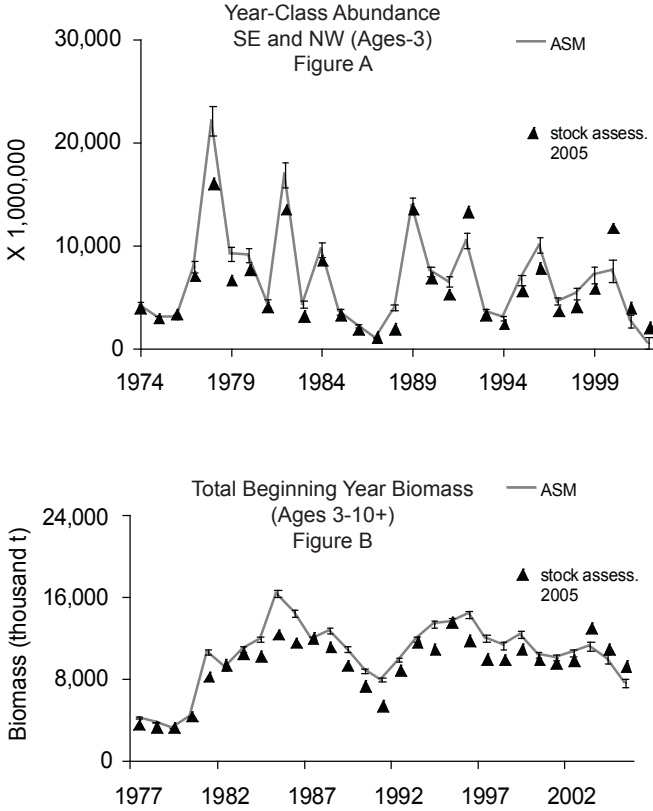


Figure 4. Year-class abundance (Fig. A) and total beginning year biomass (Fig. B) for the ASM model (with 95% confidence intervals) compared to the 2005 stock assessment standard model results (Iannelli et al. 2005).

only somewhat fitted the yearly observed bottom trawl survey and EIT survey numbers in the NW and SE, the ASM model fitted the survey age composition data well. The poorer fits may be a function of the limitations of the survey (Barbeaux and Dorn 2003) or due to the weighting factors (variances) on the data sets.

There were a few notable patterns in the residuals for the ASM model (results not shown). First, all the residuals were positive for the yearly EIT_NW data. Second, there were all negative residuals after 1990 for age-3 and after 1977 for age-4 NW_A fishery catch numbers, and after 1992, for ages-10+ NW_B fishery catch numbers. Third, after 1990, there were more negative residuals for ages-3 and 4 SE_A fishery

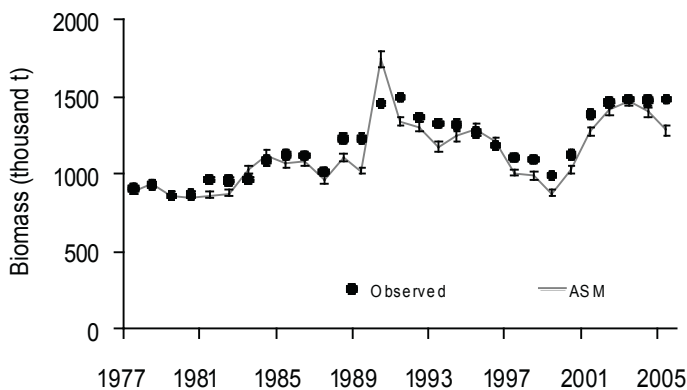


Figure 5. ASM model fit to the total catch biomass (1977-2005) with 95% confidence intervals.

catch numbers. Finally, there were more positive residuals for the yearly NW_B, SE_A, and SE_B fishery yield data.

A standard non-movement model that assumed two independent NW and SE EBS stocks of the ASM model was also fitted to the data (181 total estimated parameters). All equations were the same except the migration parameters were omitted and the recruitment function was independent by region (eq. 1 and 2). Each stock had a separate mean recruitment and stochastic processes on age and year, and the scalar allocating the fraction of recruitment between regions was eliminated. The results were nonsensical since cumulative estimates (i.e., year-class abundance in the NW and SE, total beginning year numbers for ages-3+, total beginning year biomass ages-3+) in some regions were much higher for the non-movement model than for either the ASM model or the 2005 stock assessment standard model estimates (Ianelli et al. 2005). Consequently, we did not present abundance estimates from the non-movement model.

Discussion

Other assessment models that have attempted to incorporate movement include bulk transfer models applied to eastern Pacific yellowfin tuna (*Thunnus albacares*) (Ishii 1979), to western Pacific skipjack tuna (*Katsuwonus pelamis*) (Sibert 1984), and to southern bluefin tuna (*Thunnus maccoyii*) (Hampton 1991), difference equations applied to the school shark (*Galeorhinus galeus*) (Punt et al. 2000), and advection-

diffusion models applied to various tuna species (Deriso et al. 1991, Kleiber and Hampton 1994, Sibert et al. 1999). These studies differed from ours in that they had direct movement rates through extensive tagging data.

We developed the ASM model in an attempt to estimate walleye pollock migration between the NW and SE EBS. The first hypothesis that we tested was that the age-specific movement (ASM) model can estimate migration without movement (tagging) data, but with a great deal of uncertainty. This hypothesis was not rejected; under moderate assumptions, this study showed that reasonable estimates of most population and movement parameters could be obtained from existing disaggregated assessment survey and fishery data. While some population parameters remain uncertain and high correlation exists between some parameters, most movement parameters could be estimated with confidence for the ASM model with only four estimated migration parameters. More realistic migration estimation would vary by year (1977-2005) and age (ages-3 to 10+). Having additional information from tagging studies or other movement studies would probably be necessary to stabilize such a complex model.

The second hypothesis we tested was that the ASM model performs better than a non-movement version of the spatial, two-season ASM model. The results of the non-movement model were nonsensical showing that movement must be included in any spatial model of EBS pollock.

The next step for evaluating the ASM model is to examine a third hypothesis: the ASM model would not be as robust as the region-wide, standard stock assessment model until additional information from tagging studies or other movement studies becomes available. Further analysis of the ASM model through robustness tests and management strategy evaluations (MSEs) need to be done through simulation experiments with known population and migration parameters (e.g., Fu and Quinn 2000) before the ASM model is used for assessment purposes.

A similar attempt using an age-structured stock assessment model that incorporated migration based on parasitological analyses was developed to test the migration effects on the assessment and management of the western and central Baltic herring (*Clupea harengus membras*) stocks (Horbowy 2005). Compared to the spatial model, the migration model produced higher (lower) spawning stock biomass estimates for the western (central) stock. Herring migration effects on catch and biomass ranged from low (less than 5% change) to moderate (up to 20% change). In comparison, the ASM model generally produced higher abundances (ages 3-10+) in the NW as compared to the SE (66% of the time) (Fig. 6).

Currently, there is one yearly total allowable catch (TAC) for the whole EBS that is divided by sectors and seasons by a fixed percentage. The TAC is allocated temporally by the A (40%) and B (60%) fishery sea-

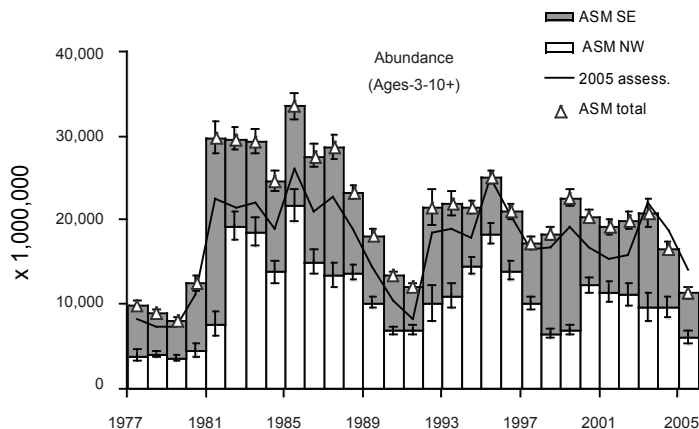


Figure 6. Estimated total abundance and abundance by area (with 95% confidence intervals) for the ASM model for the A-season compared to the 2005 stock assessment results (Iannelli et al. 2005).

sons. Unlike the standard model used for the current stock assessment that is only able to estimate walleye pollock abundances for the entire EBS, the ASM model was able to estimate abundances by season for the NW and SE separately (Fig. 6). This provides more in-depth information for fishery management and allocation of quota both spatially and temporally. Instead of fixed percentages, managers would be able to allocate quota by both region and availability. For simplicity, the ASM model only included ages 3+, one type of movement (age-specific changes), two regions (NW and SE EBS), and fishery selectivity related to gear-only effects rather than both availability and gear effects. Future elaborations should include: a larger range of ages (1+), age- and/or year-specific movements, fishery selectivity by year, region, and/or season, finer spatial and temporal scales in the EBS, and a sensitivity analysis of the weighting factors used (Deriso et al. 2007).

The key finding of our study is that more in-depth information on finer spatial and temporal scales is likely from spatially explicit studies of EBS walleye pollock. Not only will we likely gain information on their biology and changes in migration with age and environmental influences, more complex information of their intra-annual distribution will likely further management and conservation of the species.

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Changes in Fecundity in a Stressed Population: Northern Cod (*Gadus morhua*) off Newfoundland

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Abstract

Recently determined relationships in stock fecundity off Newfoundland are compared with historical data from Newfoundland, Iceland, Norway, Baltic, and the North Sea and are used to establish baseline relationships between fecundity and size at age in Atlantic cod (*Gadus morhua*). A total of 200 prespawning female cod were sampled in 1999 and 2003 in three Northwest Atlantic management areas. For southern Newfoundland stocks that have fared relatively well in the 1990s and early 2000s, fecundity-size relationships did not differ from historical norms, although age at maturity was lower. In the highly stressed northern stock off Labrador, however, age at maturity was much lower than historical norms or in southern stocks, and fecundity much higher in small and young fish. Mortality rates were higher in the northern fish. We discuss these changes in the context of changed life histories and rebuilding in stressed gadoid stocks.

Introduction

Fecundity is a fundamental property of reproductive potential. Despite this importance, and the long history of Atlantic cod (*Gadus morhua*) fisheries in the North Atlantic, there have been relatively few fecundity studies on this species. The first studies were done by Earll (1880) and Fulton (1890), and later in the twentieth century by Powles (1958). In the northwest Atlantic, May (1967), Postolakii (1967), and Pinhorn (1984) provided estimates of fecundity for several stocks. More recently, many stocks off Newfoundland and Labrador have experienced exceptional

declines in biomass and remain at all time low levels (e.g., Lilly et al. 2000). Despite evidence of change in life history characteristics such as depressed age at maturity (Olsen et al 2004), growth (Dutil et al. 1999), and lower condition (Rose and O'Driscoll 2002) there has been no reassessment of historical fecundity information for these stocks.

In general, fecundity is the reproductive output of an individual, or number of offspring produced (Thain and Hickman 1994). There are three main types of fish fecundity described in Murua et al. (2003) and Kraus et al. (2000): *Relative fecundity* is the number of oocytes per unit body weight; *realized fecundity* is the total number of eggs spawned per season; and *potential fecundity* is the number of developing oocytes per female fish prior to spawning.

Our objective was to quantify the potential fecundity of Atlantic cod and its relationship with growth parameters in three major management areas. We then compare our results with historical data from the same stocks and from other cod stock areas across the North Atlantic.

Materials and methods

Study areas

Cod fecundity was investigated within three populations in NAFO (Northwest Atlantic Fisheries Organization), subdivisions 2J, 3KL and 3Ps (Fig. 1). Hawke Channel in subdivision 2J is located between Hamilton and Belle Isle Banks, and was the northernmost sampling site. Acoustic trawl surveys and fisheries research have been conducted in this area since 1994 (e.g., Anderson and Rose 2001). Samples from 3KL were taken from two areas; the offshore site, Bonavista Corridor, straddles the southeast limit of 3K and the northeast boundary of 3L. The Bonavista Corridor is the most southern migration route of northern cod and held the last large spawning aggregations in the early 1990s (Rose 1993). The inshore site, Smith Sound, Trinity Bay (Fig. 1A) is a fjord within subdivision 3L and currently holds the largest known concentration of overwintering northern cod, estimated at 26,000 tons in 2001. The cod that migrate along the Bonavista Corridor cross the 3K and 3L subdivision boundary lines, hence these areas were combined into 3KL for analysis. The third and final sampling area was Placentia Bay (Fig. 1B), which forms part of the inshore component of the subdivision 3Ps stock. Of all the cod stocks in the Northwest Atlantic, 3Ps rebounded the quickest after rapid decline in the late 1980s. This stock has had a small commercial fishery (average TAC of 15,000 t per year) since 1997. Placentia Bay cod have been under intensive study since 1996 (e.g., Lawson and Rose 2000, Mello and Rose 2005, Rose et al. 2008).

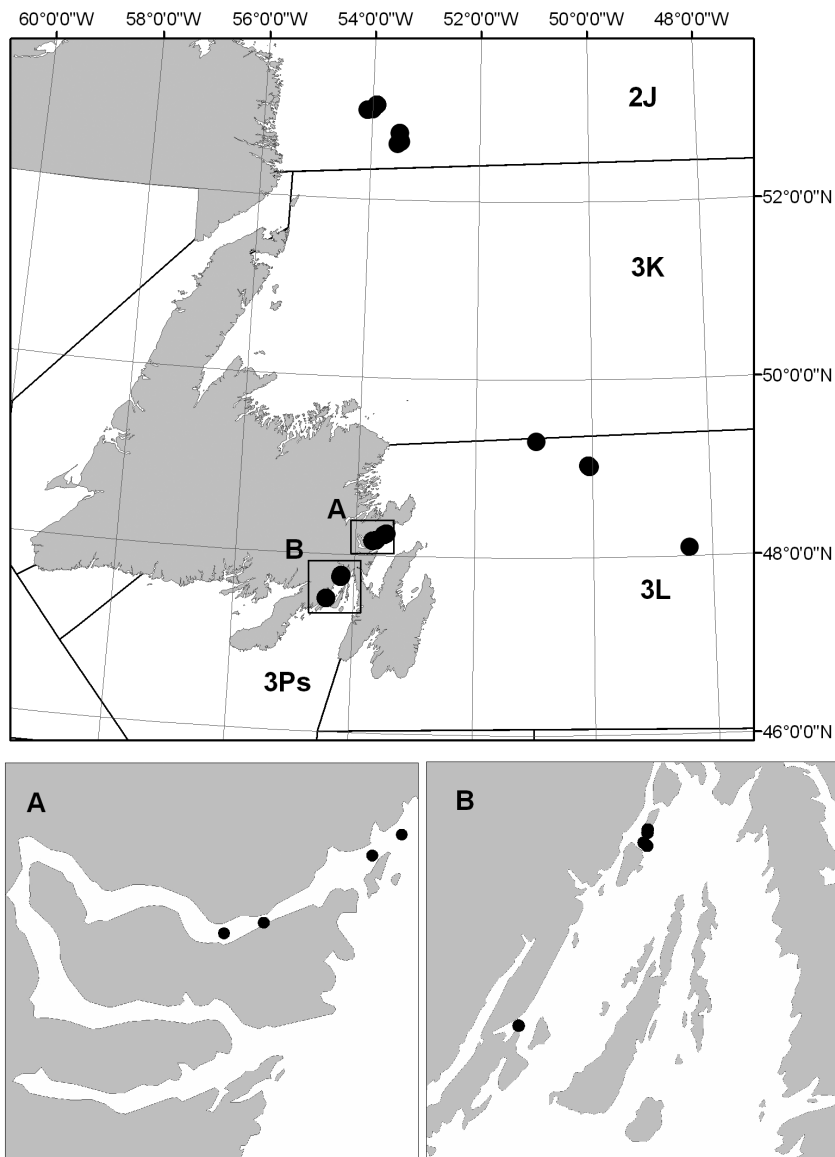


Figure 1. Sampling sites (●) and NAFO subdivisions for 1999 and 2003. Inserts represent coastal sampling sites Placentia Bay (A) and Smith Sound (B).

Table 1. Summary of female cod sampled during 1999 and 2003 within three NAFO subdivisions 2J, 3KL, and 3Ps. Information includes number of fish sampled, size (lengths and gutted weights), ranges, and standard deviations.

| Area | Year | Sample size | Standard length (cm) | | Gutted weight (kg) | |
|-------|------|-------------|----------------------|------------------|--------------------|-------------------|
| | | | Range | Average \pm SD | Range | Average \pm SD |
| 2J | 1999 | 31 | 40-60 | 48.6 \pm 4.7 | 0.465-1.81 | 0.918 \pm 0.270 |
| | 2003 | 12 | 42-61 | 49.3 \pm 7.0 | 0.540-1.63 | 0.927 \pm 0.396 |
| 3KL | 1999 | 27 | 35-82 | 62.0 \pm 10.5 | 0.355-3.95 | 2.02 \pm 0.962 |
| | 2003 | 60 | 40-94 | 56.5 \pm 12.0 | 0.472-6.60 | 1.53 \pm 1.27 |
| 3Ps | 1999 | 18 | 56-84 | 68.3 \pm 9.3 | 1.21-4.61 | 2.57 \pm 1.12 |
| | 2003 | 52 | 45-72 | 59.0 \pm 5.2 | 0.653-2.61 | 1.61 \pm 0.850 |
| Total | - | 200 | - | - | - | - |

Collections and preparation

Before spawning, a female cod gonad contains three sizes of eggs: large translucent eggs approximately 1.5 mm in diameter that are ready for release; middle-sized yolked eggs that will be released within weeks; and small whitish eggs (May 1967). The large and middle-sized eggs are first generation eggs and will be released in the current spawning season. The small whitish eggs are second-generation eggs, which will not be released until the following spawning year. Release of the large translucent eggs begins soon after oocytes become hydrated; therefore in order to measure fecundity gonads must be sampled before any hydrated eggs are visible (Raitt 1932). Female cod were sampled prior to and during the spawning seasons of 1999 and 2003. In 2J and 3KL, fish were sampled with a research otter trawl (Campelen 1800), whereas samples were caught using handlines in 3Ps.

Standard lengths, and whole, gutted, liver and gonad weights were recorded, with otoliths taken for aging. Fish sizes varied between areas (Table 1). In all analyses, gutted weight was used as opposed to whole weight to reduce bias resulting from seasonal changes and variations due to feeding. Extracted ovaries were cut down the middle and placed in a labeled jar, and Gilson's fluid (Simpson 1951) was then added to cover the ovary, to aid in the breakdown of connective tissues and the separation of eggs from each other and the ovarian wall. Samples were topped up with fluid and agitated once a week to help speed the breakdown process, and then were left for an average of three months before processing. When separation was complete, each sample was passed through a series of interlocking sieves of differing mesh sizes (1.4 m, 1.0 m, 500 m, 300 m, 180 m, 125 m). Remnant ovarian wall tissue and

second-generation eggs were discarded, and eggs were stored in jars with 90% ethanol until processed.

Subsampling and counting

Most methods used to measure fecundity involve taking a subsample of the total volume of eggs in an ovary. The Motoda splitter (Motoda 1959) is primarily used for plankton subsampling, but has been used in fecundity studies (Allain 1999) and was used in the present study. The splitter produces subsamples by successive fractionations. Counts were done manually using a stereomicroscope and handheld counter; two subsamples from each gonad were counted three times. All samples met the required <5% variation. The combined total 6 counts were averaged and used in the estimation for the total number of eggs in that sampled ovary. The potential fecundity per fish was determined by the following equation:

$$N_{eggs} = N_{eggs\ in\ subsample} \times \text{Subsample split fraction}$$

For comparison, six egg samples of random sizes were subsampled a second time using the whirling vessel. Average difference of potential fecundity estimates between the Motoda splitter and the whirling vessel was 10%. Using a paired *t*-test, no significant difference was found in the determined fecundities between the two methods ($p > 0.05$, $\alpha = 0.05$).

Fecundity analyses

Initially all data were pooled and a series of regressions were performed to determine the presence or absence of general relationships between fecundity and specific measured growth variables. Fecundity was investigated in relation to fish length, age, gutted weight, and liver and gonad indices. Liver index (LI) and gonad index (GI) are defined as:

$$LI = \text{Liver weight/Total weight} \quad (2)$$

$$GI = \text{Gonad weight/Total weight} \quad (3)$$

Fecundity was also investigated in relation to condition (Fulton's *K*). Fulton's condition examines the relation between length and weight and is used to quantify the state of well-being of a fish (Wootton 1990a), and is measured as:

$$K = \text{Total weight (kg)/length}^3 \text{ (cm)} \quad (4)$$

Significant relations were further explored through a series of 3-factor ANCOVAs, after which the data were categorized by study area. Results include samples from 1999 and 2003 except for the offshore area of Bonavista Corridor within 3KL (Fig. 1). Data were transformed into base

Table 2. Comparison of original fecundity-weight relations in cod of different geographic regions of the North Atlantic.

| Population/ area | Original function | Weight units | n | Source |
|---------------------|------------------------|-----------------|-----|---------------------------------------|
| NAFO 2J | $F = 2.09W + 6.04a$ | kg | 43 | This study |
| 2J-3K | $F = 0.48W + 0.01a$ | kg | 8 | May 1967 |
| Labrador | $F = 0.2118W + 0.041b$ | g | 65 | Postolakii 1967 |
| | $F = 569W - 80,7000$ | g | 92 | Oosthuizen and Daan 1974 |
| North sea | $F = 526W - 548,000$ | g | 47 | Schopka 1971 |
| | $F = 790W - 41,600$ | g | 49 | Botros 1962 |
| Norway | $F = 0.334W1.126$ | kg | 240 | Kjesbu et al. 1998 (weighted average) |
| | $F = 633W + 88,791$ | g | 807 | Kraus et al. 2000 (weighted average) |
| | $F = 860W - 297,000$ | g | 71 | Botros 1962 |
| Baltic | $F = 746W + 95,000$ | g | 84 | Schopka 1971 |
| | $F = 519W$ | g | 42 | Joakimsson 1969 |
| Iceland | $F = 584W - 832,000$ | g | 49 | Schopka 1971 |

^aLog-log regression.

^bFecundity in thousands of eggs.

10 logarithms to standardize variance and facilitate historical comparisons (e.g., Pinhorn 1984).

A comparison of linear regressions of fecundity-weight relations of cod from different geographic regions of the North Atlantic was also performed. Available data and original equations were gathered from 11 published studies, representing Labrador, North Sea, Norway, Baltic, and Iceland (Table 2).

Results

The overall range of lengths, weights, and ages of cod sampled was 40-94 cm, 0.355-4.61 kg, and 4-14 years, respectively (Table 1, Fig. 2). On average, mature female cod sampled from 2J were of lesser length, weight, and age than those at the other sites in both sampled years (Table 1); mature 2J cod were all less than 7 years of age (Fig. 3).

Regression analyses indicated the strongest predictors of fecundity were weight, length, and age respectively (Table 3). The regressions of fecundity on these variables were significant in all regions, with the amount of explained variation ranging from 31 to 72%. Fecundity was also associated with Fulton's K in all regions ($p < 0.05$). No overall association was evident between fecundity and liver (LI) or gonad index (GI); however, fecundity was significantly correlated with liver index in 2J, and to gonad index in 3Ps. Month was factored into a GLM model to

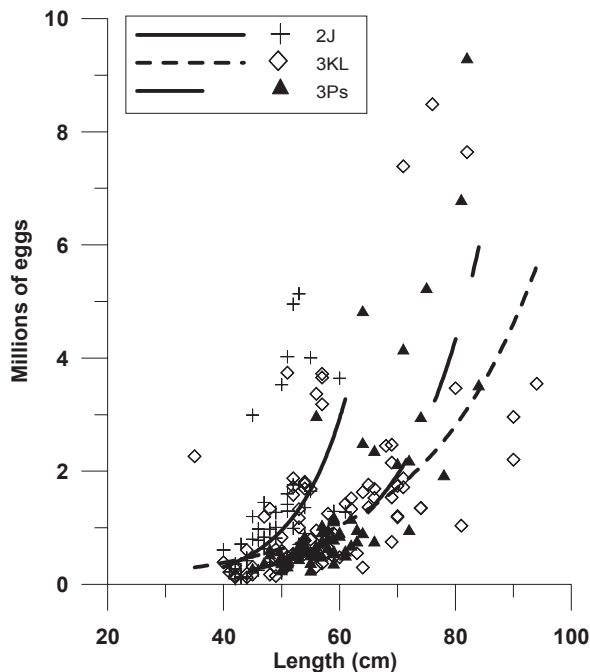


Figure 2. Scatter diagram of fecundity against length for the three NAFO areas sampled; 2J, 3KL, and 3Ps.

control for seasonality. It was found that the relation of fecundity to gonad index did not change across months sampled in 2J, 3KL, or 3Ps.

Fecundities differed significantly between the two years of sampling (1999 and 2003) by a factor of 2-4. In a 3-way ANOVA using year, region and gutted weight as factors, year and region were significant effects but did not interact ($p = 0.08$). Hence for all subsequent analyses data were pooled by year.

Analysis of covariance indicated that the slopes of the regression lines of fecundity on length, age, and weight differed significantly between 2J, 3KL, and 3Ps (p 's < 0.01). Among the years the relationships were strongest in 3Ps cod (Table 3). Cod in 2J had much higher fecundities at small sizes and younger ages than did cod from other regions. In 2J and adjacent 3KL, fecundities differed greatly from those reported by May (1967) and Postolakii (1968). At age 5 cod had fecundities similar to those at age 12 historically (Fig. 5), and with cod six times their size (Fig. 6).

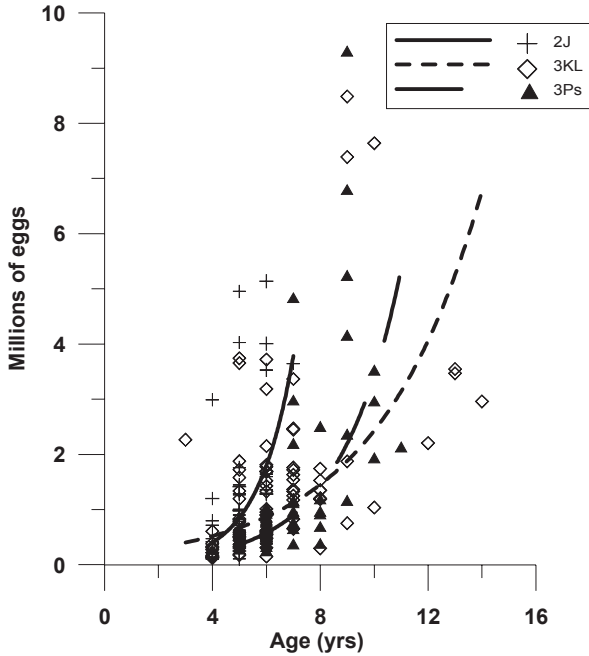


Figure 3. Scatter diagram of fecundity against age for the three NAFO areas sampled; 2J, 3KL, and 3Ps.

Additional fecundity and weight data for six North Atlantic cod populations were examined (Labrador area, NAFO subdivisions 2J-3K, Baltic (east and west), North Sea, Iceland, and Norway (Barents Sea) (Table 2, Fig 7). Where more than a single fecundity relationship was available for an area (except Norway), weighted averages were used to produce a representative regression. Due to large variance between the samples from Norway, these data sets are separated, but both indicate some of the highest weights and fecundities overall. Historical data from 863 female cod from 2J-3K (Postolakii 1967 and May 1967) have the lowest fecundities (and smallest weights) of all the stocks examined, but in the present study cod from this area had much higher fecundities at the same weights.

Discussion and conclusions

Results of the present study indicate that potential fecundity of Atlantic cod is strongly correlated with weight, length, and age and less so with somatic and liver condition. A relationship between gamete production

Table 3. Log_{10} regression parameters and significance results for relations of cod fecundity and growth variables in various NAFO regions.

| Relation | Area | Log_{10} regression parameters | | | | | |
|------------------|------|---|-----------|-------|-------|--------|-----|
| | | Slope | Intercept | R^2 | P | F | N |
| Fecundity-length | 2J | 5.70 | -3.70 | 0.36 | <0.01 | 23.56 | 43 |
| | 3KL | 3.01 | 0.69 | 0.38 | <0.01 | 53.08 | 87 |
| | 3Ps | 4.96 | -2.85 | 0.68 | <0.01 | 145.43 | 70 |
| | All | 3.15 | 0.44 | 0.36 | <0.01 | 111.02 | 200 |
| Fecundity-age | 2J | 3.73 | 3.34 | 0.31 | <0.01 | 18.58 | 43 |
| | 3KL | 1.87 | 4.52 | 0.32 | <0.01 | 40.36 | 87 |
| | 3Ps | 3.28 | 3.21 | 0.56 | <0.01 | 87.71 | 70 |
| | All | 1.91 | 4.46 | 0.28 | <0.01 | 77.65 | 200 |
| Fecundity-weight | 2J | 2.09 | 6.04 | 0.42 | <0.01 | 30.15 | 43 |
| | 3KL | 1.04 | 5.84 | 0.43 | <0.01 | 64.95 | 87 |
| | 3Ps | 1.63 | 5.64 | 0.72 | <0.01 | 178.40 | 70 |
| | All | 1.11 | 5.82 | 0.41 | <0.01 | 138.27 | 200 |
| Fecundity, K | 2J | 6.09 | 4.92 | 0.10 | 0.03 | 4.80 | 43 |
| | 3KL | 3.74 | 6.22 | 0.15 | <0.01 | 15.15 | 87 |
| | 3Ps | 2.84 | 6.08 | 0.06 | 0.04 | 4.31 | 64 |
| | All | 3.24 | 15.9 | 0.09 | <0.01 | 20.35 | 194 |
| Fecundity, GI | 2J | 0.47 | 6.58 | 0.07 | 0.07 | 3.40 | 43 |
| | 3KL | 0.23 | 6.35 | 0.02 | 0.21 | 1.58 | 87 |
| | 3Ps | -0.53 | 5.13 | 0.07 | 0.04 | 4.55 | 64 |
| | All | 0.08 | 6.07 | 0.00 | 0.49 | 0.49 | 194 |
| Fecundity, LI | 2J | 2.32 | 8.96 | 0.23 | <0.01 | 12.53 | 43 |
| | 3KL | 0.36 | 6.46 | 0.01 | 0.33 | 0.96 | 87 |
| | 3Ps | -0.23 | 5.59 | 0.01 | 0.59 | 0.29 | 64 |
| | All | 0.47 | 6.58 | 0.01 | 0.07 | 3.40 | 194 |

Fecundity is number of eggs, K represents Fulton's condition factor, GI is gonad index, and LI is liver index. Results rounded to the nearest 0.01.

and fish size was recognized in the 1800s and has been continuously documented (Earll 1880, Fulton 1967). May (1967) found strong correlations between fecundity and length, weight, and age in cod sampled off Newfoundland and Labrador as did Postolakii (1967) in what he called the Labrador cod stock (2J).

Spatial variations in cod fecundity were evident in all three management areas, as well as between offshore (Bonavista Corridor) and inshore (Smith Sound) cod groups. These differences parallel others in group states and life histories. Cod in the northern offshore regions

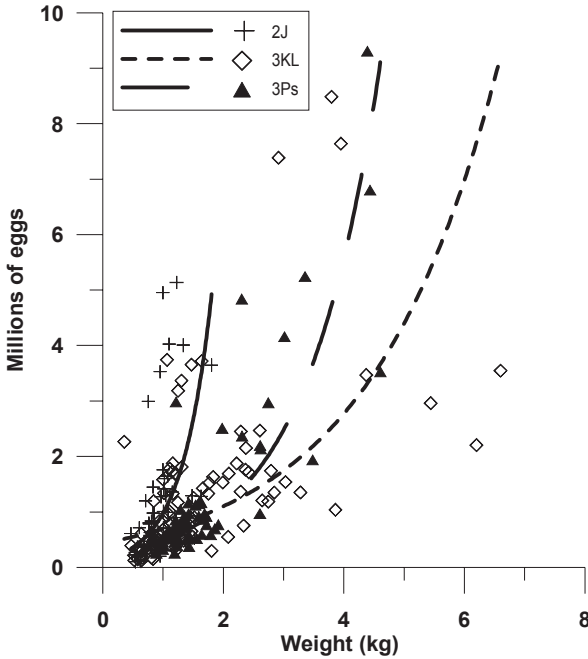


Figure 4. Scatter diagram of fecundity against weight for the three NAFO areas sampled; 2J, 3KL, and 3Ps.

are not seen beyond age 7 and occur at relatively low densities, while inshore cod that overwinter in Smith Sound from the same stock (3KL) consist of a wide size range (35-120 cm) and ages reaching 15-20 years and occur at very high densities (DFO 2004a, Rose 2000). North Atlantic studies by Postolakii (1967), McIntyre and Hutchings (2003), as well as studies for Newfoundland cod stocks by May (1967) and Pinhorn (1984), have all demonstrated differences in fecundity-growth correlations between areas. Temporal variation in fecundities between 1999 and 2003 in Smith Sound cod may be related to reproduction suppression or atresia (Rideout et al. 2000). Rideout and Rose (2006) found that for cod sampled from Smith Sound during 1999-2004, the 1999 sample had the highest rate of skipped spawning. This event was positively correlated with population age structure and diet.

The strongest fecundity to size, age, and condition relationships were evident in cod from Placentia Bay, where stock rebuilding following a fishing moratorium in 1993 enabled reopening of a modest commercial fishery in 1997 (average harvest about 15,000 t per year). In

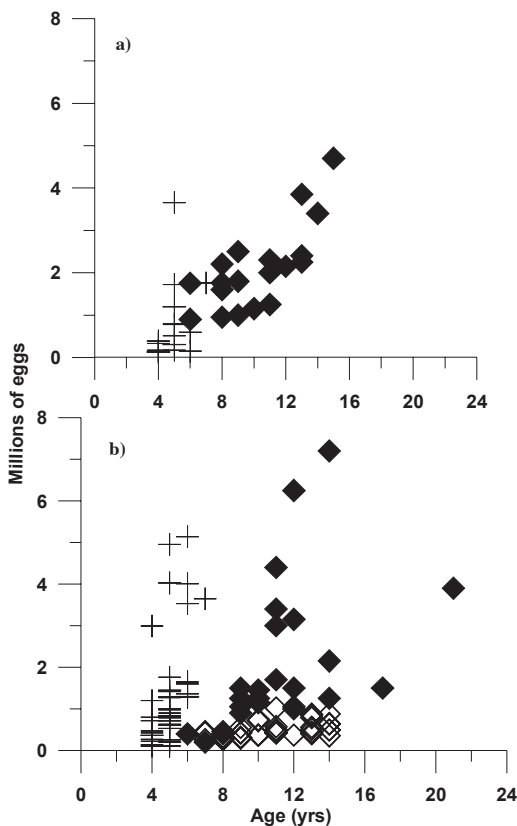


Figure 5. Fecundity at age for this study (+) and historical data from May 1967 (◆) and Postolakii 1968 (◇). Data from NAFO subdivisions 3L (a) and 2J-3K (b).

most respects the 3Ps cod stock, is the northwest Atlantic stock in the best condition. (Lawson and Rose 2000, DFO 2004b). This stock has the biomass, migrations, growth rates, reproductive potential, and condition closer to historical norms than in the formerly larger cod stocks on the Grand Bank and to the north (Sherwood and Rose 2005). In terms of fecundity, our results differ little from those of Pinhorn (1984) for this area.

In comparison, cod life histories in the northern offshore areas (Hawke Channel and Bonavista Corridor) bear little resemblance to historical norms. Cod here historically matured at earlier ages and smaller sizes than cod inhabiting southern waters (Fleming 1960, May 1967, Lilly et al. 2005). However, lengths-at-age and weights-at-age declined in the

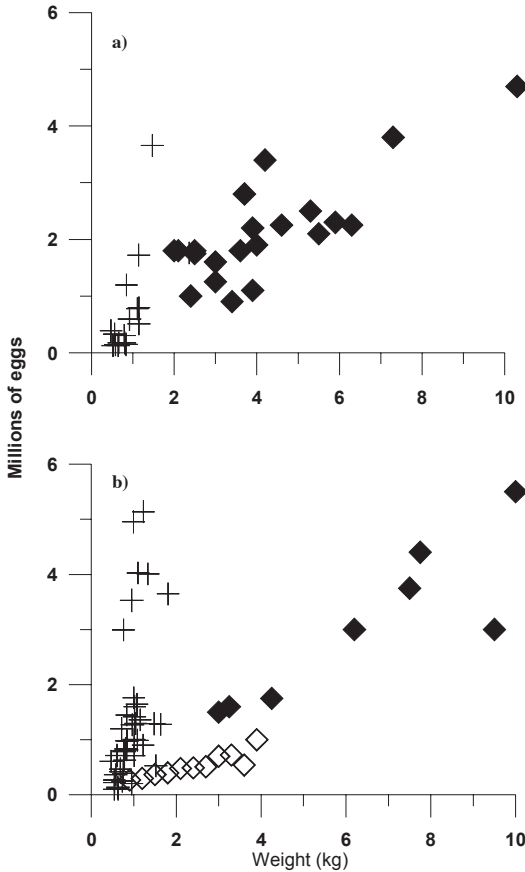


Figure 6. Fecundity at weight for this study (+) and historical data from May 1967 (◆) and Postolakii 1968 (◇). Data from NAFO subdivisions 3L (a) and 2J-3K (b). Weight is gutted except for Postolakii 1968 data, for which only whole weights were available.

1980s and early 1990s, with the greatest declines occurring in the northernmost extents of the stock. The age composition of this population has become extremely truncated and since the early 1990s very few cod older than 6 years have been found (Lilly et al. 2005). Furthermore, an increasing proportion of these fish are maturing at even younger ages. In the early 1960s, 15% of females were mature at 6 years of age; this increased to 50% in the 1970s to 80s and to 80% in the 1990s (Fleming 1960, Lilly et al. 2005). Currently, the average age at maturity for cod in 2J is 4-5 years whereas historically it was 6-7 years (this paper; Lilly et

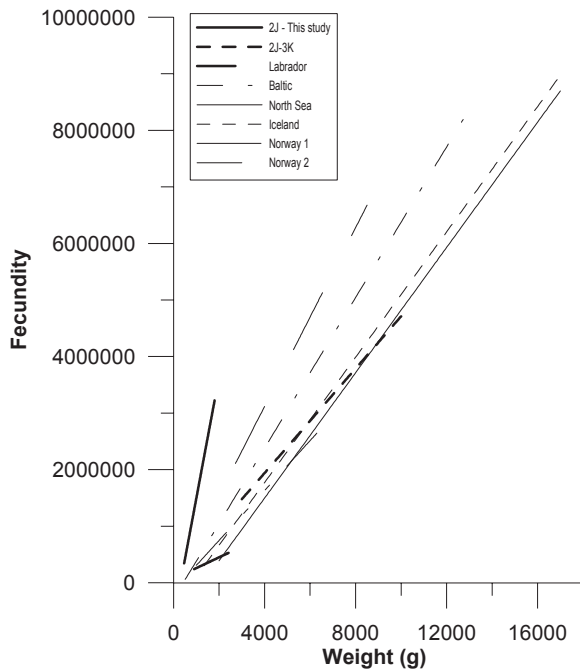


Figure 7. Comparison of linear regressions of fecundity-weight relations in cod of different geographic regions of the North Atlantic. Data were combined by weighted averages for Baltic, North Sea, and Iceland (Table 2). Norway 1 represents data from Botros 1962; Norway 2 data are weighted averaged data from Kjesbu et al. 1998. Weights are whole weights except for cod sampled from Labrador for which only gutted weights were available. Bold lines include data from the Newfoundland and Labrador region.

al. 2000). Cod sampled by May in the mid-1960s from offshore 2J-3K in similar areas to the present study were of greater age and size ranges (5-15 yrs; 3-9 kg, respectively) than were cod found in this study (4-6 years of age and 0.5-2 kg in weight).

This study also looked at a comparison of the fecundity-weight relation across North Atlantic cod stocks. May (1967) noted that the relatively high fecundity from the western Baltic and Norway might result from the low age and small size at maturation, and was not necessarily representative of the northeast Atlantic as a whole. Oosthuizen and Daan (1974) confirmed that Baltic and Norwegian cod fecundities are among the highest of all stocks, and that Newfoundland-Labrador cod fecundities were significantly lower. This has changed; our data

show that not only are cod from 2J maturing at earlier ages but they are producing a higher number of eggs at equivalent sizes and ages than in any other reported study for any cod stock.

There are several hypotheses for these changes in life history, and although the present work does not allow us to resolve these, a few comments are appropriate. Drinkwater (2002) provides evidence that severe climate conditions (cold temperatures) played a role in the slower growth rates and reduced size at age evident in the 1990s. Pörtner et al. (2001) showed a significant relationship between temperature fluctuations and recruitment, and found that a cold-induced shift in energy budget occurs which is unfavorable for growth performance and fecundity. In addition, capelin (*Mallotus villosus*) all but disappeared in the northern areas surrounding Newfoundland and Labrador after 1990 and shifted their range southward, followed by a southward shift in cod (Narayanan et al. 1995, Carscadden et al. 1997, Rose et al. 2000b). Historically capelin has been the most important food of northern cod (Carscadden et al. 2001, Lilly 1994), and a primary energy source for the development of eggs (Henderson et al. 1984); but in the 1990s few offshore cod could locate them (Rose and O'Driscoll 2002). A poor diet may be contributing to the lack of survivorship past age 6, and the related early maturation and high fecundity in the offshore areas (2J-3K). Growth and reproduction at some level compete for the limited resources of available energy. If food availability is sufficient and maintenance energy costs are taken care of, the surplus energy will bolster energy reserves and production of eggs (Wootton 1990b). Our results suggest that northern cod are investing a large amount of relatively scarce energy reserves into reproduction and in doing so may be subject to an increased risk of mortality (Lambert and Dutil 2000). Changed life history parameters could also be a survival tactic in response to the present low state of the population, the lowest recorded in history (Waiwood 1982, deYoung and Rose 1993, Sinclair and Murawski 1997). Another hypothesis is that life history changes are genetic and induced by fishing. Olsen et al. (2004) suggested that the pressures of size-selective exploitation could change the life history of cod, and that early maturation may be a genetic response to increased mortality. However, there is still no quantitative evidence linking fecundity and genetic change.

This study provides contemporary data on cod fecundity in the northwest Atlantic. Southern cod groups have fecundity schedules similar to historical norms, but the formerly dominant northern fish are maturing at earlier ages and smaller sizes, and dying young.

Early maturation, early mortality, and high fecundity are likely to be linked life history responses to environmental, population, or genetic changes. Further investigation of these changes is needed for fisheries management.

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Rebuilding Atlantic Cod: Lessons from a Spawning Ground in Coastal Newfoundland

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Abstract

Atlantic cod (*Gadus morhua*) was studied at the Bar Haven, Placentia Bay, Newfoundland (NAFO 3Ps stock unit) spawning ground from 1996 to 2003. Lessons applicable to management of rebuilding stocks derived from these studies are reviewed: (1) cod spawn in the same area each year, but numbers and timing vary (spawning biomass varied from 2,000 to 25,000 t, with timing protracted over at least 100 days); (2) courtship and spawning behavior is complex, and includes lekking, sound production, and vertical rituals; (3) large fish in good condition are necessary to large egg potential because fecundity increases exponentially with fish size—total egg potential varied considerably from year to year with spawning abundance, age changes, and mean liver condition in spawning females; (4) retention of early life stages did not explain local recruitment and rankings of annual densities of eggs, larvae and juveniles did not match with local recruitment during three years of study; (5) dispersal of early life stages, juveniles, and adults was density-dependent; (6) individual adults homed to the same spawn-

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ing ground in sequential years, but others strayed; (7) egg potential was correlated with the return of adults to the spawning ground 4-5 years later ($r^2 = 0.33$, d.f. 3), and with recruitment to the full stock area (NAFO subdivision 3Ps) ($r^2 = 0.96$, d.f. 5), with only weak compensation in survival at low stock size; (8) fishing on spawning aggregations may harm reproductive potential; and (9) seasonal fisheries influence fishing mortality, commercial yield, and value. Management implications are discussed.

