

How does stocking density affect enhancement success for hatchery-reared red king crab?

William Christopher Long, Peter A. Cummiskey, and J. Eric Munk

Abstract: Stock enhancement of red king crab (*Paralithodes camtschaticus* (Tilesius, 1815)) could increase the crab population near Kodiak, Alaska, which collapsed in the 1980s and has not recovered. We conducted a field experiment examining the effect of juvenile red king crab density on enhancement success. Hatchery-reared crabs were released in plots near Kodiak at three densities: 25, 50, and 75 m⁻². Crab densities were monitored for 6 months after release. Predation risk was measured via tethering experiments and predator density via quadrat and transect surveys. Neither migration nor mortality changed with crab density, but mortality rates decreased over time. Crab density did not affect predator density or predation risk, although predation risk decreased with time. Excluding the high initial mortality rate of 67.5%, the predicted survival after 6 months was 34%, which is better than the survival observed in a wild population. This suggests that red king crab enhancement is not predation limited and can occur at high densities. Further, processes affecting juvenile red king crab may not be strongly density dependent, at least at the scales and habitats tested.

Résumé : La mise en valeur des stocks de crabes royaux (*Paralithodes camtschaticus* (Tilesius, 1815)) pourrait accroître la population de crabes près de Kodiak (Alaska), qui s'est effondrée dans les années 1980 et ne s'est pas rétablie depuis. Nous avons mené une expérience de terrain pour examiner l'effet de la densité de crabes royaux juvéniles sur le succès de la mise en valeur. Des crabes élevés en écloseries ont été lâchés dans des parcelles à proximité de Kodiak à raison des trois densités suivantes : 25 m⁻², 50 m⁻² et 75 m⁻². La densité de crabes a été surveillée pendant six mois après le lâcher. Le risque de prédation a été mesuré dans des expériences avec des crabes attachés et la densité de prédateurs a été mesurée par échantillonnage par quadrats ou le long de transects. Aucune variation de la migration ou de la mortalité en fonction de la densité de crabes n'a été notée, mais les taux de mortalité ont diminué au fil du temps. La densité de crabes n'avait pas d'incidence sur la densité de prédateurs ou le risque de prédation, bien que ce dernier ait diminué au fil du temps. En excluant le taux de mortalité initial élevé de 67,5 %, le taux de survie prédit après six mois était de 34 %, ce qui est supérieur à la survie observée dans une population sauvage. Cela donne à penser que la mise en valeur du crabe royal n'est pas limitée par la prédation et peut se faire à fortes densités. En outre, les processus qui ont une incidence sur les crabes royaux juvéniles pourraient ne pas dépendre fortement de la densité, du moins aux échelles et dans les habitats étudiés. [Traduit par la Rédaction]

Introduction

Red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), was a major fishery species in Kodiak Island, Alaska, waters during the 1970s and 1980s, but the population declined in the late 1970s and early 1980s and the commercial fishery was closed in the early 1980s (Bechtol and Kruse 2010). Since then, the population has not returned to its previously high levels. The reason for the decline and the subsequent failure to recover is not well understood, but the decline was likely linked to a combination of overfishing (Orensanz et al. 1998), recruitment failure (Blau 1986), recovery failure due to predator abundance (Bechtol and Kruse 2009), and climatic shifts towards warmer temperatures (Zheng and Kruse 2000). As fishery reductions have not led to the recovery of the stock, stock enhancement has been considered as a means to facilitate stock recovery (Stevens 2006).

Red king crab have a complex life-history involving both pelagic and benthic stages. Females brood eggs for about a year and larvae hatch in the spring, immediately after which the females molt, mate, and extrude a new batch of eggs (Stevens and Swiney 2007). Fecundity, which is dependent on the size of the crab, whether the crab is primiparous or multiparous, and the age of the crab,

ranges from about 30 000 to 400 000 eggs (Swiney et al. 2012; Swiney and Long 2015). Larvae spend around 2–3 months in the plankton, where they pass through four zoeal stages and one glaucothoe stage (Shirley and Shirley 1989). The glaucothoe seek complex habitat, where they settle and molt to the first crab stage (Stevens 2003). Glaucothoe and early benthic juveniles are cryptic (Daly and Long 2014b) and prefer complex biogenic habitat such as algae and hydroids (Sundberg and Clausen 1977) and non-biogenic habitat such as rocks or shells (Stevens and Kittaka 1998; Loher and Armstrong 2000). This is likely because predation, both by fish (Stoner et al. 2010) and crustaceans (Stevens and Swiney 2005), is significantly lower in such habitats, although food availability may also be a factor (Stevens and MacIntosh 1991; Pirtle and Stoner 2010). After the first 2 years, crabs transition to a podding behavior (Powell and Nickerson 1965), which is also thought to decrease predation risk as they grow to maturity (Dew 1990).

Red king crab may be a good candidate for stock enhancement. In the wild, red king crab suffer high mortality at the larval stage, perhaps 0.1% survival to the glaucothoe stage (Shirley and Shirley 1989), and potentially much lower survival to the first crab stage, especially if the glaucothoe are not advected to the right habitat types (Stevens and Kittaka 1998). If the major population bottle-

Received 9 August 2017. Accepted 12 March 2018.

W.C. Long, P.A. Cummiskey, and J.E. Munk. NOAA, National Marine Fisheries Service, Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering Division, Kodiak Laboratory, 301 Research Ct., Kodiak, AK 99615, USA.

Corresponding author: William Christopher Long (email: chris.long@noaa.gov).

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from [RightsLink](https://www.elsevier.com/locate/permissions).

neck occurs prior to settlement to the benthos, then hatchery culture, which can increase survival to the first crab stage to up to 63% (Persselin and Daly 2010; Swingle et al. 2013), could help overcome this bottleneck. In addition, the red king crab's large size and high value make them an economically attractive species for stock enhancement (Hamasaki and Kitada 2008).

Post-release survival of hatchery-reared juveniles depends on a number of factors and optimizing survival is key to the success of a stock enhancement program. Hatchery-reared juveniles can be less fit than their wild counterparts, resulting in higher mortality (Stoner and Davis 1994). Sometimes this can be reduced or eliminated by conditioning animals prior to release (Davis et al. 2004; Leбата et al. 2009); in hatchery-reared red king crab, there is evidence that conditioning juveniles via contact with predators can increase cryptic behavior, suggesting that conditioning could be useful (Daly et al. 2012). The size of released animals can be important, as larger crabs may be less vulnerable to predation (Johnson et al. 2008; Pirtle et al. 2012; Daly et al. 2013). In addition, the season of release can be important if there is strong seasonal variation in predator pressure; survival of released hatchery-reared juvenile blue crab, *Callinectes sapidus* M. J. Rathbun, 1896, is much higher if they are released in fall after the summer peak in predation (Johnson et al. 2008).

The density of released juveniles can be an important factor in stock enhancement success and it can be mediated by either top-down or bottom-up processes. Given that in most cases juvenile crabs are small and do not have high energetic demands relative to food availability in their habitats, food limitation is not likely. For example, for juvenile blue crab, prey availability is not a significant determinant of habitat quality (Long et al. 2011), and there is no evidence of food limitation in blue crab release experiments (Seitz et al. 2008). A more likely bottom-up limitation for cryptic species is competition for shelter; juvenile European lobster, *Homarus gammarus* (Linnaeus, 1758), show such a response (van der Meer 2005). However, for juveniles, predation is the density-dependent process mostly likely to have a significant effect (Johnson et al. 2008).

The predator functional response describes how predation rates change with prey density and is typically either type I (density-independent), type II (inversely density-dependent), or type III (density-dependent) (Holling 1959; Hassell et al. 1977). This can be further modified by the predator aggregation response, which is an effect of prey density on predator density (e.g., Seitz et al. 2003). The functional response can vary, both quantitatively and qualitatively, with a number of factors including habitat (Alexander et al. 2012; Daly and Long 2014a), the size of the predator or prey (Aljetlawi et al. 2004; Alexander et al. 2013), the spatial arrangement of prey (Hines et al. 2009; Santos et al. 2009; Long and Hines 2012), environmental variables (Taylor and Eggleston 2000; Long et al. 2014), or predator density (Murdoch 1973). Although functional response experiments are generally performed in the laboratory, they can be predictive of what occurs in the field (Eggleston et al. 1992) and can explain whether prey species can maintain populations in particular habitats (Seitz et al. 2001). This can be very important for stock enhancement: blue crab stocking success decreases rapidly with density (Hines et al. 2008), which is predicted by the type III functional response (Long et al. 2012a).

