

# Predation of hatchery-cultured juvenile red king crabs (*Paralithodes camtschaticus*) in the wild

Benjamin Daly, Ginny L. Eckert, and Timothy D. White

**Abstract:** The ecologically and commercially important red king crab (*Paralithodes camtschaticus*) is depleted throughout much of the North Pacific and thought to be recruitment-limited, making it an appropriate candidate for stock enhancement efforts. Information on predation of newly settled red king crabs in nearshore habitats is needed to assess the feasibility of large-scale releases. We tethered hatchery-cultured red king crabs of two sizes (range: 1.75–4.08 mm carapace width) in the field for 24 h trials in July and September 2011 and used underwater video cameras to identify predators and predation susceptibility. We identified hermit crabs (*Pagurus* spp.), Alaskan ronquill (*Bathymaster caeruleofasciatus*), Arctic shanny (*Sticheus punctatus*), northern rock sole (*Lepidopsetta polyxystra*), and kelp greenling (*Hexagrammos decagrammus*) as predators. Survival did not vary by body size or deployment month; however, small crabs were consumed sooner than large crabs. Most predation events occurred in daylight hours, with the exception of Alaskan ronquill. Our results suggest stock enhancement efforts should consider predator assemblages when developing release strategies. Future studies should investigate spatial variation in predation pressure at multiple locations on broad temporal scales to optimize release strategies and understand population-level effects.

**Résumé :** Les stocks de crabe royal (*Paralithodes camtschaticus*), une espèce d'importance écologique et commerciale, sont décimés dans une bonne partie du Pacifique Nord et leur abondance serait limitée par le recrutement. Cette espèce serait donc un bon candidat pour des efforts de mise en valeur des stocks. Des données sur la prédation de crabes royaux nouvellement établis dans les habitats littoraux sont nécessaires pour évaluer la faisabilité de lâchers à grande échelle. Nous avons attaché des crabes royaux élevés en alevinière (largeur de carapace : 1,75–4,08 mm) sur le terrain pour des essais de 24 h en juillet et septembre 2011 et utilisé des caméras vidéo sous-marines pour en identifier les prédateurs et la susceptibilité à la prédation. Les prédateurs ainsi identifiés sont des bernard-l'ermite (*Pagurus* spp.), la ronquille à nageoires bleues (*Bathymaster caeruleofasciatus*), la stichée arctique (*Sticheus punctatus*), la sole *Lepidopsetta polyxystra* et le sourcil de varech (*Hexagrammos decagrammus*). Si la survie ne variait pas en fonction de la taille du corps ou du mois de déploiement, les petits crabes étaient néanmoins consommés plus rapidement que les plus grands. La plupart des événements de prédation se produisaient durant le jour, à l'exception de ceux mettant en cause la ronquille à nageoires bleues. Nos résultats donnent à penser que l'élaboration de stratégies de lâchers dans le cadre d'efforts de mise en valeur des stocks devrait tenir compte des assemblages de prédateurs. Des travaux futurs devraient se pencher sur les variations spatiales de la pression de prédation en différents endroits et à grande échelle temporelle afin d'optimiser les stratégies de lâchers et d'en mieux comprendre les effets au niveau des populations. [Traduit par la Rédaction]

## Introduction

Stock enhancement through the release of cultured juveniles has been used to increase abundance in recruitment-limited stocks with varying degrees of success worldwide (Leber et al. 2004; Bell et al. 2006). The foci of previous enhancement efforts were often hatchery production and numbers of individuals released, rather than optimizing postrelease survival (Secor et al. 2002; Lorenzen 2005; Stevens 2006a). Predation is the greatest ecological hurdle for hatchery-cultured juveniles released in the wild (Bell et al. 2005, 2008; Hines et al. 2008), and intense predation pressure can limit survival of released individuals rendering stock enhancement programs ineffective (Stoner and Davis 1994; Kitada and Kishino 2006). Evaluating predation susceptibility is necessary to assess the feasibility of stock enhancement programs; however, adequate experiments are often not conducted, making the effectiveness of many large-scale releases uncertain (Blankenship and Leber 1995; Lorenzen et al. 2010).