Introduction

Fish population dynamics at low stock sizes may differ fundamentally from those at higher stock levels and are not well understood (deYoung and Rose 1993). As a consequence, assumptions and models based on extrapolations from higher population states have proven to be unrealistic in predicting rebuilding rates, such as those for Newfoundland and Labrador cod (e.g., Roughgarden and Smith 1996, Myers et al. 1999, Hutchings 1999). Recent evaluations of stock-recruitment relationships have emphasized the need to better understand the “low end” of the stock-recruitment relationship in stocks that have entered this domain (Walters and Martell 2004), in particular because of the possibility of depensation, which describes a population state in which growth rates do not increase and may even decline at low stock sizes (Liermann and Hilborn 2001). Although Myers et al. (1995) concluded that there was little evidence for depensation across a broad sweep of fish stocks, there is considerable evidence that at least some of the cod stocks in Newfoundland and Labrador waters entered just such a state in the 1990s (Frank and Brickman 2000, Anderson and Rose 2001, Rose 2004, Shelton et al. 2006). Nevertheless, it is not at all clear at what life stage depensatory mortality occurs, or if all stocks in this region are in this state.

The place to start in attempting to understand the dynamics of rebuilding in fish stocks is on the spawning grounds. Very few studies have focused on multiyear studies of spawning grounds in marine fishes, with attempts to track the dynamics of a population from spawning fish through the egg and juvenile stages and back to spawning recruits. No study of which we are aware has attempted to do this with a stock at a depressed population level. In the present work, we review the results of a study based at a key spawning ground for Atlantic cod (*Gadus morhua*) on the south coast of Newfoundland (NAFO subdivision 3Ps management unit), located on the Bar Haven shoals in Placentia Bay (Fig. 1). At the beginning of this work in the mid-1990s, the stock was recovering from a depressed state. Over the past decade it has rebuilt somewhat, although not to historic levels, and now supports the largest fishery in the northwest Atlantic (Bratley et al. 2004). It was during this

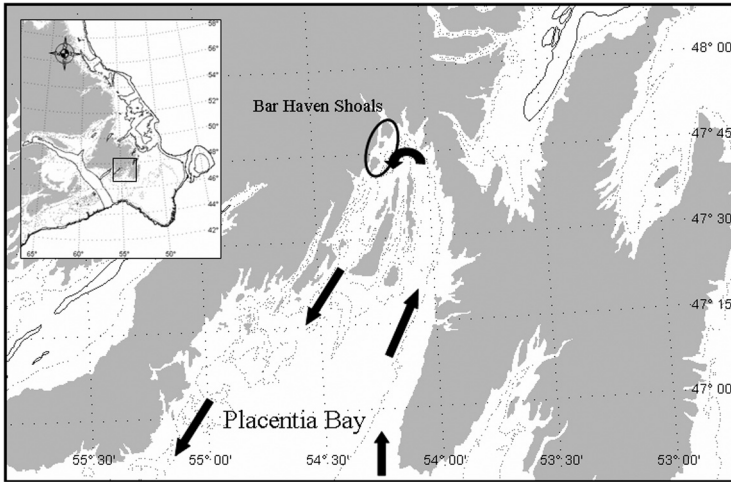


Figure 1. Map of Placentia Bay showing the Bar Haven spawning shoals and dominant currents.

period of moderate growth from a low stock size that we attempted to capture the dynamics of the life history of these fish from spawning to returning next generation adults.

The first objective of this work was to learn about the dynamics of cod populations, especially at low population sizes. Several “lessons,” used in the sense of “something learned by study or experience,” (Allen 2000) may be gleaned from this work. These form the basis of this review, which represents a synthesis of published research as well as new and more comprehensive interpretations of the data that have been collected. We add new syntheses from egg production and population models that enable comparisons of egg, larval, and juvenile concentrations with recruitment to the local spawning group and to the full management unit stock. We also examine the persistence of the Bar Haven spawning ground. A chronological approach is taken, from spawning adults, their distribution, density, and behavior, through the early life stages, and ending at next-generation recruitment back to the spawning ground and to the full stock.

It was also an objective to use this work to provide information that could advise management. Such advice often assumes compensatory population dynamics (Cook 1998, Frank and Brickman 2000) such that as abundance declines, individual and population growth rates are assumed to increase. These controversial assumptions point to the importance of this study in providing a better understanding of population processes at low stock sizes.

Methods

Acoustic surveys and stations

The timing and distribution of spawning at the Bar Haven ground in Placentia Bay was monitored over eight years (1996-2003) using acoustic survey methods employing calibrated Simrad EK500 split-beam or BioSonics single beam DT4000 echosounders (38 and 120 kHz, 6-7° half-power beam widths) (Lawson and Rose 2000a, Mello and Rose 2005a). Surveys were conducted in June 1996, from April to September in 1997-1999, and in April-early May and June from 2000 to 2003. In addition to the surveys, the CCGV *Shamook* was moored over the spawning aggregation at the Bar Haven grounds for periods of 24-36 hours in April 2002 while acoustic data were collected continuously with a calibrated EK500 split-beam echosounder with a 38 kHz transducer deployed in a fixed position adjacent to the vessel. A video camera for species and behavioral identification and passive acoustic listening hydrophone to monitor sounds made by spawning fish were also deployed at the mooring site.

Tagging

Cod were tagged at the Bar Haven grounds with Floy T-tags in 1997 and with transmitting sonar tags in experimental releases in 1998, 2000, and 2002. In all cases, cod were caught with feather hooks on lines fished from the CCGS *Shamook* in depths ranging from 10 to 70 m. In April and May 1997, 1,813 cod were tagged with Floy Ts at the Bar Haven grounds, and several thousand fish were tagged at other locations in Placentia Bay (Lawson and Rose 2000b). Recaptures were made by the commercial and scientific fisheries. The acoustic tag was the Lotek CAFT 16-3, designed to transmit a high volume (-59 dB) coded pulse every 5 seconds for up to 3 years. These tags were surgically implanted in adult cod (Robichaud and Rose 2001) at the Bar Haven grounds (Table 1). Tagged fish were released at the capture location on the grounds and translocated from the site in the various experiments. All telemetry surveys were made with Lotek SRX-400 receivers from small vessels (4 m Zodiac and 6 m RV *Gecho*) equipped with hydrophones.

Egg potential

During all acoustic surveys, the proportions of females, the condition of their gonads (immature, ripening, spawning, or spent), and their size were routinely assessed ($n = 144, 441, 504, 678, 336, 907, 347,$ and 365 females sampled from 1996 to 2003, respectively, ranging in length from 45 to 120 cm). Fecundity was determined from females sampled in 1999 and 2003 at Bar Haven (Fudge and Rose 2008). Spawning intensity was defined as the number of ripe females on the ground during the consecutive surveys. Spawning (egg) potential was estimated through

Table 1. Homing summary from acoustic telemetry experiments conducted with adult spawning cod at Bar Haven from 1998 to 2003. All fish were tagged with Lotek CAFT-16 long term coded pinger tags. Most mortality in these fish has resulted from fishing (30-40% returns from the fishery), with a maximum time at liberty of over 4 years. "No." is the number of fish at liberty during the homing year from each experiment.

| Experiment | Release year | No. | Relocation | Homing year | Homing % | Reference |
|------------|--------------|-----|-------------|-------------|----------|-----------|
| 1 | 1998 | 48 | No | | na | 1 |
| 1 | 1998 | 26 | No | 1999 | 39 | 1 |
| 1 | 1998 | 15 | No | 2000 | 53 | 1 |
| 2 | 2000 | 4 | No | 2000 | na | 2 |
| 2 | 2000 | 11 | Upcurrent | 2000 | 64 | 2 |
| 2 | 2000 | 8 | Downcurrent | 2000 | 25 | 2 |
| 3 | 2002 | 16 | No | 2002 | na | 3 |
| 3 | 2002 | 17 | On route | 2002 | 51 | 3 |
| 3 | 2002 | 15 | Off route | 2002 | 13 | 3 |
| 3 | 2002 | 11 | na | 2003 | 49 | 3 |
| 3 | 2002 | 9 | na | 2003 | 79 | 3 |
| 3 | 2002 | 9 | na | 2003 | 20 | 3 |

¹ Robichaud and Rose 2001.

² Robichaud and Rose 2002.

³ Windle and Rose 2005.

two calculations. First, the average acoustic backscattering coefficient for females on the grounds was calculated for each year from April to June encompassing the main spawning period in all years:

$$S_a(\text{females}) = \sum_n (S_a f) n^{-1} \quad (1)$$

where f = the proportion of females from catch data, and n is the number of surveys. Next, the numbers of females of each 10 cm length group was determined by decomposing the mean S_a (females) by the length composition determined from the catch and the mean acoustic target strength for each length class according to TS (dB) = $10 \times \log_{10}$ (length [cm]) - 67.5 (Rose unpubl.). Egg potential was estimated from the total number of females of 10 cm length groups, the percent maturity of those groups, and their mean fecundity:

$$\text{Egg potential} = \sum_{L_{10}} (S_{L_{10}} \times M \times F) \quad (2)$$

where $S_{L_{10}}$ was the number of spawning females of each 10 cm length group, M was the percent maturity of the group, and F their mean fecundity.

Finally, estimates of total spawning numbers over each year were made by integrating over 100 days (based on the detailed chronological data from 1997 to 1999 and assuming a 20 day residence for each female cod, Robichaud and Rose 2002).

Egg and larval surveys

Egg, larval, and demersal juvenile density and distribution were monitored from 1997 to 1999. Eggs and larvae were sampled over a grid of 45 stations throughout the spawning and post-spawning periods from April to August in 1997 and 1999, and from April to September in 1998, using a 4 m² Tucker trawl and double oblique tows to 40 m depth. Cod eggs were staged I-IV and all stage I eggs were assumed to be cod (had-dock and witch flounder with similar eggs are uncommon in Placentia Bay, Bradbury et al. 2000). Predictions of egg development time were based on mixed layer temperature (Pepin et al. 1997).

Juvenile surveys

Demersal juveniles were surveyed with a 25 m bottom seine once a month from September to December 1997-1999 at 18 sites around the shoreline of the bay that contained eelgrass habitat (Robichaud and Rose 2006). Numbers and standard length of cod caught were recorded. Hatch dates were calculated from an age-length relationship developed using standard lapillus daily-otolith-ring counts (D. Robichaud unpubl. data).

Recruitment

Recruitment was assessed from acoustic surveys at the Bar Haven spawning grounds at ages 4-5, and over the full management unit (NAFO 3Ps) using results from sequential population model Adapt run E, a middle estimate among several that varied (see Bratney et al. 2004). It is important to note that the sequential population analysis (SPA) was tuned primarily with two bottom trawl survey indices that do not cover the Bar Haven area. Hence the surveys do not overlap in space, but the main trawl survey was conducted at the same time in April as the acoustic survey at Bar Haven. The indices of recruitment differ in interpretation: the Bar Haven index reflects subadult and adult presence on this spawning ground (ages 4-5), whereas the stock index reflects survival of juveniles to age 3 over a greater proportion of, but not the full, stock range. Beverton-Holt stock-recruitment models were used to compare egg potential and recruitment, using a nonlinear fitting procedure assuming lognormal errors (Hilborn and Walters 1992).

Results and discussion

The Bar Haven spawning grounds

The Bar Haven area in northwest Placentia Bay is dominated by a series of islands and underwater shoals that rise to within 50 m of the surface (Fig. 1). A deep channel (to 200 m) penetrates the main area between Bar Haven and Woody Islands, but the main spawning area is in the shallower waters (30-80 m) at the margins of this channel (Windle and Rose 2006). The dominant flow in Placentia Bay is the inshore branch of the Labrador Current that hooks around the Avalon Peninsula and flows counter-clockwise around the bay. The complex bathymetry and variable winds result in many eddies and local variations to these dominant flows. Tidal elevations are variable spatially but reach peak heights of 3-4 m in the Swift Current area near the Bar Haven grounds. Temperatures are generally cool as a result of the Labrador Current waters, but surface waters warm seasonally to 10-15°C. During the spawning season, surface waters are warming but at depths of over 40-50 m retain near zero or even subzero temperatures.

The spawning biomass at Bar Haven, as estimated from acoustic surveying, ranged from a few thousand tons in 2000 to over 25,000 t in 1998 (Fig. 2). Total stock spawning biomass estimated from sequential population models ranged from about 60,000 t in 1996 to about 85,000 t in 1998 and 1999 (Bratney et al. 2004). Bar Haven represented between about 2 and 30% of the spawning biomass of the stock. The two series were weakly correlated when fit with a log model with zero intercept ($r = 0.48$; $p = 0.07$) (Fig. 3).

Lesson 1: Cod spawn in same area each year, but numbers and timing vary.

Cod spawned at the Bar Haven grounds in all years from 1996 to 2003 (Figs. 2, 3). The strongest year classes on the grounds were those born in 1990, 1992, and 1997 (Fig. 4). From 1997 to 1999, and particularly in 1998, there were numbers of fish older than 7 years. From 2000 to 2003 there were very few such older fish, likely a result of a concentration of fishing effort and catch in the Bar Haven area from 1998 to 2000 (Bratney et al. 2004). From 1997 to 1999, when spawning activity was monitored near year-round, spawning was highly protracted, but peaked from April to June with a secondary peak in June or early July (Fig. 5). Early spawning coincided with export of eggs and larvae from Placentia Bay, whereas later spawning was associated with higher retention of early life stages.

The protracted spawning observed made single or short-term measures of spawning density potentially misleading in terms of spawning potential. Our measures spanned the spawning from 1997 to 1999 and the major peak from April to June in the later years (1996 was a start-

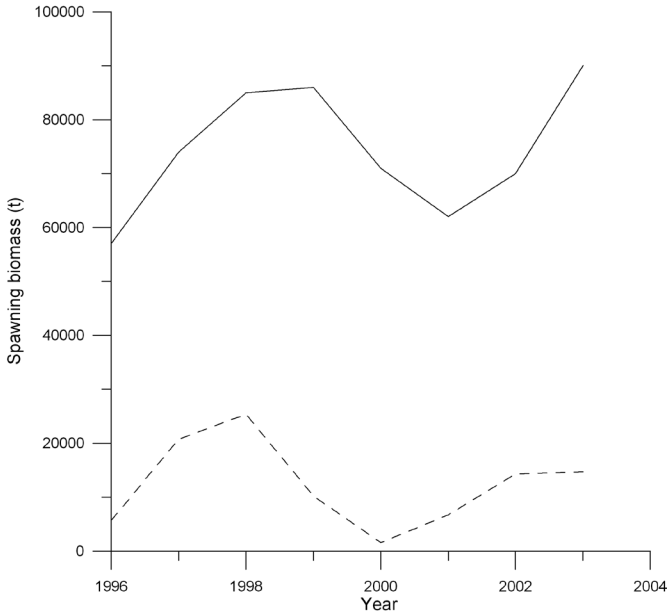


Figure 2. Spawning biomass from acoustic surveys at Bar Haven (dashed) and in the 3Ps stock.

up year with only a single measure in June). April-June measures are thought to capture the year-to-year variations (ranking the same if the full season had been used in those years, 98 > 97 > 99).

The location of the spawning grounds relative to current and tidal flows results in eggs and larvae being transported seaward and out of the bay if spawning occurs early in cold waters, or more likely being retained within the bay if spawning is later under warmer conditions. Surface drifters released at the Bar Haven grounds were retained within the land-sea complex of the inner bay, many at locations similar to the distribution of eggs and juveniles (Bradbury et al. 2000, Robichaud and Rose 2006).

Lesson 2: Spawning behavior is complex, involving lekking and sound production by males and extended courtship.

In cod, courtship behavior and spawning may extend over a period of weeks or months and follows structured rituals. Males generally arrived first on the grounds (Robichaud and Rose 2002) and undertook a form of lekking behavior, in which they competed with other males in attempts to attract females (Hutchings et al. 1999, Nordeide and Folstad

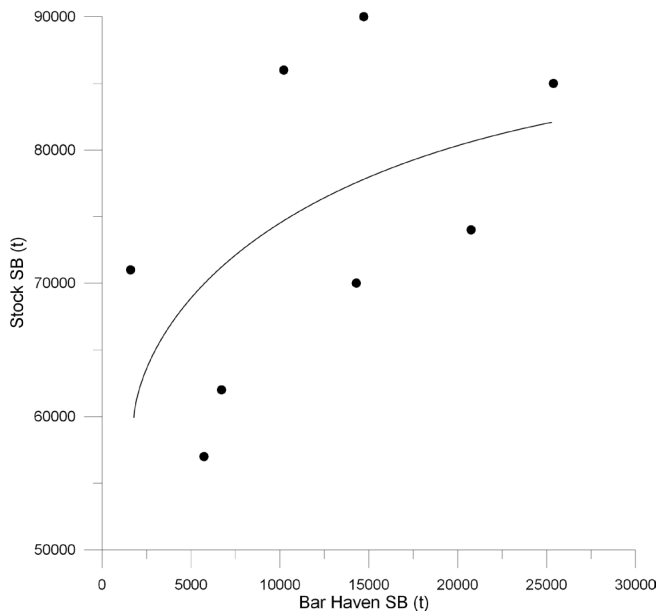


Figure 3. Spawning biomass at Bar Haven from acoustic surveys vs. the 3Ps stock spawning biomass, where x and y are the spawning biomass of Bar Haven and the 3Ps stock, respectively.

2000, Windle and Rose 2007). Males made grunting noises periodically by contracting muscles around their swim bladder (S.B. Fudge unpubl.). These grunts were recorded primarily at night. Females moved on and off the lekking arenas as their eggs ripened, with larger females batch spawning several times over a period of a few weeks (Robichaud and Rose 2003). Courtship and spawning involved vertical movements in the water column (the height depending on the depth of water), most notably in the evening, and can be observed as rises and falls in small groups of fish that have the appearance of columns (Rose 1993, Lawson and Rose 2000a). From a fixed station, the rises and falls of fish in a spawning group appear as a wave (Fig. 6).

Lesson 3: Large fish in good condition enhance egg potential.

There were large inter-annual differences in the spawning potential, with a major peak in 1997 and 1998 (1998 highest) (Fig. 7). This peak reflected for the most part a large total number of fish on the ground but also an older age structure (Fig. 4). For example, a large total number of fish was observed in 2003, but spawning potential was less than in 1997 and 1998 because of a younger age and smaller size structure. The

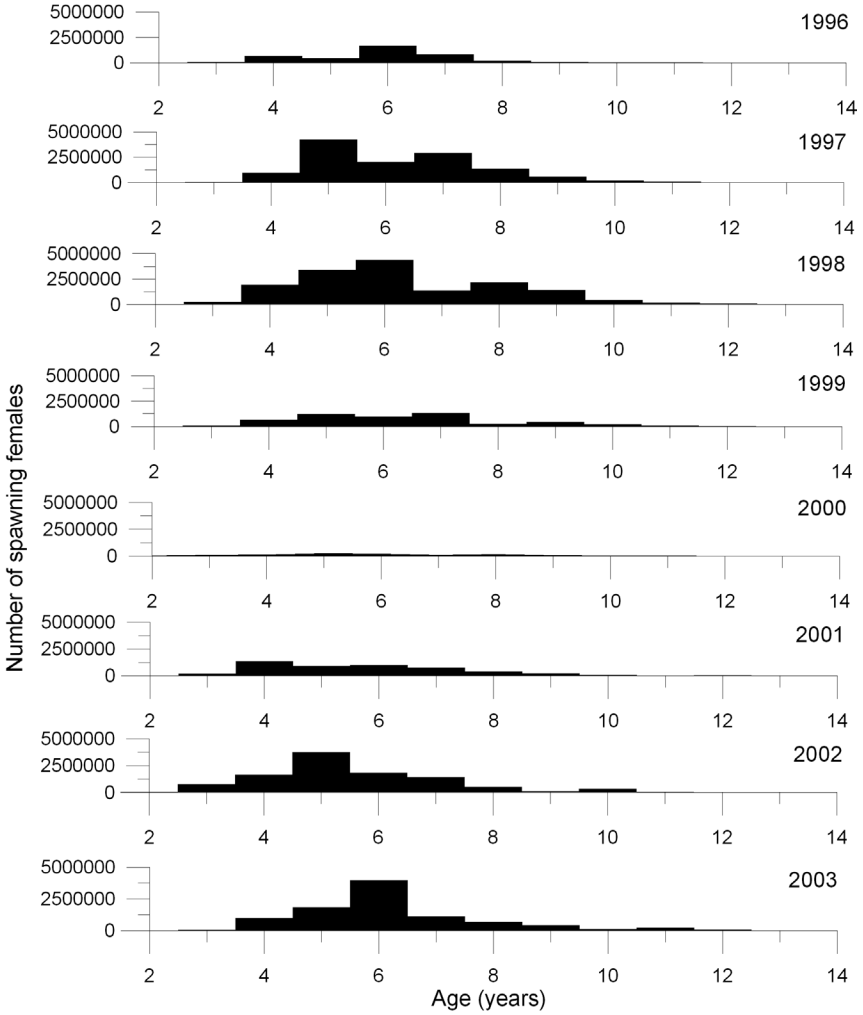


Figure 4. Age structure of cod at the Bar Haven spawning area, 1996-2003.

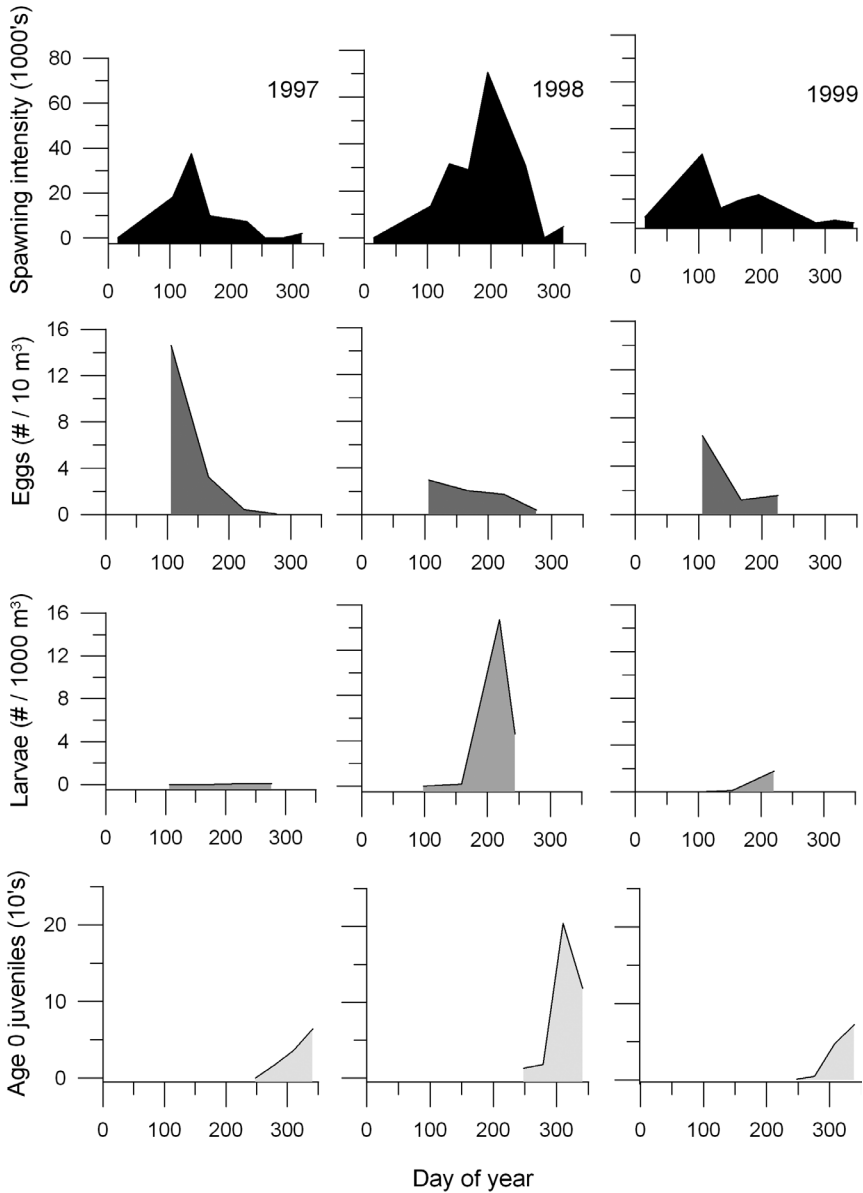


Figure 5. Spawning intensity (ripe female numbers), egg, larval, and juvenile concentrations from 1997 to 1999 in Placentia Bay.

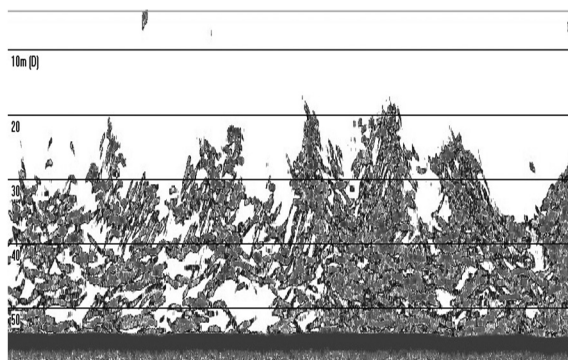


Figure 6. Echogram from stationary transducer (38 kHz) over spawning aggregation at Bar Haven in 2003. The x-axis represents time (approximately 15 minutes) and the y-axis depth (as indicated). The rises and falls of the individual fish, which form columns (Rose 1993) when observed from a moving platform, can be clearly seen.

percentage of cod aged 8 years and older reached about 14% in 1998 and 1999, but declined quickly to 9% in 2000 and 5% by 2002. Estimated annual egg production rapidly declined by 2000, but increased somewhat in 2002 and 2003.

Liver condition in mature female cod of all size classes varied among years (ANOVA, $p < 0.05$). Larger fish varied less in liver condition than smaller fish. Years of highest condition were 1997, 1998, and 2003. Mean annual liver condition in spawning females was correlated with annual egg potential (Fig. 8). In turn, cod with superior liver condition had isotope signatures characteristic of pelagic feeding (Sherwood et al. 2007), primarily a function of the availability of capelin in Placentia Bay (Mello and Rose 2005a). Liver condition in cod is known to be strongly related to reproductive success (Marshall et al. 2000).

Lesson 4: Retention of early life stages does not explain local recruitment.

In the three years of study of all life stages, retention did not appear to be key to resultant survival to spawning recruitment. The 1997 year class, the strongest to return to the Bar Haven grounds from 1996 to 2003, was poorly retained within the bay, with concentrations of eggs, larvae, and juveniles the lowest measured from 1997 to 1999 (Fig. 5).

Temporal trends in the progression of life stages differed substantially among years (Fig. 5). In 1997, the highest adult spawner and early

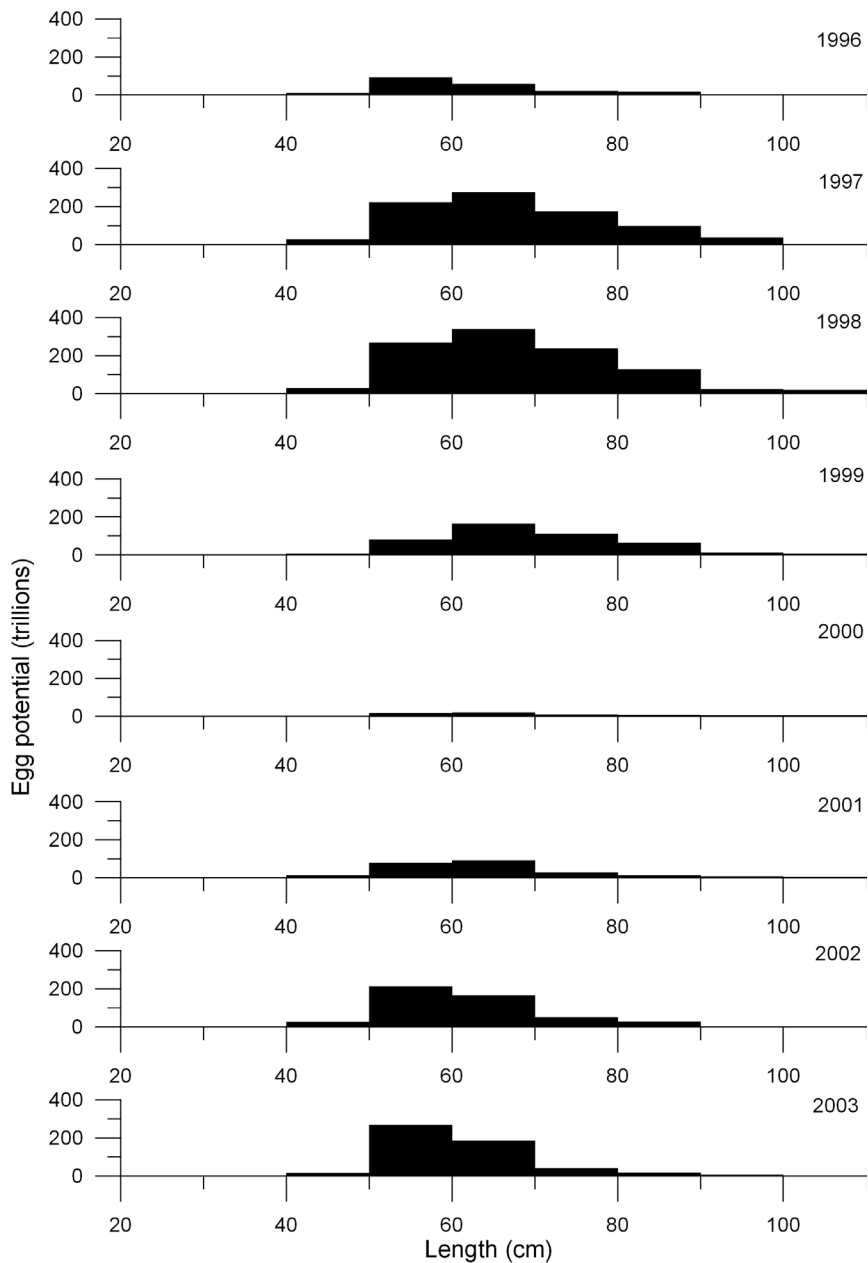


Figure 7. Annual egg production by length group at Bar Haven, 1996-2003.

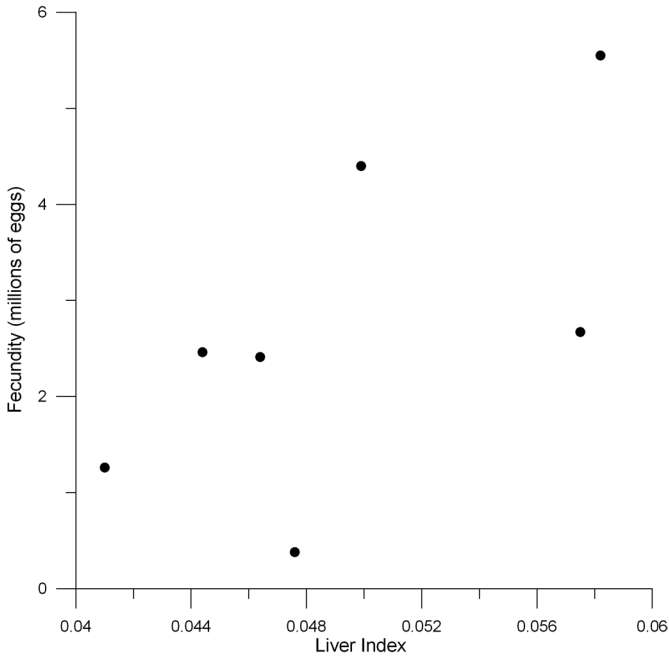


Figure 8. Annual egg potential and the mean liver index of female cod, April-June 1997-2003. Each datum is an annual average of the females measured (1996 is excluded because of singular sampling) ($r = 0.64$; $p < 0.05$). Fecundity based on Fudge and Rose 2008.

stage egg concentrations were found in April (mean surface temperature 0.0°C), but only low concentrations of larvae and demersal juveniles were subsequently observed in the bay. These findings suggest that early spawning at inevitably cold temperatures led to extended development times that resulted in few larvae or juveniles being retained within the bay. In 1998, peak spawning was delayed until June when surface temperatures were 11°C , and late stage eggs, larvae, and juveniles were more abundant within the bay (juveniles were 5 times more abundant in 1998 than in 1997). In keeping with these results, juveniles within the bay were virtually all spawned during the later peak in spawning in all years studied. Back calculations of spawning dates using otolith ages and expected egg stage durations indicated that locally retained juveniles resulted from spawning that occurred from June onward in all years. Larvae and demersal juveniles that were spawned before June were rarely observed despite an abundance of pre-June spawning in all years (Robichaud and Rose 2006).

Annual rankings of the concentrations of the three life history stages, eggs, larvae, and juveniles, did not match with local recruitment to the Bar Haven grounds (97 > 98 >> 99). The ranking of juvenile (and to a lesser extent larval) density matched that of full stock recruitment, as well as annual egg potential at Bar Haven (98 > 97 >> 99).

Potential annual fecundity at Bar Haven predicted the independently modeled juvenile recruitment to the larger stock area more precisely than local spawning recruitment, which also suggests that retention was not the key factor in local recruitment. We note that these conclusions are based on three years of data only (it was not feasible to extend this part of the study), and these results must be interpreted in that light. Nonetheless, these findings, in tandem with our findings on homing behavior, are consistent with recent studies indicating that homing in cod sustains population structures (Svedang et al. 2007), although at some larger scale retention is likely to be important.

Lesson 5: Dispersal of both early life stages and adults is density-dependent.

Juvenile dispersal was highly density-dependent (Robichaud and Rose 2006). When densities of juveniles were higher, they were more dispersed. This result differs substantially with past studies conducted at lower resolution on the northeast coast of Newfoundland, in which density-dependence of juveniles was not detected (Schneider et al. 1997).

Adults disperse from the Bar Haven grounds after spawning, in some years venturing around the Avalon Peninsula as far north as Trinity Bay (Lawson and Rose 2000a,b). Fish of larger size travel farther, with the exception of very large fish that become more sedentary (Lawson and Rose 2000a,b). In years of higher abundance, more fish will migrate farther. Tagging results reported in Lawson and Rose (2000b) and Bratney et al. (1999), suggest that the extent of the post-spawning migration to the north from fish tagged in Placentia Bay may have been greater in 1997 and 1998 than in the following years when the numbers of fish spawning at Bar Haven were lower.

Lesson 6: Adults home in sequential years to the same spawning ground.

Telemetry experiments conducted at the Bar Haven grounds from 1998 to 2003 showed that adult cod are capable of precise homing both in subsequent years and in the same year after being transplanted back along the spawning migration route (Table 1). The only experiments in which cod did not home at a high rate were those in which cod were displaced to what was likely to be unfamiliar territory not on the migration path (Robichaud and Rose 2002, Windle and Rose 2005; Table 1). Overall, discounting those transplant experiments, homing averaged about 60%. It is important to recognize that this work does not address

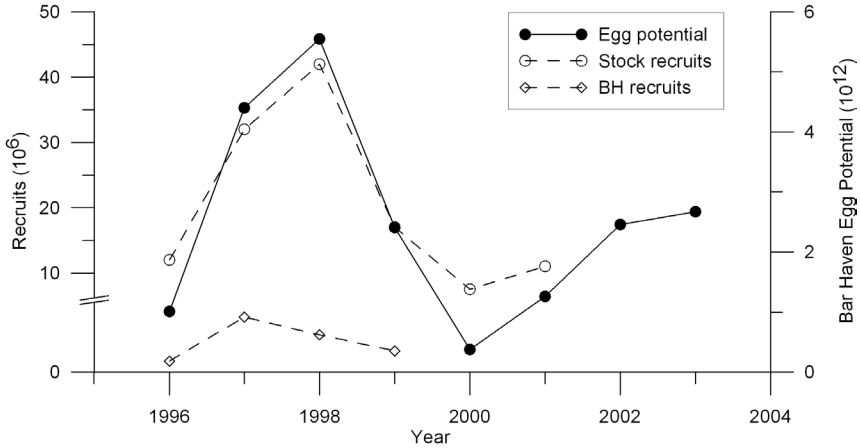


Figure 9. Egg potential at Bar Haven (closed circles), and recruits at age 3 to 3Ps stock (open circles) and to the Bar Haven grounds at age 4-5 years (open diamonds).

natal homing. The present data are not adequate to address that issue. Nevertheless, the demonstrated homing that takes place to the Bar Haven grounds is likely the mechanism that sustains this spawning group (Robichaud and Rose 2001, Windle and Rose 2005). It is equally important to note that on average 40% of cod did not home, but strayed, presumably to other spawning grounds. As many of these fish were subsequently caught in the fisheries, there is no evidence of elevated mortality as a cause of non-returning fish.

Lesson 7: At low stock sizes, egg potential predicts recruitment.

Overall annual spawning potential (eggs) at the Bar Haven ground from 1996 to 2000 was correlated with recruitment to the Bar Haven ground four and five years later ($r^2 = 0.41$) and to the full fisheries management unit (NAFO subdivision 3Ps) ($r^2 = 0.95$) in Beverton-Holt models (Figs. 9, 10). Surprisingly, the full stock relationship was the stronger of the two, based on six years of independent data (only four years of data were available from Bar Haven). The correlation between egg potential and local recruitment may be explained by homing, but why the strong relationship exists with the full stock recruitment series is uncertain. One possibility is that Bar Haven spawning could be driving recruitment in the full stock, but it seems more likely that egg production is widely correlated. We cannot distinguish between these two notions. Nevertheless, the predictive power of the stock-recruitment relation-

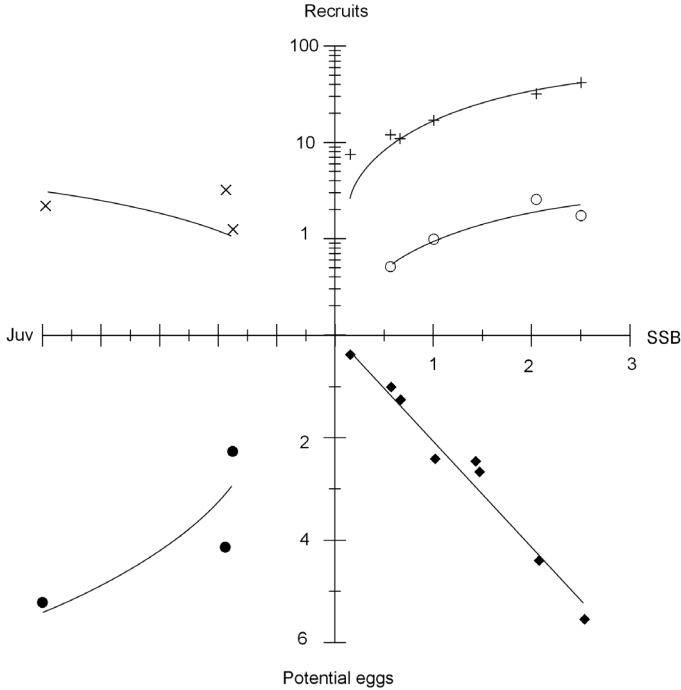


Figure 10. Paulik or life history diagram (Nash and Dickey-Collas 2005) of cod showing relationships between spawning stock biomass (SSB), egg potential, juvenile density, and recruits both to the Bar Haven grounds and to the full 3Ps stock. SSB in 10^4 t; Potential eggs $\times 10^{12}$; Juveniles indexed; and recruits $\times 10^6$. Juveniles have no units (index only).

ship offers the possibility that recruitment might be predicted several years in advance by a relatively simple monitoring of one key spawning ground. It is also important to note that although potential fecundity appears to be a much more reliable index of actual stock size for stock-recruitment analyses than is biomass or numbers (Marshall et al. 1998), and this was true in our study, most of the variability in egg production was explained by the more easily measured spawning stock biomass.

A lower slope of the stock (egg production)-recruitment relationship at Bar Haven relative to the full stock suggests that at lower stock sizes there will be a greater tendency for local recruitment, and that at larger stock sizes more dispersion of recruits to a greater area will take place. This relationship has important implications for rebuilding of Atlantic cod stocks, and perhaps those of other species, where some sub-stock

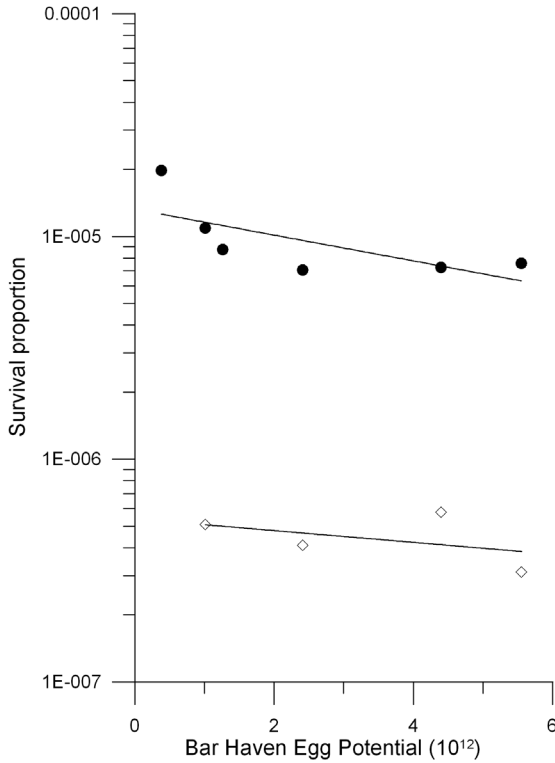


Figure 11. Survivorship from egg potential spawned at Bar Haven to subsequent spawning recruits back to Bar Haven (open diamonds) and to the full stock (closed circles).

components have fared better than others, and where expansion of the more productive components may be key to rebuilding.

It is important to note that there was little evidence in our data of strong compensation in survival rates from egg to adult (Fig. 11). Nor was there evidence of strong depensation, which has been postulated for the more depressed stocks of northern and Grand Bank cod (e.g., Frank and Brickman 2000, Anderson and Rose 2001, Rose 2004). At Bar Haven, recruitment was more or less directly related to egg potential, with similar rates of survival evident at all but the lowest production. The relationship with the full stock is also shown in Fig. 11, although we make no claims of cause and effect.

Lesson 8: Differential fishing mortality may harm spawning components.

The NAFO division 3Ps cod stock includes several spawning grounds that may comprise reproductive populations (Lawson and Rose 2000a,b; Bradbury et al. 2000). The fishery opened in 1997 tended to concentrate effort in Placentia Bay, and in particular in the Bar Haven area. From 1998 to 2000 the fishing intensity was extreme during the spring and late fall, when cod tend to aggregate at Bar Haven. As much as 35-40% of the total catch from 3Ps came from Placentia Bay during these years (FRCC 2002), and as much as 33% from the resident population (Mello and Rose 2005a). A steep decline in the numbers of fish spawning at Bar Haven is evident after 1998, preceding the decline in the full stock (Fig. 2). In addition, the rate of increase in spawning biomass in the full stock suggested by the population model has been much more modest at the Bar Haven grounds. The year-to-year decline in returns of spawning cohorts of ages 5-10 years averaged 0.85 from 1997 to 2003 (equivalent to instantaneous mortality Z with the assumption of sequential homing or similar proportion of the stock returning to Bar Haven each year). This assumption was almost certainly violated in year 2000 when fish did not return to the grounds. (The reasons are not known but large concentrations of fish were located in the deep channel of the bay in spawning condition, but they did not come to the Bar Haven grounds that year.) Hence, the data show a systematic decline in all age classes in 2000 and an untenable increase in 2001, but in all other years the assumption of homing is reasonable. In contrast, estimates of fishing mortality from the SPA population model, pooled over the same ages, ranged from less than 0.2 to about 0.4 during the same period (add 0.2 for M) (Bratley et al. 2004). These data suggest that the mortality rate of the Bar Haven spawning fish was considerably higher than in the general population, and a decline in egg production and then recruitment were immediate and delayed results, respectively. Additional tagging experiments conducted at Bar Haven support this conclusion (see Bratley et al. 2004).