In this experiment, we examined how release density affects short-term stock enhancement success for juvenile red king crabs. Given the functional response of predators on red king crab in the laboratory (Long and Whitefleet-Smith 2013), we expected a strong density-dependent response in success, with proportional mortality, driven by predation, increasing with density. Although the motivation for this experiment was optimizing stock enhancement, this experiment also addresses important questions about density-dependent processes at this early and difficult to study portion of the red king crab life history.

Methods

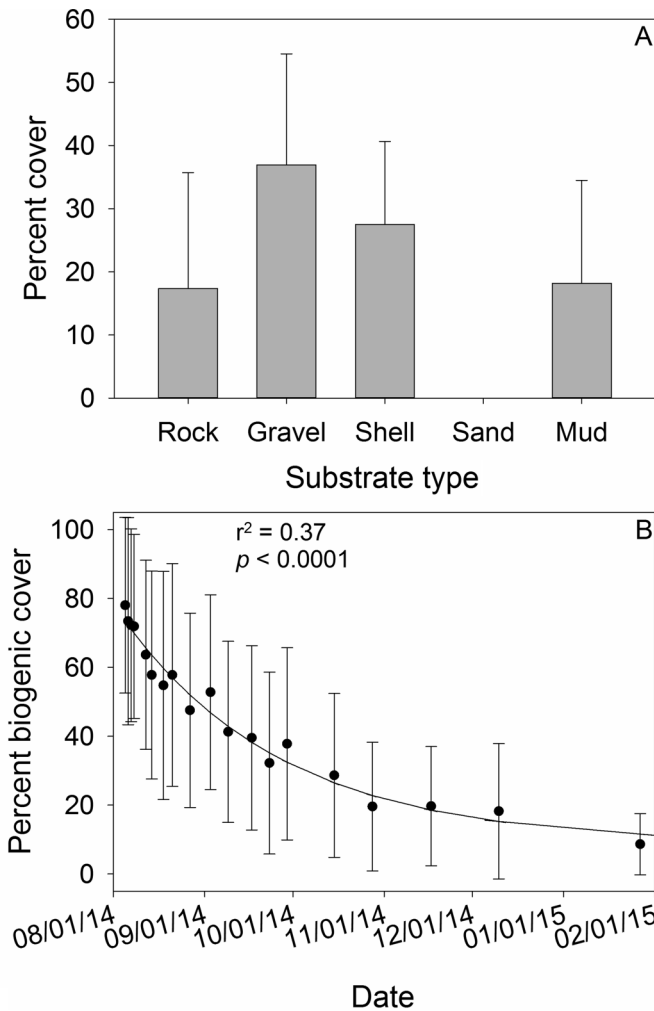
Juvenile red king crab used in this project were reared at the Alutiiq Pride Shellfish Hatchery using females captured in crab pots in Alitak Bay, Kodiak Island, as per Swingle et al. (2013). Females were held in tanks at the hatchery in flowing seawater at ambient temperature and salinity and fed to satiation on frozen herring and squid. Larvae were collected and reared to the juvenile stage on a diet of *Artemia* sp. enriched with DC DHA Selco (INVE Aquaculture, UT, USA). Juveniles were transported to the Kodiak Laboratory in coolers and reared on a diet of frozen *Artemia* (Brine Shrimp Direct, Ogden, Utah, USA), frozen bloodworms (Brine Shrimp Direct, Ogden, Utah, USA), frozen Cyclop-eeze (Argent Laboratories, Redmond, Washington, USA), Cyclop-eeze flakes, and Gelly Belly mixed with Cyclopeeze powder and Walleye Pollock (*Gadus chalcogrammus* Pallas, 1814) bone powder (U.S. Department of Agriculture, Agricultural Research Service, Kodiak, Alaska, USA) three times per week to excess.

The experiment was performed in Trident Basin, Kodiak Island, Alaska. The site was chosen because it is well-sheltered and had abundant suitable red king crab habitat in preliminary surveys and previous surveys found juvenile red king crab there (Dew 1991). The substrate was mixed rocks and shells covered by a dense bed of macroalgae. Twelve plots were established along a transect line that ran parallel to the shoreline at a depth of ~8 m. Each plot was 5 m × 5 m (25 m²) and was marked with a square of ground-line held in place with reinforcing bar (rebar) stakes. Plots were positioned 10 m apart from each other.

Crabs were released on 4 August, 2014, and were probably mostly at the C3 to C4 stage. Each plot was randomly assigned to one of three initial starting densities within the range of densities (95% CI estimated visually) in wild populations of year-0 crab (Loher and Armstrong 2000): 75, 50, 25 crab m⁻², or a control (0 crab m⁻²); each treatment including the control was replicated three times. To spread the crabs out as evenly as possible over the plots, each plot was divided into four 2.5 m × 2.5 m sub-quadrats using a temporary frame and the correct number of crabs for each plot's density treatment was counted out, transported to the bottom in individual containers, and released into each of the sub-quadrats. At release, a subsample of crabs was measured with digital calipers; the average carapace width of the crabs (including spines) was 3.3 ± 0.4 mm (±SD).

Crab densities were sampled by a diver using a 50 cm × 50 cm quadrat. Three quadrats were haphazardly sampled inside each plot. Additionally, three more quadrats were taken outside each of the plots at 0 m (right on the edge of the site) on three randomly chosen sides of each plot to estimate emigration rates. Each quadrat was carefully searched, and all red king crab were counted. In each quadrat, the percent cover of any structure-forming biota (macroalgae, hydroids, anemones, etc.) was recorded. Also, any potential predators present in the quadrat were identified and counted. Prior to the release, the plots were sampled to establish the background density of red king crab in each plot. After release, densities were sampled the day after release (day 1), days 2, 3, and 4, twice a week for the next 2 weeks, once a week for the next 3 weeks, every 2 weeks for the next 2 months, and then approximately monthly; each plot was sampled 19 times during this experiment. At times, particularly later in the project, a set of quadrat samples was taken over 2 days, and in these cases, they were analyzed as if they had all been taken on the same day, assuming changes in density over that time to be negligible. During the initial sampling, substrate composition (mud, sand, shell hash, gravel, and rock) was also recorded. Substrate composition was analyzed with an ANOSIM on a Euclidean distance similarity matrix with Treatment and Plot (nested within treatment) as factors. All multivariate analyses in this paper were performed in Primer v6.1.5 (Plymouth, UK). Substrate did not differ among treatments (Global R = 0.083, *p* = 0.257) and mostly consisted of com-

Fig. 1. (A) Mean percent cover of substrates in experimental plots at the beginning of the experiment. Error bars are one standard deviation. (B) Average percent biogenic cover for each sampling date throughout the release experiment. Best fit regression = $9.0 + 65.6e^{-0.018t}$, where t is the time in days from initial release. Error bars are one standard deviation.



plex substrates such as rock, shell, and gravel (Fig. 1). Percent biotic cover was dominated by the sugar kelp, *Saccharina latissima*, and did not vary with treatment (ANOVA, $F_{[3,1,178]} = 2.546$, $p = 0.055$; data square-root transformed to achieve homogeneity of variance), but it did decrease over time as the kelp senesced in the fall and winter (Fig. 1). All ANOVA type analyses in this paper were performed in Systat v13.00.05 (San Jose, CA).