Red king crabs (*Paralithodes camtschaticus*) have substantial commercial and ecological importance throughout the North Pacific; however, population abundances in Alaska, USA, declined in the early 1980s, and six of the nine stocks remain depressed even with decades of no fishing (Orensanz et al. 1998), with only the Bristol Bay and Norton Sound fishing areas consistently open. The Southeast Alaska fishery is intermittently open and closed because of fluctuating estimates of stock abundance (Stratman et al. 2011). Population fluctuations are likely caused by recruitment variability, but our understanding of mechanisms driving recruitment variability is limited. Hypotheses include overfishing, climate change, groundfish predation, shifts in spatial distribution, and disease (Orensanz et al. 1998; Loher and Armstrong 2005; Stevens 2006b; Zheng and Kruse 2006; Bechtol and Kruse 2009), but links between environmental factors and population abundance are not yet fully understood. Other theories suggest that abundances in the 1960s were abnormally high, driven by record crab recruitment that may have been associated with a regime shift or other

Received 27 November 2012. Accepted 16 December 2012.

Paper handled by Associate Editor Bernard Sainte-Marie.

B. Daly.\* School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 201 Railway Avenue, Seward, AK 99664, USA.

G.L. Eckert. Juneau Center, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 17101 Point Lena Loop Road, Juneau, AK 99801, USA.

T.D. White. University of California Los Angeles, 405 Hilgard Avenue, Los Angeles, CA 90095, USA.

Corresponding author: Benjamin Daly (e-mail: ben.daly@noaa.gov).

\*Present address: Kodiak Laboratory, Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 301 Research Court, Kodiak, AK 99615, USA.



environmental effects (Bechtol and Kruse 2009), which may imply that the decline was inevitable with a shift in the environment. Regardless, recruitment limitation has been suggested as a contributing factor for a lack of recovery (Blau 1986), indicating populations may be below carrying capacity, which makes red king crabs a suitable candidate for stock enhancement efforts (Stevens 2006b). The Alaska King Crab Research and Rehabilitation and Biology (AKCRRAB) program was created in 2006 to assess the feasibility of stock enhancement for king crabs in Alaska and is the first and only US aquaculture program to successfully demonstrate that king crabs can be cultured on a large scale in a hatchery setting (Daly et al. 2009). However, hatchery production does not ensure stock enhancement success.

Ecological studies are necessary to develop optimal release strategies for maximizing postrelease survival. Factors including sufficient nursery habitat (Kitada and Kishino 2006), size at release (Leber 1995; Willis et al. 1995), and release season (Glazer and Jones 1997; Stoner and Glazer 1998; Leber et al. 1997; van der Meer 2000) impact postrelease survival for several fish and invertebrate species. For example, increasing body size reduces predation rates of juvenile American lobsters (*Homarus americanus*) (Wahle and Steneck 1992). Further, survival of hatchery-cultured juvenile blue crabs (*Callinectes sapidus*) increases with body size, but optimal size varies depending on season (Johnson et al. 2008). Critical habitat requirements have been documented for juvenile red king crabs (Loher and Armstrong 2000; Stevens and Swiney 2005; Stoner 2009; Pirtle and Stoner 2010; Pirtle et al. 2012); however, information on predation of red king crab juveniles in nearshore habitats is scarce, and the importance of body size and seasonality is unknown for early benthic phase red king crabs, especially newly settled individuals.

Red king crabs have a complex life cycle including four pelagic larval (zoeal) stages, a postlarval (glaucothoe) stage, and benthic juvenile and adult stages (Marukawa 1933). Glaucothoe settle to nearshore nursery habitats and molt to the first juvenile instar where they take the adult-like form (Donaldson et al. 1992; Loher and Armstrong 2000). Juveniles are solitary and cryptic, associating with complex biogenic substrates such as structural invertebrates until approximately age-2 when they begin to display social-aggregative behavior (podding) and are less cryptic (Powell and Nickerson 1965; Dew 1990, 1991; Stone et al. 1993; Loher and Armstrong 2000). We use the terminology “early benthic phase” to define this solitary, cryptic life history stage (age-0 to age-2), which is ecologically distinct from older juveniles (Wahle and Steneck 1991; Loher and Armstrong 2000). Though size varies regionally likely because of environmental and genetic effects, early benthic phase red king crabs in southeast Alaska range ~1.8–25.0 mm carapace width (CW) and belong to instar stages C1 to ~C15 (Stevens 1990; Loher and Armstrong 2000, 2001).