Lesson 9: Seasonal fisheries may influence fishing mortality and commercial yield and value.

Cod exhibited strong seasonality in weight and condition, reaching highest levels in late fall and lowest in spring during spawning (Mello and Rose 2005b). Simulations based on data collected during this research indicated that fishing during spawning required mortality to be 8-17% higher to catch the same quota by weight as a fall fishery. Moreover, spring and summer fisheries resulted in lower yield (6%) and quality (5-26%) of fish products (Mello and Rose 2005b).

Conclusions

Detailed study of a part of the range of a fish stock, in particular key spawning grounds, with subsequent linkages through the life history and the next generation of recruits, can yield insights into the population dynamics of a fish stock that might be lost with the broader but less detailed measures typical of most stock assessments (e.g., Bratley et al. 2004). We believe that our observations are of particular importance to cod and other stocks that are at low population levels, where former sub-stock structures have either been reduced or even eradicated by overfishing or failing production. We draw the following conclusions with reference to the ecology and management of rebuilding cod (and other) stocks:

1. Monitoring of the abundance and age structure of spawning groups and their egg potential offers a simple and effective means of tracking the present state and future potential of a fish stock;
2. Fishing on spawning grounds without restricting catch quotas to that local group risks differential reduction and overfishing of critical spawning components in fish stocks having multiple spawning grounds (such as the one studied here);
3. Fishing on spawning grounds risks differential removal of the largest spawners and hence reducing disproportionately egg potential and recruitment. Spawning behavior is complex hence intrusive fishing could reduce reproductive success;
4. During the spawning season, cod are in their poorest somatic condition, and commercial quality and yield will be poorer than during the fall period;
5. A reasonable number of large cod in a spawning population (ca. 15%), here 8 years and older, will enhance potential fecundity, and provide an indication that fishing mortality is not too high. Large numbers of younger, smaller spawners are less likely to produce strong recruitment; and
6. Compensatory rates of survival of early life stages may not occur at low stock sizes. The formerly dominant offshore spawning groups of cod in Newfoundland waters were reduced to perhaps 1-2% of their historic levels in the last half of the twentieth century, and are very likely to be in a depensatory state (Rose 2004). The Placentia Bay cod, although reduced, at their lowest point were likely not less than 10-20% of historical levels, and appear to exhibit neither strong compensation nor depensation.

Finally, evaluation of alternative management strategies and tests of the population effects of the biological hypotheses advanced here could be based on simulations (e.g., Kell et al. 2007). For example, the close relationship between egg potential and stock recruitment from 1996 to 2000 predicts that recruitment will decline in the early 2000s in the NAFO 3Ps cod stock, with some recovery in the 2002-2003 year classes (this prediction will be tested in the coming years). Our results also highlight the importance of conserving local cod spawning groups (Wroblewski et al. 2005), indeed allowing their abundances to increase (Shelton et al. 2006), as a step toward rebuilding the formerly larger components of stocks.

Acknowledgments

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Disentangling the Effect of Adult Biomass and Temperature on the Recruitment Dynamics of Fishes

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Abstract

Here we analyzed the relation between recruitment dynamic (recruitment or recruitment success) and temperature of 57 commercial fish stocks of the North Atlantic. We showed that, although the effect of temperature was generally significant, spawning biomass is the main factor governing recruitment dynamic. A significant effect of spawning biomass was evident for 67% of all stocks analyzed in this study. For gadoids, the effect of spawning biomass was larger than the effect of temperature (both in terms of number of stocks and proportion of variance explained). For clupeids, spawning biomass was more important than temperature for a higher number of stocks, but the strength of the two effects, when present, was similar. Also, stocks living in colder and warmer areas showed, respectively, a positive and negative response to temperature for both families. Our results highlight that failing to account for spawning biomass effect in climate-recruitment studies could mask the influence of climate variability on recruitment dynamic. In this context, although management of several exploited fish populations cannot be entirely decoupled from the effect of climate on stock reproductive success, it is likely that the observed changes in exploited fish population dynamics are mainly the consequences of an unsustainable human impact and not climate changes.

Introduction

The physical environment has been long recognized as an essential factor in the regulation of fish population in marine ecosystems (Cushing

1982, Steele 1985). Among environmental factors, temperature is often the principal variable investigated since it regulates the rate in many ecological and physiological processes (Brett 1979). Therefore, there are strong justifications for studying the link between fish recruitment and temperature, and this information may be crucial for the management of marine resources and to predict the long-term consequence of climate changes on fisheries (Myers 1998). It is now recognized that the twenty-first century will show a significant global warming trend induced by an increase in atmospheric greenhouse effect (Houghton et al. 2001). This will also imply that a global change in the oceanic climate may propagate to the upper level of the food webs (Sarmineto et al. 1998) and consequently affect important marine resources (i.e., Loukos et al. 2003, Drinkwater 2005). Therefore, there is an increasing interest on the relation between climate and fisheries, both at the ecological and economic level (Bopp et al. 2001, Eide and Heen 2002), and evidence suggests that there is a direct link between climate and fish population dynamics (Marshall et al. 2001, Bakun and Broad 2002). In this context, life history traits might constitute a powerful means to unravel the interaction between climate and fish population. Among those, the number of recruits per unit of spawning stock biomass (SSB), i.e., the stock recruitment success (R_s), is one of the most important parameter proxies for population productivity (MacKenzie et al. 2003, Stige et al. 2006).

In this study we explored recruitment data in relation to spawning stock biomass and temperature for exploited fish stocks in the North Atlantic—57 selected demersal gadoids (cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; saithe, *Pollachius virens*; and whiting, *Merlangius merlangus*) and pelagic clupeids (herring, *Clupea harengus*; and sprat, *Sprattus sprattus*). Common patterns in life histories and population dynamics are evident only after data from several stocks, species, and areas are combined and standardized in ways that enable fair and unbiased comparisons (Myers 1998, MacKenzie et al. 2003). First, we revised available information to disentangle the effect of spawning stock biomass and temperature on R_s for the selected stocks. Successively, we investigated the potential differences in the strength and sign of these effects between families (gadoids and clupeids) and areas. We deliberately limited the analysis to SSB and temperature, although we were aware that other abiotic factors (i.e., precipitation, wind direction, currents, ice cover, etc.) and biotic factors (i.e., predation, competition, stock structure, food availability, fecundity, condition of the spawners, etc.) play an important role on recruitment processes.

Materials and methods

Time series

Stock and recruitment data

We compiled data of spawning stock biomass (*SSB*) and number of recruits (*R*) available at the International Council for the Exploration of the Sea (ICES), www.ices.dk, at the Northwest Atlantic Fisheries Organization (NAFO), www.nafo.ca, and the Ransom Myers Web site, www.msos.dal.ca/~myers/welcome.html (Table 1). For geographical distribution the reader can refer to www.ices.dk and www.nafo.ca. All estimates are derived from VPA (virtual population analysis) models and thus do not include any assumptions on the form of stock-recruitment curve.

Temperature data

The temperature data appropriate for comparisons of North Atlantic stocks should fulfill several requirements (Planque and Frédou 1999): they must be available for every stock, be consistent and sufficiently long, and correspond to large oceanic areas to be representative of the change in temperature experienced by the stock over its area of distribution. It is well known (see discussion in Ottersen et al. 1998) that environmental temperature does not strictly correspond to “ambient” temperature, although the population generally experiences higher temperature in warm years and vice versa (Planque and Frédou 1999). At the same time, it is likely that sea surface temperature (*SST*) reflects more closely ambient temperature of pelagic fish than demersal species. Anyhow, to accomplish all listed criteria, we used sea surface temperature data from the International Comprehensive Ocean Atmosphere Dataset (ICOADS) available at www.cdc.noaa.gov/coads/coads_cdc_netcdf.shtml. Monthly average at the spatial resolution of 2 degrees of latitude and 2 degrees of longitude were available for all stocks from 1800. For each stock, we calculated the annual average (*SST*) and the average temperature of the time series at the geographical centroid of the stock distribution (*SST-A*) (available at www.msos.dal.ca/~myers/welcome.html) (Table 1). The latter was used as a proxy for the mean ambient temperature occurring in the area of distribution of each stock.

Statistical analysis

To allow for stock comparisons, we chose to estimate *R* as the number of age 1 individual. For those stocks for which the numbers of age 1 individuals were not available, the logistic equation (Hilborn and Walters 1992) was applied using values of natural and fishing mortality estimated for the adjacent age class. In order to make comparable spring and autumn herring spawners, the number of 1-year-old individuals of

Table 1. List of the stocks used in this study with the stock acronyms, the fishing area as defined by ICES and NAFO, latitude and longitude corresponding to the centroid of the stock distribution, the geographical location (i.e., area, NEA = Northeast Atlantic; NWA = Northwest Atlantic), and the age of recruitment to the fisheries and the period of available data. SST-A is the average temperature experienced by the stock in the time-series, measured at the centroid of the stock distribution.

| Acronym | Fishing area | Latitude | Longitude | Area | SST-A | Age of recruits (year) | Years |
|---------|--------------|----------|-----------|------|-------|------------------------|-----------|
| CA | I&II | 68 | 15 | NEA | 7.6 | 3 | 1946-2003 |
| CEB | III d | 56 | 19 | NEA | 8.8 | 2 | 1966-2003 |
| CF | Vb | 62 | -8 | NEA | 11.0 | 2 | 1961-2003 |
| CI | Va | 63 | -21 | NEA | 8.6 | 3 | 1955-2003 |
| CK | III a | 57 | 12 | NEA | 9.0 | 1 | 1971-2003 |
| CNS | IV | 55 | 4 | NEA | 9.9 | 1 | 1963-2003 |
| CWB | III c&d | 55 | 13.5 | NEA | 8.8 | 1 | 1970-2003 |
| CVIA | VI a | 58.5 | -6 | NEA | 10.8 | 1 | 1966-2003 |
| CVIIA | VII a | 54 | -5 | NEA | 10.8 | 0 | 1968-2003 |
| CVII EK | VII e-k | 51 | -5 | NEA | 13.0 | 1 | 1971-2003 |
| HA | I&II | 68 | 15 | NEA | 7.6 | 3 | 1950-2003 |
| HF | Vb | 62 | -8 | NEA | 11.0 | 2 | 1961-2003 |
| HI | Va | 63 | -21 | NEA | 8.6 | 2 | 1981-2003 |
| HNS | IV | 55 | 4 | NEA | 9.9 | 0 | 1963-2003 |
| HVIB | Vb | 57.25 | -15 | NEA | 11.0 | 3 | 1985-2003 |
| SA | I&II | 68 | 15 | NEA | 7.6 | 3 | 1960-2003 |
| SF | Vb | 62 | -8 | NEA | 11.0 | 3 | 1961-2003 |
| SI | Va | 63 | -21 | NEA | 8.6 | 3 | 1962-2003 |
| SNS | III a&IV&VI | 55 | 4 | NEA | 9.9 | 3 | 1967-2003 |
| WNS | IV | 55 | 4 | NEA | 9.9 | 1 | 1980-2003 |
| WVIA | VI a | 58.5 | -6 | NEA | 10.8 | 1 | 1978-2003 |
| WVIIA | VII a | 54 | -5 | NEA | 10.8 | 1 | 1980-2003 |
| WVII EK | VII e-k | 51 | -5 | NEA | 13.0 | 0 | 1982-2003 |
| CESS | 4W-4Vs | 44 | -59 | NWA | 8.8 | 1 | 1958-1993 |
| CFC | 3M | 47 | -45 | NWA | 8.4 | 1 | 1972-2001 |
| CG | 1 | 59 | -44 | NWA | 5.4 | 3 | 1952-1992 |
| CGEO | 5Ze | 41 | -67 | NWA | 12.8 | 1 | 1977-1998 |
| CLAB | 2J-3KL | 50 | -52 | NWA | 4.1 | 3 | 1959-1992 |
| CNSL | 3Pn-4SR | 49 | -60 | NWA | 5.7 | 3 | 1974-1997 |
| CSGB | 3NO | 44.5 | -51.5 | NWA | 8.5 | 3 | 1956-1993 |
| CSSL | 4T-Vn | 47.5 | -63.5 | NWA | 6.2 | 3 | 1947-1993 |
| CSTP | 3Ps | 46 | -55.5 | NWA | 6.6 | 3 | 1956-1993 |

Table 1. (continued.)

| Acronym | Fishing area | Latitude | Longitude | Area | SST-A | Age of recruits (year) | Years |
|---------|------------------|----------|-----------|------|-------|------------------------|-----------|
| CWSS | 4X | 43 | -65.5 | NWA | 9.4 | 1 | 1948-1994 |
| HGEO | 5Ze | 41 | -67 | NWA | 12.8 | 1 | 1931-1998 |
| HWSS | 4X | 43 | -65.5 | NWA | 9.4 | 1 | 1970-1998 |
| SESS | 4VWX5Zc | 44 | -59 | NWA | 8.8 | 1 | 1982-2002 |
| HCB | IIIId (SDs25-29) | 57 | 21 | NEA | 8.8 | 1 | 1974-2003 |
| HCS | VIIe-j | 51 | -5 | NEA | 12.9 | 1 | 1958-2003 |
| HGR | IIIId (SD 32) | 57.3 | 23.4 | NEA | 7.9 | 1 | 1977-2003 |
| HIS | VIIaN | 54 | -4.5 | NEA | 10.8 | 1 | 1961-2003 |
| HISS | Va | 63 | -21 | NEA | 8.6 | 2 | 1981-2003 |
| HNBB | IIIId (SD 31) | 65 | 23 | NEA | 6.9 | 1 | 1980-2003 |
| HNSAS | IV&VIIId&IIIa | 58 | 2 | NEA | 9.9 | 1 | 1960-2003 |
| HNSS | II&IVa | 65 | 8 | NEA | 8.8 | 1 | 1950-2003 |
| HSBB | IIIId (SD 30) | 62 | 20 | NEA | 6.4 | 1 | 1973-2003 |
| HWBSS | IIIa&SDs 22-24 | 55 | 12 | NEA | 8.8 | 1 | 1991-2003 |
| HWI | Via(S)&VIIb-c | 54.3 | -12 | NEA | 12.1 | 1 | 1970-2003 |
| HWS | Via (N) | 57 | -9 | NEA | 11.1 | 1 | 1958-2003 |
| SBS | IIIb-d | 57 | 21 | NEA | 8.8 | 1 | 1974-2003 |
| SNS | IV | 58 | 2 | NEA | 9.9 | 1 | 1984-2003 |
| HNFBTB | 3KL | 48.25 | -52.45 | NWA | 5.5 | 2 | 1971-2002 |
| HNFBPB | 3KL | 46.4 | -54 | NWA | 6.3 | 2 | 1970-2002 |
| HNFWBNB | 3KL | 50 | -55 | NWA | 4.9 | 2 | 1971-2002 |
| HSSLAS | 4T | 47 | -63 | NWA | 6.3 | 2 | 1978-2002 |
| HSSLSS | 4T | 47 | -63 | NWA | 6.3 | 2 | 1978-2002 |
| HWNFSS | 4R | 49.25 | -59 | NWA | 5.4 | 2 | 1965-2002 |
| HWNSAS | 4R | 49.25 | -59 | NWA | 5.4 | 2 | 1965-2002 |

spring spawner stocks was negatively adjusted for a natural mortality of 0.075 per month for 2 months as in Toresen (2001).

The annual stock-specific recruitment success (R_s) was estimated for each stock and year as the natural logarithm of the ratio between R_y and SSB_{y-1} (Hilborn and Walters 1992, Beverton 2002). We are aware that SSB does not completely reflect the reproductive potential of a stock. For example, stock structure (i.e., proportion of older individuals, see Marshall et al. 1998; Cardinale and Arrhenius 2000) and/or variability in fecundity or condition of the spawners (e.g., Olsen et al. 2005, Scott et al. 2006) are not included in SSB estimation, although they are known to affect the reproductive output of the stock. However, SSB is the only estimate of the reproductive potential that is available for every stock, has a sufficiently long time series, and is consistently calculated to allow for comparisons among North Atlantic fish species.

Here we followed the procedure suggested by Cardinale and Hjelm (2006) and Stige et al. (2006). The first step is to test for and disentangle the SSB effect on R . In one of his last lectures at Woods Hole, Beverton (2002) suggested an approach for exploring this relationship. Because of the biological mechanisms behind the classical SSB - R relationships, recruitment success (R_s) should improve as SSB decreases (Fig. 1 in Cardinale and Hjelm 2006). However, if recruitment is also mediated by physical environmental events, this negative relationship may not be as obvious. For example, when the stock is declining, a negative effect of climate on R will result in a decrease in R_s ; this is reversed in the case of a positive effect of climate on R . Therefore, the variability around the relationship between R_s and SSB can be considered as a proxy for recruitment anomalies (R_a) and it is assumed to be partially determined by the stochasticity in the physical environment (Beverton 2002). However, it is worth it to emphasize that R_a can be used in climate-recruitment analysis only when a significant effect of SSB on R_s can be demonstrated. Conversely, when SSB has no significant effect on R_s , climate variables can be directly correlated to recruitment (R). It is also important to highlight that, if SSB has no effect on R_s , using R_a instead of R can actually mask any recruitment-climate relationship. The rationale behind these assumptions is mathematically formalized in the classical Ricker (1954) or Beverton and Holt (1995) recruitment functions, which are in turn based on sound ecological mechanisms (e.g., cannibalism and predation). Being that R_s is an index of recruitment scaled by SSB , the properties of R and R_s and their relationships with SSB are mathematically very different and cannot be directly compared.

The number of recruits in a fish species is generally related to egg production or SSB that is, in turn, considered a proxy of egg production (Myers and Barrowman 1996). Thus, we fitted a simple deterministic linear model:

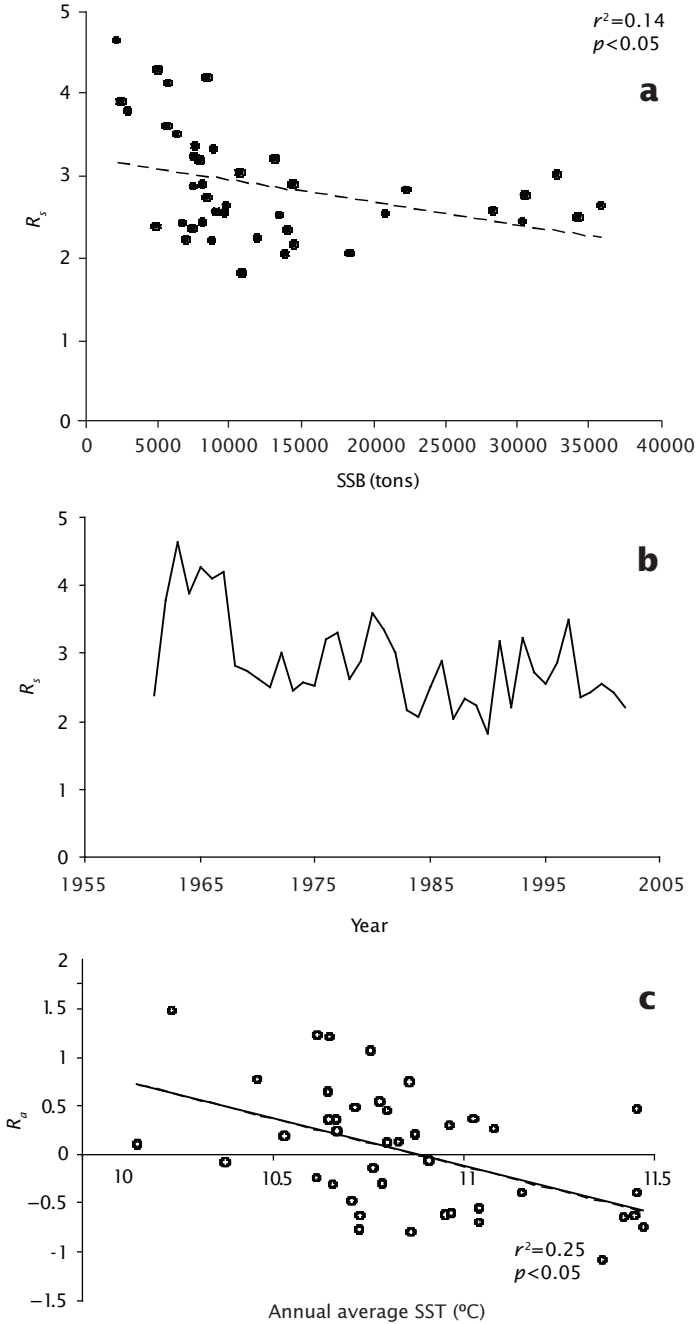


Figure 1. Example (Irish Sea herring stock) of the procedure used in the analysis. (a) relationship R_s -SSB with residuals (R_s); (b) trends in R_s over time, and (c) relationship R_s -SST.

$$R_s = \alpha - \beta \times SSB \quad (\text{Eq. 1})$$

For those stocks where the slope of β was significantly different from 0, the residuals were estimated. The residuals from Eq. 1 are defined hereafter as annual recruitment anomalies (R_a). R_a values were successively tested for correlation with annual average *SST* for each stock. For those stocks where the relationship between R_s and *SSB* was not significant, the relationships between R (in numbers of individuals) and *SST* were tested fitting a simple deterministic linear model as for Eq. 1. Trends in R_a and R are defined as recruitment dynamic thereafter. An example of the procedure described above is shown in Fig. 1 for the Irish Sea herring stock.

In our analysis we also investigated the following.

1. The proportion of stocks with an effect of *SSB* on R_s and the proportion of stocks with an effect of *SST* on R_a (or R for those stocks where an *SSB* effect was not evident). Differences between and within families were calculated using the Fisher exact test.
2. The strength (i.e., r^2 in absolute terms) of the effect of *SSB* on the R_s and of the effect of *SST* on R_a (or R for those stocks where an *SSB* effect was not evident). Differences between and within families were calculated using the Kruskal-Wallis test.

We also investigated the proportion of stocks with a positive sign in the effect of *SST* on R_a (or R for those stocks where an *SSB* effect was not evident) and the difference in the strength of the *SSB* effect compared to that of *SST* between and within families.

Finally, we plotted the r^2 of those stocks for which a significant effect of *SST* on R_a (or R for stocks where an *SSB* effect was not found) was demonstrated against the average ambient temperature in the area of distribution of each stock during the time series (*SST-A*) for gadoids and clupeids separately.

The models used do not take temporal autocorrelation into account. The level of significance was set at 5% for all the statistical tests used in this study. Statistical analysis was performed using S-PLUS (Insightful Corporation 2005) and Statistica (Statsoft Inc. 2003) computer software.

Results

There were no statistically significant differences (Fisher exact test) between families (gadoids against clupeids) in the proportion of stocks with an *SSB* effect on R_s (test 1) as well as a *SST* effect on R_a (or R depending on the stocks) (test 2; Table 2). There was also no statistical

Table 2. Results of the Fisher exact test. Between: between-family (gadoids and clupeids) differences in the proportion of stocks with an effect of SSB on R_s (test 1), in the proportion of stocks with an effect of SST on R_a (or R) (test 2), and in the sign of the effect of SST on R_a (or R) (test 3). Within: within-family (gadoids and clupeids) differences in the proportion of stocks with an effect of SSB on R_s compared to the effect of SST on R_a (or R) (tests 4 and 5). All stocks: differences in the proportion of stocks with an effect of SSB on R_s compared to the effect of SST on R_a (or R) (test 6); p is the significance value of the tests and n the number of stocks used in the analysis.

| | | Fisher test | | | | |
|--------------|---|-------------|----------|------------------|-----|------|
| Variable | | Gadoids | Clupeids | p | n | Test |
| Between | Proportion of stock with an effect of SSB on R_s | 61% | 76% | 0.27 | 38 | 1 |
| | Proportion of stock with an effect of SST on R_a (or R) | 31% | 29% | 0.87 | 17 | 2 |
| | Proportion of stocks with a positive effect of SST on R_a (or R) | 36% | 67% | 0.24 | 17 | 3 |
| | | SSB | SST | | | |
| Within | Gadoids Proportion of stocks with SSB compared to SST effect | 61% | 31% | <0.01 | 33 | 4 |
| | Clupeids " | 76% | 29% | <0.001 | 22 | 5 |
| All stocks " | | 69% | 31% | <0.001 | 55 | 6 |

difference between families concerning the sign of SST effect on R_a (or R depending on the stocks) (test 3).

On the other hand, there was a statistical difference in the proportion of stocks with an SSB effect on R_s compared to those with an SST effect on R_a (or R) for both gadoids and clupeids (tests 4 and 5) with a statistically larger proportion of stocks with a SSB effect on R_s (tests 4-6; Table 2).

There was no difference (Kruskall-Wallis test) concerning the strength of the SSB effect on R_s (test 7) and SST effect on R_a (or R depending on the stocks) (test 8) between families (Table 3). On the other hand, there was a statistical difference in the strength of the SSB effect compared to the SST effect for gadoids (test 9) and for all stocks combined (test 11), while the same was not found for clupeids (test 10; Table 3).

We plotted the r^2 of the SST effect on R_a (or R) against the average temperature in the area of distribution of each stock during the time series ($SST-A$) (see Table 1). Only those stocks where a significant effect of SST on recruitment dynamic was found were used (see Table 4). The

Table 3. Results of the Kruskal-Wallis test. Between: between-family (gadoids and clupeids) difference in the strength (r^2) of the effect of *SSB* on R_s (test 7) and in the strength of the effect of *SST* on R_a (or R) (test 8). Within: within-family (gadoids and clupeids) differences in the strength of the effect of *SSB* on R_s compared to the strength of the effect of *SST* on R_a (or R) (test 9 and 10). All stocks: differences in the strength of the effect of *SSB* on R_s compared to the strength of the effect of *SST* on R_a (or R) (test 11). The strength of the relationships is shown as median of r^2 ; p is the significance value of the tests and n the number of stocks used in the analysis.

| | | Kruskal-Wallis test | | | | | |
|---------|---|--|------------|------|-----------------|------|----|
| Between | Strength [r^2] | Gadoids | Clupeids | p | n | Test | |
| | | Effect of <i>SSB</i> on R_s | 0.31 | 0.33 | 0.89 | 38 | 7 |
| | Effect of <i>SST</i> on R_a (or R) | 0.16 | 0.26 | 0.61 | 17 | 8 | |
| | | <i>SSB</i> | <i>SST</i> | | | | |
| Within | Gadoids | <i>SSB</i> compared to <i>SST</i> effect | 0.31 | 0.16 | <0.01 | 33 | 9 |
| | Clupeids | " | 0.33 | 0.26 | 0.25 | 22 | 10 |
| | All stocks | " | 0.32 | 0.19 | <0.01 | 55 | 11 |

analysis showed that stocks living in colder areas present a positive effect of *SST* on R_a (or R), and vice versa, for both families (Fig. 2).

Discussion

Recruitment (R) is considered generally related to egg numbers or stock spawning biomass (*SSB*) (a proxy for egg numbers) (Myers and Barrowman 1996) and this was confirmed in our study by the fact that a significant effect of *SSB* on recruitment success (R_s) was evident for 67% of all stocks analyzed. This again highlights that failing to account for the *SSB* effect in climate-recruitment studies could mask the influence of climate variability on recruitment dynamic (Myers 1998, Cardinale and Hjelm 2006). Therefore, our approach, as advocated by Beverton (2002) and previously used by Cardinale and Hjelm (2006) and Stige et al. (2006), is able to unravel stock productivity and climate by using the deviation from the theoretical relation between *SSB* and R_s . During the last decade, most of the published papers on meta-analysis of fish and climate (for instance, see ICES Journal of Marine Science 58(5) and 62(7) and references herein) have used some climate proxy to explain observed variability in R or R_s without exploring and disentangling the effect of adult biomass on recruitment. This makes difficult a comparison between previous studies and our analysis (see Cardinale and Hjelm 2006 for a useful discussion). Also, R_s and recruitment is not the same

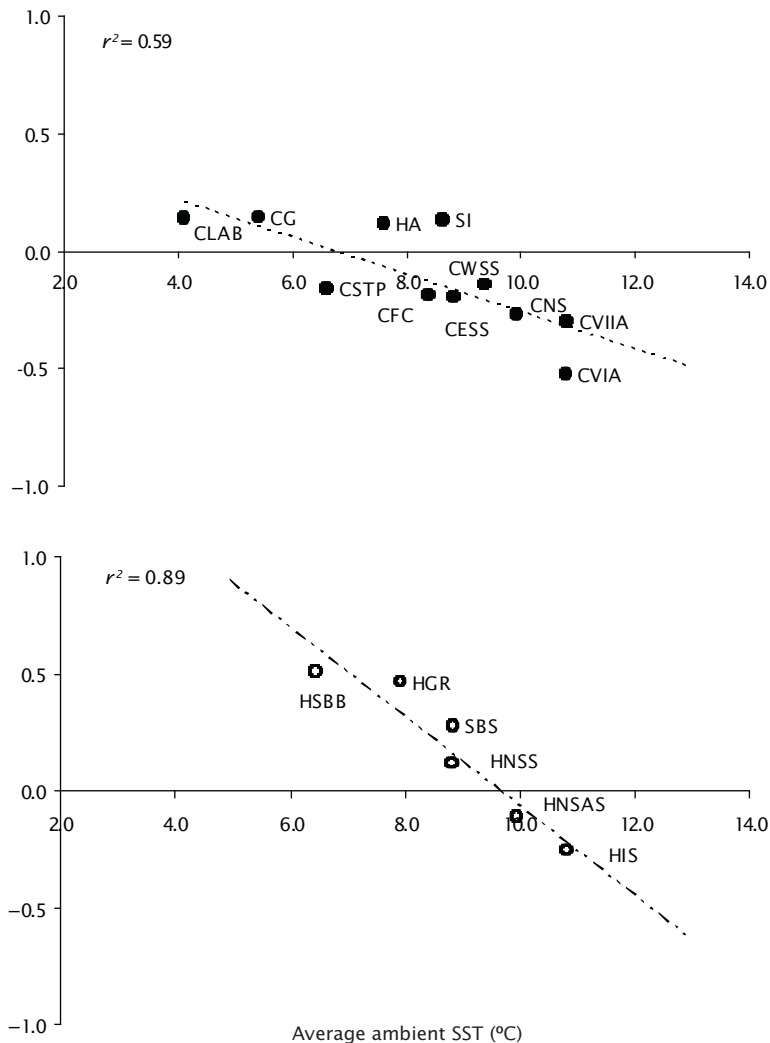


Figure 2. Relationships (both significant at $p < 0.01$) between the average SST experienced by the stock in its area of distribution during the time series and the correlation coefficient (r^2) of the SST effect on R_a (or recruitment depending on the stock) for gadoids (a) and clupeids (b). Only stocks where the relationship between SST and R_a (or recruitment depending on the stock) was statistically significant were used in the analysis.

Table 4. Results of linear regression analysis between R_s and SSB; between the residuals of the R_s -SSB regression (i.e., recruitment anomalies, R_a) and SST; and between R and SST for all stocks analyzed. ns = not significant relationship. The sign in front of r^2 indicate whether the relationship is negative or positive.

| Stock | $R_s \sim \text{SSB}$ | | $R_s \sim \text{SST}$ | | $R \sim \text{SST}$ | |
|--------------------------------|-----------------------|-------|-----------------------|-------|---------------------|------|
| | r^2 | p | r^2 | p | r^2 | p |
| Northeast arctic cod | -0.26 | <0.01 | 0.05 | ns | - | - |
| Eastern Baltic cod | -0.18 | <0.01 | -0.023716 | ns | - | - |
| Faroe cod | -0.42 | <0.01 | -0.047089 | ns | - | - |
| Iceland cod | -0.48 | <0.01 | 0.01 | ns | - | - |
| Kattegat cod | -0.09 | ns | - | - | 0.01 | ns |
| North Sea cod | -0.1 | <0.05 | -0.269361 | <0.01 | - | - |
| Western Baltic cod | -0.06 | ns | - | - | -0.031329 | ns |
| Scotland cod | -0.28 | <0.01 | -0.521284 | <0.01 | - | - |
| Irish cod | -0.2 | <0.01 | -0.297025 | <0.01 | - | - |
| Celtic cod | -0.01 | ns | - | - | -0.082369 | ns |
| Northeast arctic haddock | -0.01 | ns | - | - | 0.12 | 0.02 |
| Faroe haddock | -0.21 | <0.01 | -0.054756 | ns | - | - |
| Iceland haddock | -0.12 | ns | - | - | 0.09 | ns |
| North Sea haddock | -0.13 | <0.05 | -0.01 | ns | - | - |
| Northeast arctic saithe | -0.52 | <0.01 | -0.01 | ns | - | - |
| Rockall haddock | -0.25 | <0.05 | -0.083521 | ns | - | - |
| Faroe saithe | -0.45 | <0.01 | -0.01 | ns | - | - |
| Iceland saithe | -0.3 | <0.01 | 0.13 | 0.02 | - | - |
| North Sea saithe | -0.49 | <0.01 | 0.08 | ns | - | - |
| North Sea whiting | -0.29 | <0.01 | -0.04 | ns | - | - |
| Scotland whiting | -0.44 | <0.01 | -0.01 | ns | - | - |
| Irish whiting | -0.66 | <0.01 | -0.01 | ns | - | - |
| Celtic whiting | -0.46 | <0.01 | -0.01 | ns | - | - |
| Eastern Scotian Shelf cod | -0.41 | <0.01 | -0.192721 | <0.01 | - | - |
| Flemish Cap cod | -0.11 | ns | - | - | -0.186624 | 0.02 |
| Greenland cod | -0.01 | ns | - | - | 0.15 | 0.02 |
| Georges Bank cod | -0.09 | ns | - | - | 0.01 | ns |
| Labrador Grand Bank cod | -0.02 | ns | - | - | 0.14 | 0.04 |
| North Gulf of St. Lawrence cod | -0.01 | ns | - | - | 0.08 | ns |
| Southern Grand Bank cod | -0.01 | ns | - | - | -0.016129 | ns |
| South Gulf of St. Lawrence cod | -0.35 | <0.01 | -0.03 | ns | - | - |

Table 4. (continued.)

| Stock | $R_s \sim SSB$ | | $R_s \sim SST$ | | $R \sim SST$ | |
|---|----------------|--------|----------------|--------|--------------|--------|
| | r^2 | p | r^2 | p | r^2 | p |
| St. Pierre Bank cod | -0.31 | <0.01 | -0.16 | 0.02 | - | - |
| Western Scotian Shelf cod | -0.28 | <0.01 | -0.142129 | <0.01 | - | - |
| Georges Bank haddock | -0.01 | ns | - | - | 0.01 | ns |
| Western Scotian Shelf Haddock | -0.02 | ns | - | - | 0.08 | ns |
| Eastern Scotian Shelf Saithe | -0.2 | ns | - | - | 0.13 | ns |
| Central Baltic herring | -0.31 | 0.001 | 0.03 | ns | - | - |
| Celtic Sea herring | -0.15 | <0.001 | 0.10 | ns | - | - |
| Gulf of Riga herring | -0.01 | ns | - | - | 0.47 | <0.001 |
| Irish Sea herring | -0.14 | 0.015 | -0.25 | <0.001 | - | - |
| Iceland summer spawning herring | -0.1 | ns | - | - | 0.06 | ns |
| Northern Bothnian herring (SD 31) | -0.33 | 0.003 | 0.01 | ns | - | - |
| North Sea autumn spawners herring | -0.41 | <0.001 | -0.11 | 0.03 | - | - |
| Norwegian spring spawning herring | -0.11 | 0.001 | 0.12 | 0.01 | - | - |
| Southern Bothnian herring (SD 30) | -0.01 | ns | - | - | 0.51 | 0.002 |
| Western Baltic spring spawners herring | -0.62 | 0.001 | 0.08 | ns | - | - |
| West of Ireland herring | -0.35 | <0.001 | 0.04 | ns | - | - |
| Herring west of Scotland | -0.2 | 0.002 | 0.02 | ns | - | - |
| Baltic Sea sprat | -0.1 | ns | - | - | 0.28 | 0.003 |
| North Sea sprat | -0.08 | ns | - | - | 0.007 | ns |
| Newfoundland herring Bonavista Bay & Trinity Bay | -0.59 | <0.001 | 0.04 | ns | - | - |
| Newfoundland herring St. Mary's Bay & Placentia Bay | -0.33 | 0.001 | 0.01 | ns | - | - |
| Newfoundland herring White Bay & Notre Dame Bay | -0.3 | 0.002 | 0.06 | ns | - | - |
| South Gulf of St Lawrence herring autumn spawners | -0.67 | <0.001 | 0.01 | ns | - | - |
| South Gulf of St Lawrence herring spring spawners | -0.64 | <0.001 | 0.06 | ns | - | - |

Table 4. (continued.)

| Stock | $R_s \sim SSB$ | | $R_s \sim SST$ | | $R \sim SST$ | |
|--|----------------|--------|----------------|-----|--------------|-----|
| | r^2 | p | r^2 | p | r^2 | p |
| West coast of Newfoundland herring spring spawners | -0.29 | 0.001 | 0.05 | ns | - | - |
| West coast of Newfoundland herring autumn spawners | -0.49 | <0.001 | 0.08 | ns | - | - |

thing. Recruitment success is in a linearized form and therefore, in this different numerical context, properties of R and R_s against SSB are mathematical very different and cannot be comparable. Thus, a lack of relationship between R_s and SSB does not contradict the fact that a significant relationship has been found for the same stock in other studies using R in absolute numbers (i.e., Rätz and Lloret 2005). Nevertheless, it is also important to stress that part of the observed variability around the relationship between SSB and R_s might be dependent on other factors, as structure of the stock (i.e., maternal effect; Marshall et al. 1998), changes in fecundity and conditions of the spawners (Olsen et al. 2005, Scott et al. 2006) and Allee effect (Frank and Brickman 2000), although the investigation of these factors was beyond the scope of the paper.

The historical dynamic of fish stocks is usually related to both natural external factors and anthropogenic influences, among which fishery is generally considered the most important (Myers and Worm 2003). For instance, the high fishing mortality in coincidence of a period of poor recruitment may explain the rapid decline in several herring commercial stocks during the 1960s (Toresen and Oestvedt 2000, Toresen 2001). A similar trend has been observed for some cod stocks in the Northwest Atlantic, with a rapid decline of the populations in coincidence with the development of fisheries techniques intertwined with unfavorable condition for survival of juvenile cod (Drinkwater 2003). A classical explanation is that the coincidence of those two factors accelerated the declining process (Fiksen and Slotte 2002; Toresen 2001). Here we show that the proportion of stocks with a significant SSB effect on R_s was significantly larger than the proportion of stocks with a significant SST effect on R_a (or R) for both gadoids and clupeids. Moreover, for gadoids, the strength of the relationships $SSB-R_s$ was significantly higher than the strength $SST-R_a$ (or R). Results as shown here underline that although the effect of temperature on recruitment dynamic is significant for some stocks spawning biomass has generally a much larger impact than climate on the recruitment dynamic of North Atlantic fish.

There were no significant differences between demersal gadoids and pelagic clupeids concerning the sign of the effect of *SST* on R_a (or R), although a difference was evident (36% against 67% stocks with a positive effect of *SST*). The lack of significance is possibly due to the low numbers of stocks where a *SST* effect was found and thus the low sample size used in the Fisher test. Anyhow, a clear relationship was found between the sign of the effect of the *SST* on R_a (or R) and the average temperature in the distribution area of the stocks, with stocks living in colder areas responding positively to increasing temperature, and vice versa, for both families. Gadoids showed an average ideal *SST* around 7-8°C for optimal R_s , whereas for clupeid this value was around 9-10°C. Those results are generally in accordance with other studies for cod (Planque and Frédou 1999, Rätz and Lloret 2005, Drinkwater 2005) (i.e., variation in R with temperature for cod stocks at the border of the species distribution), while the same pattern has never been demonstrated for clupeids. Interestingly, the relationship is much stronger for clupeids compared to gadoids. This might be explained by the existence of a stronger coupling between temperature and recruitment for pelagic fishes, but it could also be due to the fact that *SST* reflects more closely the ambient temperature experienced by the pelagic stocks.

Conclusions

It has been argued that resilience to climate changes in unexploited populations is significantly larger than in highly exploited or overfished stocks (Brander 2005). Nevertheless, we showed that spawning biomass play the fundamental role in the regulation of the dynamic of fish stocks. Therefore, although management of exploited fish populations cannot be decoupled from the effect of temperature on their reproductive success, it is likely that the observed shifts in exploited fish communities are mainly the consequences of an unsustainable fishing mortality (Pauly et al. 1997, Myers and Worm 2003, Hutchings 2004) and not of a climate changes.

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Temperature Effects on Recovery of Pacific Cod Following Exhaustive Exercise

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Abstract

We examined post-exhaustive exercise recovery in Pacific cod acclimated to either 2°C or 7°C. We collected blood samples prior to an exhaustive swimming protocol, immediately after and up to four hours of recovery. Plasma concentrations of cortisol, glucose, lactate, Na⁺, and Cl⁻ were determined. Concentrations of cortisol, glucose, and lactate significantly increased post-swim as compared to samples collected pre-swim irrespective of temperature treatment. For either temperature treatment, sample concentrations of cortisol, glucose, and lactate of cod remained elevated and did not return to pre-swim levels after four hours of recovery.

Introduction

Swimming performance is a critical aspect of the natural history of fish because it relates to migration, predator avoidance, and prey capture

(Beamish 1978) and many studies have sought to examine swimming performance in fishes, such as coho (*Oncorhynchus kisutch*, Davis et al. 1963, Lee et al. 2003), chinook (*Oncorhynchus tshawytscha*, Davis et al. 1963, Lee et al. 2003), and sockeye salmon (*Oncorhynchus nerka*, Brett 1964, Farrell et al. 1998), Atlantic cod (*Gadus morhua*, Nelson et al. 1996, Martinez et al. 2004, Herbert and Steffensen 2005), and cutthroat trout (*Oncorhynchus clarki clarki*, MacNutt et al. 2004). A number of metrics of performance can be assessed using swim trials including sprint speed, rate of acceleration, and endurance swimming (see review by Wood 1991). Critical swimming speed (U_{crit}) is an accepted evaluation of prolonged swimming performance (Beamish 1978) and has been used widely to determine the effects of environmental change on the physiological performance of fish (Farrell et al. 1998, Lee et al. 2003, MacNutt et al. 2004). In general, swim trials used to assess U_{crit} force a fish to swim in a flume against an increasing current for pre-set durations until it can no longer maintain its position in the flume. Additionally, repeated determination of U_{crit} has been used to assess the general health or condition of a fish (Jain et al. 1998, Farrell et al. 1998). In repeat swim trials, fish are forced to swim to exhaustion (U_{crit1}), allowed to rest for a specified period of time, and then forced to swim to exhaustion again (U_{crit2}). A reduced U_{crit2} suggests that the fish did not have sufficient time to recover from the initial exercise. The ability to recover from exhaustion can have profound impacts on fish in the wild and may limit subsequent swimming performance (Milligan 1996), impact survival, and ultimately affect fitness.