To assess the counting efficiency of the divers, caged crab trials were performed. For each plot, a random number of crabs selected by the diver establishing the plot was placed within a 50 cm × 50 cm quadrat that was located at the same depth and in the same habitat as the plots but separated from them by a distance of at least 50 m. A cage made of 6 mm mesh hardware cloth lined on the inside with 1 mm mesh fiberglass screen was placed over the crabs. The cage was made to just fit within the quadrat. The quadrat was removed and the sides of the cage were worked into the substrate, and surrounding substrate was pushed up along the edges of the cage to seal all exits. The cage was stabilized by placing several rocks on the top. The next day, after the crabs had been given a chance to hide, the cage was removed and the quadrat searched for crabs as above. Each diver established plots for another diver and each diver counted five quadrats. On some

plots, some of the crabs had climbed onto the cage and were clinging to the inside; these were not included in the analysis. The proportion of crabs found on each plot was calculated and analyzed with an ANOVA with diver as the factor. The counting efficiency of the divers was 0.74 ± 0.06 (standard error, SE), did not differ among divers (ANOVA; $F_{[2,12]} = 2.942$, $p = 0.091$), and was used to calculate actual density from the quadrat counts done throughout the experiment.

Movement of the crabs was modeled with a random walk model, which models movement of animals as a series of steps that are each in a random direction (Manly 1977). As there was abundant suitable habitat, tens to hundreds of meters' worth, in every direction, there is no reason to suppose the crabs would demonstrate directional movement. If treated as a continuous process, then the solution for a random walk model is the same as diffusion (Othmer et al. 1988). Thus, we modeled movement of the crabs as two-dimensional diffusion from a patch with radius a over which crabs were distributed evenly with an initial density of C_0 such that

$$C(r, t) = aC_0 \int_0^{\infty} J_1(ua)J_0(ur)e^{-Du^2} du$$

where C is the density, r is the distance from the center of the initial distribution, t is the time, u is a parameter of integration, D is the diffusion parameter, and J_0 and J_1 are Bessel functions of the first kind of order 0 and 1, respectively (Crank 1975). D is proportional to the rapidity of spreading, with larger numbers indicating more rapid spreading. This model only accounts for movement of crab, but mortality is easily incorporated by multiplying the C by a survival term, S (Socolofsky and Jirka 2005). We modeled mortality in two ways. In the first, the mortality rate was held constant over time

$$S(t) = (1 - m_i)e^{-mt}$$

where m_i is the initial mortality immediately after release and m is the instantaneous mortality rate. We estimated m_i as 0.675 by averaging the proportional decrease in the densities in all the plots over the first 24 h. In addition, to model a mortality rate that changed over time, we modeled S as a difference equation such that

$$S_t = (1 - m_i)(1 - m_t)S_{t-1}$$

where S_t is the survival at time t (in days) and m_t is the mortality rate at time t . We modeled the density of crabs with a Poisson distribution of errors and calculated the expected mean number found in searched quadrats at a given t as

$$\lambda = Ac_e S \int_x^y 2\pi r C(t, r) dr$$

where A is the area searched and c_e is the counting efficiency (determined above via caging experiments). By setting x and y to 0 and a , respectively, we were able to estimate the average number expected in the counts inside the plots, and by setting x and y to a and $a + 0.5$, respectively, we were able to estimate the number outside the plots. To avoid pseudoreplication, quadrant counts at each plot were aggregated and treated as a single sample with an A of 0.75 m² for both the inside and outside samples. Because no wild crabs were detected in control plots (see Results below), we did not have to account for wild crabs. The counts of red king crab in the quadrats was fit in R 3.1.2 (Vienna, Austria) using maximum

likelihood to a series of models in which the diffusion coefficient, D , and the mortality rate, m , were allowed to vary with release density (modeled as a discrete factor). Models were included where m_t decreased exponentially with time such that $m_t = m_0 e^{-bt}$, where m_0 is the mortality rate at release and b describes how quickly the mortality rate decreases with time and where D , m_0 , and b were allowed to vary with density treatment and plot (nested within treatments). The models were ranked using Akaike's information criterion corrected for small sample size (AIC_c) and the best model selected. Models where the AIC_c differed by <2 were considered to explain the data equally well (Burnham and Anderson 2002).

Relative predation risk was assessed through tethering experiments. The crabs tethered were from the same batch of juvenile crabs released but were held in the laboratory for this purpose. Thus, they were the same age, and presumably size, as the crabs that were released. Individual hatchery crabs were tethered with 1 kg test monofilament line attached to their carapaces with cyanoacrylate glue. The line was 15 cm long and attached to a marker flag using a fishing swivel. Three crabs were tethered in each plot separated by at least 1 m. Tethered crabs were deployed in the late afternoon and were checked the next morning and again the next afternoon. To avoid disturbances, no quadrat counts were performed during the tethering experiments. Crabs that had molted, as evidenced by an intact exoskeleton remaining on the tether, were excluded from analysis. This experiment was performed in August, September, and October. The number of tethered crabs that were still alive during each check, aggregated by plot to avoid pseudoreplication, was fit to the equation $N_t = N_0 e^{-pt}$, where N_t is the number surviving at time t , N_0 is the initial number, and p is the predation rate. The data were fit, using maximum likelihood, to a series of models in which the predation rate was allowed to vary with release density (modeled as a discrete factor), month, or time of day (day or night) in R 2.14.0. The models were ranked using AIC_c and the best model selected as above.

Fish predators were sampled by diver transects at the same times as the tethering experiments. At each plot, one diver swam along a 5 m transect at the top (shallowest) side and another diver swam a 5 m transect on the bottom (deepest) side of each plot. All mobile potential predators within 1 m of the transect line were identified to the lowest taxonomic level possible and recorded. The total number of potential predators was calculated for each plot. Predator densities from both quadrat counts (which were aggregated within each plot on each sampling date to avoid pseudoreplication) and transects were square-root transformed prior to analysis. They were visualized using non-metric multidimensional scaling (nMDS) based on a Bray–Curtis similarity matrix and analyzed using an analysis of similarity (ANOSIM) with Treatment and Date as factors.

Results

No juvenile red king crabs were found in any quadrat counts in any of the control plots throughout the experiment or any of the counts performed prior to the release, indicating that the wild king crab population was at a density that was below detectable limits. Other than right after release, crabs were highly cryptic in their behavior. Although no quantitative data were collected, they were most frequently found under rocks and bivalve shells and inside macroalgae holdfasts. In the best fit model for crab density inside and outside the plots, the mortality rate decreased over time (Table 1; Figs. 2 and 3). No model in which the emigration rate or mortality rate varied with release density had any support (Table 1) because the proportional loss of crabs from plots did not differ among treatments (Fig. 2B); similarly, there was no support for models in which emigration or mortality varied with plot (nested within density treatment). Crab density in plots decreased rapidly at first (Fig. 2A) due to a combination of both movement

Table 1. AIC_c values of models of mortality and diffusion (emigration) of released red king crabs in plots.

Model	K	AIC_c	ΔAIC_c	Likelihood	AIC_c weight
D, m	2	1296.26	133.43	0.00	0.00
$D(R), m$	4	1296.89	134.06	0.00	0.00
$D, m(R)$	4	1299.78	136.95	0.00	0.00
$D(R), m(R)$	6	1278.78	115.95	0.00	0.00
$D, m(t)$	3	1162.83	0.00	1.00	1.00
$D(R), m(t)$	9	1268.90	106.06	0.00	0.00
$D(R, P), m(t, R, P)$	27	1238.10	75.27	0.00	0.00

Note: Model indicates how diffusion (D) and mortality (m) were modeled. Where R or P are included parenthetically, it indicates that the parameter was a function of release density (treated as a discrete factor) or plot (nested within density treatment), respectively. $m(t)$ indicates a model in which mortality rate decreased with time. K is the number of parameters in each model. Sample size was 337. See text for full model descriptions.

out of the plots (Fig. 2C) and mortality (Fig. 3). Mortality was very high at first, particularly the first week after release, but decreased rapidly with time (Fig. 3). We could account for the emigration from the plots and use the estimated mortality rate to calculate the overall survival of all crabs both inside and outside the plots using the difference equation for survival (above); predicted survival after 6 months when we stopped sampling was 34%, ignoring initial mortality. Including initial mortality, 11% of all crabs released were predicted to have survived the first 6 months after release.