Predation of juveniles could create a population bottleneck for red king crab. Increases in groundfish abundances coincided with declines in crab populations in Alaskan waters (Zheng and Kruse 2006; Bechtol and Kruse 2009, 2010), yet the role of predation in nursery areas remains uncertain. Groundfish gut content analysis shows that fish eat juvenile red king crabs >50 mm carapace length (CL) (Livingston 1989, 1991; Livingston et al. 1993; Tyler and Kruse 1996), which are approximately 3 years old (Lysenko and Gaidav 2005), yet most of these observations are outside shallow king crab nursery areas, making it difficult to discern population-scale effects of predation on early benthic phase red king crabs that are presumably most vulnerable to predation. Sculpin (Cottidae), Alaska ronquil (*Bathymaster caeruleofasciatus*), and Pacific halibut (*Hippoglossus stenolepis*) consume age-0 and age-1 red king crab in laboratory and nearshore field experiments (Stoner 2009; Pirtle and Stoner 2010; Daly et al. 2012a; Pirtle et al. 2012), yet recent evidence shows Pacific cod (*Gadus macrocephalus*) are uninterested in tethered early benthic phase red king crabs in the field (Pirtle et al. 2012; this study), which contradicts the belief that Pacific cod

are major predators of early stage red king crabs in the wild (Bechtol and Kruse 2010). Fish predation greatly reduces recruitment of other crab species in Alaska. For example, stomach content analysis off Kodiak Island shows that Pacific cod consumed over 365 million juvenile Tanner crabs (*Chionoectes bairdi*) (10–45 mm CW) in a single bay over 429 days; however, stomach contents did not include red king crabs (Urban 2010). Estimates indicate over 4 billion Tanner crabs (4–34 mm carapace width) were consumed by Pacific cod in the eastern Bering Sea during 1985 (Livingston 1989).

Recent crustacean stock enhancement efforts suggest the importance of predation and postrelease survival of hatchery-cultured individuals (e.g., Bannister and Addison 1998; van der Meer 2000; Ball et al. 2001; Castro et al. 2001; Davis et al. 2005; Zohar et al. 2008), yet predation on hatchery-cultured red king crabs in the wild has not been documented. We tethered hatchery-cultured red king crabs in Southeast Alaskan waters to evaluate predation on newly settled early benthic phase crabs with the goal to identify predator species in a nearshore habitat and to assess relative predation pressure during the first juvenile instar stages as part of a king crab stock enhancement feasibility study. We hypothesized that crabs are consumed by a range of predator species, survival rates vary temporally, and that larger crabs have higher survival than smaller crabs.

## Methods

### Source of juvenile crabs

We cultured juvenile red king crabs as part of AKCRRAB program using established rearing techniques (Swingle et al. 2013). Twenty ovigerous females were captured with baited pots in Stephens Passage, Alaska, during October 2010. Crabs were transported to the Alutiiq Pride Shellfish Hatchery in Seward, Alaska, and placed in 2000 L tanks containing flow-through ambient seawater and fed 20 g chopped herring and squid per crab twice per week. Once hatching began (spring 2011), larvae from each female were mixed and raised in 1200 L cylindrical tanks until the first juvenile instar stage (C1) in June 2011. Larvae were fed enriched San Francisco Bay strain *Artemia* nauplii daily. *Artemia* nauplii were enriched with DC DHA Selco (INVE Aquaculture, Utah, USA) enrichment media in 100 L cylindrical tanks for 24 h. Juvenile (C1) crabs were shipped to the University of Alaska Fairbanks, Juneau Center, in June 2011 where they were held at a density of ~2000 crabs·m<sup>-2</sup> in 670 L tanks until field experiments began. Holding tanks had flow-through seawater (8 °C), which is representative of ambient conditions, and clumps of commercial gillnet for vertical structure. Juvenile crabs were fed Cyclop-eeze (Argent Chemical Laboratories, Washington, USA) and Otohime B1 and B2 (Reed Mariculture, California, USA) every other day. At 1 month postsettlement (July), average (±SE) crab size was 2.2 ± 0.03 mm CW (range: 1.8–2.9 mm CW, stages C1–C2) and grew to 2.9 ± 0.08 mm CW (range: 1.8–4.1 mm CW, stages C1–C4) at 3 months postsettlement (September) (Table 1), which are representative of recently settled red king crabs found in the field in Southeast Alaska (Loher and Armstrong 2000).