Fish exposed to exhaustive exercise in the laboratory exhibit increased concentrations of lactate in plasma and white muscle, decreased glycogen reserves in white muscle and a disturbance of osmotic balance (Wood 1991). Lactate from the tissue moves into the blood, although peak levels in the blood may not be reached until 2 hours after exhaustion (Milligan 1996). Recovery from exhaustion involves the replenishment of tissue glycogen reserves, decrease of lactate concentrations, and the normalization of tissue pH to pre-exercise values (Milligan and Wood 1986, Wang et al. 1994). Although recovery times differ among species and studies, an exhausted fish will generally clear lactate to pre-swim levels within 12 hours (Kieffer 2000) and will recover glycogen reserves within 24 hours (Milligan and Wood 1986). However, there is increasing evidence that glycogen replenishment and lactate removal post-exercise are inhibited by increased cortisol concentrations in the blood due to the exercise trial (see review by Milligan 1996).

Metabolic recovery rate is influenced by temperature (Galloway and Kieffer 2003), but the specific relationship is not always clear. In Atlantic salmon (*Salmo salar*), rates of glycogen synthesis, lactate catabolism, and restoration of pH balance following exhaustive exercise were higher

for fish acclimated at warm (18-23°C) compared to cool temperature (12°C) (Wilkie et al. 1997). However, Kieffer et al. (1994) found that rainbow trout (*Oncorhynchus mykiss*) acclimated to a higher temperature (18°C) had similar glycogen and lactate recovery times compared to fish acclimated to a lower temperature (5°C). These contrasting findings illustrate the need for further investigation into the effects of acclimation temperature on metabolic recovery post-exercise.

In a previous experiment we found that Pacific cod (*Gadus macrocephalus*), acclimated to two different temperatures (4°C and 11°C), showed no significant difference between U_{crit1} and U_{crit2} when swum to exhaustion twice with a one hour rest period in between swims (Hanna 2006) suggesting that one hour was an ample period for fish to recover between swim trials. Whereas analyses of survey catch data indicate that Pacific cod preferentially inhabit waters slightly above 7°C (Perry et al. 1994), Paul et al. (1988) examined oxygen consumption rates of Pacific cod held at different temperatures and found differences in fish held between 3.5°C and 7°C but no differences in fish held between 7°C and 12°C. This suggests that these fish can acclimate to maintain metabolic rate between 7°C and 12°C but adjust their metabolic rate at temperatures between 3.5°C and 7°C. We set out to determine temperature effects on rates of metabolic recovery of wild-caught Pacific cod held at 2°C and 7°C. To assess metabolic recovery we collected blood samples both before and after swim trials and after two and four hours of recovery. Samples were analyzed for hematocrit and plasma concentrations of cortisol, lactate, glucose, total protein, Na^+ , and Cl^- . Because Pacific cod swum at different temperatures did not differ in their U_{crit1} and U_{crit2} , we hypothesized that they would not differ in their rates of recovery.

Materials and methods

In June 2005, we captured adult Pacific cod (weight, 0.9-3.6 kg; total length, 44-68 cm) near Kodiak Island with pots (145 × 130 × 70 cm) at a depth of approximately 20 m and transported them back to the Kodiak Fisheries Research Center wet lab facilities. We measured each fish for total length (± 1.0 cm), weight (± 0.01 kg), and width and height (just posterior to the pectoral fins; ± 0.1 mm). Each fish was marked using a unique number coded tag (T-bar tag FD-68B, Floy Tag®, Seattle, WA) prior to being placed into one of two 6 m³ tanks supplied with sand filtered seawater drawn from Trident Basin at a depth of 25 m.

In November 2005, two weeks before the initiation of swim trials, six male and eight female fish were placed into a single tank maintained at 2°C and five males and three females were placed into another tank maintained at 7°C. All fish were fed Pacific herring (*Clupea pallasii*) to satiation every three days.

After the two week acclimation period, we captured each fish from the tanks using a low abrasion dipnet and immersed them in a 30 L solution of anesthetic (tricaine methansulfonate; 100 ppm) for up to two minutes. Once each fish was anesthetized, we placed it on a V-board and collected 0.5 ml of blood from the caudal vasculature using a 21-gauge needle and 3 ml syringe. We again measured fish for total length, standard length, width, height, and weight as described above. We then placed the fish back into their respective tanks for an average of 27 days prior to swim trials.

We placed individual blood samples into labeled vials coated with an anticoagulant, ammonium heparin, for the preparation of plasma samples. We determined hematocrit of each sample in duplicate by drawing blood into micro-hematocrit capillary tubes (Fisherbrand®, Pittsburgh, PA) followed by centrifugation in a micro-hematocrit centrifuge (Unico®, Dayton, NJ) at 12,000 RPM for 10 minutes. The remainder of the blood sample was separated via centrifugation (2,500 rpm for 15 minutes, Fisherbrand® accuSpin™ Micro R) ≤ 30 min after collection. We drew off plasma using a Pasteur pipette and placed it into a labeled vial, which was stored at -50°C for later analysis.

Immediately preceding each swim trial, fish were fasted for either four days (high temperature group) or five days (low temperature group) to minimize the effect of digestion and assimilation on metabolism (Paul et al. 1988). We captured fish from tanks using a low abrasion dipnet and placed them into a 370 L Brett-type swim flume maintained at the acclimation temperature of the fish. The swimming section of the flume was constructed of Lexan® and measured 1.87 m long with a diameter of 20 cm. Measures of total length, width, and height were used to calculate solid blocking effect of individual fish in the swim flume (Bell and Terhune 1970). Before the actual swim trial, we trained fish through exposure to stepwise increases in water velocity until the fish could no longer swim away from the back of the flume. We then allowed the fish to acclimate to 0.5 BL s^{-1} for 36 hr and then performed two U_{crit} trials with a 1 hr rest period in between trials. During each U_{crit} trial we increased water velocity 0.1 BL s^{-1} every 30 min until the fish failed to swim away from the back of the flume. Immediately after determination of the second U_{crit} , we removed the fish from the swim flume and collected a blood sample (as above) and placed the fish back into its respective tank but separated from the other fish via netting. We allowed the fish to recover for either two or four hours. Half of the fish in each temperature group (seven low temperature and four high temperature fish) were allowed a two hour recovery and the other half were allowed a four hour recovery. A slow, circular current ($<0.5 \text{ BL s}^{-1}$) was maintained in the tanks allowing the fish to swim during the recovery period. After the recovery period, we removed the fish and killed it with a sharp blow to the head. We obtained a 1 ml blood sample and weighed and measured the fish for standard morphometrics (as above).

We assayed plasma for concentrations of glucose, lactate, and protein using enzymatic assay kits (Glucose: Wako Pure Chemical Industries, Richmond, VA.; Lactate: Trinity Biotech, St. Louis, MO.; Protein: Pierce, Rockford, IL) according to manufacturers protocols adapted for use in 96-well microplates. A SPECTRAmax[®] microplate spectrophotometer and SOFTmax[®] PRO software (Molecular Devices, Sunnyvale, CA) were used. We assayed samples in triplicate to determine a mean optical density. A standard curve of optical density to concentration of each constituent was created.

We determined plasma Na⁺ and Cl⁻ concentrations using a Medica EasyElectrolytes ion meter (Medica Corporation, Bedford, MA). We diluted samples with deionized water in the ratio 11:5 to fit plasma concentrations into the working range of the instrument. We assayed all samples in duplicate. The mean intra-assay variation was 0.2% determined by running a control every 15 samples.

Concentrations of plasma cortisol were determined using radioimmunoassay techniques originally described by Foster and Dunn (1974) and further modified by Redding et al. (1984) and verified for Pacific cod (courtesy of G. Feist, Oregon State University). Samples were assayed in duplicate.

We determined differences in blood parameters over time (pre-swim to recovery) and between temperatures using two-way repeated measures analysis of variance. Separate tests were performed for the two hour recovery group and the four hour recovery group. Multiple comparisons were made using the Holm-Sidak method. A *t*-test was used to test for differences in U_{crit1} between temperature groups and paired *t*-tests were used to determine differences between U_{crit1} and U_{crit2} . All tests were performed at $\alpha = 0.05$. Data are presented as mean \pm standard error of measure. SigmaStat 3.0 statistical software (Systat Software, Inc., Richmond, CA) was used for all statistical analyses.

Results

The mean U_{crit1} for low (0.97 ± 0.03 BL s⁻¹) and high (0.99 ± 0.04 BL s⁻¹) temperature acclimated Pacific cod was not significantly different between groups ($P = 0.772$). U_{crit2} was significantly lower than U_{crit1} in the low temperature group (0.94 ± 0.03 BL s⁻¹, $P = 0.022$) but not in the high temperature group (0.96 ± 0.05 BL s⁻¹, $P = 0.093$).

Plasma cortisol concentrations increased significantly from pre- to post-swim in fish held at both temperature treatments at both sampling schedules (2 hr: $P < 0.001$; 4 hr: $P < 0.001$; Fig. 1). Concentrations of cortisol did not significantly differ between temperature treatments in either the two hour ($P = 0.907$) or four hour ($P = 0.925$) sampling intervals nor did they differ between fish sampled immediately post-swim and either samples collected two hours (low temperature: $P = 0.813$,

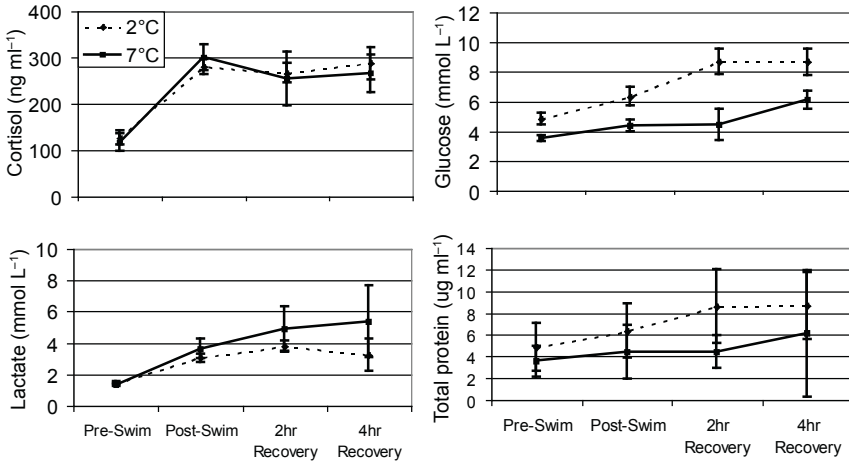


Figure 1. Interrelationships among swim state, acclimation, temperature, and circulating levels of blood constituents \pm SE for Pacific cod acclimated to 2°C (14 fish) and 7°C (8 fish). Blood samples were taken pre-swim, immediately post-swim, and at 2 and 4 hr of recovery post-exhaustion.

high temperature: $P = 0.260$) or four hours (low temperature: $P = 0.496$, high temperature: $P = 0.460$) after swimming in either temperature treatment. The intra-assay variation was $<5\%$ and the inter-assay variation was $<10\%$.

Likewise, concentrations of plasma lactate increased significantly from pre- to post-swim in both the high and low temperature acclimated fish (2 hr: $P < 0.001$; 4 hr: $P < 0.001$) but did not differ between temperature treatments at two hours ($P = 0.249$) or four hours ($P = 0.233$) after the swim test (Fig. 1). Plasma lactate concentrations remained elevated in both temperature groups during recovery and were not significantly different from samples collected immediately post-swim after two hours (low temperature: $P = 0.629$, high temperature: $P = 0.330$) or four hours (low temperature: $P = 0.660$, high temperature: $P = 0.907$). Plasma protein concentrations did not significantly differ between temperature groups for fish sampled at two hours ($P = 0.517$) and four hours ($P = 0.426$) after the swim test, nor was there any difference in plasma protein concentrations over time (2 hr: $P = 0.108$; 4 hr: $P = 0.939$; Fig. 1). Plasma glucose concentrations increased significantly from pre- to post-swim and further increased during recovery in both the two hour ($P = 0.006$) and four hour ($P < 0.001$) recovery groups (Fig. 1). Concentrations of plasma glucose were consistently higher in the low temperature group

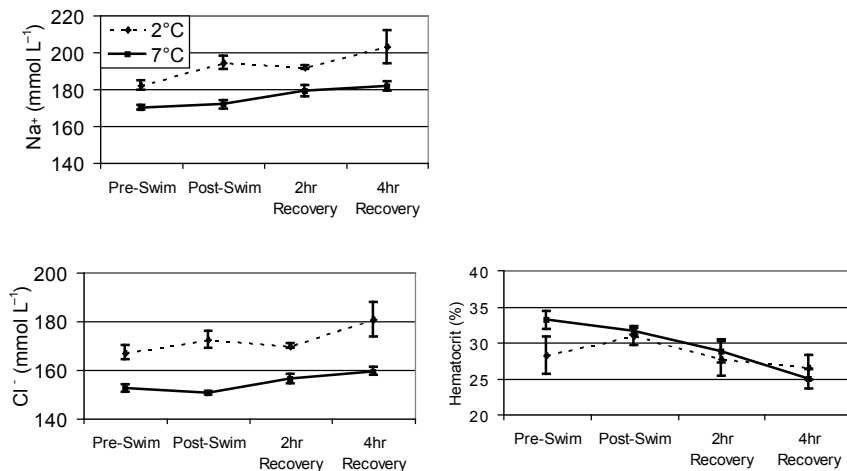


Figure 2. Interrelationships among swim state, acclimation temperature, and circulating levels of blood constituents \pm SE for Pacific cod acclimated to 2°C (14 fish) and 7°C (8 fish). Blood samples were taken pre-swim, immediately post-swim, and at 2 and 4 hr of recovery post-exhaustion. Significant interactions existed between temperature and time for plasma Na⁺ concentrations and hematocrits in the 2 hr recovery group and for plasma Cl⁻ concentrations in the 4 hr recovery group.

than the high temperature group at both two and four hours post-swim. Glucose concentrations were significantly different between temperature groups in the two hour recovery group ($P = 0.008$) but not in the four hour ($P = 0.107$) recovery group. The mean intra-assay variation for the glucose, lactate, and protein assays were <4% and the mean inter-assay variations were <10%.

A statistically significant interaction existed between temperature and time for plasma Na⁺ concentrations in the two hour recovery group ($P = 0.023$). Plasma Na⁺ concentrations increased in both temperature groups in the four hour recovery group from pre- to post-swim and during recovery ($P < 0.001$, Fig. 2). Plasma Cl⁻ concentrations were consistently higher in the low temperature group than the high temperature group but only significantly higher in the two hour recovery group ($P < 0.001$). A statistically significant interaction existed between temperature and time for plasma Cl⁻ concentrations in the four hour recovery group ($P = 0.011$). Cl⁻ concentrations significantly increased from pre- to post-swim and during recovery in the two hour recovery group ($P = 0.023$).

A statistically significant interaction existed between temperature and time for hematocrit in the two hour recovery group ($P = 0.022$) and did not significantly differ between temperature groups in the four hour recovery group ($P = 0.836$). Additionally, hematocrit values significantly decreased from pre-swim to recovery in the four hour recovery group ($P = 0.020$).

Discussion

Pacific cod acclimated to 2°C and 7°C and exercised to exhaustion exhibited marked physiological disturbances as evidenced by plasma cortisol, glucose, lactate, and ions. These constituents remained elevated up to four hours post exhaustion and showed no signs of returning to pre-swim values in either temperature group. Based on these data we concluded that the temperatures utilized in this experiment have no significant effect on short term recovery following exhaustive exercise in Pacific cod and are consistent with previous studies we have conducted that indicate no significant difference in U_{crit1} and U_{crit2} between temperature treatments (Hanna 2006).

Although physiological recovery was incomplete four hours after exhaustion, it is interesting to note that swimming performance decreased only slightly during the second swim. With only a one hour rest period between swim trials, fish were able to perform almost as well as during the first swim with only a slight decrease in the low temperature group. Similar results were found in juvenile rainbow trout in which fish maintained swimming performance after only a 45 minute recovery period (MacFarlane and McDonald 2002). Therefore, it seems that complete physiological recovery is not necessary to maintain swimming performance in this species based on this particular test of performance.

Also consistent with our results, rainbow trout exhibit increased concentrations of plasma glucose post-exercise and during recovery and remained elevated four hours after exhaustion (Milligan and Wood 1986, Wood et al. 1990). Additionally, glucose concentrations in this study are similar to those for Atlantic cod in which pre-swim plasma glucose was between 4 and 7 mmol L⁻¹ and after four hours of recovery was between 8 and 10 mmol L⁻¹ (Nelson et al. 1996). Glucose concentrations increase in stressed fish due to combined effects of glycogenolysis and gluconeogenesis (Wendelaar Bonga 1997) and may be mediated by increases in plasma cortisol. Cortisol aids in the mobilization of energy stores and stimulates release and synthesis of glucose (see review by Mommsen et al. 1999) and can result in increased concentrations of plasma glucose. However, the differences in glucose concentrations between temperature groups found in this study are not consistent with a previous study on Pacific cod (Hanna 2006) and are only significant within the two hour

recovery group and not the four hour recovery group. This may be indicative of higher rates of glycogenolysis/gluconeogenesis in the low temperature acclimated fish or a reduced usage of glucose in these fish compared to high temperature acclimated fish. Similar differences in plasma Cl⁻ concentrations between temperature groups combined with differences in plasma glucose concentrations suggest low temperature acclimated fish may be more stressed than the higher temperature acclimated fish.

High concentrations of plasma cortisol pre-swim suggest that both temperature groups were stressed prior to the swim trials. The stress may have been due to the acclimation temperatures or simply captivity. In a previous experiment we found that Pacific cod acclimated to 4°C had higher plasma cortisol concentrations than those acclimated to 11°C (Hanna 2006). However, Pacific cod are known to inhabit waters slightly above 7°C (Perry et al. 1994). Therefore, we might expect the 2°C fish to be stressed from the low temperatures but not the 7°C fish. Although these increased levels of cortisol may not have affected swimming performance (Gregory and Wood 1999), the role of cortisol in slowing the recovery process is well known (Milligan 1996) and therefore may have inhibited recovery in these fish.

Cortisol, lactate, glucose, and ion concentrations did not return to resting levels after four hours of recovery in this study. Cortisol plays a key role by slowing the recovery process through influences on lactate metabolism and glycogen resynthesis (see review by Milligan 1996). When cortisol synthesis is blocked, rates of lactate clearance and glycogen resynthesis are increased (Pagnotta et al. 1994). Cortisol levels may remain elevated for several hours (see review by Milligan 1996) or days to weeks (Haukenes and Buck 2006) following exposure to a stressor. Cortisol does not increase in rainbow trout that are allowed to swim at low velocity after exhaustive exercise and thus lactate is cleared within two hours of recovery (Milligan et al. 2000). This suggests that either the fish in this study may not have been swimming fast enough to limit cortisol accumulation and thus metabolic recovery may have been delayed or that increased rates of clearance or inhibition of synthesis of cortisol due to exercise during the recovery period is not manifested in Pacific cod as in rainbow trout. It would also be interesting to examine the effects of high concentrations of cortisol on tissue glycogen and lactate recovery in Pacific cod. However, due to our location on Kodiak Island, we did not have access to liquid nitrogen for freeze clamping and so were unable to properly collect muscle samples from fish.

Plasma Cl⁻ and Na⁺ concentrations were consistently higher in the low temperature fish than in high temperature fish throughout the experiment indicating greater osmoregulatory disturbance in the low temperature fish (Redding and Schreck 1983). Fish in the low temperature group were not able to ionoregulate as well as their high tempera-

ture counterparts possibly due to the stress associated with the lower temperatures. Redding and Schreck (1983) also indicate decreases in hematocrit associated with stress; yet, this effect was not observed in our study. The increases in plasma lactate and glucose in association with exercise has been observed in rainbow trout (Milligan and Wood 1986, Wood et al. 1990). These data, combined with the lack of change in plasma total protein concentrations, suggest that there was little net movement of water between the extracellular fluid and muscle of the fish (Wang et al. 1994).

Because neither temperature group experienced any measurable amount of metabolic recovery in any variable we assessed, we cannot say that temperature does not affect rates of recovery. However, the temperatures chosen do not seem to affect short term recovery after exhaustion in Pacific cod. Differences in recovery rate seen in other studies occurred over wider temperature ranges than those examined in this experiment and included three temperature groups. Wilkie et al. (1997) acclimated Atlantic salmon to 12, 18, and 23°C and Galloway and Kieffer (2003) examined Atlantic salmon at 6, 12, and 18°C. To effectively demonstrate a temperature effect on recovery, one would need to greatly increase the observation time post-exhaustion. Thus, adding more and broader temperature treatments might help to elucidate a relationship between recovery rate and ambient temperature in Pacific cod.

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Ontogenetic, Temporal, and Spatial Variation of Feeding Niche in an Unexploited Population of Walleye Pollock (*Theragra chalcogramma*)

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Abstract

Stable isotope ratios of carbon and nitrogen were measured in an unexploited population of walleye pollock (*Theragra chalcogramma*) from Prince William Sound, Alaska (PWS) as a metric of feeding niche. Stable isotope data of pollock were compared with each other and with stable isotope data of age-0 herring (*Clupea pallasii*). There were significant species, location, and time period differences in synoptically sampled age-0 pollock and herring. Age-0 pollock were generally ^{13}C -enriched relative to herring even as carbon isotope values varied with time. A positive relationship between ^{13}C content and length of pollock from Zaikof Bay, PWS, was consistent with a pattern of low ^{13}C being attributable to food subsidies, most likely oceanic zooplankton.

The carbon isotope difference between age-0 pollock and age-0 herring increased when ^{13}C decreased. This coincided with a relative increase in age-0 pollock food chain length compared to age-0 herring. This is posited to reflect reduced overlap in food supply and thus competition during a period of inferred high food subsidies. Subsidies are further posited to vary according to hypothesized oceanic zooplankton population cycles.

A systematic increase in nitrogen isotope values with respect to size suggested an average ontogenetic food chain length increase of about 1.3 trophic levels over a pollock's life span after age-0. Trophic level variability was consistent with facultative planktivory for all adult sized pollock, including those with lengths over 400 mm, above which there was a sharp trophic level increase. The ability for pollock to maintain

a relatively low trophic level for most of their life is hypothesized to enhance the species' ability to sequester energy. Stable isotopes may provide a useful metric for detecting trophic change in terms of subsidies as well as food chain length.

Introduction

An unexploited population of walleye pollock, *Theragra chalcogramma*, the dominant gadid of the subarctic Pacific Ocean, was discovered in Prince William Sound, Alaska (PWS), during the mid-1990s (Willette et al. 1999). Pollock, along with Pacific herring (*Clupea pallasii*) and juvenile pink salmon (*Oncorhynchus gorbuscha*) were found to be the dominant constituents of the PWS pelagic fish fauna (Cooney et al. 2001). Willette et al. (1999) found that as well as being facultative planktivores, immature and adult pollock preyed upon nekton in PWS. Squid were the most common nekton prey of adult pollock. The nekton prey of immature pollock consisted of juvenile gadids, mainly pollock, as well as salmonids, mainly pink and chum salmon (*O. keta*). The proportion of nekton in diets was inversely correlated with abundance of large calanoid copepods (Willette et al. 1999). Pollock switched to principally consuming large calanoids and other zooplankton above certain threshold levels. This prey-switching facility has also been observed in Bering Sea pollock (e.g., Dwyer et al. 1987). Age-0 pollock, which were consistently sampled alongside age-0 herring in protected bays of PWS (Paul and Paul 1998, Paul et al. 1998, Kline 1999), fed on food chains of approximately the same length, which were consistent with zooplanktivory (Kline 2001, 2007).

Stable isotope ratios are useful for food web analysis because of predictable relationships in the isotopic compositions of consumers and their forage (reviewed by Michener and Schell 1994). Age-0 pollock and age-0 herring, as well as other "forage fish" taxa, reflect carbon subsidies from the adjacent Gulf of Alaska by concomitant shifts in stable isotope composition throughout PWS (Kline 1999, 2007). Continental slope zooplankton populations were posited to be the source of occurrences of low $^{13}\text{C}/^{12}\text{C}$ abundance occasionally measured in PWS fishes (Kline 1999). Low $^{13}\text{C}/^{12}\text{C}$ values measured in PWS fishes were thus posited to reflect oceanic carbon subsidies. The natural abundance of $^{13}\text{C}/^{12}\text{C}$ expressed as $\delta^{13}\text{C}$ ' (see Materials and methods) of PWS zooplankton was more than -21‰ whereas that of zooplankton of the same species sampled in the Gulf of Alaska was less than -22‰ (Kline 1999). Because of trophic enrichment of ^{13}C of $\sim 1\text{‰}$ per feeding step (reviewed by Michener and Schell 1994), zooplanktivores such as age-0 pollock feeding exclusively on one of these sources would have correspondingly higher values than these, which was reflected in actual observations (Kline 1999).

Whereas oceanic subsidies were observed in all forage taxa in late 1995, the relative effect in terms of inferred dependency based on $\delta^{13}\text{C}$ values varied by species (Kline 2007). Sand lance (*Ammodytes hexapterus*), a nearshore fish species, had the highest $\delta^{13}\text{C}$ values prior to late 1995 and had the highest $\delta^{13}\text{C}$ values during late 1995. However, their $\delta^{13}\text{C}$ values during late 1995 were lower than for herring prior to the shift. Age-0 pollock were second to herring in terms of having the greatest qualitative response to oceanic subsidies. Interactions among species in PWS in their response to oceanic subsidies of potential food can thus be inferred from differences in $^{13}\text{C}/^{12}\text{C}$ composition.

Age-0 pollock in PWS were found to increase in energetic content during the winter, whereas age-0 herring lost energy, which was hypothesized to reflect species differences in foraging strategies (Paul and Paul 1998, Paul et al. 1998). To test whether differences in foraging strategy could be detected with stable isotopes, in particular differences in response to oceanic subsidies, this paper examines new as well as previously published age-0 pollock and herring stable isotope data. This context required greater detail in the analysis than previous studies (Kline 1999, 2007). Kline 1999 was limited to qualitative comparison of juvenile pollock and herring from two time periods, autumn 1994 and autumn 1995. Additional data of age-0 pollock from 1994 and 1996 are presented here. Supplementing these data are age-0 herring data for those time periods for which age-0 pollock data are available. These data are examined quantitatively by species, sampling period, and sampling site to assess the relative response of oceanic subsidies in terms of $\delta^{13}\text{C}$ value. This is a finer scale analysis than done previously (Kline 2007). Additionally, previously unpublished stable isotope data of larger size classes of pollock are presented to consider ontogenetic relationships, if any, to oceanic subsidies as well food chain length, or trophic level (TL), which is reflected by $\delta^{15}\text{N}$ value.

Materials and methods

Fish sampling

Pollock and herring were sampled primarily by trawling and seining (Kline 1999). Samples were collected for multiple projects. The juvenile pollock and herring samples analyzed for stable isotopes were also analyzed for whole-body energetic content reported by Paul et al. (1998).

The scope of sampling for pollock varied in time (Tables 1 and 2). Sampling in 1994 was limited whereas broadscale surveys in October–November 1995 and March 1996 covered PWS in its entirety (Fig. 1). Subsequent sampling focused on four representative bays (Norcross et al. 2001). There are five sampling periods, A to E (Table 1), for which both age-0 pollock and age-0 herring stable isotope data are available. Sampling periods C and D, corresponding to the period when exten-



Figure 1. A map of the Prince William Sound study area showing the locations where pollock and herring were sampled for this study. The location codes for this map are given in Tables 1 and 2.

sive surveys were conducted, also corresponded to when there was an inferred strong pulse of oceanic subsidies (Kline 2007). Sampling periods A, B, and E are assumed to be a period when oceanic subsidies were lower than that inferred during C and D and collectively are referred to as the low subsidy period. Pollock over 125 mm in length were sampled at the same times as age-0 fish, but were fewer in total number (Table 2). Accordingly, these larger size classes of pollock were stratified into two time-integrated temporal groups, one corresponding to the inferred high subsidy period, and one corresponding to the low subsidy period. Only two of the 209 pollock from the high subsidy period were sampled during D. Within these two temporal strata, high and low subsidy, pollock over 125 mm in length were stratified by sampling site in PWS (Table 2).

Epaxial muscle was dissected from larger size class pollock, whereas whole age-0 pollock and herring were analyzed. Fish tissues were freeze-dried and then ground to a fine powder. Powdered samples were sent to the University of Alaska Fairbanks Stable Isotope Facility

Table 1. Age-0 pollock and herring carbon and nitrogen stable isotope data stratified by sampling period and sampling location with *P* values of statistical analyses. *P* values are for Mann-Whitney U-tests (MWU) and Kruskal-Wallis tests (KW) reported in the text. Asterisks under columns A1 and A2 indicate data used for ANOVAs reported in the text. Under the column vote, a Y is given if the $\delta^{13}\text{C}'$ value was $\leq -20.0\text{‰}$ and an N if the $\delta^{13}\text{C}'$ value was $> -20.0\text{‰}$. SE, $\Delta^{15}\text{N}$, and ΔTL values that were <0.1 are indicated as 0.0. The map codes correspond to the sites shown in Fig. 1.

| Location | Map code | Species | N | Vote | $\delta^{13}\text{C}'$ | SD | SE | $\Delta^{15}\text{N}$ | MWU | KW | $\delta^{15}\text{N}$ | SD | SE | $\Delta^{15}\text{N}$ | ΔTL | MWU | KW | A1 | A2 |
|-------------------------------------|----------|---------|-----|-------|------------------------|-----|-----|-----------------------|---------|---------|-----------------------|-----|-----|-----------------------|-------------------|---------|---------|---------|---------|
| A. June 1994 | | | | | | | | | | | | | | | | | | | |
| Knight Island Passage | 4 | Pollock | 21 | N | -18.9 | 0.7 | 0.1 | 0.4 | 0.0059 | | 13.2 | 0.9 | 0.2 | 0.2 | 0.1 | 0.0108 | | | |
| | | Herring | 24 | N | -19.3 | 0.4 | 0.1 | | | | 12.9 | 0.3 | 0.1 | | | | | | |
| B. September to October 1994 | | | | | | | | | | | | | | | | | | | |
| Paddy Bay | 7 | Pollock | 20 | N | -19.3 | 0.2 | 0.1 | 0.8 | 0.0867 | | 11.4 | 0.1 | 0.0 | -1.3 | -0.4 | 0.0224 | | | |
| | | Herring | 2 | N | -20.1 | 1.0 | 0.7 | | | | 12.7 | 0.1 | 0.0 | | | | | | |
| Port Gravina | 8 | Pollock | 11 | N | -19.0 | 1.4 | 0.4 | 0.9 | 0.0377 | | 12.4 | 0.6 | 0.2 | -0.5 | -0.1 | 0.0687 | | | * |
| | | Herring | 25 | N | -20.0 | 0.6 | 0.1 | | | | 12.8 | 0.7 | 0.1 | | | | | | * |
| Windy Bay | 14 | Pollock | 25 | N | -19.3 | 0.4 | 0.1 | 0.2 | 0.8332 | | 12.5 | 0.2 | 0.0 | 0.3 | 0.1 | <0.0001 | | | |
| | | Herring | 27 | N | -19.5 | 0.7 | 0.1 | | | | 12.2 | 0.2 | 0.0 | | | | | | |
| Three sites | | Pollock | 56 | N | -19.3 | 0.7 | 0.1 | 0.5 | 0.0022 | 0.8800 | 12.1 | 0.6 | 0.1 | -0.4 | -0.1 | 0.0050 | 0.0006 | | |
| | | Herring | 54 | N | -19.7 | 0.7 | 0.1 | | | 0.0189 | 12.5 | 0.6 | 0.1 | | | | <0.0001 | | |
| C. October to November 1995 | | | | | | | | | | | | | | | | | | | |
| Eaglek Bay | 2 | Pollock | 25 | Y | -20.6 | 0.5 | 0.1 | 0.8 | <0.0001 | | 12.9 | 0.2 | 0.0 | 0.2 | 0.1 | 0.0130 | | | * |
| | | Herring | 25 | Y | -21.4 | 0.5 | 0.1 | | | | 12.7 | 0.3 | 0.1 | | | | | | * |
| Hogg Bay | 3 | Pollock | 25 | Y | -20.6 | 0.3 | 0.1 | 0.7 | <0.0001 | | 13.0 | 0.2 | 0.0 | 0.4 | 0.1 | <0.0001 | | | |
| | | Herring | 25 | Y | -21.3 | 0.2 | 0.0 | | | | 12.7 | 0.3 | 0.1 | | | | | | |
| Port Gravina | 8 | Pollock | 25 | N | -20.4 | 0.3 | 0.1 | 1.2 | <0.0001 | | 13.4 | 0.3 | 0.1 | 0.7 | 0.2 | <0.0001 | | | * |
| | | Herring | 25 | Y | -21.6 | 0.6 | 0.1 | | | | 12.6 | 0.4 | 0.1 | | | | | | * |
| Sawmill Bay | 9 | Pollock | 25 | Y | -20.7 | 0.3 | 0.1 | 0.8 | <0.0001 | | 13.1 | 0.4 | 0.1 | 0.3 | 0.1 | 0.0018 | | | |
| | | Herring | 25 | Y | -21.5 | 0.3 | 0.1 | | | | 12.8 | 0.3 | 0.1 | | | | | | |
| Simpson Bay | 11 | Pollock | 25 | Y | -20.6 | 0.4 | 0.1 | 0.8 | <0.0001 | | 13.2 | 0.3 | 0.1 | 0.4 | 0.1 | <0.0001 | | | * |
| | | Herring | 25 | Y | -21.4 | 0.4 | 0.1 | | | | 12.7 | 0.3 | 0.1 | | | | | | * |
| Whale Bay | 13 | Pollock | 25 | Y | -20.5 | 0.4 | 0.1 | 1.4 | <0.0001 | | 12.9 | 0.3 | 0.1 | 0.6 | 0.2 | <0.0001 | | | * |
| | | Herring | 25 | Y | -21.9 | 0.2 | 0.0 | | | | 12.3 | 0.2 | 0.0 | | | | | | * |
| Zaikof Bay | 15 | Pollock | 25 | Y | -20.5 | 0.4 | 0.1 | 0.8 | <0.0001 | | 13.1 | 0.4 | 0.1 | 0.3 | 0.1 | 0.0126 | | | * |
| | | Herring | 25 | Y | -21.3 | 0.2 | 0.0 | | | | 12.8 | 0.3 | 0.1 | | | | | | * |
| Seven sites | | Pollock | 175 | Y | -20.6 | 0.4 | 0.0 | 0.9 | <0.0001 | 0.0754 | 13.1 | 0.3 | 0.0 | 0.4 | 0.1 | <0.0001 | <0.0001 | | |
| | | Herring | 175 | Y | -21.5 | 0.4 | 0.0 | | | <0.0001 | 12.7 | 0.3 | 0.0 | | | | <0.0001 | | |
| D. March 1996 | | | | | | | | | | | | | | | | | | | |
| Drier Bay | 1 | Pollock | 10 | N | -19.3 | 0.7 | 0.2 | 1.3 | <0.0001 | | 13.2 | 0.4 | 0.1 | 0.6 | 0.2 | 0.0008 | | | * |
| | | Herring | 25 | Y | -20.6 | 0.4 | 0.1 | | | | 12.5 | 0.4 | 0.1 | | | | | | * |
| Eaglek Bay | 2 | Pollock | 10 | N | -20.1 | 0.3 | 0.1 | 0.9 | <0.0001 | | 13.1 | 0.4 | 0.1 | 0.7 | 0.2 | <0.0001 | | | * |
| | | Herring | 25 | Y | -21.0 | 0.5 | 0.1 | | | | 12.5 | 0.4 | 0.1 | | | | | | * |
| Orca Bay | 6 | Pollock | 20 | N | -19.3 | 0.7 | 0.2 | | | | 13.6 | 0.3 | 0.1 | | | | | | * |
| | | Herring | 10 | N | -19.9 | 0.2 | 0.1 | 1.1 | <0.0001 | | 12.8 | 0.3 | 0.1 | 0.7 | 0.2 | 0.0001 | | | * |
| Paddy Bay | 7 | Pollock | 10 | N | -19.4 | 0.2 | 0.1 | | | | 13.7 | 0.2 | 0.1 | | | | | | * |
| | | Herring | 10 | N | -19.4 | 0.2 | 0.1 | | | | 13.7 | 0.2 | 0.1 | | | | | | * |
| Port Gravina | 8 | Pollock | 10 | N | -19.9 | 0.3 | 0.1 | | | | 13.1 | 0.3 | 0.1 | | | | | | * |
| | | Herring | 10 | N | -19.4 | 0.3 | 0.1 | 0.9 | <0.0001 | | 13.0 | 0.4 | 0.1 | 0.5 | 0.2 | 0.0022 | | | * |
| Sawmill Bay | 9 | Pollock | 10 | N | -19.4 | 0.3 | 0.1 | | | | 13.2 | 0.4 | 0.1 | | | | | | * |
| | | Herring | 25 | N | -20.3 | 0.5 | 0.1 | | | | 12.7 | 0.4 | 0.1 | | | | | | * |
| Simpson Bay | 11 | Pollock | 80 | N | -19.6 | 0.5 | 0.1 | 1.1 | <0.0001 | <0.0001 | 13.4 | 0.5 | 0.1 | 0.8 | 0.2 | <0.0001 | <0.0001 | | |
| | | Herring | 100 | Y | -20.7 | 0.6 | 0.1 | | | <0.0001 | 12.6 | 0.5 | 0.1 | | | | | | <0.0001 |
| E. October 1996 | | | | | | | | | | | | | | | | | | | |
| Eaglek Bay | 2 | Pollock | 25 | N | -19.3 | 0.5 | 0.1 | 1.0 | <0.0001 | | 12.4 | 0.2 | 0.0 | 0.4 | 0.1 | 0.0083 | | | * |
| | | Herring | 24 | N | -20.3 | 0.4 | 0.1 | | | | 11.9 | 0.6 | 0.1 | | | | | | * |
| Simpson Bay | 11 | Pollock | 25 | N | -19.1 | 0.4 | 0.1 | 0.7 | 0.0005 | | 12.7 | 0.3 | 0.1 | 0.6 | 0.2 | 0.0003 | | | * |
| | | Herring | 14 | N | -19.8 | 0.5 | 0.1 | | | | 12.1 | 0.5 | 0.1 | | | | | | * |
| Whale Bay | 14 | Pollock | 19 | N | -18.6 | 0.5 | 0.1 | 1.1 | 0.0001 | | 12.3 | 0.5 | 0.1 | 0.3 | 0.1 | 0.2545 | | | * |
| | | Herring | 18 | N | -19.7 | 0.8 | 0.2 | | | | 12.0 | 0.7 | 0.2 | | | | | | * |
| Zaikof Bay | 15 | Pollock | 23 | N | -19.5 | 0.6 | 0.1 | 0.1 | 0.7820 | | 12.5 | 0.4 | 0.1 | 0.0 | 0.0 | 0.9830 | | | * |
| | | Herring | 24 | N | -19.6 | 0.7 | 0.1 | | | | 12.5 | 0.4 | 0.1 | | | | | | * |
| Four sites | | Pollock | 92 | N | -19.1 | 0.6 | 0.1 | 0.7 | <0.0001 | <0.0001 | 12.5 | 0.4 | 0.0 | 0.3 | 0.1 | 0.0002 | 0.0017 | | |
| | | Herring | 80 | N | -19.9 | 0.7 | 0.1 | | | 0.0006 | 12.2 | 0.6 | 0.1 | | | | 0.0043 | | |
| All data | Period | Pollock | 424 | | | | | | | <0.0001 | | | | | | | | <0.0001 | |
| | | Herring | 433 | | | | | | | <0.0001 | | | | | | | | <0.0001 | |
| Species | Pollock | 424 | N | -19.8 | 0.8 | 0.0 | 0.9 | <0.0001 | | | 12.9 | 0.6 | 0.0 | 0.3 | 0.1 | <0.0001 | | | |
| | | Herring | 433 | Y | -20.7 | 1.0 | 0.0 | | | | 12.5 | 0.5 | 0.0 | | | | | | |

Table 2. Carbon and nitrogen stable isotope linear regression data for pollock >125 mm in length stratified by inferred low and high subsidy periods defined in text and by sampling site. The dependent variable is as given in the table; the independent variable was length. Asterisks under the column ANCOVA indicate data used for the analysis of covariance reported in the text. The lower block compares regression statistics for linear as well as 2nd and 3rd order polynomials for the collective data. The map codes correspond to the sites shown in Fig. 1.

| Graph | Subsidy Site period | Map code | Dependent variable | R^2 | P | N | ANCOVA |
|--------|---------------------|-----------------------|-------------------------|--------|---------|-----|----------------|
| Fig. 5 | Low | Zaikof Bay | 15 $\delta^{13}C'$ | 0.0030 | 0.8003 | 27 | * |
| | | Whale Bay | 13 $\delta^{13}C'$ | 0.3140 | 0.0299 | 15 | * |
| | | Wells Passage | 12 $\delta^{13}C'$ | 0.1200 | 0.0003 | 103 | * |
| | | Port Gravina | 8 $\delta^{13}C'$ | 0.2930 | 0.0076 | 23 | |
| | | Orca Bay | 6 $\delta^{13}C'$ | 0.0730 | 0.3317 | 15 | |
| | | Montague Strait | 5 $\delta^{13}C'$ | 0.0190 | 0.6282 | 15 | |
| | | Knight Island Passage | 4 $\delta^{13}C'$ | 0.0740 | 0.4171 | 11 | |
| | | All | | 0.0030 | 0.4122 | 209 | |
| Fig. 6 | High | Zaikof Bay | 15 $\delta^{13}C'$ | 0.7130 | <0.0001 | 30 | * |
| | | Whale Bay | 13 $\delta^{13}C'$ | 0.6480 | <0.0001 | 26 | * |
| | | Wells Passage | 12 $\delta^{13}C'$ | 0.3460 | <0.0001 | 40 | * |
| | | Simpson Bay | 11 $\delta^{13}C'$ | 0.3500 | 0.0427 | 12 | |
| | | Sheep Bay | 10 $\delta^{13}C'$ | | | 2 | |
| | | All | | 0.1510 | <0.0001 | 112 | |
| Fig. 7 | Low | Zaikof Bay | 15 $\delta^{13}C'_{TL}$ | 0.2040 | 0.0181 | 27 | |
| | | Whale Bay | 13 $\delta^{13}C'_{TL}$ | 0.2560 | 0.0546 | 15 | |
| | | Wells Passage | 12 $\delta^{13}C'_{TL}$ | 0.0460 | 0.0304 | 103 | |
| | | Port Gravina | 8 $\delta^{13}C'_{TL}$ | 0.0580 | 0.2679 | 23 | |
| | | Orca Bay | 6 $\delta^{13}C'_{TL}$ | 0.0560 | 0.3974 | 15 | |
| | | Montague Strait | 5 $\delta^{13}C'_{TL}$ | 0.0200 | 0.6175 | 15 | |
| | | Knight Island Passage | 4 $\delta^{13}C'_{TL}$ | 0.0280 | 0.6233 | 11 | |
| | | All | | 0.2450 | <0.0001 | 209 | |
| Fig. 8 | High | Zaikof Bay | 15 $\delta^{13}C'_{TL}$ | 0.6210 | <0.0001 | 30 | |
| | | Whale Bay | 13 $\delta^{13}C'_{TL}$ | 0.0890 | 0.1399 | 26 | |
| | | Wells Passage | 12 $\delta^{13}C'_{TL}$ | 0.2610 | 0.0008 | 40 | |
| | | Simpson Bay | 11 $\delta^{13}C'_{TL}$ | 0.1770 | 0.1728 | 12 | |
| | | Sheep Bay | 10 $\delta^{13}C'_{TL}$ | | | 2 | |
| | | All | | 0.0150 | 0.2028 | 112 | |
| Fig. 2 | Low | Zaikof Bay | 15 TL | 0.2610 | 0.0065 | 27 | |
| | | Whale Bay | 13 TL | 0.0010 | 0.9261 | 15 | |
| | | Wells Passage | 12 TL | 0.1730 | <0.0001 | 103 | |
| | | Port Gravina | 8 TL | 0.3390 | 0.0036 | 23 | |
| | | Orca Bay | 6 TL | 0.4100 | 0.0101 | 15 | |
| | | Montague Strait | 5 TL | 0.4690 | 0.0048 | 15 | |
| | | Knight Island Passage | 4 TL | 0.1370 | 0.2618 | 11 | |
| | | All | | 0.4480 | <0.0001 | 209 | |
| Fig. 3 | High | Zaikof Bay | 15 TL | 0.5780 | <0.0001 | 30 | |
| | | Whale Bay | 13 TL | 0.6180 | <0.0001 | 26 | |
| | | Wells Passage | 12 TL | 0.0130 | 0.4901 | 40 | |
| | | Simpson Bay | 11 TL | 0.8510 | <0.0001 | 12 | |
| | | Sheep Bay | 10 TL | | | 2 | |
| | | All | | 0.5700 | <0.0001 | 112 | |
| Fig. 4 | All | All | TL | 0.4620 | <0.0001 | | Model |
| | | All | TL | 0.4810 | <0.0001 | | Linear |
| | | All | TL | 0.5090 | <0.0001 | | 2nd order poly |
| | | All | TL | 0.5090 | <0.0001 | | 3rd order poly |

where stable isotope analysis was performed using Europa 20/20 and Finnegan Delta Plus units equipped with continuous flow elemental analyzers. A single stable isotope analysis generated the following data: $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios expressed in standard delta units, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, and %C and %N. The delta notation used to express stable isotope ratios is reported as the parts per thousand deviation relative to international standards, air N_2 for nitrogen, and Vienna Peedee belemnite for carbon. The delta notation used to express stable isotope ratios relative to international standards is defined by the following expression:

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000\text{‰} \quad (1)$$

where $R = ^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. By definition, the isotope standards have delta values of zero, i.e., $\delta^{15}\text{N} = 0$ for atmospheric N_2 . Mass spectrometric analysis quality assurance protocols consisted of running of laboratory standards before and after groups of five “unknowns.”