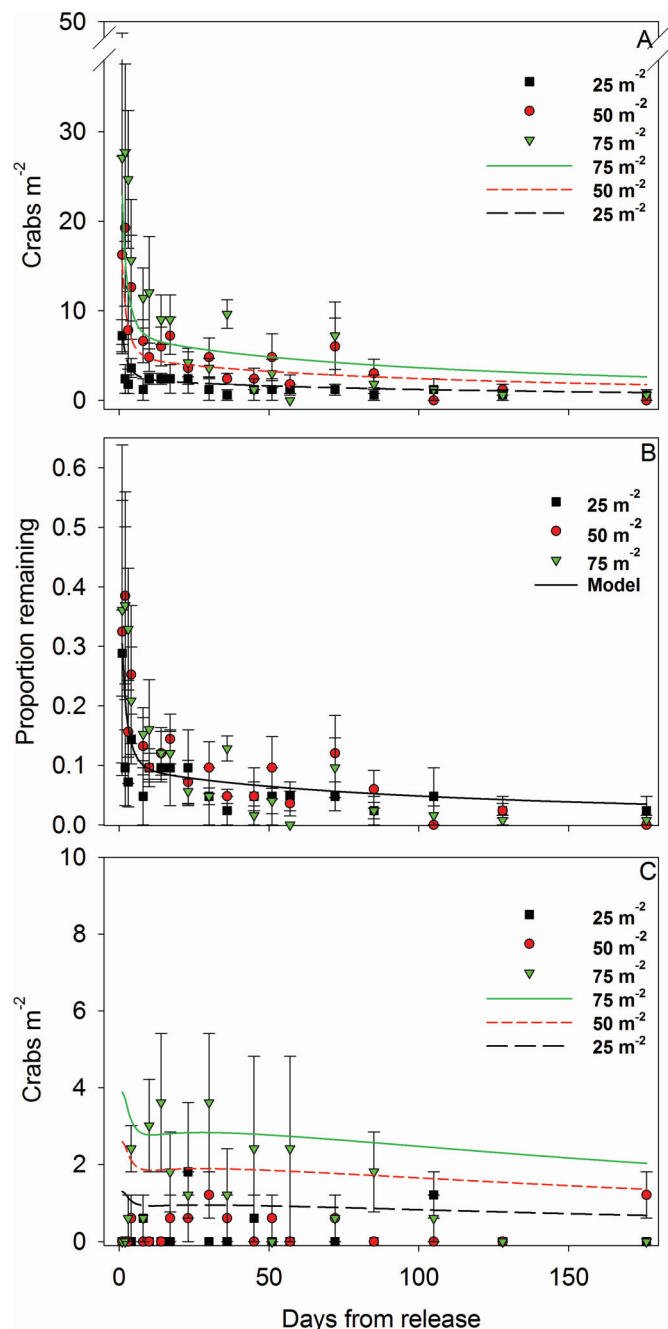
Two models fit the tethering experiment data equally well. In the best model, predation rate varied among months and the time of day, and in the second best model, it varied only with month; there was no support for any model in which the predation rate varied with the release density (Table 2). The results for the first model are presented (Fig. 3A). Predation rates decreased from August through October and were lower during the day than during the night. The decline in observed predation rate over time matched the decline in mortality rates in the best fit model for crab density (Fig. 3).

The densities of smaller predators counted in quadrats did not vary among treatments (ANOSIM, Global $R = 0.009$, $p = 0.31$; Fig. 4). There was a statistical difference among dates (ANOSIM, Global $R = 0.026$, $p = 0.028$), but a Global R value so close to zero indicated that the differences were biologically negligible (Clarke and Warwick 2001), and examination of pairwise comparisons among dates failed to reveal any patterns suggesting a change in the predator assemblage over time. Smaller predators included hermit crabs (primarily *Elassochirus gilli* (J. E. Benedict, 1892) and *Elassochirus tenuimanus* (Dana, 1851)), dock shrimp (*Pandalus danae* Stimpson, 1857), Arctic shanny (*Stichaeus punctatus* (Fabricius, 1780)), crescent gunnel (*Pholis laeta* (Cope, 1873)), and Alaskan ronquil (*Bathymaster caeruleofasciatus* Gilbert and Burke, 1912). The density of larger and (or) mobile predators counted in predator transects did not vary among months (ANOSIM, Global $R = 0.082$, $p = 0.160$) or release densities (Global $R = 0.03$, $p = 0.360$; Fig. 4). Common predators included juvenile rockfish (*Sebastidae* spp., mostly dusky rockfish, *Sebastes ciliatus* (Tilesius, 1813)), Alaskan ronquil, greenlings (*Hexagrammidae* spp.), and sculpins (*Cottoidea* spp., with red Irish lords, *Hemilepidotus hemilepidotus* (Tilesius, 1811), being the most common).

Discussion

This experiment provides strong evidence that stock enhancement of red king crabs is ecologically viable at least through the first year in Kodiak, estimates the natural mortality rate of juveniles in the region in known good habitat, and answers important questions about density-dependent processes in juvenile red king crab in this habitat. Released red king crabs survived well compared with wild crabs after release despite high mortality imme-

Fig. 2. Red king crab juveniles counted in quadrats inside and outside of release plots over time. (A) Density of crabs inside release plots. (B) Proportion of released crabs remaining in release plots over time. (C) Density of crabs outside plots. Points represent mean (averaged among replicate plots) and error bars are one standard error (SE). Lines are the best fit models of mortality and emigration (see text for details). Emigration rate (diffusion) = $0.02415 \text{ m}^2/\text{day} \pm 0.00004 \text{ (SE)}$. See Fig. 3 for mortality rate. [Colour online.]



diately after release. An estimated 11% of all released crabs survived 6 months after release, the period of benthic life when they are likely most vulnerable to predation. Despite releasing crabs at a high density, we found no density dependence in anything we measured, including predation rate, predator density, mortality rate, or diffusion rate. This work adds substantially to our understanding of the early benthic life history stage of red king crab and paves the way for future work on red king crab

Fig. 3. (A) Effects of month and time of day on predation rates on tethered juvenile red king crabs. Bars represent best fit model estimates and error bars are one standard error. Statistical differences among treatments are indicated with different letters and cases. (B) Best fit model for mortality rate of released crabs based on quadrat count data. Parameter estimates are: $m_0 = 0.409 \pm 0.059 \text{ (SE)}$ and $b = 0.352 \text{ day}^{-1} \pm 0.061 \text{ (SE)}$. See text for model details.

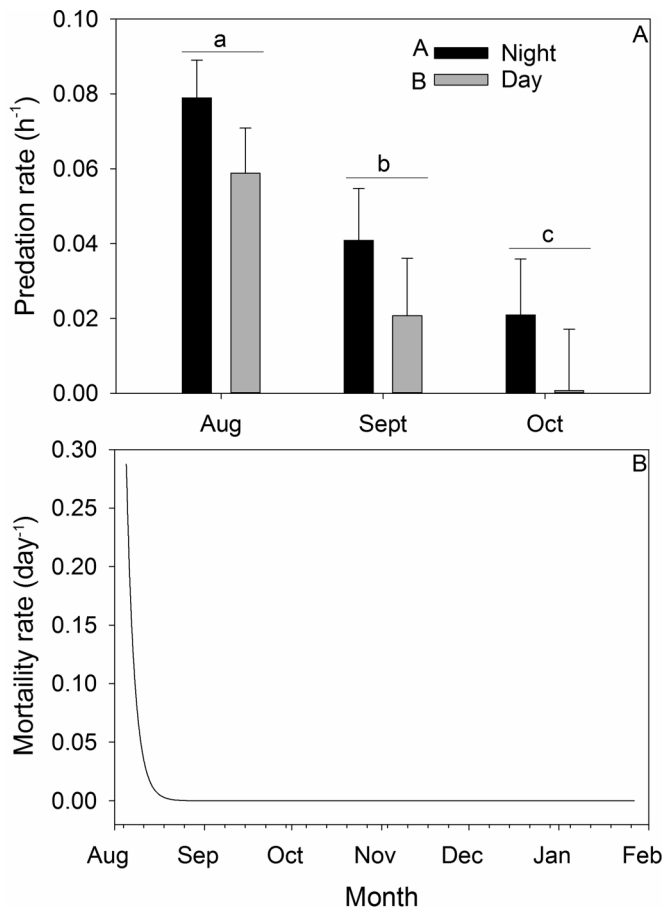


Table 2. AIC_c values of models of predation rate (*p*) on tethered red king crab.