### Study site

The study site at Yankee Cove (58°35.431'N, 134°54.366'W) near Juneau, Alaska, is composed of shallow (0–12 m) nearshore rocky reefs that host dense stands of the kelps *Saccharina subsimplex*, *Laminaria yezoensis*, and *Agarum clathratum*, several species of prostrate red algae, encrusting algae, and benthic invertebrates (see Pirtle et al. 2012). These reefs transition into flat, sandy substrate at approximately 8 m depth. A wide range of vertebrates and invertebrates were observed at the study site and are considered potential predators of early benthic phase red king crabs based on relative size differences. We conducted a series of ten 45 min dives within an area of ~900 m<sup>2</sup> at the study site over a 1-week time span in early July and late August 2011 to document potential

**Table 1.** Red king crab (*Paralithodes camtschaticus*) average, minimum, maximum, and standard error (SE) carapace width (CW) measurements, sample size, and estimated juvenile instar stage for “small” and “large” crabs used in July and September tethering trials.

Month	Size class	Average CW (mm)	Minimum CW (mm)	Maximum CW (mm)	±SE (mm)	Sample size	Instar stage
July	Small	1.90	1.75	2.00	0.014	31	C1
	Large	2.40	2.20	2.90	0.027	45	C2
September	Small	2.07	1.80	2.25	0.012	66	C1, C2
	Large	3.86	3.60	4.08	0.017	56	C4

predators at the study site. Additionally, we noted the presence of potential predators during video analyses (described below).

### Experimental design

We tested the effect of body size, deployment time, and camera light on survival of recently settled red king crabs during July and September 2011. In each of these 2 months, we subdivided juvenile red king crabs into two size classes (Table 1) representing the upper and lower size range at each time period and compared CW of crabs using *t* tests. Carapace width was greater for large crabs compared with small crabs in both July (*t* test,  $t = 14.369$ ,  $p < 0.001$ ) and September, (*t* test,  $t = 87.488$ ,  $p < 0.001$ ). We tethered individual hard-shelled intermolt crabs by gluing 15 cm of monofilament fishing line (1.59 kg breaking strength) to the dorsal side of the carapace using a small drop of cyanoacrylate glue (e.g., Heck and Thoman 1981). Tethered crabs were held in the laboratory for approximately 18 h prior to deployment to ensure crabs survived the tethering process and could actively move. Tethered crabs were placed in the field by attaching the monofilament line to a bolt anchored to a concrete disk, which was buried in the substrate and covered with ambient gravel and cobble (~2–30 mm diameter) so that the substrate was flush. Each tethering station was separated by approximately 5 m, and all were at a depth of 8–10 m. On each of 8 consecutive days in both July and September, we deployed 12 crabs in the field for 24 h trials starting at approximately 0900–1000 h. We ensured that crabs were alive and actively moving in situ by observing the crabs for several minutes immediately after deployment. In all cases, crabs could move on their tethers, find crevice space within the substrate, and establish crypsis. Of the 12 crabs tethered per day, four (two small, two large) were individually enclosed in separate 2 mm mesh enclosures to prevent predation and escapement during the experiment to assess effects of handling stress (procedural control). Of the remaining eight crabs, four (two small, two large) were tethered without mesh enclosures and with underwater cameras attached to sand anchors and positioned 60 cm above each crab. The remaining four crabs (two small, two large) were tethered without mesh enclosures or cameras. We assessed survival after 24 h and returned crabs remaining at the end of the trials to the laboratory but did not redeploy them. Including the procedural control, a total of 192 crabs were tethered throughout the experiment.

The underwater HD color video cameras (Well-Vu Nature Vision Inc., Manual Wind Color System) (704 × 480 resolution at 7 images per second) were used to record predator interactions using methods similar to Pirtle et al. (2012). The cameras had LED lights to improve observations in low light conditions. Lights were adjusted to minimum levels that still allowed for clear observations at night. Cameras were connected to a shore digital video recorder via underwater cable and powered externally by a 12 V battery bank (four marine batteries in series; see Pirtle et al. 2012 for details). Trials were excluded from the video analysis if cameras flooded or produced poor image quality. A total of 55 tethered crabs had usable video, of which predators consumed 33 crabs. Though we could not always observe crab behavior in video analysis because of their cryptic nature (hiding in interstitial spaces within the substrate) and small size, some individuals were visible

by video. When attacked, the location of crabs was obvious either by fish attack behavior, direct observation of the crab, or by movement of the tether itself. We reviewed videos to identify all species in the field of view as potential predators, actual predators, and quantify time from deployment to the first and mortal attack.