The method of McConnaughey and McRoy (1979) was used to calculate lipid-normalized $^{13}\text{C}/^{12}\text{C}$. The method is based on using the C/N ratio derived from the %C and %N data generated for each sample, assumes a C/N ratio of 4.0 is normal, and adjusts $\delta^{13}\text{C}$ accordingly. The parameter L based on C/N was calculated first:

$$L = 93/[1 + 1/(0.246 \times \text{C/N} - 0.775)] \quad (2)$$

L and the uncorrected $\delta^{13}\text{C}$ value was then used to calculate a lipid-normalized value ($\delta^{13}\text{C}'$):

$$\delta^{13}\text{C}' = \delta^{13}\text{C} + 6[3.9/(1 + 287.1/L) - 0.2068] \quad (3)$$

In general, normalization reduces a source of $^{13}\text{C}/^{12}\text{C}$ variability, enabling comparisons without the confounding effects of varying lipid content.

The $\delta^{13}\text{C}'$ values of age-0 pollock and age-0 herring were compared through subtraction and expressed as:

$$\Delta^{13}\text{C}' = \delta^{13}\text{C}'_{\text{pollock}} - \delta^{13}\text{C}'_{\text{herring}} \quad (4)$$

Trophic level

Relative trophic level of good precision can be estimated based on the trophic enrichment of $\delta^{15}\text{N}$, $\epsilon_N = 3.4$. The following formula was used to calculate trophic level:

$$TL_i = 2 + (\delta^{15}\text{N}_i - \delta^{15}\text{N}_H)/\epsilon_N \quad (5)$$

where TL_i is the trophic level of organism i , $\delta^{15}\text{N}_i$ is the $\delta^{15}\text{N}$ value of organism i , and $\delta^{15}\text{N}_H$ is the reference $\delta^{15}\text{N}$ value (assumed to be an herbivore, $TL = 2$). A value of 8.4‰ was used for $\delta^{15}\text{N}_H$ based on the copepod *Neocalanus cristatus* (Kline 2001). The maximum error when estimating

relative TL is $0.3TL$ (Kline 2001) based on temporal and spatial variability of $\delta^{15}N$ values of the *Neocalanus* reference. Because the uncertainty based on SE of a sample is less than $0.1 TL$, fish species were compared to each other (Kline 2001). TL relative to herring sampled synoptically with pollock was calculated by subtracting the mean juvenile herring $\delta^{15}N$ value from the mean juvenile pollock $\delta^{15}N$ value and dividing by ϵ_N . Thus:

$$\Delta TL = \Delta^{15}N/\epsilon_N = (\delta^{15}N_{\text{pollock}} - \delta^{15}N_{\text{herring}})/\epsilon_N \quad (6)$$

ΔTL computed using formula (6) is assumed to eliminate the uncertainty of $0.3 TL$ intrinsic to TL calculated relative to a zooplankton reference (formula 5), which is due to temporal variation of $\delta^{15}N$ at the food chain base (Kline 2001). Synoptically sampled age-0 pollock and herring are assumed to have shifted concordantly to baseline shifts.

Correcting trophic enrichment of $\delta^{13}C'$ values allows one to compare organisms with large differences in TL (e.g., Kline et al. 1998). This is based on an assumed trophic enrichment ratio of 3.4:1 for $\delta^{15}N$ vs. $\delta^{13}C'$ and uses the following formula (after Kline et al. 1998):

$$\delta^{13}C'_{TL} = \delta^{13}C' - \epsilon_C/\epsilon_N(\delta^{15}N_i - \delta^{15}N_H) \quad (7)$$

where $\delta^{13}C'_{TL}$ is the TL normalized carbon isotope ratio derived from $\delta^{13}C'$, $\epsilon_C = 1$, and $\epsilon_N = 3.4$. The reference value of $\delta^{15}N_H = 8.4\text{‰}$ is the same that was used for calculating TL , formula (5) above, and similarly, carries a maximum uncertainty of 0.3‰ . $\delta^{13}C'_{TL}$ is used mainly for adult fishes when TL is likely to be variable and higher than $TL \sim 3$. If TL can be assumed to be nearly constant, e.g., when comparing $\delta^{13}C'$ of planktivores, then TL normalization is not necessary. It is assumed that age-0 pollock and herring are planktivores. An advantage to not normalizing TL is that $\delta^{13}C'$ and $\delta^{15}N$ analyses will be independent.

Results

Age-0 fishes: pollock vs. herring

Carbon isotopes

All $\delta^{13}C'$ observations of both species were more than -20.5‰ during periods A and B and during period E. During period C most $\delta^{13}C'$ observations of both species were less than -20.5‰ . The most negative $\delta^{13}C'$ values of both age-0 pollock and age-0 herring were observed in periods C and D. During period C the mean $\delta^{13}C'$ values of age-0 pollock by sampling site ranged from -20.4 to -20.7‰ and the mean $\delta^{13}C'$ value was -20.6‰ (SD = 0.4; Table 1). During periods A, B, and E age-0 pollock site mean values ranged from -18.6 to -19.5‰ , i.e., 1 to 2‰ ^{13}C enriched relative to period C (Table 1). Period D age-0 pollock $\delta^{13}C'$ values were intermediate, ranging among sites from -19.3 to -20.1‰ (Table 1).

Overall, age-0 pollock were $\delta^{13}\text{C}'$ enriched relative to age-0 herring by 0.9‰, which was statistically significant ($P < 0.05$, Mann-Whitney U-test; Table 1). Each species varied significantly in $\delta^{13}\text{C}'$ with respect to sampling period (Kruskal-Wallis test; Table 1). Within sampling periods B and C age-0 pollock did not vary significantly among sites, whereas age-0 herring did (Kruskal-Wallis test; Table 1). Within sampling periods D and E, age-0 pollock and age-0 herring each varied significantly among sites (Kruskal-Wallis test; Table 1). Each species varied significantly in $\delta^{13}\text{C}'$ value with respect to sampling period (site effect ignored; Kruskal-Wallis test; Table 1).

There were statistically significant species and time period effects but no species-time interaction ($P = 0.4785$) when $\delta^{13}\text{C}'$ values of age-0 pollock and age-0 herring from Port Gravina from periods B and C were compared (ANOVA, A2 in Table 1). The mean difference in $\delta^{13}\text{C}'$ value between periods B and C of 1.3‰, and the mean difference between the species of 0.8‰, were statistically significant (Fisher's PLSD).

There were statistically significant site, species, and time period effects as well as statistically significant site-time, site-species, time-species, and site-time-species interactions when $\delta^{13}\text{C}'$ values of age-0 pollock and age-0 herring from Eaglek Bay, Simpson Bay, Whale Bay, and Zaikof Bay from periods C and E were compared (ANOVA, A1 in Table 1). The difference of 0.2‰ between Zaikof Bay and Eaglek Bay was the only difference in mean site value that was statistically different (Fisher's PLSD). The difference of 1.6‰ between sampling times was statistically different (Fisher's PLSD). The mean difference between the species was 0.9‰, which was statistically significant (Fisher's PLSD).

$\Delta^{13}\text{C}'$ value differences, which ranged from 0.2 to 1.4‰, were generally statistically significant (Mann-Whitney U-test; Table 1). Mean period $\Delta^{13}\text{C}'$ during C and D were 0.9 and 1.1‰, respectively, which was qualitatively higher than that during periods A, B, and E.

Nitrogen isotopes

The least positive $\delta^{15}\text{N}$ values of age-0 pollock were observed in periods B and E when values were less than +13‰ (Table 1). At other times mean $\delta^{15}\text{N}$ values of age-0 pollock were more than $\sim +13$ ‰. Whereas period mean $\delta^{15}\text{N}$ values of age-0 pollock ranged by 1.3‰, period mean $\delta^{15}\text{N}$ values age-0 herring ranged by just 0.7‰. The greatest $\delta^{15}\text{N}$ value disparity between the species, $\Delta^{15}\text{N} = +0.8$ ‰, occurred during period D. $\Delta^{15}\text{N}$ was +0.4‰ during period C. At other times, $\Delta^{15}\text{N}$ ranged from -0.4 to $+0.3$ ‰. There was an increasing trend for time period averaged ΔTL , from -0.1 in period B to $+0.2$ in D, but was $+0.1$ during periods A and E.

Age-0 pollock and age-0 herring generally differed significantly in $\delta^{15}\text{N}$ values at given sites within given sampling periods (Mann-Whitney U-test; Table 1). The main exception was during period E when they were not significantly different at two of four sites ($P = 0.2545$ and 0.9830).

Time period averaged $\Delta^{15}\text{N}$ was consistently statistically significant (Mann-Whitney U-tests; Table 1). Overall, age-0 pollock were significantly (Mann-Whitney U-test; Table 1) $\delta^{15}\text{N}$ enriched relative to age-0 herring by 0.3‰, corresponding to a ΔTL of 0.1. Within each sampling period, the $\delta^{15}\text{N}$ values of age-0 pollock and age-0 herring were statistically different (Kruskal-Wallis test Table 1). Each species varied significantly in $\delta^{15}\text{N}$ value with respect to sampling period (site effect ignored; Kruskal-Wallis test; Table 1).

There were statistically significant time period effects and species-time interactions but no significant species effects ($P = 0.2141$) when $\delta^{15}\text{N}$ values of age-0 pollock and age-0 herring from Port Gravina from periods B and C were compared (ANOVA, A2 in Table 1). The mean difference in $\delta^{15}\text{N}$ value between period B and C of 0.3‰ and the mean difference between the species of 0.3‰ were statistically significant (Fisher's PLSD).

There were statistically significant site, species, and time period effects as well as statistically significant site-species and site-time-species interactions when $\delta^{15}\text{N}$ values of age-0 pollock and age-0 herring from Eaglek Bay, Simpson Bay, Whale Bay, and Zaikof Bay from periods C and E were compared (ANOVA, A1 in Table 1). Only the site-time and species-time interactions were not significant ($P = 0.0736$ and 0.6183 , respectively). Mean site $\delta^{15}\text{N}$ differences of, respectively, 0.2, 0.2, 0.3 and 0.3‰ between Eaglek Bay and Simpson Bay, Zaikof Bay and Eaglek Bay, Zaikof Bay and Simpson Bay, and Zaikof Bay and Whale Bay were statistically different (Fisher's PLSD). However, mean site $\delta^{15}\text{N}$ differences of, respectively, 0.1 and less than 0.1‰, between Eaglek Bay and Whale Bay, and between Zaikof and Simpson Bay were not significant ($P = 0.1919$ and 0.9136 , respectively, Fisher's PLSD). The difference of 0.5‰ between sampling times was statistically different (Fisher's PLSD). The mean difference between the species was 0.3‰, which was statistically significant (Fisher's PLSD).

Ontogenetic assessments

A systematic increase in nitrogen isotope values with respect to size suggested an average ontogenetic food chain length increase of about 1.3 trophic levels over a pollock's life span after age-0. There were significant relationships between $\delta^{15}\text{N}$ -based TL and length during both high and low subsidies periods at most sites (Table 2). The significant correlations were somewhat lower during the low subsidies period ($R^2 = 0.17$ to 0.47 ; Fig. 2) than during the high subsidies period ($R^2 = 0.57$ to 0.85 ; Fig. 3). There was at least one site per period for which there was no significant relationship that may have been driven by the limited size range found there (Figs. 2 and 3). Collectively, length explained 45% of TL variability during the low subsidy period and 57% during the high subsidy period (Table 2). Aggregating all of the data, the R^2 for a linear

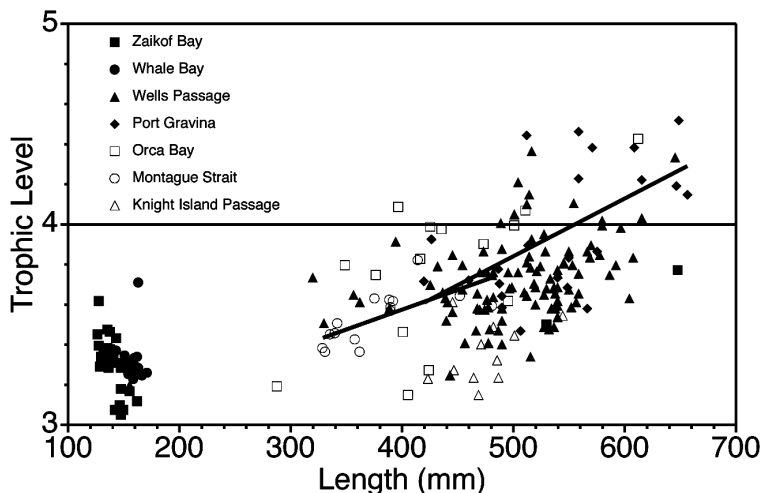


Figure 2. Trophic level based upon $\delta^{15}\text{N}$ values of pollock >125 mm in length from the low subsidy period, by sampling site, as a function of length. Regression lines are shown for Zaikof Bay and Montague Strait data; correlation statistics are given in Table 2.

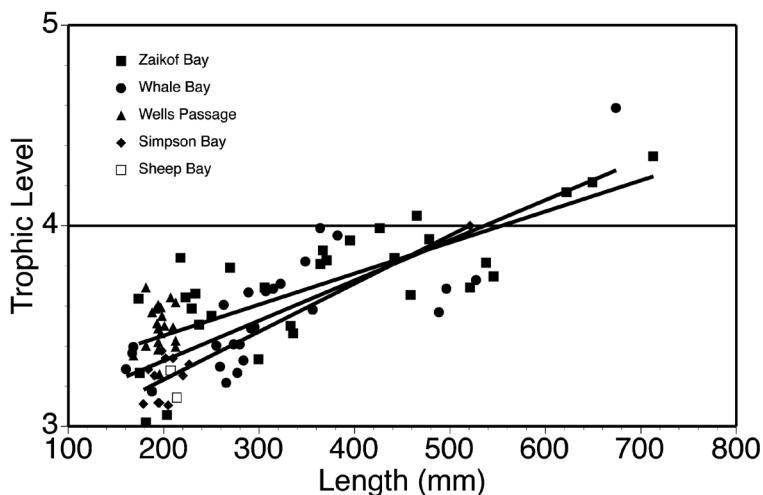


Figure 3. Trophic level based upon $\delta^{15}\text{N}$ values of pollock >125 mm in length from the high subsidy period, by sampling site, as a function of length. Regression lines are shown for Zaikof Bay, Whale Bay, and Simpson Bay data; correlation statistics are given in Table 2.

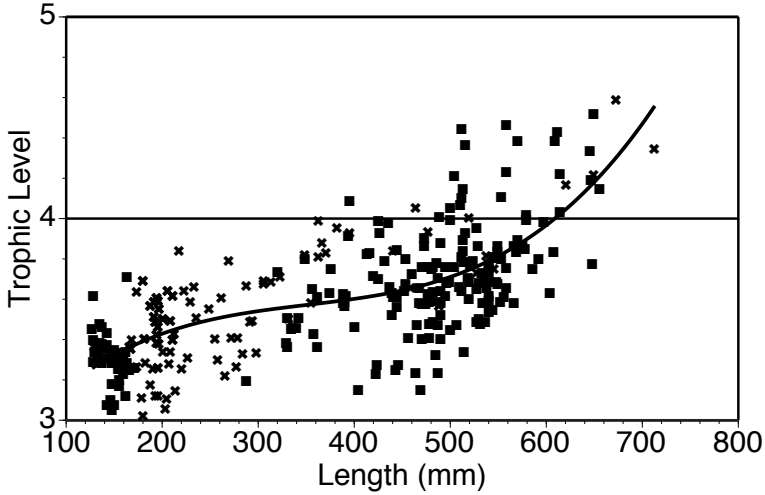


Figure 4. Trophic level based upon $\delta^{15}\text{N}$ values of pollock >125 mm in length as a function of length for all data. A third-order polynomial regression line is shown. Symbols distinguish low (x) from high (solid squares) sampling periods; correlation statistics are given in Table 2.

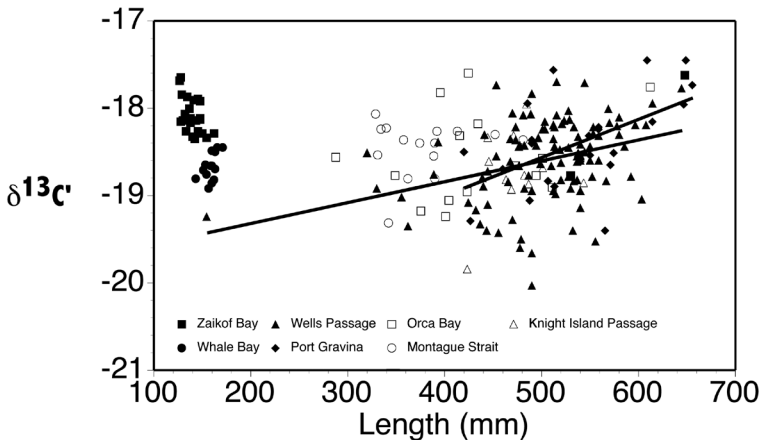


Figure 5. Carbon stable isotope analyses reported as $\delta^{13}\text{C}'$ values of pollock >125 mm in length from the low subsidy period, by sampling site, as a function of length. Regression lines are shown for Wells Passage and Port Gravina data; correlation statistics are given in Table 2.

regression was 0.462 (Table 2). A third order polynomial increased the correlation to 0.509 (Table 2, Fig. 4). Up to about 500 mm length, most pollock fit between $TL = 3$ and 4 (Fig. 4). Above 500 mm, pollock were increasingly higher than $TL = 4$.

Analysis of covariance (ANCOVA) suggested that there was a significant difference in $\delta^{13}C'$ value between high and low subsidy periods, whether TL or length was used as the covariate. The covariates and interactions between $\delta^{13}C'$ and the covariates were significant for both analyses. During the low subsidies period there was a significant relationship between $\delta^{13}C'$ and length at three sites (Table 2, Fig. 5). However, these correlations were lower (R^2 from 0.12 to 0.31) compared to those from the high subsidies period (R^2 from 0.35 to 0.71). During the high subsidies period $\delta^{13}C'$ was significantly correlated to length in all sites (Table 2, Fig. 6).

Correlations between $\delta^{13}C'_{TL}$ and length were reduced compared to $\delta^{13}C'$ and length in most cases (Table 2; compare Fig. 7 with Fig. 5 and compare Fig. 8 with Fig. 6). During the high subsidies period the R^2 for Zaikof Bay was reduced to 0.62 from 0.71, whereas it was reduced from $R^2 = 0.648$ to no correlation ($P = 0.1399$) at Whale Bay (compare Figs. 6 and 8). Length explained about 15% of $\delta^{13}C'$ based on the collective data during the high subsidies period, but none after normalization to $\delta^{13}C'_{TL}$.

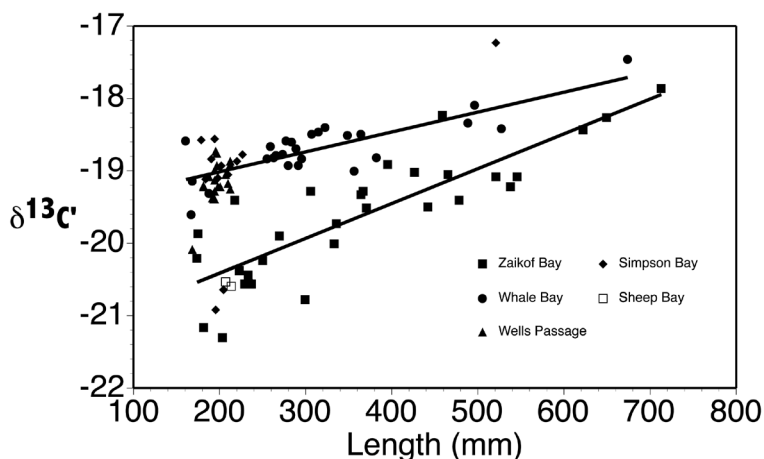


Figure 6. Carbon stable isotope analyses reported as $\delta^{13}C'$ values of pollock >125 mm in length from the high subsidy period, by sampling site, as a function of length. Regression lines are shown for Whale Bay and Zaikof Bay data; correlation statistics are given in Table 2.

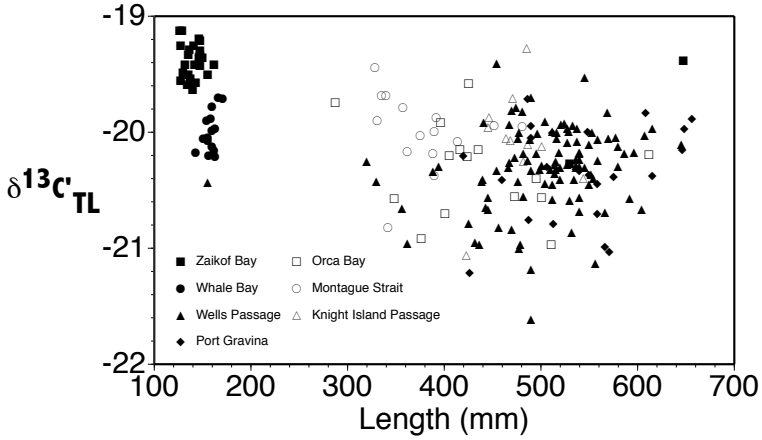


Figure 7. Carbon stable isotope analyses reported as $\delta^{13}C'_{TL}$ values of pollock >125 mm in length from the low subsidy period, by sampling site, as a function of length.

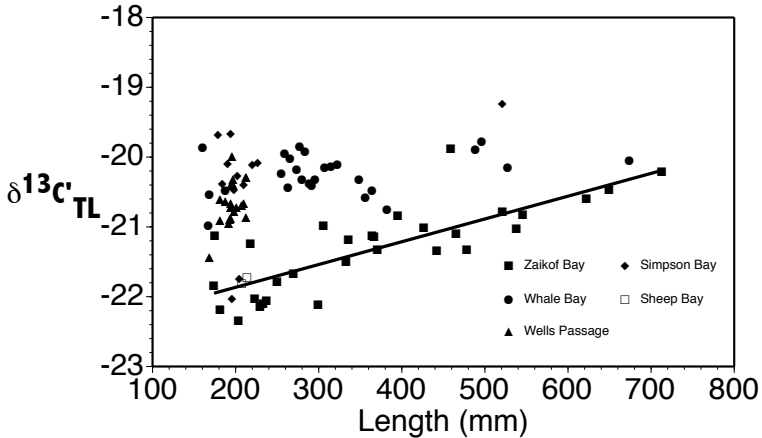


Figure 8. Carbon stable isotope analyses reported as $\delta^{13}C'_{TL}$ values of pollock >125 mm in length from the high subsidy period, by sampling site, as a function of length. Regression line is shown for Zaikof Bay data; correlation statistics are given in Table 2.

Discussion

Trophic flexibility at age-0

Stable isotope analysis revealed subtle shifts in the trophic relationships of age-0 fishes in PWS. The difference in value of $\delta^{13}\text{C}$ between the species of up to 1.4‰ in a given location and 1.1‰ within a time period was somewhat less than the maximum temporal shift observed within a species. Furthermore, within-species and within-timeframe spatial variation of $\delta^{13}\text{C}$ values was even less at 0.0 to 0.6‰. Between the autumns of 1994 and 1995, age-0 pollock decreased by 1.3‰ and herring decreased by 1.8‰. Between autumn 1995 and March 1996, pollock rebounded by 1.0‰ and herring by just 0.8‰ and by autumn of 1996 pollock and herring were within 0.2‰ of what their values were during the autumn of 1994, i.e., essentially the same. The qualitative difference in their $\delta^{13}\text{C}$ rebound in March 1996 is as revealing as the shift itself. That herring in March 1996 were more similar in $\delta^{13}\text{C}$ value to herring the previous autumn compared to pollock reflected that they had not turned over as much of their low ^{13}C carbon as pollock, which is consistent with reduced feeding and energy gains by herring compared to pollock. For example, 70% of herring stomachs may be empty during the winter period when zooplankton stocks are low (Foy and Norcross 1999). Pollock are able to forage successfully enough during the winter to gain energy whereas herring cannot (Paul et al. 1998). Foraging during the winter apparently took place on carbon of higher ^{13}C content than what occurred in the autumn, otherwise there would not have been these shifts. Pollock feeding during the winter leading up to March 1996 also depended on a longer food chain, which was evident by their highest $\delta^{15}\text{N}$ values observed during this study of up to 13.7‰, and maximum difference of 0.8 TL with respect to herring. Age-0 pollock foraging may be more adaptable and able exploit a broader range of food sources than age-0 herring. This trophic flexibility may be an adaptive strategy contributing to this species resiliency. The net energy gain may also reflect a reduced energy expenditure compared to herring. These differences could be physiological or may be related to behavior. For example, there may be differences in energy expenditure during predator avoidance. Regardless of the cause, pollock juveniles appear to be better able adapt to changes in food compared to herring. This advantage may confer resilience to changes in their food supply such as those that may come about from climate change.

Did the fish or their food move?

Because fish are motile, observed isotopic shifts could be due to movement of fish or their food. For example, stable isotope analysis has been useful for detecting fish migration (e.g., Kline et al. 1998). A scenario, although highly unlikely, that could explain the simultaneous multiple

species and multiple-site $\delta^{13}\text{C}'$ shifts would have involved concerted migrations by pollock and herring to locations where food sources had $\delta^{13}\text{C}'$ values like those observed during the shifts. The fish would thus have had to migrate out to the Gulf of Alaska and then back into PWS to the locations where they were sampled. A far more likely explanation for the shifts is that their plankton prey moved with currents, either near the surface via the Alaska Coastal Current or below the surface such as through fjord deepwater or estuarine exchange (Niebauer et al. 1984). This exchange, which can be episodic, has been observed through drifter buoys and moored current meters (Vaughan et al. 2001). Vaughan et al. (2001) observed net inflow at depth during the summer. Occurrence of diapausing Gulf of Alaska origin copepods in deep waters of PWS provides evidence for deepwater biological exchange (Kline 1999).

The variable and ontogenetic $\delta^{13}\text{C}'_{TL}$ patterns of the larger sized pollock provide additional evidence that 0-age $\delta^{13}\text{C}'$ shifts were due to movement of their planktonic food. The variable response to subsidies in the form of plankton is consistent with pollock switching to planktivory above density thresholds (Willette et al. 1999) given the safe assumption that plankton density was spatially variable. Only at Zaikof Bay was there evidence of these shifts affecting most of the population. There were, however, a few individual fish from Simpson and Sheep bays with $\delta^{13}\text{C}'_{TL} \sim -22\%$. The slope of Zaikof Bay pollock $\delta^{13}\text{C}'_{TL}$ values with respect to length is consistent with the expected turnover time of older, larger fish, which may be more than 1 year (Hesslein et al. 1993). The trend to higher $\delta^{13}\text{C}'_{TL}$ values (i.e., there was less of a shift to low $\delta^{13}\text{C}'_{TL}$ values, or no shift at all) of larger sizes of pollock is consistent with longer turnover time. Furthermore, if Zaikof Bay pollock were immigrants from the Gulf of Alaska (GOA), a reverse slope to that observed would be expected: because of slower turnover, the larger size classes would more likely resemble GOA carbon and the smaller sizes classes PWS carbon, which is the opposite of the observation. Zooplankton subsidies of low $\delta^{13}\text{C}'$ content are assumed to be transient, and thus affected principally age-0 fishes. Immigration from the GOA, however, is not precluded and may explain why a few individual large size-class pollock had $\delta^{13}\text{C}'_{TL}$ values less than -21% during the low subsidies period.

Ontogenetic food chain length shifts

Trophic level based upon $\delta^{15}\text{N}$ values provides a convenient metric of trophic level that is consistent with the observation that pollock in PWS switch prey according to their size as well as prey availability (Willette et al. 1999). If pollock were strictly zooplanktivores, their TL would be ~ 3 whereas if they were strictly primary piscivores, their TL would be ~ 4 . Most sizes of pollock ranged between $TL = 3$ and 4 consistent with a mixture reflective of prey switching. If pollock consumed only nekton that in turn were piscivorous (i.e., the pollock were secondary

piscivores), those pollock would be expected to be $TL = 5$. A mixture of 50% piscivorous prey and 50% zooplankton prey would yield pollock of $TL = 4$. Thus no size class of pollock is precluded from consuming zooplankton given the TL range observed here.

The sharp increase in TL for pollock more than 500-600 mm may reflect consuming a greater proportion of piscivorous prey, which is presumably enabled by their larger gape. Removal of these larger size classes of pollock from a population by fishing would thus be consistent with the "fishing down marine food webs" hypothesis (Pauly et al. 1998).

Long-term prospects?

Brodeur and Ware (1992) reported that zooplankton populations in the northeast subarctic Pacific Ocean fluctuate on inter-decadal time scales, which was postulated to be a climate-driven process for explaining observed long-term changes in nekton populations. Periods of high levels of zooplankton were characterized by their dense occurrence on continental slope waters. There should be an increased likelihood for oceanic subsidies to enhance coastal fishes during periods when slope zooplankton populations are high compared to when slope zooplankton populations are low. Oceanic subsidies in PWS are thus posited to benefit coastal fishes in proportion to inter-decadal fluctuations in slope zooplanktons.

This study provided evidence that subsidies may benefit coastal fish populations like those in PWS by supplementing their carbon base because both pollock and herring shifted more or less in concert. However, pollock values were always slightly less negative than herring, suggesting a lesser dependency on oceanic subsidies. A greater separation in the isotopic composition between these two species in winter is consistent with decreased diet overlap, hence decreased potential for competition, reflected by the greater disparity in mean isotope values during the high subsidy period. Zooplankton abundance may drive competition between pollock and competing species feeding near $TL = 3$. For example, when herring likely depended >50% on oceanic subsidies during October 2005 to March 2006, pollock likely depended $\leq 50\%$ on oceanic subsidies. At other times, pollock had little to no oceanic subsidy dependence.

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Juvenile Walleye Pollock Aggregation Structure in the Gulf of Alaska

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Abstract

Size and shape patterns of juvenile walleye pollock (*Theragra chalcogramma*) aggregations in the Gulf of Alaska are described in relation to biophysical factors such as depth of the aggregation in the water column, water temperature, and age and body condition of the aggregation members. Aggregation characteristics were measured with acoustic data collected with a vertically oriented echosounder, and biophysical data were collected with a large midwater trawl and temperature-depth sensors from two areas near Kodiak Island, Alaska, during 1995-1997 and 2000-2002. Juvenile walleye pollock spatial patterns were expressed using fish aggregation length, height, fractal dimension, and density. Redundancy analysis (RDA) was used to examine the associations of the biophysical factors with the size and shape descriptors of juvenile walleye pollock aggregations. Fish aggregation height increased as a function of fish age, and there was a negative association between depth of the aggregation in the water column and density of fish in the aggregation. There was also a negative association between body condition of the fish and the fractal dimension of the aggregation. These results demonstrate that relatively easily measurable environmental and biological factors can be useful in describing and potentially predicting spatial patterns of fish aggregations. Associations in the fish aggregation structure and biophysical measurements were consistent with expectations based on predation and foraging theory.

Introduction

Many functions of fish shoaling behavior are associated with predator-prey interactions (Pitcher and Parrish 1993). For example, the attack

success of a predator declines with increasing prey group size (Neill and Cullen 1974), and fish find patchy-distributed food faster when in a school (Pitcher et al. 1982). In addition, an increase in group cohesiveness and a decrease in nearest neighbor distance often results from increased predation risk, whereas the reverse occurs as fish hunger levels increase (Morgan 1988).

Other factors contribute to the formation, maintenance, and structural characteristics of fish aggregations. Many fish species congregate at regular intervals to form spawning aggregations (Misund et al. 1998). Group structure may also change as a function of ontogeny. Adult sardines form larger and less dense schools than juveniles (Muiño et al. 2003), and some species of fish lead relatively solitary lives as adults although as juveniles they form well organized schools (Keenleyside 1979). Physical factors can influence the small-scale spatial patterns of fishes. The effect of temperature on the distribution of fish aggregations has been well documented (e.g., Krause et al. 1998, Swartzman 1997). Some species of schooling fish will avoid cold water at the expense of missed foraging opportunities (Misund et al. 1998), yet others will enter cold water only to feed (Olla et al. 1985). The effect of ambient light has also been found to influence fish shoaling structure with declining light intensities generally producing less cohesive groups of fish (O'Conner and Krause 2003).

Walleye pollock are one of the most abundant and commercially important fish in the Gulf of Alaska and Bering Sea (Megrey 1989, Kim 1990). Adults are semi-demersal and in some cases can form "carpet" aggregations near the seafloor that can extend for miles, whereas juvenile pollock are typically found higher in the water column in more discrete groupings (Wilson et al. 2003). Temperature and ambient light levels are two physical factors that influence the distribution of walleye pollock aggregations. Pollock have been observed to exhibit diel migrations to shallower nighttime depths where they form more dispersed layers (Bailey 1989, Brodeur and Wilson 1996b). Adult aggregations appear to avoid cold water regardless of prey density, yet can otherwise be associated with areas where food abundance is high (Swartzman et al. 1994, 1995; Kotwicki et al. 2005).

Although the juvenile stage of walleye pollock has been the focus of numerous behavioral and ecological studies (Brodeur and Wilson 1996a), very few field studies have described juvenile aggregation characteristics and the biophysical factors that may influence their formation and maintenance. Kang et al. (2006) described juvenile walleye pollock school characteristics but only in relation to the age of the school members. Wilson et al. (2003) described juvenile walleye pollock aggregation characteristics and related these to commercial fishing activities. Several laboratory studies have investigated the impact of trade-offs between hunger and predation risk on school patterns of

juvenile walleye pollock. For instance, juvenile walleye pollock formed less cohesive groups as food levels decreased (Sogard and Olla 1997). However, in the presence of a predator, juveniles foraging for clumped food formed more cohesive groups, but larger juveniles and those foraging for dispersed food maintained less cohesive groups (Sogard and Olla 1997, Ryer and Olla 1998b). Although additional laboratory studies have examined the effects of other factors, such as temperature and light, on the behavior of individual juvenile walleye pollock (Olla and Davis 1990, Ryer and Olla 1998a), it is unknown how these and other factors might affect juvenile walleye pollock group structure. Field studies, in particular, are needed to better understand what specific environmental cues are associated with the range of juvenile walleye pollock aggregation patterns in nature. Thus, the objective of our study is to describe juvenile walleye pollock aggregation patterns from two areas of the Gulf of Alaska, and to explore whether associations of these patterns exist with easily measured biophysical data such as depth of the aggregation in the water column, water temperature, and age and body condition of the aggregation members. We also discuss whether the detected associations between aggregation patterns and biophysical data are consistent with expectations based on predation and foraging theory.

Methods

Study area

Spatial patterns of juvenile walleye pollock were described for two areas during two seasons within the Gulf of Alaska near Kodiak Island: (1) during the summers of 2000-2002 in Chiniak and Barnabas troughs on the east side of Kodiak Island (hereafter referred to as "East Kodiak"), and (2) during the winters of 1995-1997 in Shelikof Strait on the northwest side of Kodiak Island (Fig. 1). During these years, strong year classes of juvenile pollock were detected. The abundance of juvenile aggregations during this time facilitated this work to describe aggregation patterns of juvenile pollock. Additionally, the presence of a strong year class over consecutive years provides an opportunity to study aggregation patterns of fish as a function of age.

Field methods

Acoustic-trawl surveys consisted of a series of uniformly spaced parallel transects, from 5.6 km apart southeast of the Kodiak Island to 13.9 km apart west of Kodiak Island (Fig. 1). In some instances, more than one survey pass was conducted over a study area during the same field season (Table 1). A survey pass consisted of a complete acoustic sampling of all transects within an area, and multiple passes were separated in time by 3-4 days. Echo-integration data were collected with a calibrated

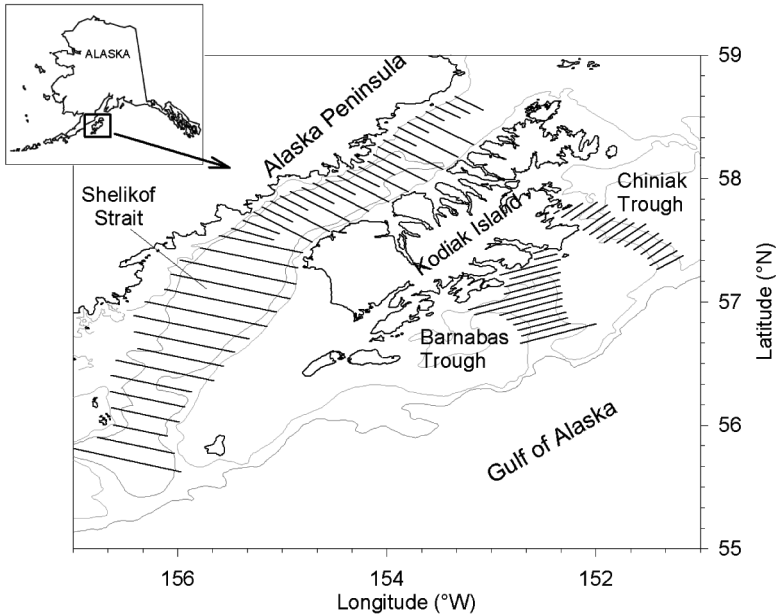


Figure 1. The two survey areas near Kodiak Island, Alaska: East Kodiak (Chiniak Trough and Barnabas Trough) surveyed in 2000-2002 and Shelikof Strait surveyed in 1995-1997. Lines indicate acoustic-trawl survey transects.

Simrad EK500 quantitative echo-sounding system operating at 38 kHz (Bodholt et al. 1989) and were initially logged with a horizontal resolution of about 5-6 m (dependent on vessel speed) and vertical resolution of 0.1-0.5 m using standard methods described in Wilson et al (2003).

Samples were collected with a large pelagic trawl (Guttormsen et al. 2002) to confirm the identity of the species attributed to specific acoustic backscatter and to provide length, weight, and age composition of walleye pollock. Trawl hauls were conducted in areas of high backscatter, so areas with high densities of fish were sampled most heavily. Catches of walleye pollock were sampled to determine fork length (FL) to the nearest 1.0 cm, total body weight to the nearest 2.0 g, and age of the fish.

Temperature profiles were obtained with a temperature-depth probe attached to the trawl headrope in East Kodiak and with a micro bathythermograph attached to the trawl headrope in Shelikof Strait. Conductivity-temperature-depth casts and expendable bathythermograph probes were used to collect water temperature profile data in East

Table 1. Survey areas, survey pass number, number of hauls, and number of analyzed aggregations from Shelikof Strait and East Kodiak (Chiniak and Barnabas troughs).

| Study year | Survey pass | No. hauls | Shelikof Strait | | |
|------------|-------------|----------------|-----------------|-----------------|----------------|
| | | | No. schools | No. schools | |
| 1995 | 1 | 19 | 483 | – | |
| 1996 | 1 | 36 | 867 | – | |
| 1997 | 1 | 28 | 812 | – | |
| | 2 | – ^a | 173 | – | |
| | | East Kodiak | | | |
| | | Chiniak Trough | | Barnabas Trough | |
| 2000 | 1 | 7 | 142 | 12 | – ^b |
| | 2 | 13 | 81 | 10 | – ^b |
| 2001 | 1 | 8 | 274 | 12 | 131 |
| | 2 | 6 | 267 | 9 | 104 |
| | 3 | 10 | 177 | 10 | 120 |
| | 4 | – | – | 2 | 169 |
| 2002 | 1 | 8 | 216 | 12 | 104 |
| | 2 | 14 | 215 | 10 | 107 |
| | 3 | 12 | 205 | 15 | 148 |
| | 4 | – | – | 2 | 179 |

^aPass 2 was a partial pass that only surveyed transects north of 57°20'N.

^bNo juveniles were detected in Barnabas Trough in 2000.

Kodiak and Shelikof Strait at selected locations throughout the study areas (e.g., NMFS 1996, Wilson et al. 2003).

Fish aggregation descriptors

Because walleye pollock in East Kodiak and Shelikof Strait disperse at night (Guttormsen et al. 2002, Wilson et al. 2003), only aggregations observed between one hour after sunrise and one hour before sunset were used in this analysis. Areas where backscatter attributed to adult pollock or unidentified organisms (e.g., euphausiids) overlapped with that from juvenile walleye pollock were also excluded from the present analysis.

Juvenile walleye pollock backscatter was classified into aggregations using Echoview software (SonarData, Tasmania, Australia). The classification designated all aggregations as schools, whether the aggregations were discrete small groupings or long low-density layers (Reid 2000). Echoview software applies school recognition algorithms that correct for pulse-length effects and beam width effects following the methods of Reid and Simmonds (1993), Barange (1994), and Diner (1998) generat-

ing corrected estimates of various school descriptors. School size and shape descriptors used in this analysis include fish aggregation length, height, fractal dimension, and density. Fractal dimension (D) relates the perimeter (P) of a fish aggregation to its area [A , where $D = 2 \ln(P/4)/\ln(A)$] and is an informative measure of shape complexity (Barange 1994, Freon et al. 1996, Coetzee 2000). A fractal dimension of one characterizes the most basic outline shape (i.e., a square), and a fractal dimension of two characterizes the most complex outline shape (Coetzee 2000). To determine fish aggregation density (i.e., number of fish within each aggregation; fish per 10^3 m^3), the mean volume back-scattering strength, S_v (dB re 1 m^{-1}), for each aggregation was converted to a mean volume back-scattering coefficient, sv (m^{-1} ; MacLennan et al. 2002). The sv was then divided by the mean backscatter cross-section, $\bar{\sigma}_{bs}$, of juvenile walleye pollock ($\bar{\sigma}_{bs}$ in m^2 per fish). The $\bar{\sigma}_{bs}$ was calculated using a target strength (TS) to fish length (L_{cm}) model for walleye pollock [$TS = 20 \log(L_{cm}) - 66$; Foote and Traynor 1988] and was based on the population length composition for a given area.