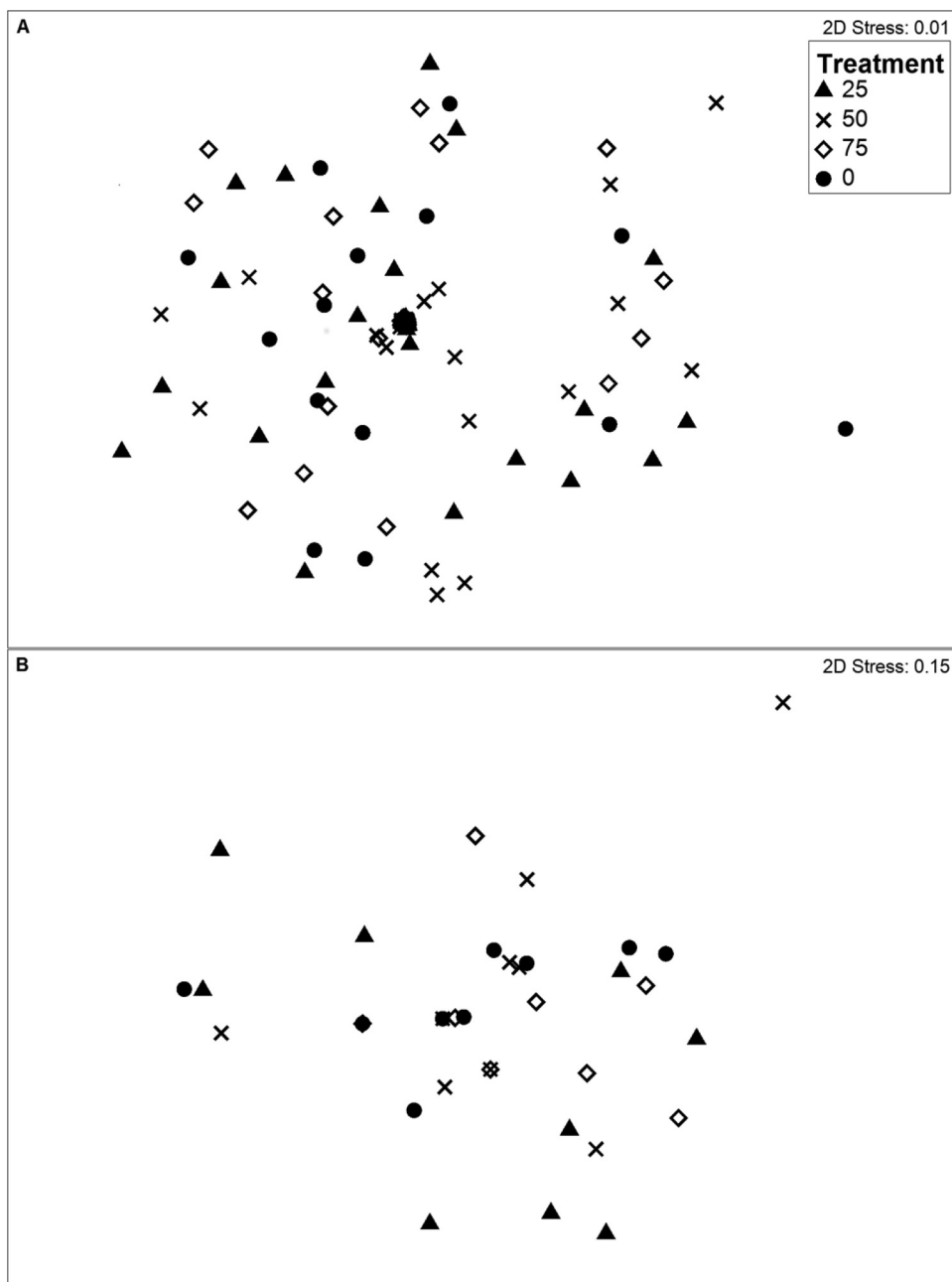
Model	<i>K</i>	AIC _c	ΔAIC _c	Likelihood	AIC _c weight
<i>p</i>	1	121.62	15.15	0.00	0.00
<i>p</i> (D)	4	125.63	19.16	0.00	0.00
<i>p</i> (T)	2	120.12	13.65	0.00	0.00
<i>p</i> (M)	3	108.29	1.83	0.40	0.27
<i>p</i> (M, T)	4	106.46	0.00	1.00	0.67
<i>p</i> (D, M)	6	112.79	6.33	0.04	0.03
<i>p</i> (D, T)	5	123.71	17.24	0.00	0.00
<i>p</i> (D, M, T)	7	112.69	6.22	0.04	0.03

Note: Model indicates how predation rate was modeled. Factors were release density (R), time of day (T), and month (M). Parenthetical factors indicate which factors were included in each model. *K* is the number of parameters in each model. Samples size was 62. See text for full model descriptions.

stock enhancement and economic analysis of stock enhancement activities.

Red king crab released in this experiment survived extraordinarily well during the experimental timeframe; of those that survived the initial mortality immediately after release, 47% were estimated to survive their 6 months. There are virtually no estimates of mortality in wild red king crab populations due to the difficulty of studying this cryptic life history stage. The only study from which a similar mortality estimate could be obtained was

Fig. 4. Non-metric multidimensional scaling plot of the assemblages of (A) small and (B) large potential predators. Small predators were enumerated in quadrat counts throughout the experiment, whereas large predators were enumerated in transects counts.



performed in Southeast Alaska; in that study, the settlement and density of red king crab juveniles was observed over approximately a year (Loher and Armstrong 2000), and juvenile red king crab densities declined about 54% 2 months after peak densities during settlement and 93% 10 months after settlement, suggesting an ~46% and ~7% survival rate for the 2 months and the first 10 months respectively (Loher and Armstrong 2000). Linear interpolation suggests a 6 month survival of about 27%. Our estimate of survival higher than this, indicating that hatchery-reared juvenile king crab in Kodiak waters survive at least as well as their wild counterparts do in a population that is commercially harvested and suggesting that the population bottleneck in Kodiak occurs before settlement to the benthos, although predation on later stages is not well documented. Likewise, survival of hatchery blue crabs, *C. sapidus*, matches the survival of wild blue crabs of the

same size in the same habitat (Johnson et al. 2011). This is evidence that stock enhancement is an ecologically viable mechanism for restoring red king crab populations in Kodiak.

Red king crab juveniles experienced high, 67.5% mortality within the first 24 h after release and very high mortality rates over the first week post release, and future efforts should focus on identifying ways to reduce this. Such high mortality is not atypical in the release of hatchery animals. For example, hatchery-reared European lobster, *H. gammarus*, suffer high mortality in the first hour after release, likely due to the fact that it takes them a little while to locate shelter and during this time they are highly vulnerable to predation (van der Meeren 2000). It is likely that a similar process is occurring with the red king crab. Red king crab exhibit cryptic behavior in complex habitat to avoid predation (Long and Whitefleet-Smith 2013). However, hatchery-reared juve-

niles that have not been exposed to predators exhibit less cryptic behavior than those that have been (Long et al. 2015), and this makes them more vulnerable to predation (Daly et al. 2012). As predator conditioning may increase cryptic behavior, exposing crabs before a release could improve their initial survival immediately after release (Daly et al. 2012). In addition, exposing crab to natural substrates can also help condition cryptic behavior. Hatchery-reared blue crab, *C. sapidus*, do not bury in sediment, an anti-predator behavior, until they are exposed to sediment and such pre-conditioning can improve survival in the wild (Davis et al. 2004). Other means of reducing the initial mortality include releasing at night when predation risk is lower (Daly et al. 2013), and released crabs would be at less risk while finding shelter or using some form of caging or netting to exclude predators (Beal et al. 2002).