Field and laboratory experiments revealed that predation by sunflower sea stars (*Pycnopodia helianthoides*) is likely an artifact, because untethered juvenile red king crabs can escape by actively moving away (Pirtle et al. 2012). Because sunflower sea stars can reach speeds of 12 m·h<sup>-1</sup> (Brewer and Konar 2005) and potentially cover large distances in 24 h, we removed them from the study site prior to crab tethering trials each day. During early July prior to tethering trials, we quantified natural sunflower sea star density by conducting ten 15 m × 2 m random transects in a 30 m × 30 m (900 m<sup>2</sup>) plot and then removed all sunflower sea stars from the plot over 2 days. We subsequently quantified sunflower sea star density 1, 4, 5, 6, and 7 days after the removal using ten 15 m × 2 m random transects on each day. Densities on each day were compared using repeated measures ANOVA and post hoc comparisons (Tukey's HSD). We significantly reduced sunflower sea stars (ANOVA,  $F = 7.81$ ,  $df = 5$ ,  $p < 0.001$ ) from average (±SE) initial density of  $0.20 \pm 0.025$  to  $0.02 \pm 0.007$  sunflower sea stars·m<sup>-2</sup> (Tukey's HSD,  $p < 0.001$ ) after 1 day. Sea star densities within the confines of our study site began slowly recovering but remained significantly depressed after 7 days ( $0.11 \pm 0.038$  sea stars·m<sup>-2</sup>) (Tukey's HSD,  $p = 0.044$ ; Fig. 1), suggesting removal successfully minimized predation by sunflower sea stars. Accordingly, all sunflower sea stars within 10 m of crab tethering locations (eyebolts) were removed immediately prior to each 24 h tethering trial.

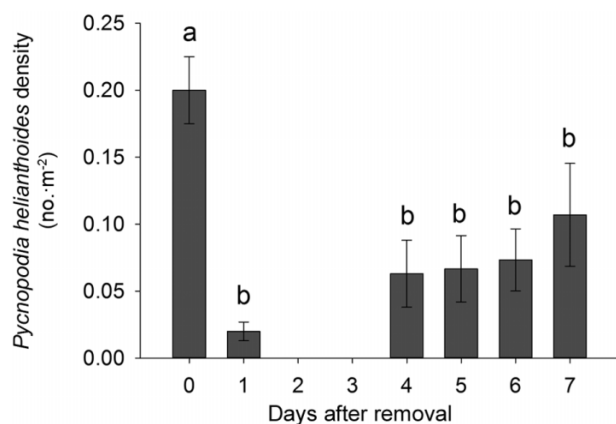
### Analyses

We quantified crab survival as percentage of deployed crabs remaining after 24 h trials. Percent survival data were arcsine square-root-transformed and compared among treatments with and without cameras (and camera lights) in July and September using ANOVA and post hoc comparisons (Tukey's HSD; Table 2). Because the camera effect was not significant ( $F = 2.94$ ,  $df = 1$ ,  $p = 0.097$ ), all replicates with and without cameras were pooled. Survival was then compared among cages (with or without mesh enclosures), sizes (small, large), and deployment months (July, September) using ANOVA and post hoc comparisons (Tukey's HSD). Time to mortal attack was compared among small and large crabs using a *t* test. Differences in time to mortal attack among predators were examined by ANOVA on square-root-transformed data. All analyses were conducted using Sigma Stat version 4 (Aspire Software International, Ashburn, Virginia, USA). Statistical significance was set at  $\alpha = 0.05$ .

### Results

We observed many potential predators at the study site (Table 3). Diver observations and video analysis suggested that Hermit crabs (*Pagurus* spp.), Pacific cod, sculpins (Cottoidea), northern rock sole (*Lepidopsetta polyxystra*), and kelp greenling (*Hexagrammos decagrammus*) were numerically dominant compared with other species such as Alaskan ronquil, Arctic shanny

**Fig. 1.** Average  $\pm$  SE sunflower sea star (*Pycnopodia helianthoides*) density over time. Densities were lower on each day after the initial removal (day 0) (repeated measures ANOVA,  $F = 7.81$ ,  $df = 5$ ,  $p < 0.001$ ). Different letters indicate statistical significance (Tukey's HSD,  $p \leq 0.05$ ).