The classification of acoustic backscatter into schools by Echoview software required a series of user-controlled parameters. These parameters were examined over a range of values and evaluated, and the final criteria were chosen based on their ability to provide the best definition of a juvenile walleye pollock aggregation when compared by eye to the original echograms. The final values selected were S_v threshold (-70 dB), minimum school length (40 m), minimum height (5 m), minimum connected length (5 m), minimum connected height (2 m), maximum vertical linking distance (5 m), and maximum horizontal linking distance (20 m). These values were used for all analyses. The criteria chosen to define an aggregation likely contain substantial and unknown biases, and it has been shown that changing the criteria can affect the results (Burgos and Horne 2007). However, if the criteria are kept constant, as in the present study, they should provide useful comparative information about the variability of the fish aggregation structure (Freon et al. 1996, Reid et al. 2000).

Biophysical factors

Water temperature at the location of each fish aggregation (hereafter referred to as "temperature") was determined by matching the mean depth of the aggregation in the water column (hereafter referred to as "aggregation depth") to the corresponding temperature of the nearest vertical temperature profile. The age and body condition of fish within each aggregation were determined from the nearest haul information. The mean body condition of juvenile pollock within each aggregation was calculated using a morphometric body condition factor index determined by body weight deviations from a least-squares fitted length (L)-weight (W) relationship (Jakob et al. 1996; $W = aL^b$, where a and b are

constants). The index eliminates the effect of body size on the data. Two condition factor indices were generated: one for fish off East Kodiak and another for fish in Shelikof Strait.

Statistics

Redundancy analyses (RDA) were used to test the associations of biophysical factors with the juvenile walleye pollock aggregation descriptors using “vegan,” a community ecology package for R software (R Foundation for Statistical Computing, Vienna, Austria). Each survey area was considered a separate data set. The data for East Kodiak and Shelikof Strait are separated both in space and season, so it was not possible to discern whether patterns in the resulting ordination were due to differences in the location or the season between the two areas. RDA is a form of constrained ordination analysis that seeks to partition dominant patterns of variation into a reduced number of gradients that are maximally correlated with explanatory variables (Makarevich and Legendre 2002). For the present study, a matrix of fish aggregation descriptors was analyzed with respect to a corresponding matrix of biophysical factors. RDA assumed the matrix of biophysical factors to be dependent on the explanatory matrix of fish aggregation descriptors. RDA was appropriate for these data because it preserved the Euclidean distance among the fish aggregation descriptors. Aggregation length, height, and density estimates were natural log transformed to stabilize the variance prior to conducting the RDA, and fish aggregation descriptor data were scaled to unit variance. Differences were considered significant at $p < 0.05$.

Both biophysical factor gradients and fish aggregation descriptor gradients were represented in RDA triplot figures as vectors, where vector length is proportional to the strength of the gradient (see Results, Figs. 2-3). The vectors indicate how the gradients load along the first two RDA axes. For example, if a vector gradient bisects the first quadrant of a triplot, the fish aggregations within the first quadrant would have relatively high values for that gradient. The third quadrant is opposite the first quadrant; therefore fish aggregations within the third quadrant would have relatively low values for that gradient. Fish aggregations close to a vector gradient have higher values for the gradient, and fish aggregations with greater perpendicular distance to a vector gradient have weaker associations with the gradient.

Results

Fish aggregations in both study areas and each year were composed of juvenile walleye pollock from a single year class. In Shelikof Strait, the strong 1994 year class of fish was observed in 1995 (age 1, 11.5 mean FL); 1996 (age-2, 20.7 mean FL); and 1997 (age-3, 27.2 mean FL). In

East Kodiak, a strong age group of 2-year-old fish was present in both 2000 (19.5 mean FL) and 2001 (20.6 mean FL) and a strong age group of 3-year-old juveniles was present in 2002 (32.6 mean FL).

The redundancy analysis produced ordinations significantly different from a random distribution for both study areas. A total of 4,974 fish aggregations were analyzed, 2,639 in East Kodiak and 2,335 in Shelikof Strait (Table 1). A range of pre-log-transformed fish aggregation descriptor values and a range of biophysical values are listed in Table 2. For clarity, only the distribution centers of fish aggregation descriptors for each survey pass (e.g., Chiniak Trough 2000, 2001) are plotted in ordination space (Figs. 2-3). The first and second axes of the RDA explained 83.9% and 15.7% of the total variation in fish aggregation size and shape descriptors for the East Kodiak data. Both axes were statistically significant ($p < 0.001$). The first and second axes of the RDA explained 93.2% and 6.1% of the total variation in fish aggregation size and shape descriptors for the Shelikof Strait data. The first axis was statistically significant ($p < 0.001$).

Fish age and aggregation depth were associated with juvenile walleye pollock spatial patterns in both study areas. Fish age and aggregation depth had the highest loadings of the biophysical factors along all significant RDA axes both in East Kodiak and Shelikof Strait (Table 2). In both areas there was a positive relationship between increased age loading and aggregation height, and there was a negative relationship between increased depth loading and aggregation density (Figs. 2-4). This suggests the importance of fish age and aggregation depth in structuring juvenile walleye pollock aggregations, most specifically in structuring aggregation height and density. This also suggests fish age and aggregation depth have a consistent effect on fish aggregation structure across areas and/or between seasons.

Body condition of juvenile walleye pollock was associated with juvenile aggregation patterns only in East Kodiak, but there was no clear association between temperature and juvenile pollock aggregation patterns. Body condition had moderate loadings along the first RDA axis in East Kodiak but not in Shelikof Strait (Table 2), and in East Kodiak there was a negative relationship between increased condition loading and fish aggregation fractal dimension (Figs. 2 and 4). Temperature had moderate loadings along the first RDA axes in both East Kodiak and Shelikof Strait and had high loadings along the second RDA axis in East Kodiak (Table 2). There was a negative relationship between increased temperature loading and aggregation height in East Kodiak (Fig. 2), but there was a positive relationship between these two variables in Shelikof Strait (Fig. 3). These results suggest body condition and temperature were less important in structuring juvenile walleye pollock aggregations than were fish age and aggregation depth. These results also suggest body condition and temperature did not have a consistent effect on

Table 2. Minimum and maximum (pre-log-transformed) values of fish aggregation descriptors and biophysical factors, and loadings of the first and second RDA axes.

| | East Kodiak | | | | Shelikof Strait | | | |
|--|-------------|------------------------|-------|--------|-----------------|------------------------|-------|-------|
| | Min | Max | RDA1 | RDA2 | Min | Max | RDA1 | RDA2 |
| Aggregation descriptors | | | | | | | | |
| Length (m) | 16 | 7115 | -0.65 | 0.32 | 2 | 38121 | -0.76 | 0.40 |
| Height (m) | 4 | 162 | 0.25 | -0.31 | 4 | 124 | 1.101 | 0.23 |
| Fractal dimension | 1.06 | 1.99 | -2.13 | 0.63 | 1.02 | 1.99 | -1.64 | -0.19 |
| Density (fish/10 ³ m ³) | 0.53 | 1.30 × 10 ⁵ | 1.72 | 0.95 | 0.79 | 5.07 × 10 ⁴ | 0.85 | -0.29 |
| Biophysical factors | | | | | | | | |
| Aggregation depth (m) | 16 | 239 | -0.69 | -0.67 | 67 | 244 | -0.68 | 0.58 |
| Temperature (°C) | 5.25 | 10.26 | -0.20 | 0.61 | 2.88 | 5.24 | 0.27 | 0.31 |
| Fish age (years) | 2 | 3 | 0.39 | -0.85 | 1 | 3 | 0.73 | 0.63 |
| Body condition | -0.09 | 0.11 | 0.35 | -0.003 | -0.29 | 0.19 | 0.05 | 0.73 |
| Eigenvalue | | | 0.31 | 0.15 | | | 0.21 | 0.01 |
| % Variance | | | 83.88 | 15.72 | | | 93.24 | 6.10 |

Eigenvalues and the percent of variance explained by the RDA are given.

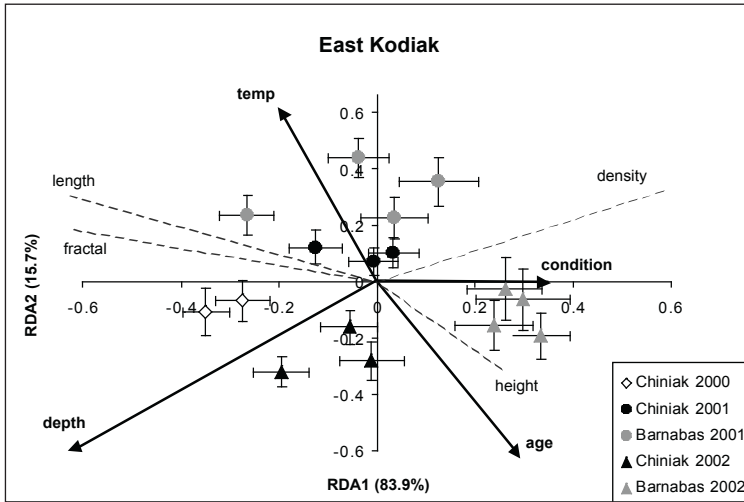


Figure 2. Redundancy analysis diagram showing the estimated distribution center for each East Kodiak trough-pass combination in ordination space. Error bars represent 95% confidence intervals about the mean of each distribution. Identical symbols are indicative of multiple survey passes. The dashed lines represent the aggregation descriptor gradients, and the solid lines represent the biophysical gradients.

aggregation structure across areas and/or between seasons as did fish age and aggregation depth.

Discussion

Many of the trends that were detected among juvenile walleye pollock aggregation descriptors and the measured biophysical factors, including aggregation depth and body condition of the fish, were consistent with expectations based on predation and foraging theory. In some cases, however, the results were more difficult to explain. The fact that aggregation height increased for older juveniles in both areas was one such finding. In this case, other researchers have reported that a spheroid school structure is advantageous to fish because it minimizes the detection envelope of the fish school to underwater predators (Pitcher and Parrish 1993). Because juvenile walleye pollock aggregations were longer horizontally than vertically, the aggregations must decrease in length and/or increase height to produce a more spherical structure. Thus, the increase in aggregation height reported in our work would serve to

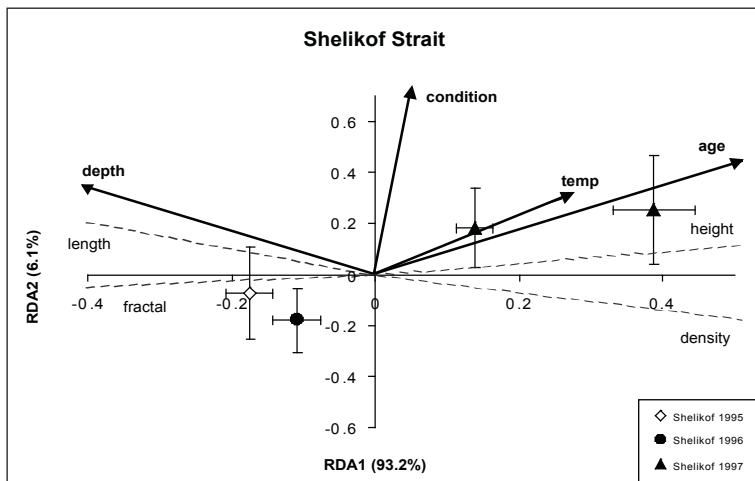


Figure 3. Redundancy analysis diagram showing the estimated distribution center for each Shelikof Strait pass in ordination space. Error bars represent 95% confidence intervals about the mean of each distribution. Identical symbols are indicative of multiple survey passes. The dashed lines represent the fish aggregation descriptor gradients, and the solid lines represent the biophysical gradients.

produce an aggregation shape less detectable to predators. However, predation intensity is typically greater for smaller individuals of many fish species, including walleye pollock (Milinski 1993, Hollowed et al. 2000). Therefore, it is puzzling that the older, larger juveniles rather than younger, smaller fish would form a more spheroid aggregation structure. Other studies have shown that swimming speeds of fishes are generally proportional to body length (Misund and Aglen 1992), and it may be that the reduced swimming speeds for smaller fish, in some way, prevents formation and maintenance of the more spherical aggregation.

Findings based on walleye pollock acoustic data collected off Japan support the association between fish age and aggregation height reported in our study (Kang et al. 2006). They reported that age-1 walleye pollock formed schools of less vertical height than age-2 and adult fish, although this was not the case when compared to age-0 walleye pollock. Their results may have been confounded because they did not use schools of pure age groups in their analyses (a school was designated based on the age group of the majority of the members). Nevertheless, the consistent results between these two studies indicate

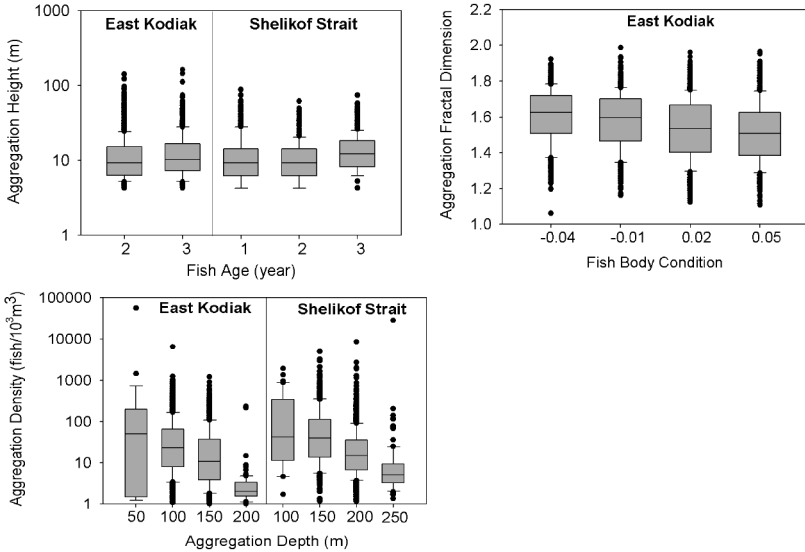


Figure 4. Box plots of the (pre-log-transformed) values of fish aggregation descriptors and biophysical factors showing the associations between fish age and aggregation height, aggregation depth and aggregation density, and body condition of the fish and aggregation fractal dimension. The box plots show the median, 10th, 25th, 75th, and 90th percentiles. Note the use of a logarithmic scale on the y-axis in two of the plots.

that the trend in fish aggregation height among age-1 and older age groups may extend over a broad geographical range.

Other results from the present study were consistent with what one might expect based on the advantages that schooling behavior confers to its members in predator-prey interactions. Fish aggregation density estimates decreased for deeper dwelling aggregations in both the East Kodiak and Shelikof Strait study areas. Although the effects of depth on spatial patterns of fishes are poorly known, numerous studies have shown that fish schools become less cohesive as light intensity decreases (Ryer and Olla 1998a, O'Conner and Krause 2003). In the presence of predators, however, fish typically form more compact schools so they can communicate rapidly and perform well-coordinated escape tactics (Pitcher and Parrish 1993). Light is essential to this communication because visual and behavioral cues are important components in information transfer among fish (Ryer and Olla 1991, Lachlan et al. 1998). Laboratory studies showed that juvenile walleye pollock will disperse as light levels decrease, even in the presence of a

predator, most likely because it becomes more difficult for the fish to see one another (Ryer and Olla 1998a). In the Gulf of Alaska, potential demersal predators of juvenile walleye pollock such as arrowtooth flounder (*Atheresthes stomia*), halibut (*Hippoglossus stenolepis*), and adult walleye pollock increase with proximity to the seafloor (Bailey 1989, Hollowed et al. 2000). The influence of diminishing light levels on the activity and foraging success for these predators is unknown. However, it is conceivable that group compaction might be favored by juvenile walleye pollock when they are deeper and in closer proximity to these demersal predators, but ambient light levels are simply too low for this to occur.

Increased body condition for juvenile walleye pollock off East Kodiak was associated with a decrease in aggregation fractal dimension. An increase in body condition is generally attributed to an increase in feeding or an increase in prey concentration (Pedersen and Jobling 1989, Kloppmann et al. 2002), and body condition can be used to approximate long- and short-term changes in food abundance and quality (Grant and Brown 1999). The high body condition of fish in Barnabas Trough in 2002 suggested that the fish had recently consumed high quality or large quantities of prey. This could have occurred prior to the fish moving into the area or while they were within Barnabas Trough. If the latter were true, then prey concentrations in the East Kodiak study area were likely greatest within Barnabas Trough in 2002. The less complex aggregation shape, as indicated by a lower fractal dimension in Barnabas during 2002, implies the fish were not dispersing from the aggregations. Other studies have demonstrated two potential mechanisms behind this observation. Group cohesiveness decreases with hunger (Morgan 1988), because fish disperse from the safety of their school to forage (Godin and Smith 1988). If the fish in Barnabas Trough in 2002 had recently consumed high quality or large quantities of prey, the need to disperse from the aggregation to seek additional prey may have been reduced. Alternatively, being part of a group often intensifies competition for food (Bertram 1978), but competition costs can be reduced if prey densities are high (Eggers 1976). If the East Kodiak prey field was more abundant within Barnabas Trough in 2002, competition costs would be reduced and the fish could have foraged from within the safety of the aggregation.

Fish aggregation size and shape patterns were not associated with body condition of juvenile walleye pollock during the winter in Shelikof Strait. Walleye pollock feed intensely in summer but only feed sporadically during winter months (Sogard and Olla 2000, Yamamura et al. 2002). As a consequence, body condition falls during winter and recovers quickly in summer (Yamamura et al. 2002). Thus, during summer, foraging behavior may be a more important component for mediating fish aggregation behavior, whereas during winter months, when

fish feed less frequently, other factors may become more influential in structuring the group.

This study demonstrated that relatively easily measurable environmental and biological factors can be useful in describing and predicting spatial patterns of juvenile walleye pollock aggregations. Because the data for East Kodiak and Shelikof Strait are separated both spatially and temporally, it was not possible to discern whether observed patterns are due to differences in location or season. However, the consistent effect that fish age and aggregation depth had on juvenile aggregation patterns across these locations and/or seasons suggest that these two factors may act as strong, stable forces that continuously influence and structure juvenile walleye pollock aggregations through predator avoidance and evasion. Foraging behavior may also be important in structuring the fish aggregations but only during times when prey availability is relatively high.

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Walleye Pollock as Predator and Prey in the Prince William Sound Ecosystem

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Abstract

Research during the Sound Ecosystem Assessment (SEA) Program during the mid-1990s identified walleye pollock and Pacific herring as the two major pelagic fish biomasses in Prince William Sound. Pollock predation was also identified as a major source of mortality on juvenile pink salmon. Subsequent research at the Prince William Sound Science Center has focused on three aspects of the role of pollock in the Prince William Sound ecosystem: (1) winter-period population abundance, (2) pink salmon predator monitoring, and (3) marine mammal predation studies. Prince William Sound Science Center conducted winter-period surveys of adult pollock from 1995 to 2003. Pollock biomass in Prince William Sound ranged from 22,000 to 43,000 metric tons. The pink salmon predator monitoring studies assessed pelagic fish abundance and distribution synoptic with spring-period zooplankton surveys from 2000 to 2006. Both pollock and herring showed progressive migrations during the spring that were consistent with predation on inshore fishes including pink salmon fry. Marine mammal assessment was added to the winter-period surveys beginning in 2000. Steller sea lion abundance and distribution were positively correlated with herring and negatively correlated with pollock. Walleye pollock and Pacific herring exhibit major differences in overwintering distributions that have substantial impacts on predator populations, especially marine mammals and sea-birds. The difference in relative dominance between these two species is likely a major factor in long-term ecosystem change.

Introduction

Walleye pollock (*Theragra chalcogramma*) is well known as a valuable commercial fish, an important forage fish for marine fish and wildlife, and as a dominant marine competitor and predator (Dwyer et al. 1987, Lloyd and Davis 1988, Springer 1992, Livingston 1993). The importance of the commercial fishery for walleye pollock is highlighted by the six million ton catch in 1985 worth over \$1 billion in ex-vessel income, which made it the world's largest single-species fishery (FAO 1996). However, the economic importance of pollock may be overshadowed by its ecological importance. Pollock dominates the pelagic fish biomass in the Bering Sea (Livingston 1993). Rice (1995) concluded that it is common for one or two planktivorous fishes to dominate arctic and subarctic marine food webs. Where such conditions exist, Rice maintained that understanding the dominant planktivores is a prerequisite to understanding the fate of changing marine production and fluctuations in satellite predator populations.

Walleye pollock populations throughout the Gulf of Alaska and Bering Sea have been studied since the 1950s (Traynor 1986, Dwyer et al. 1987, Bailey et al. 1995, Brodeur and Wilson 1996). Bottom trawl surveys that were initiated in the mid-1960s to assess red king crab (*Paralithodes camtschaticus*) were expanded in the 1970s to include demersal fish (Bakkala and Alton 1986). Since pollock was a major component of the trawl catch of demersal fish, these surveys became a major assessment tool. The first echo integration midwater trawl (EMT) survey was conducted in 1979 (Thorne 1979, Karp and Traynor 1988, Traynor et al. 1990). Subsequently, acoustic surveys have become an important component of commercial fishery management (Hollowed and Megrey 1990; Hollowed et al. 1996; Wilson 1994; Wilson et al. 1995, 1996).

Annual commercial harvests of pollock in Prince William Sound (PWS) were primarily from incidental catches and less than 4 t prior to 1995. The Alaska Department of Fish and Game (ADFG) and the National Marine Fisheries Service (NMFS) had conducted a bottom trawl survey of PWS during summer 1989 (Haynes and Urban 1991). The survey, using a 400 mesh eastern otter trawl, estimated the pollock biomass at 9,500 t. However, studies initiated after the 1989 *Exxon Valdez* oil spill suggested that walleye pollock, along with Pacific herring (*Clupea pallasii*), were the dominant pelagic fish biomasses in PWS (Thomas et al. 1997). Acoustic surveys of herring were implemented by the Prince William Sound Science Center (PWSSC) in 1993. In 1995, ADFG established an exploratory fishery on pollock with a harvest guideline of 950-2,000 t (Bechtol 2002), and PWSSC initiated winter-period EMT surveys of pollock. These surveys continued through 2003, although emphasis changed after 2000 because of concerns about relationships with the endangered western stock of Steller sea lions (*Eumetopias jubatus*)

(Ferrero and Fritz 2002). PWSSC conducted annual spring-period surveys of both pelagic fish and zooplankton from 2000 to 2006 to investigate the role of pollock as a predator on pink salmon (*Oncorhynchus gorbuscha*) fry. Limited fall-period surveys were also conducted as part of the study of herring, pollock, and Steller sea lion interrelationships. With the exception of incidental information included in papers about Steller sea lion predation on herring (Thomas and Thorne 2001, 2003), previous reporting of this extensive research effort on pollock in PWS has been limited to contract and conference reports.

Methods

Winter and fall-period surveys of pollock

PWSSC conducted seven winter-period EMT surveys of pollock in PWS between 1995 and 2003. An additional survey was conducted in 2006, but was focused on comparative observations of pollock and marine mammals rather than abundance assessment. Acoustic techniques, specifically echo integration, have been used for decades to assess abundance of pelagic fishes (Thorne 1971; 1983a,b; MacLennan and Simmonds 1992). Evidence from acoustic records suggests that adult pollock begin to accumulate in PWS in early winter, and remain in aggregations until after spawning in April. During this time, the distribution is almost exclusively pelagic between 175 and 300 m depths. The acoustic surveys were designed to take advantage of this accessible and relatively restricted distribution (Thomas et al. 1997).

The PWS survey design consisted of a three-stage sampling procedure (Cochran 1977, Scheaffer et al. 1986). First, historical patterns, information from commercial fishermen, and broad area sonar/echo-sounder surveys were used to identify the general distribution of pollock within PWS. Second, a quantitative (echo integration) acoustic survey was conducted, with sampling intensity proportional to abundance indicated in stage one. Third, midwater trawl net sampling was directed toward the surveyed concentrations to obtain biological information including length and weight (McClatchie et al. 2000). Confidence intervals around estimates were determined from repeated transects to avoid problems with autocorrelation or dependence upon model assumptions (Thomas and Thorne 2003). The 95% confidence intervals during the 1990s surveys ranged from $\pm 20\%$ to 45% of the mean estimate, but improved to $\pm 10\%$ -15% during the 2000-2003 surveys as a result of a more focused survey design. Midwater trawling was conducted by ADFG using the RV *Pandalus*. Additional biological data were obtained from ADFG sampling of commercial fishing landings in Cordova. Several quantitative scientific echosounders were used during the study, including frequencies of 38 kHz, 70 kHz, and 120 kHz. Extensive signal to

noise studies were conducted to document the detectability of the pollock at all three frequencies.

Published target strength relationships for pollock (Traynor and Williamson 1983, Traynor 1996) were used to convert echo integration values to absolute density estimates. The validity of the target strength assumptions was verified by in situ measurements at multiple frequencies in PWS.

Visual counts of Steller sea lions and whales from both vessels and airplanes were added to the acoustic surveys in 2000. Twenty-seven aerial surveys were conducted from 2000 to 2006. The aerial surveys used a survey plane equipped with a global positioning system (GPS) linked computer system. Surveys were flown at an altitude of 300 m. Sea lions, whales, and aggregations of marine birds can readily be seen and identified from this altitude. GPS-recorded flight paths and the locations of marine birds and mammals were plotted on a map of PWS. The aerial survey estimates were supplemented by census from the acoustic survey vessel. The acoustic surveys for pollock were primarily conducted during daytime, although pollock diel vertical migration is minimal during winter in PWS. All marine mammals within visual range were counted during the daytime transects. Herring surveys were primarily conducted at night. Infrared scanners were used synoptic with these surveys, as well as with the infrequent nighttime surveys for pollock (Thomas and Thorne 2001). The focus on Steller sea lion/herring/pollock interrelationships also led to fall-period surveys in 2001, 2004, and 2006. The primary objective of these surveys was to document seasonal changes in herring distribution, but observations were also made on both adult and juvenile pollock.

Spring surveys

The Prince William Sound Science Center conducted annual monitoring of the spring abundance and distribution of both macrozooplankton and pelagic fish populations from 2000 to 2006. This was an extensive effort that included acoustic and net sampling for zooplankton as well as synoptic acoustic measurements of pelagic fish abundance. For the purposes of this paper, the reporting is limited to the results of the fish monitoring effort.

Pollock is known to be a major predator on pink salmon fry. High concentrations of macrozooplankton, specifically the large-bodied copepods of the genus *Neocalanus*, were believed to provide both a prey-sheltering mechanism and a food source for the juvenile pink salmon (Willette et al. 2001). Six areas in PWS were sampled all seven years (Fig. 1). Three of the areas extended along the main basin of PWS from Bligh Island to the Hinchinbrook Entrance, and three extended from Perry Island Passage out through Knight Island Passage, a well-documented pink salmon nursery and out-migration corridor (Cooney et

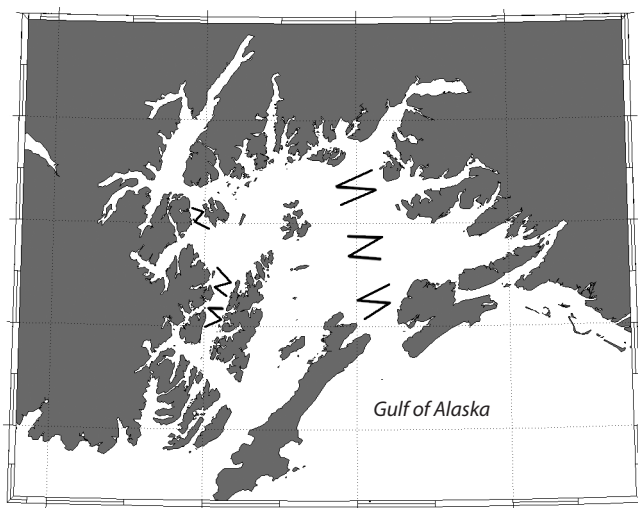


Figure 1. Location of spring-period acoustic transects in Prince William Sound.

al. 1995, Willette et al. 2001). Three surveys were conducted each year at approximately three-week intervals from late April to early June (Table 1). Several multiple-frequency systems were used during the course of the program. Fish densities were typically estimated using a 120 kHz frequency, although 70 kHz and 38 kHz systems were also used some years. Acoustic scattering from fish was measured in the upper 250 m. All systems were calibrated with standard targets following procedures of Foote et al. (1987). The acoustic data were analyzed using standard echo integration techniques (Thorne 1983a,b; MacLennan and Simmonds 1992). A generalized acoustic cross-section equivalent to -32 dB per kg was used to estimate fish biomass from the fish backscatter (Thorne 1983a).

Results

Winter-period biomass estimates and trends

The initial acoustic survey of walleye pollock biomass in PWS in 1995 produced an estimate of $37,963 \pm 9,420$ t. The biomass estimates peaked at $42,972 \pm 19,223$ t in 1998, then declined to $22,101 \pm 2,512$ in 2003 (Fig.

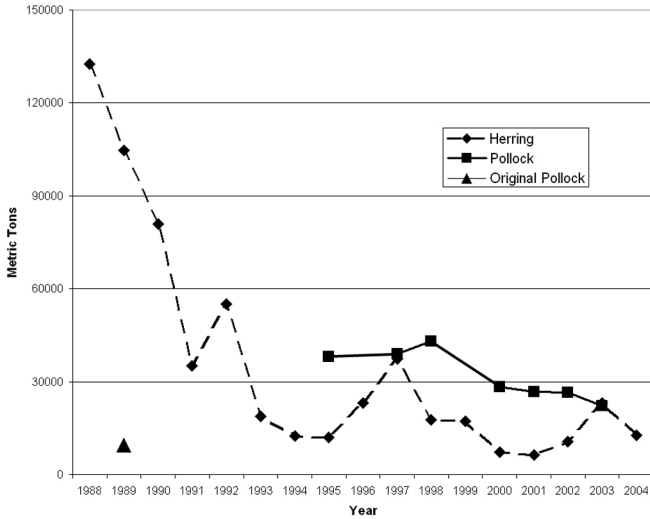


Figure 2. Comparison of herring and pollock biomass estimates in Prince William Sound, 1988 to 2004. Herring values after Thomas and Thorne (2003).

2). These estimates were considerably higher than from the bottom trawl survey in 1989. They were also higher than corresponding estimates of the Pacific herring biomass, but substantially lower than the herring biomass prior to its collapse after the *Exxon Valdez* oil spill (Thomas and Thorne 2003). The decreasing trend of pollock abundance in PWS over the 9-year period was significant at the 95% level (Table 2).

From January through March, adult pollock were distributed primarily in deeper basins adjacent to the Gulf of Alaska and at depths between 175 and 300 m (Figs. 3-4). In contrast, herring are distributed in protected bays and inlets at depths of 10-40 m (Thomas and Thorne 2001, 2003). Steller sea lion distributions were closely associated with herring distributions rather than pollock, although commercial fishing for pollock had been implicated in the decline of the western stock of Steller sea lions (NMFS 2000). Steller sea lion numbers were positively correlated (99%) with herring abundance from synoptic aerial and acoustic surveys and negatively correlated (99%) with pollock abundance (Table 2). Only one Steller sea lion was ever detected above pollock concentrations in PWS throughout the extensive winter-period aerial and vessel surveys.

Table 1. Dates of spring cruises, 2000-2006.

| Year | Cruise 1 | Cruise 2 | Cruise 3 |
|------|----------------|-----------|------------|
| 2000 | May 3-4 | May 12-13 | May 22-26 |
| 2001 | April 18-20 | May 11-14 | June 13-15 |
| 2002 | April 23-25 | May 11-13 | May 29-30 |
| 2003 | April 28-May 1 | May 15-18 | June 11 |
| 2004 | April 23-25 | May 12-14 | June 2-4 |
| 2005 | April 20-22 | May 8-10 | June 7-8 |
| 2006 | April 29-May 1 | May 12-14 | June 8-9 |

Fall-period observations

Fall-period observations of juvenile and adult pollock were incidental to surveys that investigated predation by Steller sea lions on herring. Juvenile pollock were known from Sound Ecosystem Assessment observations to be distributed primarily within bays during fall, overlapping herring distributions (Stokesbury et al. 2000). PWSSC fall-period surveys during 2001, 2004, and 2006 encountered, sampled, and measured juvenile pollock in several bays. The average juvenile pollock depth was 20.2 m at night and 44.4 m during day. Juvenile pollock schools were less dense than herring schools. No Steller sea lions were associated with the juvenile pollock schools, but humpback whales were observed diving above the schools.

Unlike during winter, adult pollock were not seen in dense, deep layers during fall. However, adult pollock were often found in shallower bays and inlets. The fish could be detected acoustically and sampled by hand line, and were extensively foraging on age 0 herring.

Spring-period monitoring

Two distinct patterns of pelagic fish movement were observed during the spring-period monitoring from 2000 to 2006. The first was a general, progressive movement out of the deep main basins and into shallower and more protected regions of PWS (Fig. 5). The highest fish biomass in the main basin was observed during the first cruise every year except 2002. For all years combined, the fish biomass in the main basin during the first cruise was significantly higher (95%) than that observed during the last cruise. The inverse was seen in the corridor. The highest fish biomass in the corridor was observed during the last cruise every year except 2004, and again the fish biomass measured during the last cruise was significantly higher (95%) than that observed during the first for all years combined.

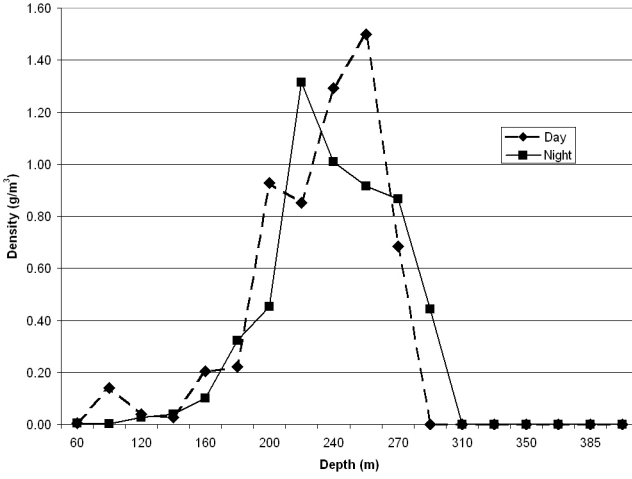


Figure 3. Typical winter-period vertical distribution of adult walleye pollock in Prince William Sound.

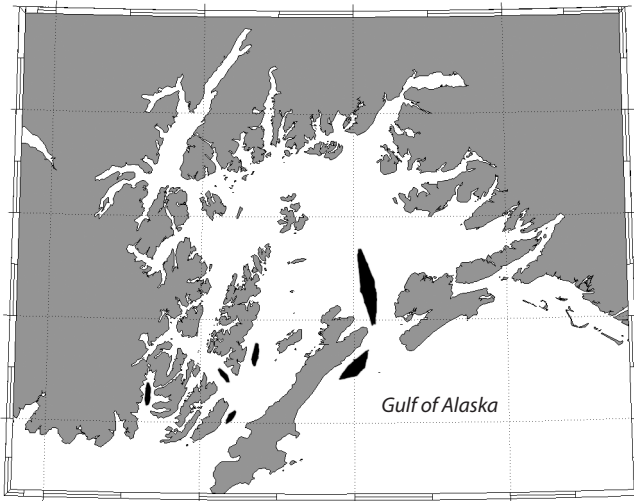


Figure 4. Typical horizontal distribution of adult walleye pollock in Prince William Sound during winter.

Table 2. Tests of linear regressions.

| Comparison | n | r | t | Significance |
|--|----|-------|------|--------------|
| Trend of pollock abundance 1995-2003. | 7 | -0.87 | 3.95 | 95% |
| Synoptic aerial survey counts of Steller sea lions and acoustic estimates of herring biomass, 2000-2006. | 18 | 0.88 | 7.41 | 99% |
| Synoptic aerial survey counts of Steller sea lions and acoustic estimates of pollock biomass, 2000-2006. | 13 | -0.60 | 2.49 | 99% |
| PWS Steller sea lions versus hindcast of herring abundance from mile-days of spawn, 1973-2005. | 13 | 0.72 | 3.41 | 99% |
| PWS Steller sea lions census, 1994-2004. | 6 | 0.26 | 0.54 | N.S. |

PWS = Prince William Sound.

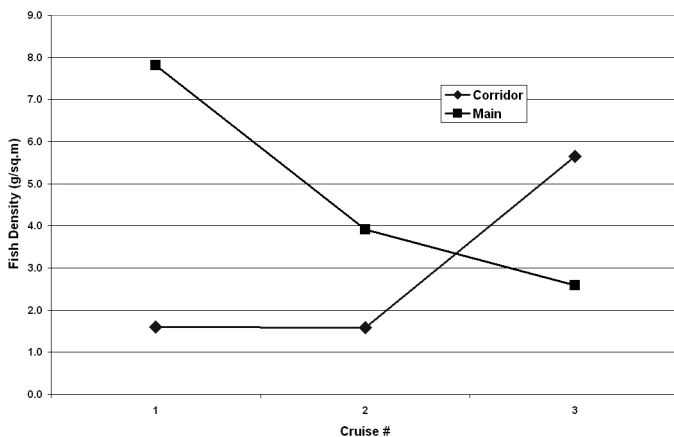


Figure 5. Progressive spring-period movement of pelagic fish, primarily pollock, out of main basins and into more protected regions of Prince William Sound. See Table 1 for cruise dates.

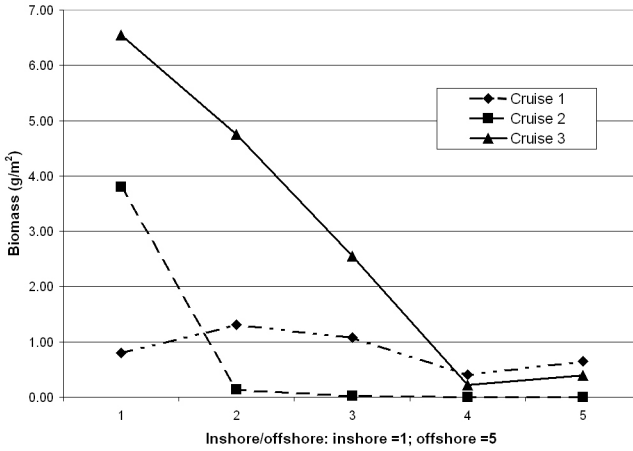


Figure 6. Progressive shoreward movement of herring and pollock during spring 2001, a year of low macrozooplankton abundance. See Table 1 for cruise dates.

The second pattern was a progressive inshore movement in the corridor region. To illustrate this, transects were divided into five equal sections, with section 1 the most shoreward 20% of each transect and section 5 the central 20% (Fig. 6). These transects are typically 3-4 km in length. The shoreward movement was associated with the odd calendar years, which were characterized by lower abundance of large copepods. The shoreward section had significantly higher (95%) fish density than the central section for odd years, but not for even (Fig. 7).

Discussion

Winter

Nearly 30 years ago, Thorne (1979) noted that adult walleye pollock in the Gulf of Alaska were distributed near the bottom above the continental shelf, but were totally pelagic off the slope. As a consequence of these distributional characteristics, both acoustic and bottom trawl surveys are critical tools in the NMFS management program for pollock in both the Gulf of Alaska and Bering Sea. In contrast, PWS is dominated by relatively deep basins. This contrast appears to impact several aspects of pollock ecology in PWS. Winter distributions of pollock in PWS appear to be exclusively pelagic. There are substantial basins with sufficient depth to accommodate the apparent preferred depth distributions of 175-300 m. The lower abundance of pollock estimated from the original

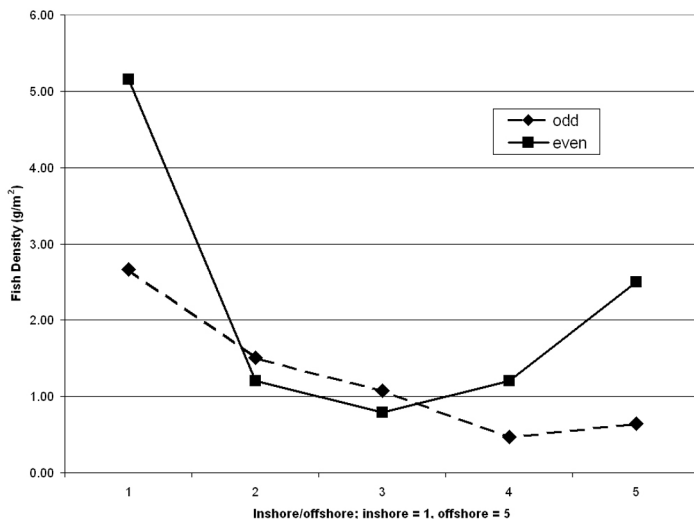


Figure 7. Average inshore/offshore distribution of fish in the corridor region for odd and even year surveys.

summer bottom trawl survey in 1989 may have a seasonal component, but the difference is more likely the result of the limited near-bottom distribution of pollock. The higher acoustic estimates are also unlikely to represent a substantial increase in abundance between 1989 and 1995, since ADFG has conducted subsequent summer bottom trawl surveys, with generally similar results to the 1989 survey (Bechtol 2002).

The different depth regimes may also explain some of the disparity in the reported role of pollock as a food source for Steller sea lions. The initial report in the journal *Nature* that Steller sea lions in PWS focused on herring rather than pollock (Thomas and Thorne 2001) was controversial, although it is now well documented. Some of the disparity is related to season, since most historical research on Steller sea lion foraging behavior was conducted during summer. However, predation by Steller sea lions on pollock in the Gulf of Alaska and Bering Sea may result from the inability of pollock to achieve the depths needed to discourage sea lion predation.

The observation in this paper that Steller sea lions in PWS focus on herring rather than pollock is supported by other data. Agency counts of Steller sea lions in Prince William Sound (Kruse et al. 2000, Sease et al. 2001) from 1973 to 2005 are positively correlated (99%) with herring abundance as measured by the magnitude of herring spawn (Table 2). There are only two years of agency Steller sea lion counts synoptic with

our pollock estimates. However, the Steller sea lion abundance in PWS from 1994 to 2004 trends upward, although not significantly (Table 2), while the pollock abundance trend in our surveys is significantly downward.

Fall

The Exxon Valdez Oil Spill Trustee Council has recently expressed concern over the lack of recovery of the PWS herring stock. Among the factors that have been suggested to hinder recovery are predation and competition. Pollock is clearly the main competitor. The limited observations during fall suggest that adult pollock may also be a major predator, especially on age 0 herring. The observations also suggest that juvenile pollock may provide important forage for humpback whales. These aspects of pollock ecology in PWS need far more study.

Spring

Spring period zooplankton monitoring in PWS showed high abundance of large copepods in 2000 and 2002 and moderate abundance in 2004 and 2006. Abundance was low in 2001 and 2003, and moderate in 2005. A significant inshore movement of pelagic fish was detected during the odd calendar years, which had the generally lower zooplankton abundance. Juvenile pink salmon are distributed near shore, while zooplankton distributions are more cosmopolitan. A shoreward movement of pollock and herring would be an expected characteristic of prey switching from zooplankton to pink salmon (Willette et al. 2001).