Higher mortality immediately after introduction into the wild appears to be driving the higher predation risk during the night that occurred in the tethering experiments. Previous research has shown that predation risk for tethered juvenile red king crab is lower at night (Daly et al. 2013). Thus, it is likely that the higher predation risk we observed during the night period was driven by the fact that the crabs were tethered in the late afternoon, so the "night" period included the time immediately after introduction into the wild when the crabs were more vulnerable.

The estimated mortality rate decreased with time and matched the observed decrease in the predation risk in tethering experiments. The match in decline between overall mortality and predation risk suggests that the primary cause of mortality in the field is predation. Supporting this, crabs held individually in the laboratory have high survival rates (Swiney et al. 2013; Westphal et al. 2014). A similar pattern occurs in Chesapeake Bay, where predation risk for blue crabs increases starting in May, peaks in August, and decreases rapidly afterwards (Hines et al. 2008), and in Norway, where predation risk for European lobsters is lower in the winter than in the summer (van der Meeren 2000). The decrease in predation over time could be explained by a number of factors or more likely a combination of them. First, predation rates likely vary seasonally, either because of changing predator density or changing feeding rates with temperature (Stoner et al. 2010). As we saw no indication of a decrease in predator density during the study, that is likely not the driving factor. It could also be driven by increasing crab size. Larger red king crab are, not surprisingly, less vulnerable to predation than smaller crab (Pirtle et al. 2012), and a similar pattern occurs for blue crab (Johnson et al. 2008). Finally, cryptic behavior can increase over the short term in the lab (Daly et al. 2012), and this increase in effective use of structure may continue over a longer time frame.

The lack of density dependence in predation and mortality of the crabs, indicating a type I functional response, was surprising. There are few observations of densities of wild year-0 red king crab, but Loher and Armstrong (2000) found average densities of just under 30 m⁻² at one of their three sites, which is similar to our highest densities after the first 24 h, which were about 24 m⁻². Laboratory experiments on the predator functional response on predators preying on year-0 king crab show a strong effect of prey density under a range of conditions (Long et al. 2012b; Long and Whitefleet-Smith 2013), and year-0 red king crab survival is reduced at high densities due to cannibalism even when no predators are present (Long et al. 2015). The functional response of predators preying on juvenile blue crabs is likewise strongly density dependent (Long et al. 2012a), and this is the likely mechanism that leads to decreased survival of released blue crabs with increasing density (Hines et al. 2008). However, for red king crab, laboratory experiments do not demonstrate good predictive power; there was no effect of density on either the overall mortality rate or on the predation risk on tethered crabs in this study. Neither was there any observed increase in predator density during or after release, as occurs when European lobster are released

(van der Meeren 2005). This may be driven by the fact that the released juvenile red king crab were small enough that even at the highest density they did not represent a significant increase in the overall biomass in the system, and therefore, predators would have no inducement to aggregate on release plots. Further, the presence of alternative prey can alter the predator functional response and significantly reduce predation pressure on juvenile crabs (Long et al. 2012a).

There was also no evidence of bottom-up limitations leading to any density dependent responses. Given the size of the crabs, their metabolic requirements, and food availability in the habitat, it seems unlikely that food would be limiting at the densities tested. Similarity, there is no indication of food limitation in released hatchery-reared blue crab either (Seitz et al. 2008). Another possibility is that the crabs might compete for habitat. Competition for shelter can reduce survival in lobsters (van der Meeren 2005) and habitat use is altered by density in juvenile red king crab (Long et al. 2015). Had such competition occurred, we would expect to see density dependence in either mortality or movement. In addition, there was no indication that crabs were limited by shelter as there were plenty of appropriately sized hiding places that did not contain any crabs. That release success is not density dependent is positive news for enhancement efforts because it suggests that crabs can be released at high densities in good habitat, which will reduce the cost of release and monitoring efforts.

This release experiment demonstrates that year-0 hatchery-reared red king crab survive at least as well as wild crabs after release. This suggests that hatchery-reared crabs could be used to restock populations in Kodiak. The lack of density dependence indicates that future experiments and releases can be performed at high density without reducing success; although experiments looking at a larger scale of release, in which emigration from the release area would have less of an effect on density over time, will be important to confirm this. It further suggests that the early juvenile stage of red king crab is not affected by density-dependent processes, at least within the large range of densities tested here. This has implications for stock dynamics and the red king crab stock-recruit relationship. Future research is needed to further optimize release strategies. In particular, testing strategies for reducing initial mortality could substantially increase success of releases. Additionally, experiments examining the effects of size and season of release and those of spatial variability in release success among different sites will be necessary before any scale-up of these techniques should be attempted.

Acknowledgements

We thank J. Hetrick and the Alutiiq Pride Shellfish Hatchery for rearing the juvenile crabs used in this experiment and M. Simeonoff for help capturing broodstock. We thank B. Daly, N. Sisson, N. Gabriel, and the staff of the Shellfish Assessment Program, Kodiak Laboratory, for help counting, tethering, and holding crabs for these experiments. Funding was provided by NMFS Office of Science and Technology, Aquaculture Program. Comments from B. Daly, R. Foy, and J. Long improved earlier versions of this paper. Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA. The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA.

References

- Alexander, M., Dick, J., O'Connor, N., Haddaway, N., and Farnsworth, K. 2012. Functional responses of the intertidal amphipod *Echinogammarus marinus*: effects of prey supply, model selection and habitat complexity. *Mar. Ecol. Prog. Ser.* 468: 191–202. doi:10.3354/meps09978.
- Alexander, M.E., Dick, J.T.A., and O'Connor, N.E. 2013. Born to kill: Predatory functional responses of the littoral amphipod *Echinogammarus marinus* Leach throughout its life history. *J. Exp. Mar. Biol. Ecol.* 439(0): 92–99. doi:10.1016/j.jembe.2012.10.006.