(*Sticheus punctatus*), and red king crab. Video analysis showed several species passing through the camera field of view but not interacting with the tethered crabs; five species were directly observed consuming crabs (Table 3). Hermit crabs were responsible for most (74%) of the mortal attacks on small crabs. Hermit crabs, Alaskan ronquil, Arctic shanny, northern rock sole, and kelp greenling consumed large crabs with relatively similar frequencies (7%–36% of total attacks on large crabs; Fig. 2). Video analysis showed that most (81%) of the mortal attacks occurred during daylight hours (Fig. 3), but Alaskan ronquil typically attacked at

**Table 2.** ANOVA for survival of uncaged red king crab (*Paralithodes camtschaticus*) juveniles deployed with and without cameras in July and September.

Effect	SS	df	MS	F	p
Camera	0.277	1	0.277	2.94	0.097
Month	0.099	1	0.099	1.05	0.315
Camera $\times$ month	0.001	1	0.001	0.01	0.926
Residual	2.639	28	0.094		

night (2300 to 0400 h). Time to mortal attack differed among predator groups (ANOVA,  $df = 2$ ,  $F = 4.81$ ,  $p = 0.016$ ; Fig. 4), with mortal attacks by Alaskan ronquil occurring later than those by hermit crabs (Tukey's HSD,  $p = 0.012$ ). Arctic shanny and kelp greenling were excluded from analysis because of low predation frequencies. Juvenile Pacific cod (~15–25 cm total length) were frequently observed in the camera field of view in nighttime hours feeding on small crustaceans attracted to the camera lights but never interacted with the tethered crabs. Generally, cod activity peaked from midnight until 0200 h.

All crabs in the procedural control survived and remained on their tethers, but survival (average  $\pm$  SE) for uncaged crabs was  $37.5\% \pm 8.70\%$  for small crabs and  $43.8\% \pm 8.91\%$  for large crabs in July and  $21.9\% \pm 7.43\%$  for small crabs and  $34.4\% \pm 8.53\%$  for large crabs in September (Fig. 5). The main effect of mesh cages was significant, with uncaged crabs having lower survival than caged (control) crabs (Table 4). The main effects of size and deployment month were not significant, and there was no size  $\times$  month interaction (Table 4; Fig. 5). Time between deployment and mortal attack was longer for large crabs ( $7.2 \pm 1.7$  h) compared with small crabs ( $3.4 \pm 1.1$  h;  $t$  test,  $t = -2.306$ ,  $p = 0.028$ ).

**Table 3.** Taxa present at the study site that were considered potential predators of recently settled red king crabs (*Paralithodes camtschaticus*).