The pelagic fish components were not separated in this study. However, pelagic fish biomass in PWS is dominated by pollock and herring. During the day in spring, adult pollock are distributed primarily as individual fish in the upper 150 m, while herring break into small, dense near-surface schools. Both components shared the inshore movement, and Willette et al. (2001) documented prey switching for both pollock and herring.

Conclusions

Rice (1995) and Cury et al. (2003) stress that understanding dominant biomasses is a key to understanding ecosystem function. The relatively long-term monitoring of pollock and herring, the two dominant pelagic biomasses in PWS, and their interactions with other species, has provided important insights into the functioning of the PWS ecosystem. One is the impact of the contrasting winter-period distributions on marine mammals and birds. Herring overwinter in protected bays and inlets at depths generally less than 40 m and are highly concentrated at densities greater than 0.1 kg per m³. This distribution is very amenable to foraging by surface-oriented marine mammals and birds. In

contrast, adult pollock overwinter in deeper, offshore basins at depths greater than 150 m and are more cosmopolitan, but at densities 100 to 1000 times lower than herring densities. It is apparent from the Prince William Sound Science Center research that Steller sea lions depend on herring for critical overwinter forage, and other research has shown that herring are critical to many species of marine birds (Irons et al. 2000). A change in the relative dominance between herring and pollock would have a major impact on ecosystems like PWS. The role of pollock as a predator on juvenile herring may be a factor in the dominance by pollock in the Gulf of Alaska and the lack of recovery of herring in PWS.

The Prince William Sound Science Center spring-period surveys provide some validation of the conclusions of the Sound Ecosystem Assessment Program with regard to pollock. The movement of pollock out of the main basin and into inshore waters during years of low abundance of large copepods was clearly consistent with the prey-switching behavior documented by Willette et al. (2001). The impact of this behavior on pink salmon survival is the object of continuing studies by Prince William Sound Science Center.

While considerable progress has been made, it is clear that far more is needed to effectively address the complex role of pollock in the Prince William Sound ecosystem.

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Variation in the Trophic Level of Pacific Cod with Changes in Size and Season

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Abstract

The effect of fishing on the marine ecosystem has been often summarized as the trend in the mean trophic level of the catch. This metric has been shown to be declining in many parts of the world, a trend popularly known as “fishing down the food web.” The method has been criticized, however, because it typically considers only a single trophic level value for each component of the catch while considerable variation is known to exist in the food habits of marine organisms both seasonally and ontogenically. Examining the seasonal food habits of Pacific cod we determine that significant differences in trophic level exist both with increasing size of the cod as well as by season. However, adjusting the mean trophic level of the entire commercial catch for changing cod trophic levels does little to change the interpretation of the status of Gulf of Alaska fisheries.

Introduction

The effect of fisheries on the marine ecosystem has been the subject of intense investigation over the last decade. One of the most influential metrics developed as an indicator of fishing effects on the ecosystem has been the mean trophic level of the fisheries landings (Pauly et al. 1998). Declining mean trophic level of the fishery is commonly thought to demonstrate the shift from a fishery based on long-lived large predator species to one dominated by smaller, shorter-lived, zooplanktivorous species (Pauly et al. 2001), a phenomenon known as “fishing down the food web” (Pauly and Palomares 2005). Changes in mean trophic levels of the catch may not always be due to fishing effects, however. Climate regime shifts have also been shown to dramatically reorganize

the marine ecosystem (Hunt et al. 2002, Litzow 2006) with resulting major changes in the composition and mean trophic level of the commercial catches (Anderson and Piatt 1999).

Trophic level (TL) represents the position of an organism in the food web where primary producers (plants and detritus) by definition have a TL of 1. The TL of marine consumers can range from a value of 2.0 for first order consumers such as herbivores and detritivores, to as high as 5.5. The latter value is rare, occurring only in specialized predators of marine mammals such as polar bears and killer whales. Trophic levels can be determined empirically through the analysis of diet composition data (Odum and Heald 1975), obtained as output from a food web trophic model such as ECOPATH (Christensen and Pauly 1992, www.ecopath.org), or assessed using the stable isotope ratio of $^{15}\text{N}/^{14}\text{N}$ which increases by 0.34% at each feeding step in the food web (DeNiro and Epstein 1981, Kline and Pauly 1998).

The use of the mean trophic level of the fisheries landings as an ecosystem indicator has not been without its detractors (Caddy et al. 1998, Essington et al. 2006). Assigning a single TL value for each species in the catch, in particular, has been criticized since it fails to take into account changes in diet that occur as animals grow larger. The trophic level of a species can change by as much as 3 levels from birth to maturity for some top predators (Caddy et al. 1998). Pauly and Palomares (2005) argue, however, that most ontogenic changes tend to be small and as a fishery removes the larger individuals of a fish stock it would also have the effect of lowering the mean trophic level assigned to that species, resulting in an underestimation of the decline caused by fishing effect on the mean trophic level of the fishery.

In addition to ontogenic changes in diet, intraspecific seasonal variations in food habits can be considerable (Daan 1973); but the diet composition data used to calculate TLs is typically taken from a limited number of data sets with seasonal food habits data sets being rare. In this study we utilize a seasonal diet composition data set of Pacific cod *Gadus macrocephalus* to determine the magnitude of both seasonal and ontogenic trophic level changes in this species. The range of cod TLs as determined empirically from seasonal diet composition is then used as an input in the calculation of the mean TL of the entire commercial catch. This approach is used to answer the question: do corrected values for Pacific cod TL appreciably change the interpretation of the changes in the mean TL?

Pacific cod are well suited for this study since they are generalist, keystone predators that feed on prey items from several trophic levels (Jewett 1978, Albers and Anderson 1985, Aydin et al. 2002, Yang et al. 2006), both up in pelagic and benthic areas. They are also an important component of the commercial fisheries in the North Pacific with

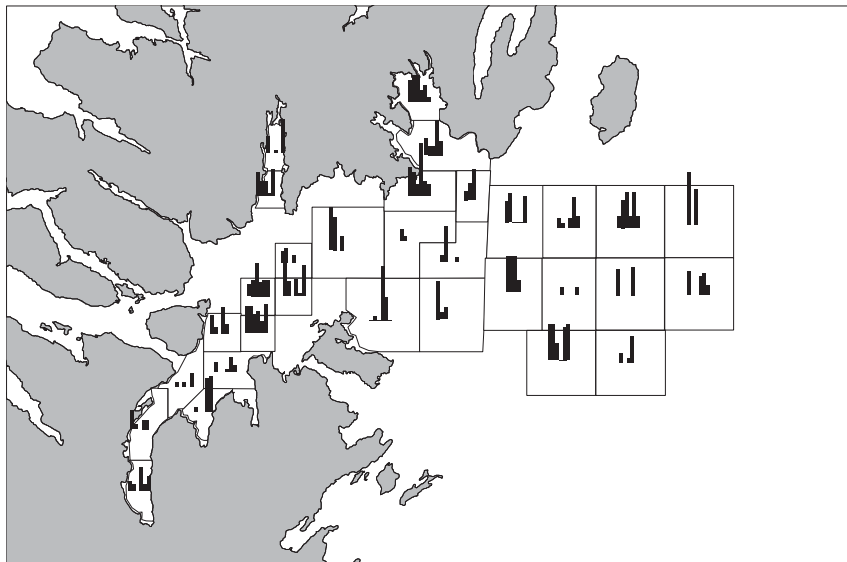


Figure 1. Station locations in Marmot Bay, Kodiak Island, Alaska, where stomachs were collected for diet composition. Each sampling period is represented by a bar with the tallest bar equaling 23 stomachs.

catches averaging over 270,000 metric tons from 1995 to 2005. While overshadowed by walleye pollock and pink salmon catches, Pacific cod catch represented 9% of the Gulf of Alaska commercial fisheries harvest from 2000 to 2004 (NPFMC 2006).

Methods

Sample collection and laboratory analysis

Pacific cod (hereafter referred to as cod) stomachs were collected during six sampling periods: June 20-24, August 24-29, October 26-31, 1998; and January 7-17, March 30-April 5, and June 19-23, 1999 from 31 stations in Marmot Bay, on the northeast corner of Kodiak Island (Fig. 1). Cod were captured by an Alaska Department of Fish and Game (ADFG) research vessel towing a 400 Eastern bottom trawl net targeting soft substrates. The vessel made one tow per station during each sampling period, the tow location being determined by the vessel captain. Mean depth, bottom temperature, and starting and ending locations of each tow were recorded.

The stomachs were collected at sea following protocols established by the National Marine Fisheries Service (NMFS) Alaska Fisheries Science Center (e.g., Yang et al. 2006). A maximum of 40 stomachs per station were collected, with a minimum sample per station of 5 stomachs. Five specimens for every 10 cm size group were targeted. Stomachs from 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 at NMFS Alaska Fisheries Science Center laboratory to the lowest taxonomic level possible and enumerated. Wet weights were recorded after the contents were blotted with paper towels. When intact, commercial fish species were measured to the nearest centimeter fork length.

Data analysis

Cod prey items were assigned a trophic level as determined by a food web model for the Gulf of Alaska developed by K. Aydin and others at the NMFS Alaska Fisheries Science Center (pers. comm.). This model includes the microbial loop, which increases the TL of animals with TL > 2.5 by 0.5 levels over estimates from models not including the microbial loop (K. Aydin, pers. comm.). For prey items that were not included in the food web model, species TL values were taken from the Fishbase database, increased by 0.5 to include the microbial loop. (www.fishbase.org, Froese and Pauly 2000). The prey were assigned a single TL based on their taxonomic identity even though there is some variation in the TL of the prey species with size. Detailed diet information by size is not available for many prey taxa. In addition, the latitude for variation in TL decreases for species lower in the food web. The trophic level of each individual Pacific cod was calculated as

$$TL_i = 1 + \sum_{j=1}^n DC_{ij} TL_j$$

where i is the individual cod, j is the n th prey, and DC_{ij} is the diet composition as fractions of each j in the diet of i (Pauly et al. 2001).

The trophic levels of cod calculated from the diet composition data were evaluated using analysis of covariance (ANCOVA) to determine if cod length or season had significant and independent effects on TL (Crawley 2002). Regression equations of cod TL on length by season were then used to calculate the TL of cod measured during sampling of the commercial fishery. Individual trophic levels were then averaged to obtain the TL of cod in the commercial catch. Nearly all cod retained in the fishery are from 40 to 80 cm fork length so this was the size range used in the analysis. The range of TL values by season from June 1998 to June 1999 calculated from the cod catch was then input into calculations of the overall TL of all commercial landings using

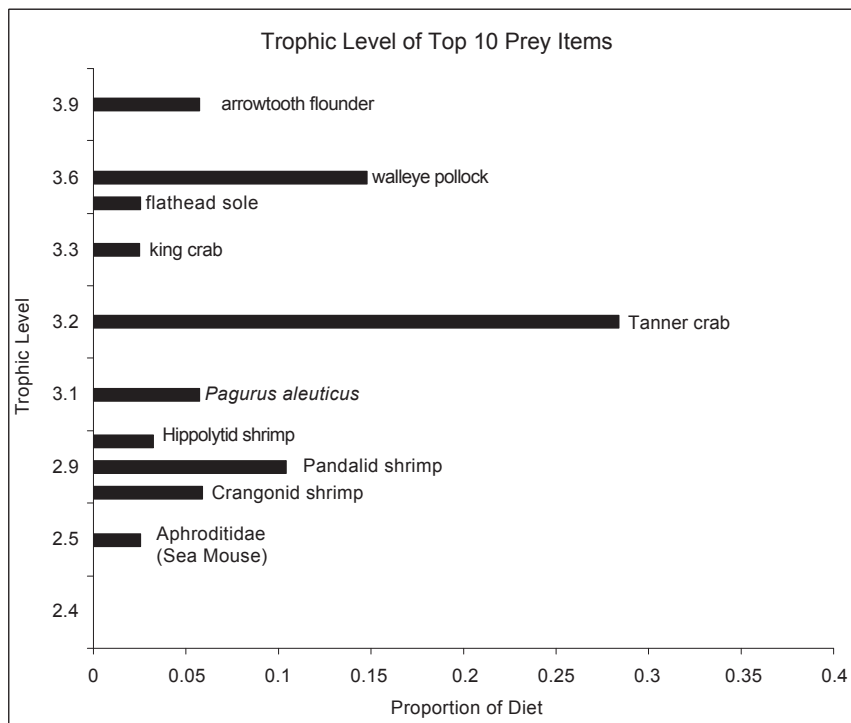


Figure 2. Trophic level and proportion in the cod diet by weight of the top ten prey items.

$$\overline{TL}_k = \frac{\sum_{i=1}^m Y_{ik} TL_i}{\sum_{i=1}^m Y_{ik}}$$

where Y_{ik} is the landings of species i by weight in year k and TL_i is its trophic level (Pauly et al. 2001).

Results

A total of 954 cod stomachs were sampled during the six sampling periods. Sufficient cod to complete the sampling protocols were not always attained especially at the ends of the length range. As reported in food habit studies from other areas, Pacific cod in Marmot Bay consumed a wide variety of prey items ranging in TL from 1.0 (red, green algae) to Pacific halibut with a TL of 4.5. The top 10 prey items by weight came from trophic levels ranging from 2.5 to 3.9 (Fig. 2). As the size of the

sampled cod increased, walleye pollock became an increasing proportion of the diet reaching 68% by weight for cod 85-90 cm in length. The proportion of Tanner crab in the diet remained constant at about 20% for cod larger than 50 cm (Fig. 3).

ANCOVA showed no significant two-way interaction between length and season ($p = 0.237$). ANCOVA also showed that length and season significantly affected Pacific cod TL ($F_{6,825} = 9.731$, $p < 0.0001$ for reduced model), but not with strong predictive characteristics ($R^2 = 0.07$). Cod tend to have an increasing TL with increasing size (Fig. 4) and there were significant changes in TL by season, however those changes were independent of size. In other words, since the interaction term was not significant, larger cod consumed prey of increasing TL, regardless of season.

Estimated TL of cod from the commercial catch ranged from 4.01 in August 1998 to 4.25 in January 1999 season (Fig. 5, Table 1). By comparison, the TL value from cod assigned by the food web model is 4.1. When our corrected range of values for cod was applied to the overall mean TL of the Gulf of Alaska commercial catch from 1956 to 2004, the resulting yearly differences in mean TL averaged only 0.01 over the period (Fig. 6).

Discussion

The mean TL of the catch in the GOA has varied considerably over the last 50 years. The well documented regime shift of the late 1970s led to a reorganization of the ecosystem (Anderson and Piatt 1999) with one group (shellfish, capelin, and herring) declining while another group (Pacific cod, walleye pollock, and salmon) increased. This is reflected in the mean TL of the commercial catch. In 1974 over 50% of the catch was shrimp (TL 2.9) and crab (TL 3.2-3.3) with a resulting mean TL of 3.59. As salmon (mostly pink salmon, TL 4.2), Pacific cod (TL 4.1), and walleye pollock (TL 3.7) came to dominate the catch, the mean TL of the catch rose to around 4.0 by 1999. This change is similar in magnitude to changes in TL associated with “fishing down the food web” effects (e.g., the east and west coasts of Canada, Pauly et al. 2001; Greek waters, Stergiou and Koulouris 2000; and globally, Pauly et al. 1998).

In contrast, calculating the mean TL of the Gulf of Alaska catch using our range of TLs for cod, the maximum resulting yearly difference was 0.03 in 1992, the year when cod catches were at their highest level of 80,000 t. The average difference was 0.01 over the period 1956-2004, which is around 3% of the difference observed due to the regime shift. While we detected statistically significant differences in TL with increasing fish size and by season, our analysis shows that adjusting the mean TL of the Gulf of Alaska commercial catch for these differences does little to change the interpretation of the status of the fisheries.

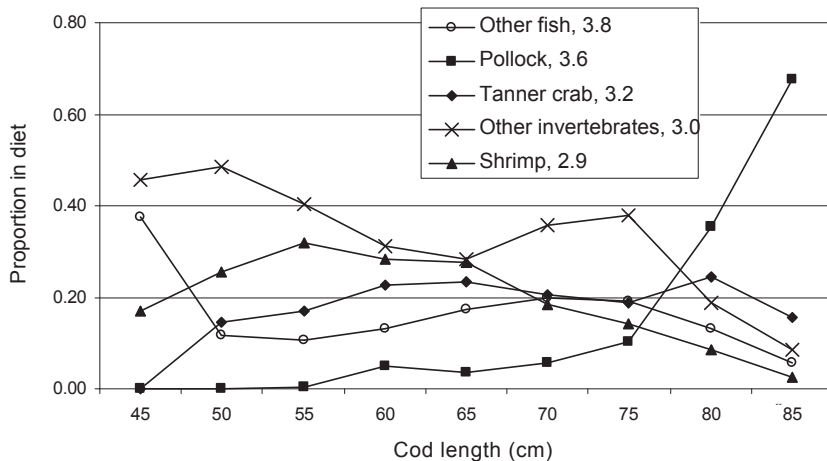


Figure 3. Changes in the proportions by weight of prey items of Pacific cod with increasing size of the cod. The number in the legend following the name is the trophic level of that prey category.

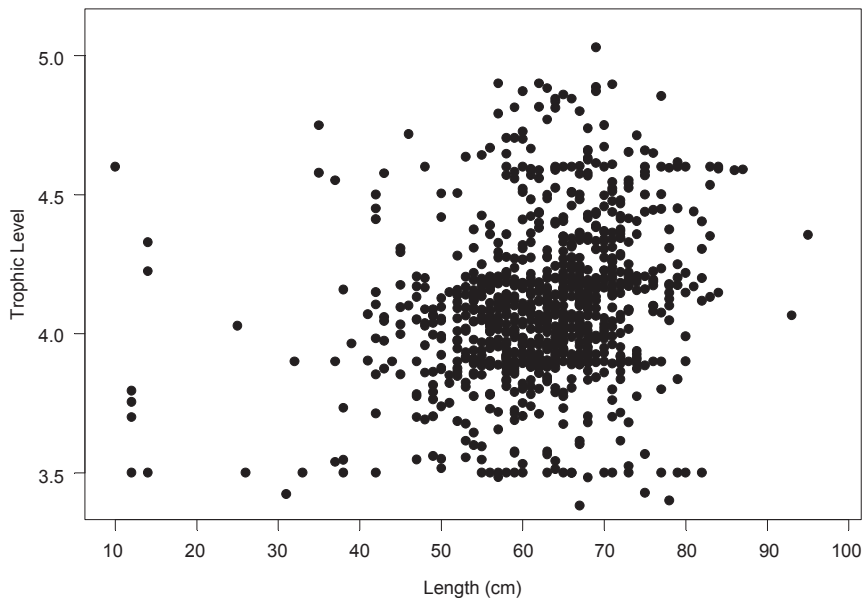


Figure 4. Trophic level of 954 Pacific cod by length as determined empirically from stomach contents.

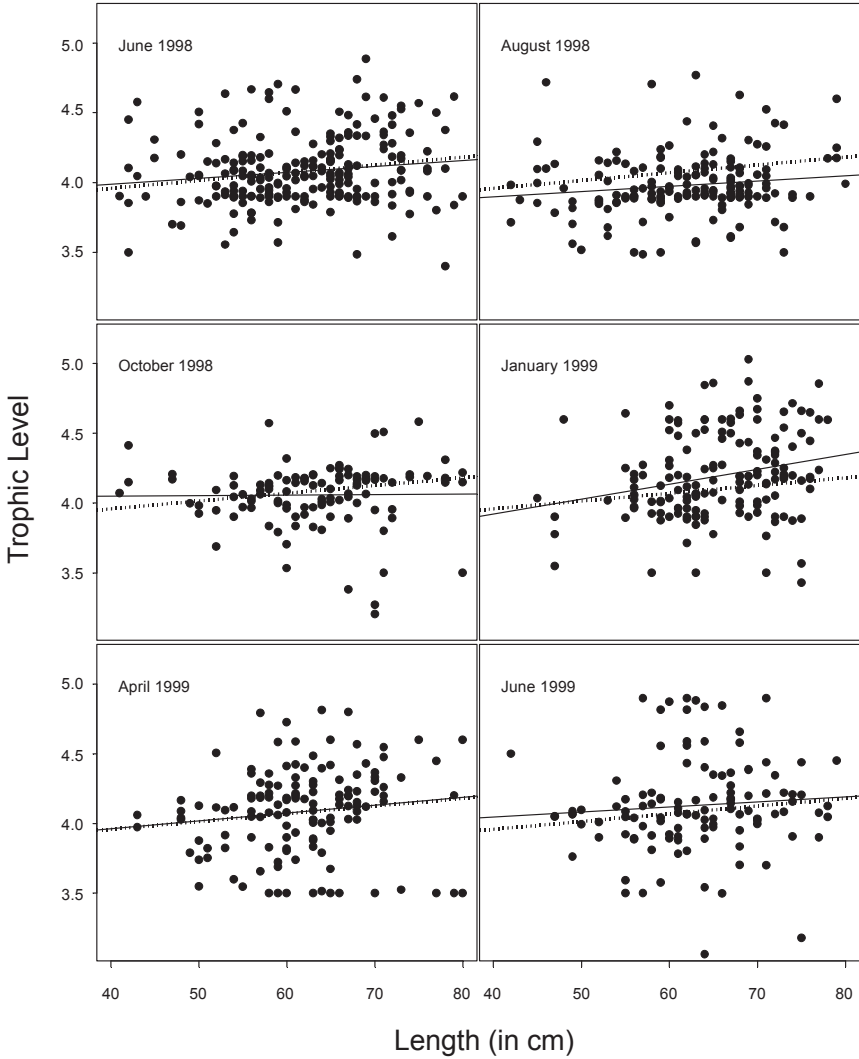


Figure 5. Changes in trophic level in cod by length and season. Solid line represents the regression of TL by length for each season while the dotted line is the overall regression line for all seasons.

Table 1. Summary of cod stomachs collected for diet composition analysis and measured for length during the commercial fishery around Kodiak Island.

| Stomachs sampled for diet composition | | Stomachs measured from commercial harvest | | |
|---------------------------------------|---------------|---|--|---------------|
| Sampling period | Stomach count | Number of measurements | Average cod length \pm SD ^a | Trophic level |
| June 1998 | 226 | 309 | 61.9 \pm 9.0 | 4.10 |
| August 1998 | 176 | 52 | 61.9 \pm 9.5 | 4.01 |
| October 1998 | 118 | 255 | 63.9 \pm 9.9 | 4.06 |
| January 1999 | 168 | 157 | 62.9 \pm 14.2 | 4.25 |
| April 1999 | 146 | 4,237 | 60.8 \pm 9.0 | 4.12 |
| June 1999 | 120 | 577 | 62.8 \pm 8.5 | 4.16 |
| Total | 954 | 5,587 | 62.3 \pm 10.3 | 4.12 |

^aCod length of the commercial catch, SD = standard deviation.

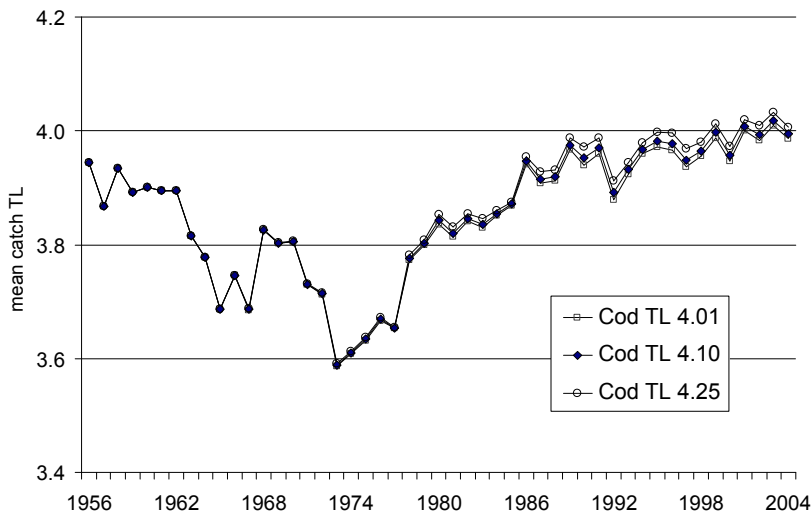


Figure 6. Mean trophic level of the commercial catch in the Gulf of Alaska, 1956 to 2004. The mean TL was calculated using three values for Pacific cod: 4.10 as determined by a food web model, and the range of 4.01 to 4.25, which was determined as the range of values seen in Pacific cod in Marmot Bay over a 1 year period, June 1998 to June 1999.

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The Management Strategy Evaluation Approach and the Fishery for Walleye Pollock in the Gulf of Alaska

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Abstract

Management strategy evaluation (MSE) is the process of using simulation testing to examine the robustness of candidate management strategies to error and uncertainty. MSE involves using (1) a model (the “operating model”) to represent the true underlying dynamics of the resource and to generate future data, (2) an estimation model to assess the state of the stock relative to agreed target and limit reference points based on the data simulated using the operating model, and (3) a decision rule to determine management actions (e.g., the acceptable biological catch, ABC) given the results of the estimation model. The latter two steps constitute the management strategy. The parameters of the management strategy can be selected to attempt to satisfy desired (but conflicting) management goals and objectives. The results of an MSE are performance measures that quantify the effectiveness of the estimation model and, more generally, the management strategy. MSE is used in this paper to evaluate the extent to which the current management strategy for the fishery for walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska (GOA) is able to satisfy the management objectives of avoid-

ing low stock size and achieving high, stable catches, given error and uncertainty regarding the data used for assessment purposes, and the form of the stock-recruitment relationship. The results of the analyses indicate that the current management strategy for GOA pollock appears to meet the management sustainability goals when the actual resource dynamics are consistent with the current stock assessment and for two scenarios with alternative stock-recruitment relationships.

Introduction

Management strategy evaluation (MSE) is the process of using simulation testing to determine how robust feedback-control management strategies are to measurement and process error, and model uncertainty (Smith 1994). For the purposes of MSE, a management strategy is the combination of the procedures related to how a resource is monitored, how its status relative to target and limit reference points is determined (the “estimation model”), and how the results of the estimation model are used to determine management actions (the “decision” or “catch control” rule). A management strategy can be complex, involving a stock assessment model coupled with a decision rule (such as that adopted for the management of commercial whaling by the International Whaling Commission; e.g., Cooke 1999, International Whaling Commission 1999), or it can be very simple, such as a decision rule that uses empirical data (e.g., those adopted for anchovy and sardine off South Africa, De Oliveira et al. 1998). In fact, any quantitative method that determines management actions, such as limits on fishing mortality or acceptable biological catch (ABC), gear restrictions, or spatial or temporal limitations, could be evaluated using MSE. The focus of MSE has been on management of single-species fisheries, but there is no reason that management strategies designed primarily to achieve ecosystem objectives could not be evaluated using the MSE approach (Sainsbury et al. 2000, Butterworth and Punt 2003).

The results of an MSE are performance measures that quantify the extent to which a management strategy is able to satisfy the (often conflicting) management goals (Kell et al. 2006). In addition, the results of an MSE can be used to determine how well estimation models are able to estimate quantities (such as current biomass) that are of interest to management. MSE has been used to evaluate current and alternative management strategies for many fisheries worldwide, including those for South African sardine and anchovy (De Oliveira et al. 1998, De Oliveira and Butterworth 2004), prawns off northern Australia (Dichmont et al. 2006), species in Australia's South East multispecies fishery (Punt et al. 2002), krill off Antarctica (Constable 2005), and flatfish in the Northeast Atlantic (Kell et al. 2005).

MSE has been argued to be an integral part of implementing the UN FAO Code of Conduct for Responsible Fisheries (FAO 1996), because it allows management strategies that are robust to several forms of uncertainty to be identified (Punt 2006). Specifically, MSE analyses can be used to evaluate the extent to which the performance of a management strategy is impacted by uncertainty, in the form of process error (e.g., recruitment variability), observation error (i.e., imprecise or inadequate data collection), and model error (e.g., uncertainty about the true form of the stock-recruitment relationship) (Francis and Shotton 1997). Model error has been identified as a potentially major, but often overlooked, source of uncertainty when considering management decisions, and particularly the selection of management strategies (Butterworth and Punt 1999).

Although the Gulf of Alaska (GOA) walleye pollock fishery has been a fully domestic U.S. fishery since the mid-1980s, it began as a directed foreign fishery in 1964 (Dorn et al. 2005). This fishery is the second largest directed fishery in the Gulf of Alaska, with annual catches between 50,000 and 120,000 metric tons (t) annually since 1986 (Dorn et al. 2005). It is managed by the North Pacific Fishery Management Council (NPFMC) based on scientific advice provided by the National Marine Fisheries Service (NMFS). The management strategy used for the GOA pollock fishery is based upon the "Tier 3 NPFMC decision rule" (NPFMC 2005a). This decision rule determines the target level of fishing mortality each year as a function of the size of the spawning biomass expressed relative to a reference level (Fig. 1). Since 2002, a slightly more conservative decision rule has been used for walleye pollock in the Gulf of Alaska (Dorn et al. 2001). This decision rule increased the buffer between the overfishing level of fishing mortality and the target level of fishing mortality when the spawning biomass is below the reference spawning biomass level to provide a greater protection against assessment uncertainty.

The management strategy for this fishery can therefore be considered as the combination of Dorn et al.'s (2001) decision rule, which produces the ABC (Eq. 1a, with $\alpha = 0.05$), and an estimation model that fits a population dynamics model using fishery, survey, and biological data to produce estimates of the biological reference points $F_{40\%}$ (the fishing mortality that reduces the spawning biomass-per-recruit to 40% of the average unfished spawning biomass-per-recruit), $SB_{40\%}$ (the spawning biomass associated with $F_{40\%}$), $SB_{47\%}$ (the spawning biomass associated with $F_{47\%}$), and the current spawning biomass. The management plan also includes an overfishing level (OFL), defined in terms of fishing mortality (Eq. 1b). If fishing mortality exceeds the overfishing level, "overfishing," as defined under the Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA), is said to be occurring. To protect endangered Steller sea lions, which consume walleye pollock, a spawning biomass of 20% of the average unfished spawning biomass,

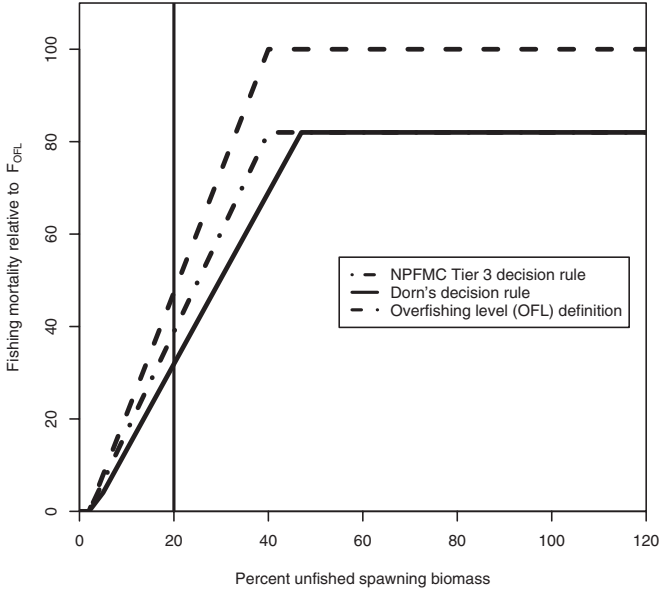


Figure 1. The overfishing level, the North Pacific Fishery Management Council (NPFMC) Tier 3 maximum level of fishing mortality, and the Dorn et al. (2001) decision rule.

$SB_{20\%}$, (the vertical line in Fig. 1), has been established as a level below which no directed fishing would be allowed.

$$F_{ABC} \leq \begin{cases} F_{40\%} & \text{if } SB / SB_{47\%} > 1 \\ F_{40\%} [(SB / SB_{47\%} - \alpha) / (1 - \alpha)] & \text{if } \alpha < SB / SB_{47\%} \leq 1 \\ 0 & \text{if } SB / SB_{47\%} \leq \alpha \end{cases} \quad (1a)$$

$$F_{OFL} = \begin{cases} F_{35\%} & \text{if } SB / SB_{40\%} > 1 \\ F_{35\%} [(SB / SB_{40\%} - \alpha) / (1 - \alpha)] & \text{if } \alpha < SB / SB_{40\%} \leq 1 \\ 0 & \text{if } SB / SB_{40\%} \leq \alpha \end{cases} \quad (1b)$$

The spawning biomass reference points (i.e., $SB_{40\%}$ and $SB_{47\%}$) are estimated by multiplying mean recruitment since 1977 by the corresponding spawning biomass-per-recruit (i.e., corresponding to $F_{40\%}$ and $F_{47\%}$). Use of recruitment during the post-1977 time period is intended to represent current stock productivity following a widely recognized cli-

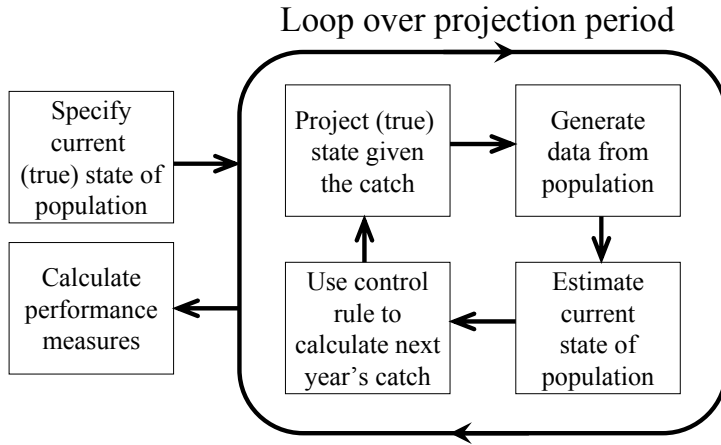


Figure 2. Outline of the key steps of a management strategy evaluation (MSE).

matic regime shift that occurred in 1977. Fishing mortality on GOA pollock since 1977 has varied, but has generally been considerably lower than $F_{40\%}$, so it is unlikely that recruitment during this period provides a suitable estimate of mean recruitment when fishing at $F_{40\%}$, except if recruitment is independent of stock size. An advantage of the MSE approach is that decision rule performance (which includes estimation of biological reference points) can be evaluated both for this idealized situation and for more realistic situations such as when recruitment depends on stock size.

The impetus for this study comes from the 2002 Goodman report (Goodman et al. 2002), which reviewed the management strategies used by the NPFMC for groundfish stocks, and recommended that “an MSE analysis . . . be undertaken to provide additional assurance that the current NPFMC ABC harvest strategy is a robust one and is likely to continue to meet the objectives of the Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA) and of NPFMC itself.” This paper therefore outlines the framework used to evaluate management strategies for the GOA pollock fishery. It then uses this framework to evaluate the current management strategy for the case in which the actual resource dynamics are similar to the assumptions that underlie the current stock assessment and harvest policy. This provides a first test of the current management strategy for GOA pollock.

Methods

Overview and operating model

Fig. 2 outlines the key components of an MSE. The operating model (see Appendix for the technical details of this model) represents the “true” state of the resource, and includes hypotheses regarding how the age-structure of the resource changes through time, and the form of the underlying stock-recruitment relationship. The operating model is age-structured, can relate recruitment to spawning biomass or estimate each independently, and includes process error in both recruitment and fishery selectivity. It is similar in structure to the population dynamics model on which the 2005 GOA pollock stock assessment (Dorn et al. 2005) was based, primarily because the latter represents the best available science regarding the status of this resource. The main difference between the operating model and the original stock assessment model is the age range that each model covers. The operating model covers ages 1 through 15 years, and the stock assessment model covers ages 2 through 10 years, with the oldest ages being the “plus” groups. Some proportion-at-age data are available for ages 1 through 15+ (e.g., the fishery for 1985, 1989-1990, and 1992-2004; the NMFS echo-integration trawl (EIT) survey for 1981, 1983-91, 1994-98, and 2000-05; and the NMFS GOA bottom trawl surveys for years 1984, 1987, 1989, 1990, 1993, 1996, 1999, 2001, and 2003), which is the reason for the age range chosen for the operating model. Both models estimate the parameters of the stock-recruitment relationship, the annual fishing mortalities, the catchability coefficients for each survey, fishery and survey selectivity, recruitment deviations, annual deviations for the fishery selectivity parameters, and the biological reference points needed to apply the decision rule.

There are two main steps to using an operating model to evaluate management strategies: (1) the operating model is fit to historical fishery and survey data using Bayesian methods based on the Markov chain Monte Carlo algorithm (Hastings 1970, Gelman et al. 2004) to determine the best estimates for the values for its parameters, and hence the numbers-at-age at the start of the projection period (2006) and to quantify the uncertainty associated with the estimates of these quantities; and (2) the operating model is used to project the simulated stock forward for a series of draws from the Bayesian posterior distribution when management is based on a simulated management strategy. Step 1, often referred to as conditioning, is undertaken to ensure that the simulations are representative of the actual problem of managing the GOA pollock fishery, as this situation is currently understood through stock assessments.

During the projection period, the operating model generates the survey and fishery data that are used by the estimation model compo-

ment of the management strategy, and characterizes the impacts, from a single-species perspective, of the ABCs set using the management strategy. In the projections, the recruitment process error, and the observation error applied to the “true” survey indices of abundance, survey catch proportions-at-age, and fishery catch proportions-at-age, are assumed to be temporally uncorrelated.

For the purposes of this study, 100 simulations were conducted for each scenario regarding the specifications of the operating model. This number of simulations was selected because it was sufficient to determine differences among alternative strategies; several previous studies have been based on a similar number of simulations per scenario. Each simulation involved projecting the simulated stock forward for 30 years (2006-2035) by annually applying the estimation model and decision rule, and then updating the “true” population dynamics. Thirty years was selected for the length of the projection period based on the suggestion of Goodman et al. (2002).

Management strategy

The management strategy considered in this paper is the combination of the decision rule in Fig. 1 and the stock assessment model on which the 2005 GOA pollock stock assessment was based (Dorn et al. 2005). This estimation model, which is similar to the operating model when the operating model assumes recruitment to be independent of spawning biomass, except for the age range considered, is designed to provide the input needed to apply the decision rule that produces the F_{ABC} and hence the ABC, i.e., the estimates of $F_{40\%}$, $SB_{47\%}$, and current spawning biomass (see Eq. 1a). With one exception, the catch removed from the simulated stock is set to the ABC calculated using the management strategy, i.e., implementation error is ignored. The exception is that the catch is set to 0.1% of the age 3+ biomass if the spawning biomass is assessed to be below $SB_{20\%}$ (rather than zero). This level of catch reflects the current levels of pollock bycatch in GOA fisheries other than the directed pollock fishery, and represents what is likely to happen in the event that the spawning biomass of pollock is assessed to be below $SB_{20\%}$ and the directed pollock fishery was closed.

Performance measures

The performance measures consist of two types (“estimation” and “management”). The estimation performance measures examine how well the estimation model estimates annual spawning biomass, annual fishing mortality, the fishing mortality needed to apply the decision rule, the biological reference points, and the ABC based on the decision rule. The “estimation” performance measures were selected because they assess the ability of the assessment model to provide the information needed to set the ABC in the following year and to determine the status of the

stock relative to biological reference points. The “management” performance measures are selected based on the goals and objectives of the NPFMC (NPFMC 2005b) and the MSFCMA. They are the number of simulations in which the “true” spawning biomass falls below the “true” $SB_{20\%}$, the number of simulations in which the “true” fishing mortality is above the “true” maximum fishing mortality threshold (MFMT), F_{OFL} (Eq. 1b), and the average catch over the projection period. The “management” performance measures were selected because they assess the ability of the management system to prevent the stock from becoming overfished, to prevent overfishing, and to maintain catches at sustainable levels.

The results are shown graphically rather than in tabular form (which would be extremely voluminous). Specifically, the ability of the management strategy to leave the spawning biomass close to the reference level of $SB_{40\%}$ and achieve high catches is summarized using a plot with the following six panels:

1. A summary of the distribution of the time-trajectory of the true spawning biomass;
2. A summary of the distribution of the time-trajectory of annual catches;
3. The time-series of the true spawning biomass for simulations 25, 50, 75, and 100;
4. The time-series of catches for simulations 25, 50, 75, and 100;
5. A summary of the distribution of the time-trajectory of the ratio of the true spawning biomass to the true reference level of $SB_{40\%}$; and
6. A histogram of the average catch during the projection period.

The estimation performance of the management strategy in assessing current stock status is summarized by plots that show the distributions for the percentage relative errors for the time-series of (1) spawning biomass and (2) fishing mortality in the final year of the assessment period; (3) the reference spawning biomass, $SB_{40\%}$ (NPFMC 2005a); (4) the target fishing mortality, $F_{40\%}$ (NPFMC 2005a); (5) the fishing mortality on which the ABC for the following year is based, F_{ABC} (see Eq. 1a); and (6) the ABC under the decision rule.

Scenarios considered

This study considers three scenarios: a base scenario in which recruitment is lognormally distributed about a mean value (Eq. A.3) so there is no impact of a reduction in spawning biomass on expected recruitment, and two scenarios in which recruitment declines with reductions in spawning biomass (Eq. A.2a and A.2b). The form of the relationship

between spawning biomass and recruitment forms the focus for this study because the form of this relationship has been identified in the past as a factor to which the performance of management strategies has been found to be sensitive (Butterworth and Punt 1999). The true value of $SB_{40\%}$ used when calculating the performance measures is defined as the product of the spawning biomass-per-recruit corresponding to $F_{40\%}$ and the recruitment expected at $F_{40\%}$.

Results and discussion

Base scenario

The base scenario involves the operating model being based on the same assumption about the form of the stock-recruitment relationship as the management strategy, i.e., that recruitment and spawning biomass are unrelated. It would be expected therefore that the management strategy would perform adequately for this scenario. The resource is maintained at the spawning biomass reference level on average for this scenario (Fig. 3, upper center panel), and there is only a small probability ($\leq 5\%$) that the spawning biomass is reduced to below $SB_{20\%}$ (Fig. 4b). There is, however, a high probability (80%) that the true fishing mortality is above the overfishing fishing mortality reference level, F_{OFL} , in the fourth and fifth years of the projection period (Fig. 4c), but this probability decreases rapidly and is much lower ($< 20\%$) during most of the projection period. North Pacific harvest policies establish a buffer between the reference fishing mortality and F_{OFL} , but some risk of unintentionally exceeding limits is unavoidable given the uncertainties in the assessment. The implications of those risks, in terms of reduction in biomass and loss in yield, could be evaluated using the results of an extension to the outputs of the current MSE.

The high level of fishing mortality in the earliest years of the projection period appears to be due to the transition from the actual data for GOA pollock to data simulated using the operating model, which leads to positive biases in the estimates of F_{ABC} and ABC for the earliest years of the projection period (Fig. 5). Bias in the estimates of spawning biomass, and particularly fishing mortality, occurs in the first few years of the projection period because, for example, the signs of the differences between the estimated biomass and an index of abundance for a year before 2006 will tend to be the same because the data for the years prior to 2006 are set to the actual values, while the differences will be centered around zero for the future (see, for example, Fig. 6). Transient behavior in the first years of the projection period for MSE studies has been observed in the past for other species (e.g., Mapstone et al. 2004). The bias of approximately 5% in $F_{40\%}$ (see the lower center panel of Fig. 5) occurs because of the difference in the plus-group ages in the operating and estimation models.