- Aljetlawi, A.A., Sparrevik, E., and Leonardsson, K. 2004. Prey-predator size-dependent functional response: derivation and rescaling to the real world. *J. Anim. Ecol.* **73**(2): 239–252. doi:10.1111/j.0021-8790.2004.00800.x.
- Beal, B.F., Mercer, J.P., and O'Conghaile, A. 2002. Survival and growth of hatchery-reared individuals of the European lobster, *Homarus gammarus* (L.), in field-based nursery cages on the Irish west coast. *Aquaculture*, **210**(1): 137–157. doi:10.1016/S0044-8486(02)00037-6.
- Bechtol, W., and Kruse, G. 2009. Analysis of a stock-recruit relationship for red king crab off Kodiak Island, Alaska. *Mar. Coast. Fish. Dyn. Manage. Ecosyst. Sci.* **1**: 29–44. doi:10.1577/C08-052.1.
- Bechtol, W.R., and Kruse, G.H. 2010. In Factors affecting historical red king crab recruitment around Kodiak Island, Alaska. *Biology and Management of Exploited Crab Populations under Climate Change*. Edited by G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby. Anchorage, AK. Alaska Sea Grant College Program, University of Alaska Fairbanks. Lowell Wakefield Fisheries Symposium: AK-SG-10-01. pp. 413–442.
- Blau, S.F. 1986. Recent declines of red king crab (*Paralithodes camtschaticus*) populations and reproductive conditions around the Kodiak Archipelago, Alaska. In *North Pacific Workshop on Stock Assessment and Management of Invertebrates*. Edited by G.S. Jamieson and N. Bourne. *Can. Spec. Publ. Fish. Aquat. Sci.* **p.** 360.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science + Business Media, New York.
- Clarke, K.R., and Warwick, R.M. 2001. Change in marine communities: an approach to statistical analysis and interpretation. 2nd ed. Plymouth Marine Laboratory, PRIMER-E, Plymouth, U.K.
- Crank, J. 1975. The mathematics of diffusion. 2nd ed. Clarendon Press.
- Daly, B., and Long, W.C. 2014a. Inter-cohort cannibalism of early benthic phase blue king crabs (*Paralithodes platypus*): Alternate foraging strategies in different habitats lead to different functional responses. *PLoS ONE*, **9**(2): e88694. doi:10.1371/journal.pone.0088694. PMID:24558414.
- Daly, B., and Long, W.C. 2014b. Intra-guild predation among early benthic phase red and blue king crabs: evidence for a habitat-mediated competitive advantage. *J. Exp. Mar. Biol. Ecol.* **451**: 98–104. doi:10.1016/j.jembe.2013.11.011.
- Daly, B., Stoner, A.W., and Eckert, G.L. 2012. Predator-induced behavioral plasticity of juvenile red king crabs (*Paralithodes camtschaticus*). *J. Exp. Mar. Biol. Ecol.* **429**: 47–54. doi:10.1016/j.jembe.2012.06.010.
- Daly, B., Eckert, G.L., and White, T.D. 2013. Predation of hatchery-cultured juvenile red king crabs (*Paralithodes camtschaticus*) in the wild. *Can. J. Fish. Aquat. Sci.* **70**(3): 358–366. doi:10.1139/cjfas-2012-0377.
- Davis, J.L.D., Young-Williams, A.C., Aguilar, R., Carswell, B.L., Goodison, M.R., Hines, A.H., Kramer, M.A., Zohar, Y., and Zmora, O. 2004. Differences between hatchery-raised and wild blue crabs: implications for stock enhancement potential. *Trans. Am. Fish. Soc.* **133**(1): 1–14. doi:10.1577/T03-004.
- Dew, C.B. 1990. Behavioral ecology of podding red king crab, *Paralithodes camtschaticus*. *Can. J. Fish. Aquat. Sci.* **47**(10): 1944–1958. doi:10.1139/f90-219.
- Dew, C.B. 1991. Characterization of preferred habitat for juvenile red king crab in three Kodiak bays. Final report to the Kodiak Island Borough, Kodiak, Alaska Contract Number 89-226. pp. 1–90.
- Eggleston, D., Lipcius, R., and Hines, A. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Mar. Ecol. Prog. Ser.* **85**(1): 55–68. doi:10.3354/meps085055.
- Hamasaki, K., and Kitada, S. 2008. Potential of stock enhancement for decapod crustaceans. *Rev. Fish. Sci.* **16**(1): 164–174. doi:10.1080/10641260701681722.
- Hassell, M., Lawton, J., and Beddington, J. 1977. Sigmoid functional responses by invertebrate predators and parasitoids. *J. Anim. Ecol.* **46**(1): 249–262. doi:10.2307/3959.
- Hines, A.H., Johnson, E.G., Young, A.C., Aguilar, R., Kramer, M.A., Goodison, M., Zmora, O., and Zohar, Y. 2008. Release strategies for estuarine species with complex migratory life cycles: Stock enhancement of Chesapeake blue crabs (*Callinectes sapidus*). *Rev. Fish. Sci.* **16**(1): 175–185. doi:10.1080/10641260701696809.
- Hines, A.H., Long, W.C., Terwin, J.R., and Thrush, S.F. 2009. Facilitation, interference, and scale: the spatial distribution of prey patches affects predation rates in an estuarine benthic community. *Mar. Ecol. Prog. Ser.* **385**: 127–135. doi:10.3354/meps08055.
- Holling, C. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.* **91**(5): 293–320. doi:10.4039/Ent91293-5.
- Johnson, E.G., Hines, A.H., Kramer, M.A., and Young, A.C. 2008. Importance of season and size of release to stocking success for the blue crab in Chesapeake Bay. *Rev. Fish. Sci.* **16**(1): 243–253. doi:10.1080/10641260701696837.
- Johnson, E.G., Young, A.C., Hines, A.H., Kramer, M.A., Bademan, M., Goodison, M.R., and Aguilar, R. 2011. Field comparison of survival and growth of hatchery-reared versus wild blue crabs, *Callinectes sapidus* Rathbun. *J. Exp. Mar. Biol. Ecol.* **402**(1–2): 35–42. doi:10.1016/j.jembe.2011.03.013.
- Lebata, M.J.H.L., Le Vay, L., Walton, M.E., Biñas, J.B., Quinitio, E.T., Rodriguez, E.M., and Primavera, J.H. 2009. Evaluation of hatchery-based enhancement of the mud crab, *Scylla* spp., fisheries in mangroves: comparison of species and release strategies. *Mar. Freshw. Res.* **60**(1): 58–69. doi:10.1071/MF08155.
- Loher, T., and Armstrong, D.A. 2000. Effects of habitat complexity and relative larval supply on the establishment of early benthic phase red king crab (*Paralithodes camtschaticus* Tilesius, 1815) populations in Auke Bay, Alaska. *J. Exp. Mar. Biol. Ecol.* **245**(1): 83–109. doi:10.1016/S0022-0981(99)00157-4.
- Long, W.C., and Hines, A.H. 2012. Scale and the predator functional response: density-dependent predation varies with plot size. *J. Exp. Mar. Biol. Ecol.* **413**: 50–55. doi:10.1016/j.jembe.2011.11.015.
- Long, W.C., and Whitefleet-Smith, L. 2013. Cannibalism in red king crab: Habitat, ontogeny, and the predator functional response. *J. Exp. Mar. Biol. Ecol.* **449**: 142–148. doi:10.1016/j.jembe.2013.09.004.
- Long, W.C., Grow, J.N., Majoris, J.E., and Hines, A.H. 2011. Effects of anthropogenic shoreline hardening and invasion by *Phragmites australis* on habitat quality for juvenile blue crabs (*Callinectes sapidus*). *J. Exp. Mar. Biol. Ecol.* **409**(1–2): 215–222. doi:10.1016/j.jembe.2011.08.024.
- Long, W.C., Johnson, E.G., Gamelin, E.F., and Hines, A.H. 2012a. Density-dependent indirect effects: apparent mutualism and apparent competition coexist in a two-prey system. *Mar. Ecol. Prog. Ser.* **456**: 139–148. doi:10.3354/meps09702.
- Long, W.C., Popp, J., Swiney, K.M., and Van Sant, S.B. 2012b. Cannibalism in red king crab, *Paralithodes camtschaticus* (Tilesius, 1815): effects of habitat type and predator density on predator functional response. *J. Exp. Mar. Biol. Ecol.* **422–423**: 101–106. doi:10.1016/j.jembe.2012.04.019.
- Long, W.C., Seitz, R.D., Brylawski, B.J., and Lipcius, R.N. 2014. Individual, population, and ecosystem effects of hypoxia on a dominant benthic bivalve in Chesapeake Bay. *Ecol. Monogr.* **84**(2): 303–327. doi:10.1890/13-0440.1.
- Long, W.C., Van Sant, S.B., and Haaga, J.A. 2015. Habitat, predation, growth, and coexistence: Could interactions between juvenile red and blue king crabs limit blue king crab productivity? *J. Exp. Mar. Biol. Ecol.* **464**: 58–67. doi:10.1016/j.jembe.2014.12.011.
- Manly, B. 1977. A model for dispersion experiments. *Oecologia*, **31**(1): 119–130. doi:10.1007/BF00348715. PMID:28309156.
- Murdoch, W. 1973. The functional response of predators. *J. Appl. Ecol.* **10**: 335–342.
- Orensanz, J., Armstrong, J., Armstrong, D., and Hilborn, R. 1998. Crustacean resources are vulnerable to serial depletion—the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. *Rev. Fish. Biol. Fish.* **8**(2): 117–176. doi:10.1023/A:1008891412756.
- Othmer, H.G., Dunbar, S.R., and Alt, W. 1988. Models of dispersal in biological systems. *J. Math. Biol.* **26**(3): 263–298. doi:10.1007/BF00277392. PMID:3411255.
- Persselin, S., and Daly, B. 2010. In Diet and water source effects on larval red king crab cultivation. *Biology and management of exploited crab populations under climate change*. Edited by G.H. Kruse, G.L. Eckert, R.J. Foy, R.N. Lipcius, B. Sainte-Marie, D.L. Stram, and D. Woodby. Alaska Sea Grant College Program, University of Alaska Fairbanks, Anchorage, Alaska. Lowell Wakefield Fisheries Symposium: AK-SG-10-01. pp. 479–494.
- Pirtle, J.L., and Stoner, A.W. 2010. Red king crab (*Paralithodes camtschaticus*) early post-settlement habitat choice: Structure, food, and ontogeny. *J. Exp. Mar. Biol. Ecol.* **393**(1–2): 130–137. doi:10.1016/j.jembe.2010.07.012.
- Pirtle, J.L., Eckert, G.L., and Stoner, A.W. 2012. Habitat structure influences the survival and predator-prey interactions of early juvenile red king crab *Paralithodes camtschaticus*. *Mar. Ecol. Prog. Ser.* **465**: 169–184. doi:10.3354/meps09883.
- Powell, G.C., and Nickerson, R.B. 1965. Aggregations among juvenile king crabs (*Paralithodes camtschaticus*, Tilesius) Kodiak, Alaska. *Anim. Behav.* **13**(2–3): 374–380. doi:10.1016/0003-3472(65)90058-8. PMID:5835854.
- Santos, C.D., Saraiva, S., Palmeirim, J.M., and Granadeiro, J.P. 2009. How do waders perceive buried prey with patchy distributions? The role of prey density and size of patch. *J. Exp. Mar. Biol. Ecol.* **372**(1–2): 43–48. doi:10.1016/j.jembe.2009.02.005.
- Seitz, R., Lipcius, R., Hines, A., and Eggleston, D. 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology*, **82**(9): 2435–2451. doi:10.1890/0012-9658(2001)082[2435:DDPHVA]2.0.CO;2.
- Seitz, R.D., Lipcius, R.N., Stockhausen, W.T., Delano, K.A., Seebo, M.S., and Gerdes, P.D. 2003. Potential bottom-up control of blue crab distribution at various spatial scales. *Bull. Mar. Sci.* **72**(2): 471–490.
- Seitz, R.D., Lipcius, R.N., Knick, K.E., Seebo, M.S., Long, W.C., Brylawski, B.J., and Smith, A. 2008. Stock enhancement and carrying capacity of blue crab nursery habitats in Chesapeake Bay. *Rev. Fish. Sci.* **16**(1–3): 329–337. doi:10.1080/10641260701696985.
- Shirley, S.M., and Shirley, T.C. 1989. Interannual variability in density, timing and survival of Alaskan red king crab *Paralithodes camtschaticus* larvae. *Mar. Ecol. Prog. Ser.* **54**(1–2): 51–59. doi:10.3354/meps054051.
- Socolofsky, S.A., and Jirka, G.H. 2005. Special topics in mixing and transport processes in the environment. Coastal and Ocean Engineering Division, Texas A&M University, College Station, Texas, Engineering lectures 172.
- Stevens, B.G. 2003. Settlement, substratum preference, and survival of red king crab *Paralithodes camtschaticus* (Tilesius, 1815) glaucothoe on natural substrata in the laboratory. *J. Exp. Mar. Biol. Ecol.* **283**(1–2): 63–78. doi:10.1016/S0022-0981(02)00471-9.
- Stevens, B. 2006. Is it possible to enhance king crab populations in Alaska? In *Alaska Crab Stock Enhancement and Rehabilitation: Workshop Proceedings*. Edited by B. Stevens. Alaska Sea Grant College Program AKSG-06-04. pp. 79–89.
- Stevens, B.G., and Kittaka, J. 1998. Postlarval settling behavior, substrate prefer-

- ence, and time to metamorphosis for red king crab *Paralithodes camtschaticus*. Mar. Ecol. Prog. Ser. **167**: 197–206. doi:10.3354/meps167197.
- Stevens, B., and MacIntosh, R. 1991. Cruise results supplement, cruise 91-1 Ocean Hope 3: 1991 eastern Bering Sea juvenile red king crab survey, May 24–June 3, 1991, National Marine Fisheries Service, Alaska Fisheries Science Center, Kodiak Fisheries Research Center, Seattle, Wash.
- Stevens, B.G., and Swiney, K.M. 2005. Post-settlement effects of habitat type and predator size on cannibalism of glaucothoe and juveniles of red king crab *Paralithodes camtschaticus*. J. Exp. Mar. Biol. Ecol. **321**(1): 1–11. doi:10.1016/j.jembe.2004.12.026.
- Stevens, B.G., and Swiney, K.M. 2007. Hatch timing, incubation period, and reproductive cycle for captive primiparous and multiparous red king crab, *Paralithodes camtschaticus*. J. Crustac. Biol. **27**(1): 37–48. doi:10.1651/S-2663.1.
- Stoner, A.W., and Davis, M. 1994. Experimental outplanting of juvenile queen conch, *Strombus gigas*: comparison of wild and hatchery-reared stocks. Fish. Bull. U.S.A. **92**(2): 390–411.
- Stoner, A.W., Ottmar, M.L., and Haines, S.A. 2010. Temperature and habitat complexity mediate cannibalism in red king crab: Observations on activity, feeding, and prey defense mechanisms. J. Shellfish Res. **29**(4): 1005–1012. doi:10.2983/035.029.0401.
- Sundberg, K., and Clausen, D. 1977. Post-larval king crab (*Paralithodes camtschaticus*) distribution and abundance in Kachemak Bay Lower Cook Inlet, Alaska, 1976. Alaska Department of Fish and Game, Alaska Department of Fish and Game, Anchorage, Environmental Studies of Kachemk Bay and Lower Cook Inlet, 5. pp. 1–36.
- Swiney, K.M., and Long, W.C. 2015. Primiparous red king crab, *Paralithodes camtschaticus*, are less fecund than multiparous crab. J. Shellfish Res. **34**(2): 493–498. doi:10.2983/035.034.0233.
- Swiney, K.M., Long, W.C., Eckert, G.L., and Kruse, G.H. 2012. Red king crab, *Paralithodes camtschaticus*, size-fecundity relationship, and inter-annual and seasonal variability in fecundity. J. Shellfish Res. **31**(4): 925–933. doi:10.2983/035.031.0403.
- Swiney, K.M., Long, W.C., and Persselin, S.L. 2013. The effects of holding space on juvenile red king crab (*Paralithodes camtschaticus*) growth and survival. Aquacult. Res. **44**: 1007–1016. doi:10.1111/j.1365-2109.2012.03105.x.
- Swingle, J.S., Daly, B., and Hetrick, J. 2013. Temperature effects on larval survival, larval period, and health of hatchery-reared red king crab, *Paralithodes camtschaticus*. Aquaculture, **384–387**: 13–18. doi:10.1016/j.aquaculture.2012.12.015.
- Taylor, D.L., and Eggleston, D.B. 2000. Effects of hypoxia on an estuarine predator-prey interaction: foraging behavior and mutual interference in the blue crab *Callinectes sapidus* and the infaunal clam prey *Mya arenaria*. Mar. Ecol. Prog. Ser. **196**: 221–237. doi:10.3354/meps196221.
- van der Meeren, G.I. 2000. Predation on hatchery-reared lobsters released in the wild. Can. J. Fish. Aquat. Sci. **57**(9): 1794–1803. doi:10.1139/f00-134.
- van der Meeren, G. 2005. Potential of ecological studies to improve survival of cultivated and released European lobsters, *Homarus gammarus*. N. Z. J. Mar. Freshw. Res. **39**: 399–424. doi:10.1080/00288330.2005.9517321.
- Westphal, M.J., Eckert, G.L., and Tamone, S.L. 2014. Comparison of first year growth among field, hatchery- and laboratory-raised juvenile red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), in Alaska. J. Crustac. Biol. **34**(3): 319–325. doi:10.1163/1937240X-00002228.
- Zheng, J., and Kruse, G. 2000. Recruitment patterns of Alaskan crabs in relation to decadal shifts in climate and physical oceanography. ICES J. Mar. Sci. **57**(2): 438. doi:10.1006/jmsc.1999.0521.