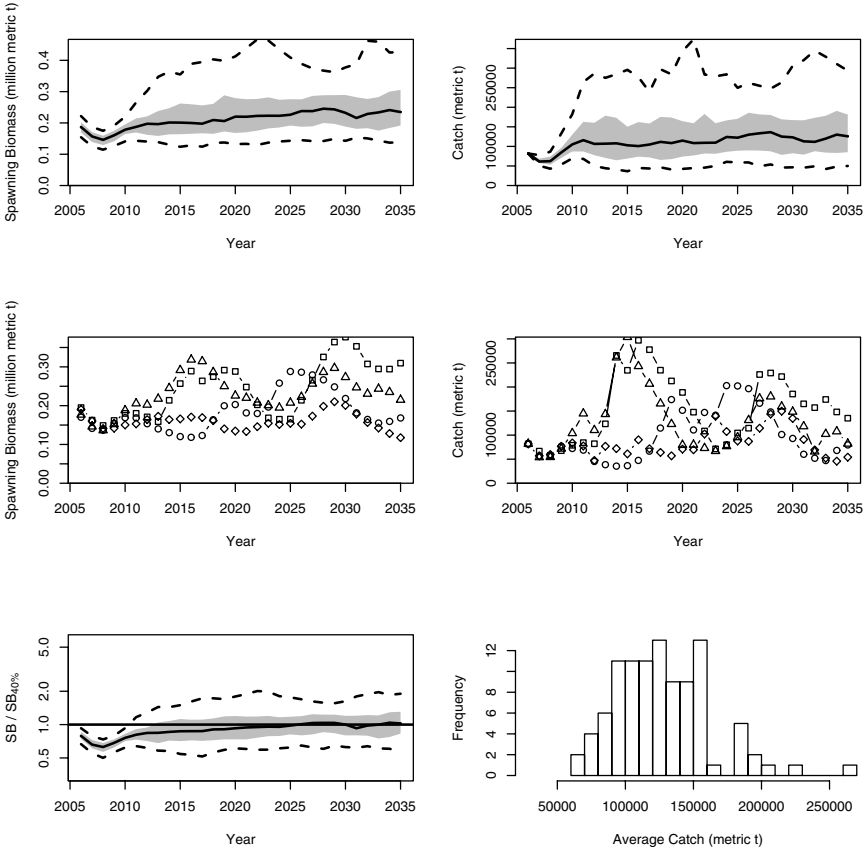


Figure 3. Results for the base operating model for the “true” spawning biomass, catch, four realizations of spawning biomass trajectories, four realizations of catch trajectories, the relative level of “true” spawning biomass (on a logarithmic scale), and the distribution of average catch over the 100 simulations. For the envelopes, the solid black line is the median, the shaded area covers the 25th through the 75th percentiles, and the dashed lines are the 5th and 95th percentiles.

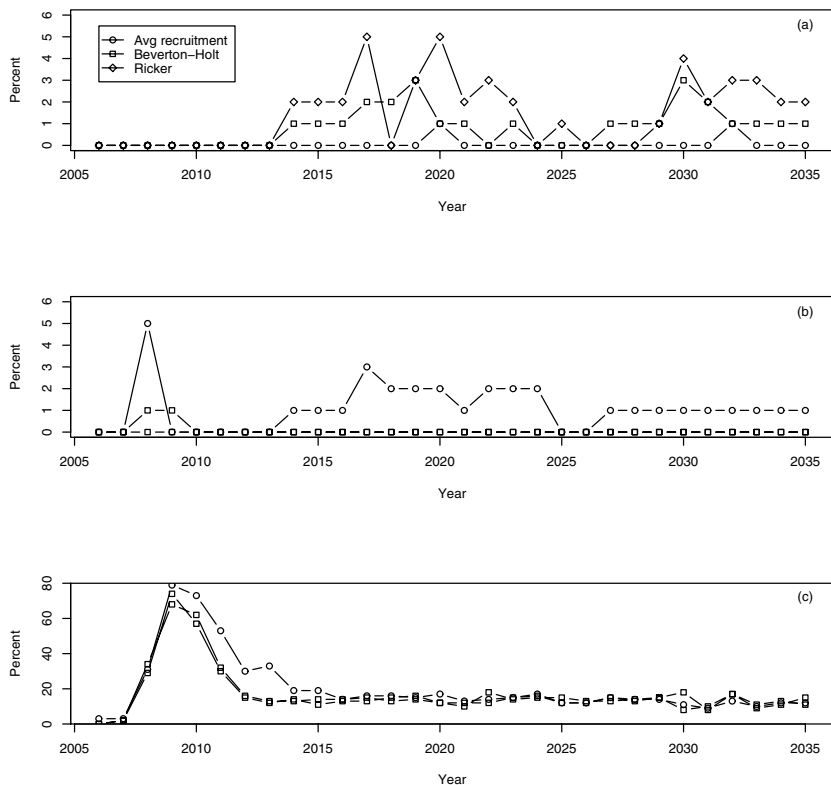


Figure 4. Number of simulations in each year where the estimated spawning biomass was below the estimated SB_{20} (a); number of simulations in each year where the “true” spawning biomass was below the “true” $SB_{20\%}$ (b); and number of simulations in each year where the “true” fishing mortality was above the “true” maximum fishing mortality threshold (MFMT), F_{OFL} (c). The results in this figure are based on the three operating model scenarios.

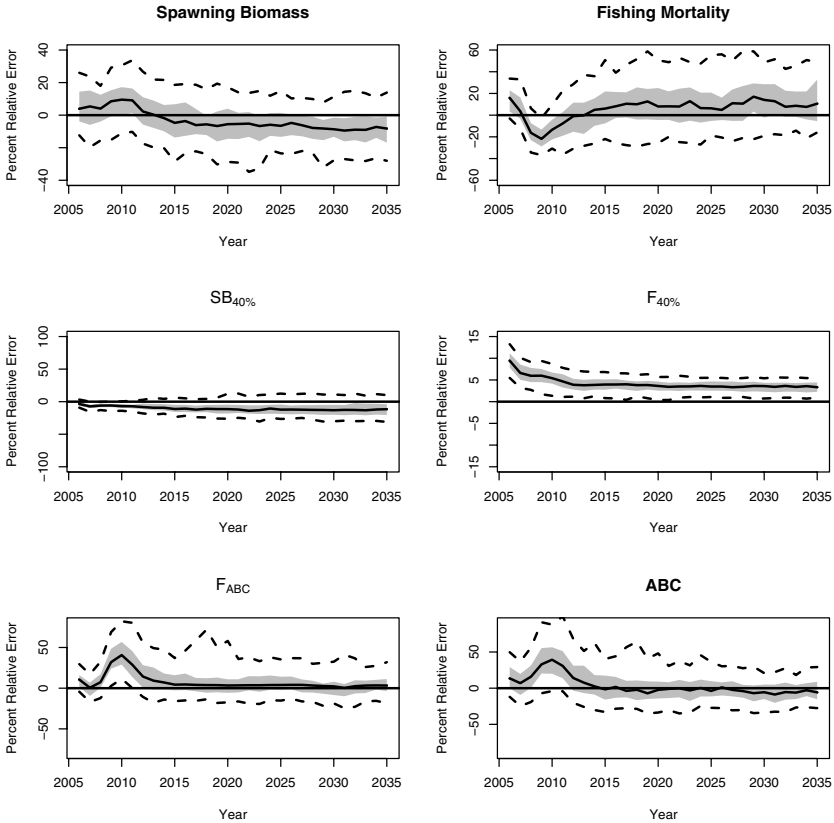


Figure 5. Results for the base operating model showing the percent relative error between the estimated and “true” values for spawning biomass, fishing mortality, $SB_{40\%}$, $F_{40\%}$, F_{ABC} , and ABC. The solid black line is the median, the shaded area covers the 25th through the 75th percentiles, and the dashed lines are the 5th and 95th percentiles.

The average level of catch during the projection period is 127,000 t, which is greater than the average level of catch during 1964-2005 (84,000 t), and greater than the average level of catch since 1986 (82,000 t). The catch variability (standard deviation of catch) over the projection period is 80,000 t, which is greater than the catch variability over the years 1964-2005 (67,000 t), and much greater than that since 1986 (20,000 t). Differences between the average catch during the projection period and during the historical period are due to several factors. First, the current control rule has been used only since 2001. Prior to 2001, a variety of rationales were used to arrive at an ABC, most of which

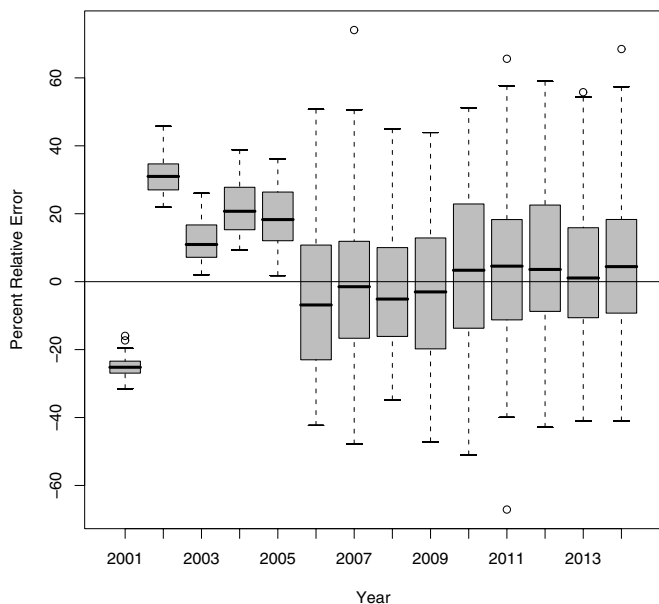


Figure 6. Box and whisker plots of the percent relative errors for the NMFS winter Gulf of Alaska (GOA) Shelikof Strait echo-integration trawl (EIT) survey indices (2001-2014) based on simulated assessments conducted in 2015. The indices for the years prior to 2006 are the actual data, while those from 2006 onward are generated by the operating model.

resulted in harvest rates lower and more stable than would be recommended under the current harvest policy. Second, during the early period of the fishery, catches were constrained more by capacity and interest than by management actions. In fact, average catches during the projection period correspond well to equilibrium catches under constant $F_{40\%}$ and $F_{50\%}$ fishing mortality rates reported by Dorn et al. (2005), indicating that the projection model is performing as expected.

The biases in Fig. 5 appear to be due primarily to the transition between actual and simulated data and differences in the fishery and survey selectivity functions between the operating model and the estimation model, as the operating model covers ages 1 through 15 and the estimation model considers only ages 2 through 10. In general, the biases of the estimation model are modest and do not compromise the implementation of appropriate harvest limits.

The results in Figs. 3-5 confirm the expectation that the management strategy appears to perform adequately, and as expected, when

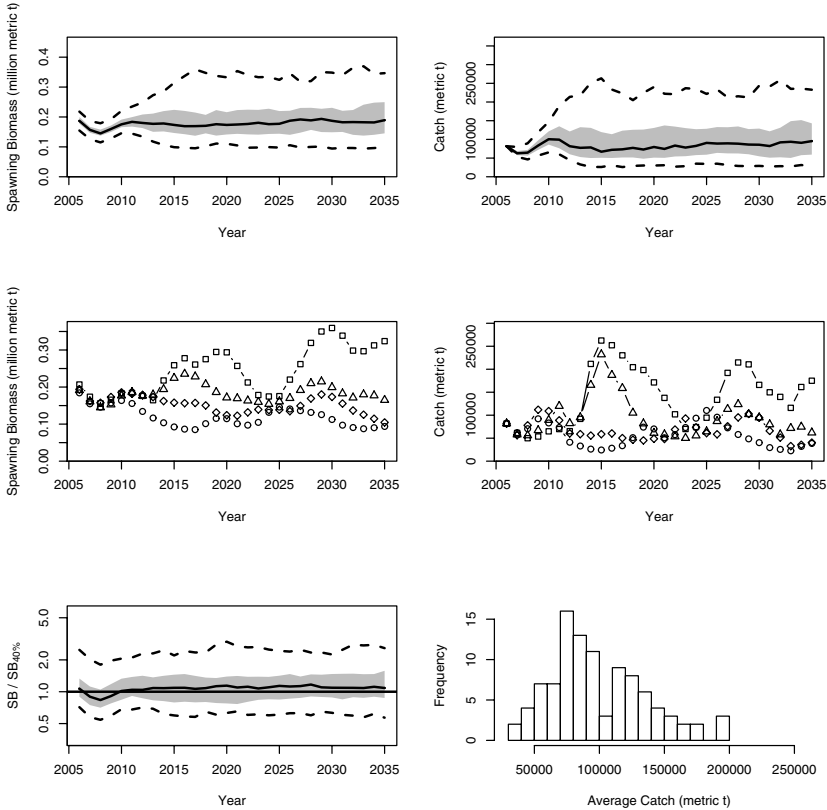


Figure 7. As for Fig. 3, except that the results pertain to the operating model in which recruitment is governed by the Beverton-Holt stock-recruitment relationship.

the dynamics of the resource nearly exactly correspond to the assessment model assumptions and mean recruitment does not decline with declining spawning biomass.

Sensitivity to the form of the stock-recruitment relationship

Figs. 7 and 8 summarize the management performance of the management strategy when a stock-recruitment relationship is included in the operating model. Estimated stock recruit relationships (Fig. 9) indicate that recruitment declines with decreasing stock size (the posterior modal estimates of steepness are respectively 0.647 and 0.465 for the Beverton-Holt and Ricker stock-recruitment relationships).

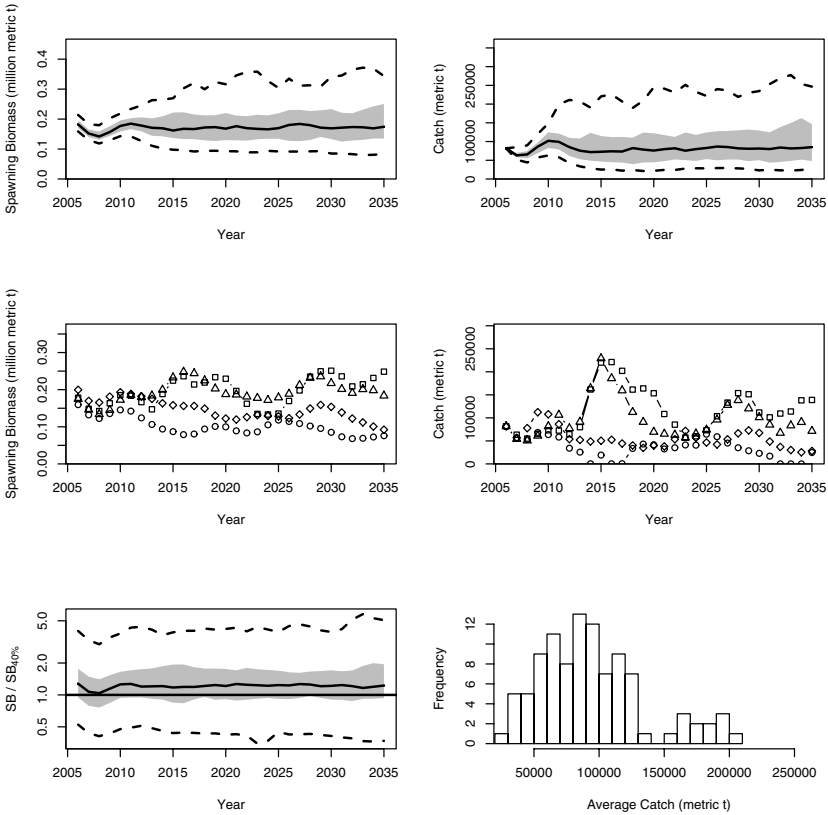


Figure 8. As for Fig. 3, except that the results pertain to the operating model in which recruitment is governed by the Ricker stock-recruitment relationship.

The stock is left above the spawning biomass reference level on average for both scenarios in which recruitment declines with reductions in spawning biomass. However, $SB_{40\%}$ for these scenarios is lower than $SB_{40\%}$ for the base scenario, as the level of recruitment expected under $F_{40\%}$ is lower for these scenarios than the average level of recruitment used to calculate $SB_{40\%}$ for the base scenario (Fig. 9).

The probability that the stock really dropped below the true $SB_{20\%}$ is lower for both scenarios in which recruitment declines with reductions in spawning biomass than for the base scenario. The converse is true for the estimated biomass values, although the probability across all scenarios is $\leq 5\%$ (Fig. 4). The reason for the lower probability of being below the

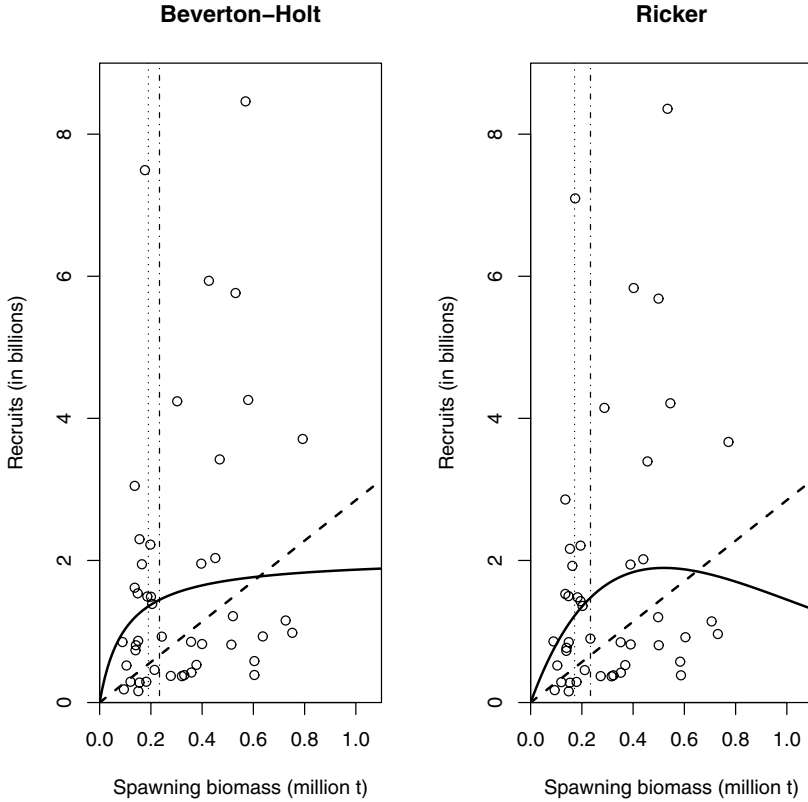


Figure 9. The stock-recruitment relationship along with spawning biomass and recruitment over the historical period based on the values for the parameters corresponding to the mode of the posterior distribution. Results are shown for the Beverton-Holt and Ricker scenarios. The dashed lines are the replacement lines corresponding to $F = 0$, the dotted vertical lines indicate $SB_{40\%}$ for each scenario, and the dot-dash vertical lines indicate $SB_{40\%}$ for the base operating model.

true $SB_{20\%}$ is that catches are adjusted much lower for the scenarios in which recruitment is related to spawning biomass according to a stock-recruitment relationship (contrast Figs. 3, 7, and 8) which is in turn related to positive bias in the estimates of $SB_{40\%}$ (see Figs. 10 and 11). One consequence of this bias is that there is an increased probability that the estimation model will assess the stock to be below $SB_{20\%}$ (see the upper panel of Fig. 4). The probability that the true fishing mortality exceeds the overfishing level is similar to that for the base scenario.

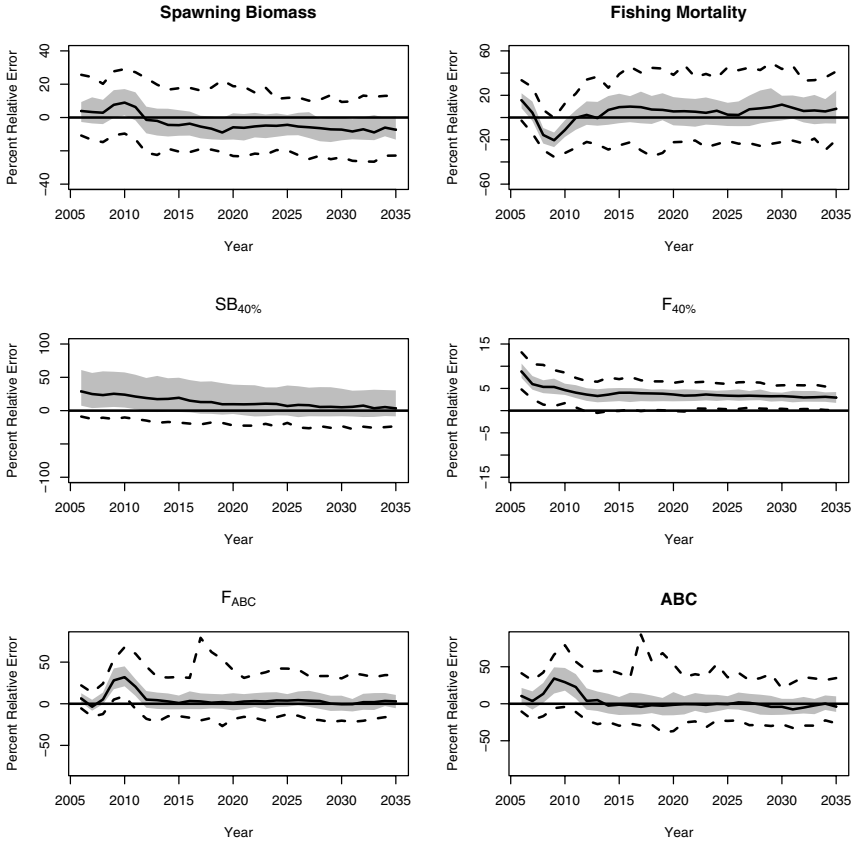


Figure 10. As for Fig. 5, except that the results pertain to the operating model in which recruitment is governed by the Beverton-Holt stock-recruitment relationship.

This is because the overfishing level (Eq. 1b) is defined in terms of fishing mortality rates that lead to particular reductions in spawning biomass-per-recruit rather than spawning biomass. The average level of catch during the projection period is 99,000 t (Beverton-Holt) and 95,000 t (Ricker), i.e., notably lower than for the base scenario. This result is not unexpected given that the population is less resilient when recruitment declines with reductions in spawning biomass. Catch variability, expressed as the standard deviation in catch, is less for the Beverton-Holt and Ricker relationships (64,000 and 65,000 t, respectively) than for the base scenario.

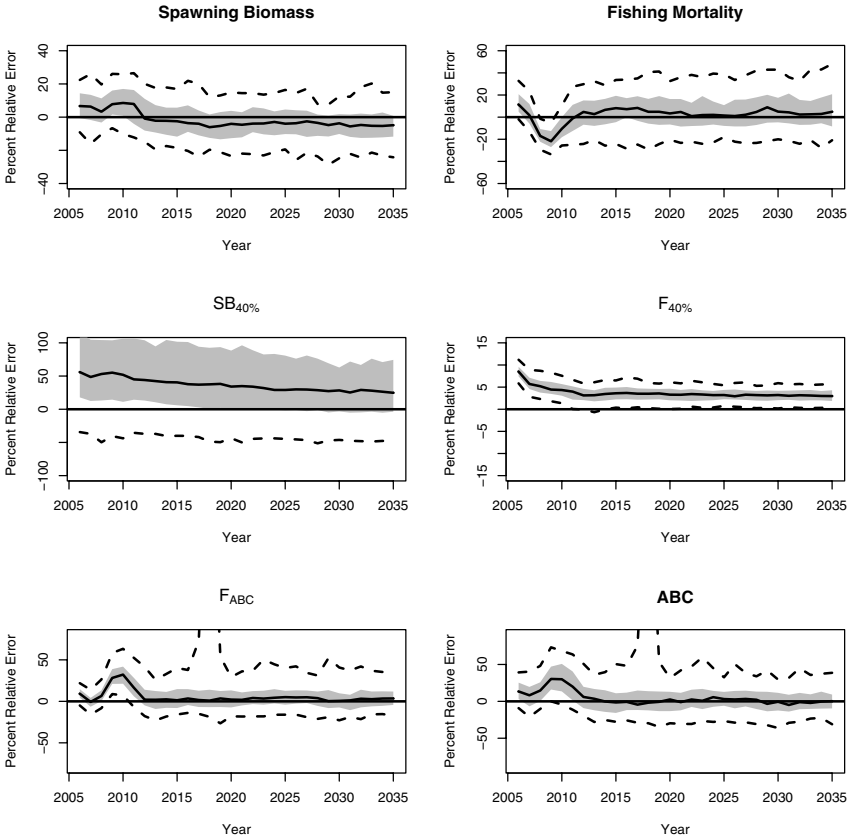


Figure 11. As for Fig. 5, except that the results pertain to the operating model in which recruitment is governed by the Ricker stock-recruitment relationship.

Somewhat surprisingly, the patterns of relative error for the scenarios in which recruitment declines with reductions in spawning biomass (Figs. 10 and 11) are remarkably similar to those for the base scenario. Specifically, spawning biomass is negatively biased and fishing mortality is positively biased by about 5%, $F_{40\%}$ is positively biased by 5%, and F_{ABC} and ABC are virtually unbiased. However, in contrast to the base scenario, $SB_{40\%}$ is positively biased, although this is not unexpected because the estimator of $SB_{40\%}$ assumes that recruitment is independent of spawning biomass.

Overall, performance for these sensitivity tests is generally fairly satisfactory because the spawning biomass is stabilized above the refer-

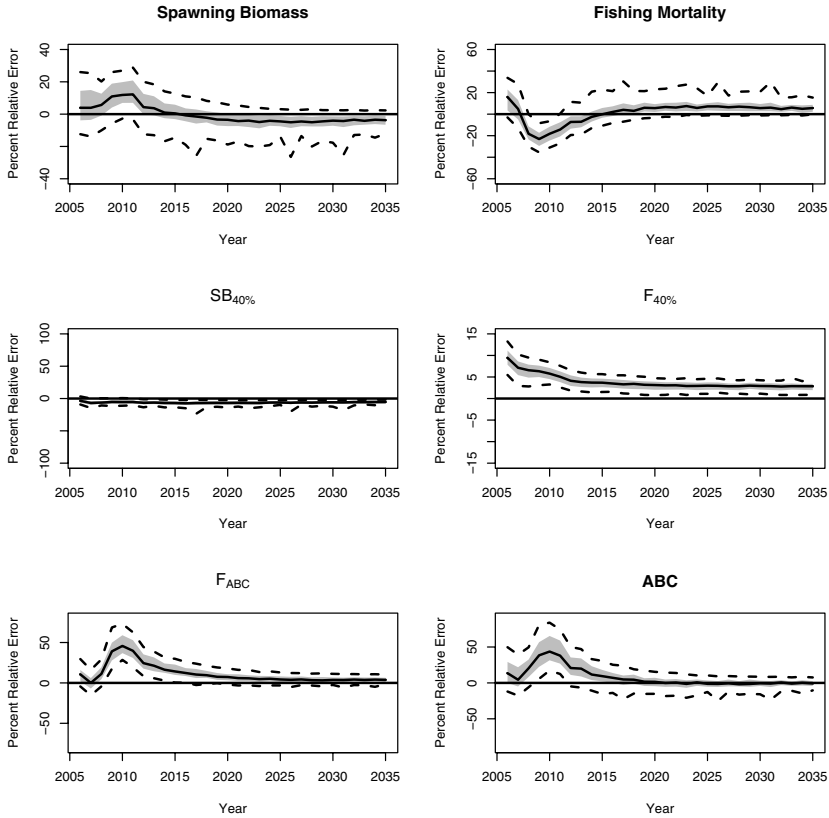


Figure 12. As for Fig. 5, except that the results pertain to the base operating model when there is no observation or process error during the projection period.

ence level and the probability of being below $SB_{20\%}$ is lower than for the base scenario. Given the differences in average catch levels, it seems clear that the decision rule is adjusting catch limits in the correct direction even though it is making incorrect assumptions about productivity when recruitment is really related to spawning biomass.

Impact of future observation and process error

An additional series of simulations was conducted in which there was no future process or observation error to more fully understand the behavior of the management strategy (Fig. 12). As expected, there is considerably less inter-annual and inter-simulation variation when there

is no error in the future (but the assessment model is not aware of this). The relative errors are somewhat smaller than was the case for the original base scenario. However, the patterns of relative error are almost identical to those for the base operating model with observation and process error. This confirms that the reasons for the biases observed in Figs. 5, 10, and 11 are likely to be due to the structural differences between the operating model and the estimation model and the nature of how the operating model is parameterized rather than to how the future data are generated.

General discussion

The current management strategy for GOA pollock appears to meet the management sustainability goals that can be inferred from the goals and objectives of the NPFMC and the MSFCMA and the estimates of management-related quantities are not unreasonably inaccurate and imprecise. Although this result was anticipated (hoped) when the analyses initiated, it is not always guaranteed that a management strategy will perform as anticipated even under fairly ideal conditions. For example, Kell et al. (2005) performed an MSE on eight North Atlantic fish stocks based on the decision rule used by the International Council for the Exploration of the Sea (ICES). The results of this MSE indicated that the ICES management strategy did not perform well. The poor performance was exacerbated by the time lags in the assessment and monitoring processes. Similarly, using an MSE, Punt and Ralston (2007) examined the possible decision rules that could be inferred from the decisions by the Pacific Fishery Management Council regarding how groundfish resources are managed, and found that the rule that most closely mimics recent decision-making performed appreciably poorer than alternative approaches in terms of inter-annual variation in catch and the need for frequent revisions to rebuilding plans.

This management strategy evaluation dealt only with the current management strategy for GOA pollock, and evaluated whether it is robust to a range of uncertainties. Additional work is planned to evaluate whether other management strategies would improve performance in achieving management goals and objectives.

The results of the simulation exercise of this paper are based on an operating model that is almost identical to the estimation model except that alternative stock-recruitment relationships can be used in the operating model. The analyses of this paper are based on fitting the operating model to the actual data for the resource in question and quantifying parameter uncertainty using samples from a Bayesian posterior distribution. While this ensures that the scenarios considered are constrained by what is understood for GOA pollock, it is questionable whether even the full range of parameter uncertainty is captured. For

example, weight-at-age is necessarily assumed to be known exactly for the purposes of sampling from the posterior distribution. Furthermore, basing the projections on samples from the posterior distribution raises the possibility that it will prove impossible for the Markov chain Monte Carlo algorithm to converge. This problem was not encountered in this study. However, given the paucity of data, the values for the parameters of the stock-recruitment relationship on which the analyses of this paper were based were very imprecise.

Future work will explore the robustness of the management strategy to the effects of (plausible) violations of the assumptions of the operating model on which this paper is based. Butterworth and Punt (1999) reviewed the uncertainties considered in past MSE analyses and found that there were no uncertainties that were important in all cases; rather the most important uncertainties were case-specific. In the context of the GOA pollock fishery, the major uncertainties that need to be examined relate to ecosystem changes, multispecies interactions, climate variability, and/or regime shifts. This is because it is unknown how changes in the species composition of the GOA have led to changes in predation on pollock and hence pollock natural mortality (Hollowed et al. 2000, Gaichas 2006). In addition, it has been postulated that climate variability and regime shifts in the GOA may account directly or indirectly for changes in pollock productivity and recruitment (Anderson and Piatt 1999, Bailey 2000). Finally, account could be taken in future work of the difference between TACs and subsequent landings.

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Appendix: The operating model

Population dynamics

The number of animals aged one and older is governed by the equation:

$$N_{y+1,a} = \begin{cases} N_{y+1,1} & \text{if } a = 1 \\ N_{y,a-1} e^{-(M_{a-1} + \tilde{S}_{y,a-1} F_y)} & \text{if } 1 < a < x \\ N_{y,x-1} e^{-(M_{x-1} + \tilde{S}_{y,x-1} F_y)} + N_{y,x} e^{-(M_x + \tilde{S}_{y,x} F_y)} & \text{if } a = x \end{cases} \quad (\text{A.1})$$

where $N_{y,a}$ is the number of fish of age a at the start of year y ;

M_a is the (time-invariant) instantaneous rate of natural mortality for fish of age a ;

$\tilde{S}_{y,a}$ is the selectivity of harvesting on fish of age a during year y ;

F_y is the fishing mortality on fully-selected ($\tilde{S}_{y,a} \rightarrow 1$) animals during year y ; and

x is the plus-group (all fish in this age-class are mature and recruited to the fishery—assumed to be age 15).

Three alternative relationships between stock size and the number of subsequent recruits (at age 1) are considered. Recruitment is lower than expected at unfished equilibrium when the spawning biomass is a small fraction of its unfished size for two of these relationships (Beverton-Holt and Ricker):

$$N_{y+1,1} = \frac{4R_1 h SB_y}{\psi_0 R_1 (1-h) + (5h-1) SB_y} e^{\phi_{y+1} - \sigma_R^2/2} \quad \phi_y \sim N(0, \sigma_R^2) \quad (\text{A.2a})$$

$$N_{y+1,1} = \frac{SB_y}{\psi_0} \exp \left[A_y \left(1 - \frac{SB_y}{\psi_0 R_1} \right) \right] e^{\phi_{y+1} - \sigma_R^2/2} \quad \phi_y \sim N(0, \sigma_R^2) \quad (\text{A.2b})$$

but not for the third:

$$N_{y+1,1} = \bar{R}_1 e^{\phi_{y+1} - \sigma_R^2/2} \quad \phi_y \sim N(0, \sigma_R^2) \quad (\text{A.3})$$

where SB_y is the female spawning biomass during year y (corresponding to 1 April):

$$SB_y = \sum_{a=2}^x w_{y,a}^{spawn} \phi_{y,a} N_{y,a} e^{-frac(M_a + \tilde{S}_{y,a} F_y)} \quad (\text{A.4})$$

| | |
|-------------------|---|
| $\phi_{y,a}$ | is the fraction of fish of age a that are mature/spawning during year y ; |
| $frac$ | is the fraction of the year at which spawning takes place (set to 3/12); |
| R_1 | is the number of age-1 animals at unfished equilibrium; |
| ψ_0 | is spawning biomass-per-recruit in the absence of exploitation; |
| h | is the steepness of the stock-recruitment relationship ($h = 1/(1 + 4e^{-A_r})$ for the Ricker model); |
| \bar{R}_1 | is average age-1 recruitment; |
| σ_R | is the log-scale standard deviation of the random fluctuations in recruitment about the underlying deterministic stock-recruitment relationship (set to 1.0; Dorn et al. 2005); and |
| $w_{y,a}^{spawn}$ | is the average mass of a spawning fish of age a during year y . |

Fishery selectivity

Following Dorn and Methot (1990), Helser et al. (2001), and Sullivan et al. (1997), Dorn et al. (2005) modeled fishery selectivity for the historical period using a double-logistic function with time-varying parameters:

$$S_{y,a} = \left[\frac{1}{1 + \exp[-\beta_1 e^{\delta_{\beta_1,y}} (a - \alpha_1 - \delta_{\alpha_1,y})]} \right] \left[1 - \frac{1}{1 + \exp[-\beta_2 e^{\delta_{\beta_2,y}} (a - \alpha_2 - \delta_{\alpha_2,y})]} \right] \quad (\text{A.5})$$

where $\alpha_1, \alpha_2, \beta_1, \beta_2$ are the parameters that determine the shape of the selectivity curve;

$\delta_{\alpha_1,y}, \delta_{\alpha_2,y}$ are the deviations in the fishery selectivity α parameters for year y ; and

$\delta_{\beta_1,y}, \delta_{\beta_2,y}$ are the deviations in the fishery selectivity β parameters for year y .

Catches

Under the assumption of continuous fishing throughout the year, the fully selected fishing mortality is calculated by solving the equation:

$$\hat{C}_y = \sum_{a=1}^x w_{y,a} \hat{C}_{y,a} ; \hat{C}_{y,a} = \frac{\tilde{S}_{y,a} F_y}{M_a + \tilde{S}_{y,a} F_y} N_{y,a} (1 - e^{-(M_a + \tilde{S}_{y,a} F_y)}) \quad (A.6)$$

where \hat{C}_y is the estimated catch (in mass) during year y ;

$w_{y,a}$ is the average mass of a fish of age a during year y (Dorn et al. 1999); and

$\hat{C}_{y,a}$ is the estimated catch of fish of age a (in numbers) during year y .

Surveys

The data used to estimate the values for the parameters of the operating model are available from six fishery-independent sources: (1) the NMFS winter GOA Shelikof Strait echo-integration trawl (EIT) survey (Guttormsen and Yasenak 2006); (2) the NMFS GOA bottom trawl survey (Martin 1997, Britt and Martin 2000); (3) the egg production estimates of female spawning biomass (Picquelle and Megrey 1993); (4) the ADFG crab/groundfish nearshore bottom trawl survey (Blackburn and Pengilly 1994); (5) the McKelvey age 1 survey (McKelvey 1996); and (6) an historical ADFG 400-mesh eastern trawl survey (Dorn et al. 2005). The data for each survey include indices of abundance, and survey size- and age-composition (see Dorn et al. (2005) for full details of the data available for each survey type).

The model estimates of the survey biomass indices are calculated using the equation:

$$\hat{I}_{d,y} = \hat{q}_d \hat{B}_{d,y}^e \quad (A.7)$$

where

\hat{I}_d is the model estimate of the biomass index for survey d ;

\hat{q}_d is the model estimate of catchability for survey d ;

$\hat{B}_{d,y}^e$ is the model estimate of the total biomass available to survey d during year y :

$$\hat{B}_{d,y}^e = \sum_{a=1}^x w_{y,a}^d \hat{N}_{d,y,a}^e = \sum_{a=1}^x w_{y,a}^d \tilde{S}_a^d N_{y,a} e^{-\text{frac}_d(M_a + \tilde{S}_{y,a} F_y)} \quad (A.8)$$

$\hat{N}_{d,y,a}^e$ is the model estimate of total number of age a animals available to survey d during year y ;

\tilde{S}_a^d is the age-specific selectivity pattern for the survey type d (assumed to be descending logistic function for the EIT survey, an ascending logistic function for the ADFG coastal survey and the historical trawl survey, and a double lo-

gistic function for the NMFS bottom trawl survey; the egg production estimates are assumed to be indices of female spawning biomass; while the McKelvey data are indices of age 1 abundance);

$w_{y,a}^d$ is the average mass of a fish of age a in year y during survey d (Dorn et al. 1999); and

$frac_a$ is the fraction of the year at which survey d takes place.

Initial conditions

The numbers-at-age at the start of 1961 are assumed to be lognormally distributed about the equilibrium numbers-at-age.

$$N_{1961,a} = N_{1961,1} e^{-\sum_{a=1}^{a-1} M_a} e^{v_a} ; \quad v_a \sim N(0, \sigma_R^2) \quad (\text{A.9})$$

Parameter estimation and Bayesian analysis

The estimable parameters of the operating model are the parameters of the stock-recruitment relationship, the deviations in recruitment (initial conditions and about the stock-recruitment relationship), the annual fishing mortalities, the parameters that define fishery selectivity and how it changes over time, and the parameters that determine survey catchability and survey selectivity. The sample of parameter vectors used for projection purposes is generated using the Markov chain Monte Carlo (MCMC) algorithm (AD Model Builder, Fournier 2006). The application of the MCMC algorithm is based on 11 million iterations, of which the results of every 10,000th iteration are saved. The objective function that forms the basis for the application of the MCMC algorithm follows that used by the actual assessment (Dorn et al. 2005) and includes components for fishery catch, fishery catch proportions-at-age, fishery catch proportions-at-length (for years for which fishery catch proportions-at-age data are not available), survey abundance indices, survey catch proportions-at-age, and survey catch proportions-at-length (for years for which survey catch proportions-at-age data are not available). This objective function also includes priors on the deviations about the deterministic stock-recruitment relationship (Eq. A.2 and A.3), on the deviations about the deterministic 1961 age-structure (Eq. A.9), and on the extent to which fishery selectivity may vary among years (Eq. A.5).

When recruitment is assumed to be related to spawning stock size according to the Beverton-Holt or Ricker relationships, a normal distribution with mean given by the average age 1 recruitment since 1977

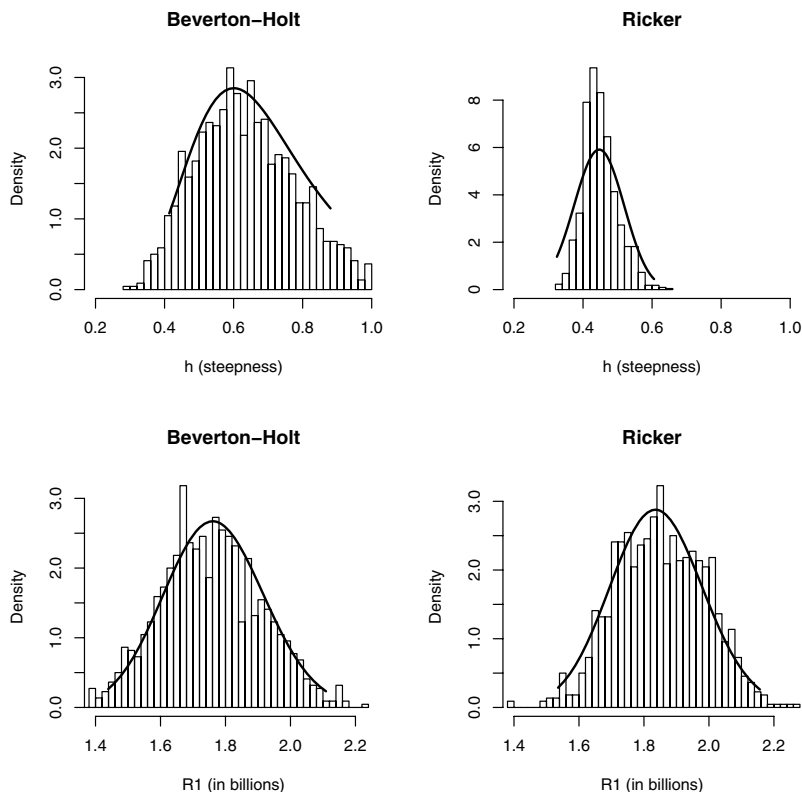


Figure A.1. Likelihood profiles (solid lines) and the marginal posteriors (histograms) for R_1 and h for the Beverton-Holt and Ricker scenarios.

from the scenario in which recruitment is independent of spawning stock size and a CV of 0.1, is used as a prior for the recruitment in the unfished state, R_1 . Fig. A.1 contrasts the posterior distributions for R_1 and h (steepness) with likelihood profiles for these quantities.

Data generation

The data available to the estimation model in the future are the data currently available (and on which the parameters of the operating model are based) along with future data generated by the operating model. The latter data are generated in a manner consistent with how they are treated in the actual GOA pollock assessment. Data are generated for fishery catch proportions-at-age (using multinomial sampling, with an

effective sample size of 400) and for the EIT, NMFS bottom trawl and ADFG coastal surveys. Future data are not generated for the egg production and historical trawl surveys because these surveys no longer take place, while the age-1 indices are sufficiently imprecise that they provide effectively no information and are consequently not simulated. The selectivity for the fishery and the surveys are constant over the projection period in both the operating model and the stock assessment model. In the operating model, the projected fishery selectivity is the average fishery selectivity for 1992-2004.

The simulated indices of abundance from the EIT and ADFG surveys are lognormally distributed with CVs of 0.2 and 0.25 respectively. The survey proportions-at-age for these two surveys are multinomially distributed with effective sample sizes of 60 and 10 respectively. The log-normal CV assumed for the NMFS bottom trawl surveys in each future year is selected at random from the historical past CVs for this survey. Similarly, the annual effective sample sizes for the proportions-at-age for this survey are selected at random from the historical effective sample sizes. The EIT and ADFG surveys are assumed to be conducted annually in the future while, consistent with actual practice, data from the NMFS bottom trawl survey are only generated for every second year in the future.

The annual weights-at-age for the fishery, all surveys, and the average population weights and weights at spawning are based on the data used in the 2005 GOA pollock stock assessment.

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