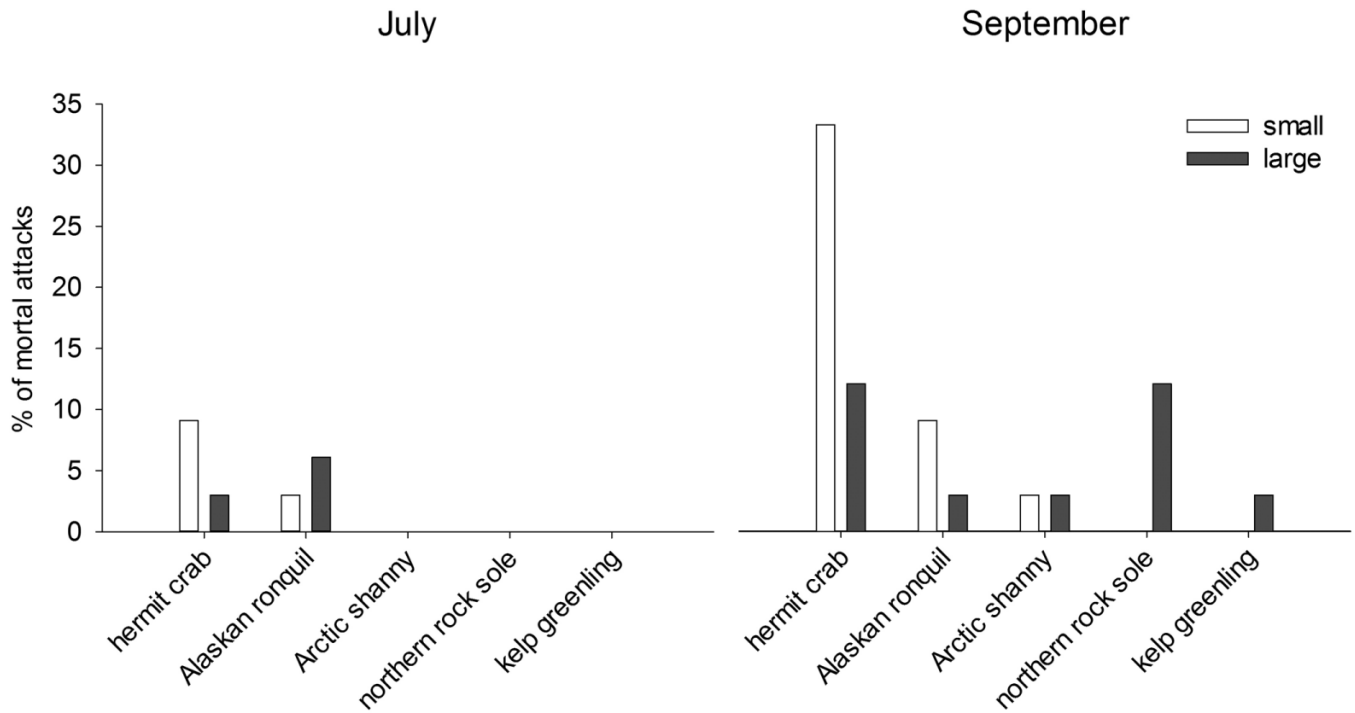
Common name	Species name	Occur	Appear	Consume	Abundance
Pacific cod	<i>Gadus macrocephalus</i>	X	X	—	H
Walleye pollock	<i>Theragra chalcogramma</i>	X	—	—	L
Kelp greenling	<i>Hexagrammos decagrammus</i>	X	X	X	H
Whitespotted greenling	<i>Hexagrammos stelleri</i>	X	X	—	L
Undefined rockfish	<i>Sebastes</i> spp.	X	—	—	M
Buffalo sculpin	<i>Enophrys bison</i>	X	—	—	M
Great sculpin	<i>Myoxocephalus polyacanthocephalus</i>	X	X	—	H
Crested sculpin	<i>Blepsias bilobus</i>	X	—	—	L
Silverspotted sculpin	<i>Blepsias cirrhosus</i>	X	—	—	M
Red Irish lord	<i>Hemilepidotus hemilepidotus</i>	X	X	—	H
Undefined sculpins	<i>Artedius</i> , <i>Clinocottus</i> , or <i>Oligocottus</i> spp.	X	X	—	M
Sturgeon poacher	<i>Podothecus acipenserinus</i>	X	X	—	H
Arctic shanny	<i>Sticheus punctatus</i>	X	X	X	M
Northern ronquil	<i>Ronquilus jordani</i>	X	X	—	M
Alaskan ronquil	<i>Bathymaster caeruleofasciatus</i>	X	X	X	M
Starry flounder	<i>Platichthys stellatus</i>	X	—	—	M
Yellowfin sole	<i>Limada aspera</i>	X	—	—	M
Northern rock sole	<i>Lepidopsetta polyxystra</i>	X	X	X	H
Crescent gunnel	<i>Pholis leata</i>	X	X	—	M
Giant Pacific octopus	<i>Enteroctopus dofleini</i>	X	—	—	L
Red king crab	<i>Paralithodes camtschaticus</i>	X	—	—	L
Graceful kelp crab	<i>Pugettia gracilis</i>	X	—	—	L
Undefined hermit crabs	<i>Pagurus</i> – <i>Elassochirus</i> spp.	X	X	X	H
Undefined shrimps	Pandalidae	X	—	—	L
Tubesnout	<i>Aulorhynchus flavidus</i>	X	—	—	M
Wolf-eel	<i>Anarrhichthys ocellatus</i>	X	—	—	L
Sunflower sea star	<i>Pycnopodia helianthoides</i>	X	X	—	H <sup>a</sup> , L <sup>b</sup>

**Note:** Taxa that were observed during dive surveys (Occur) appeared in the camera field of view (Appear) and successfully consumed a tethered crab (Consume) in video analysis are indicated with an “X”. Relative abundances are indicated as low (L), moderate (M), or high (H). We removed sunflower sea stars from the study site, resulting in no predation by sunflower sea stars on tethered crabs.

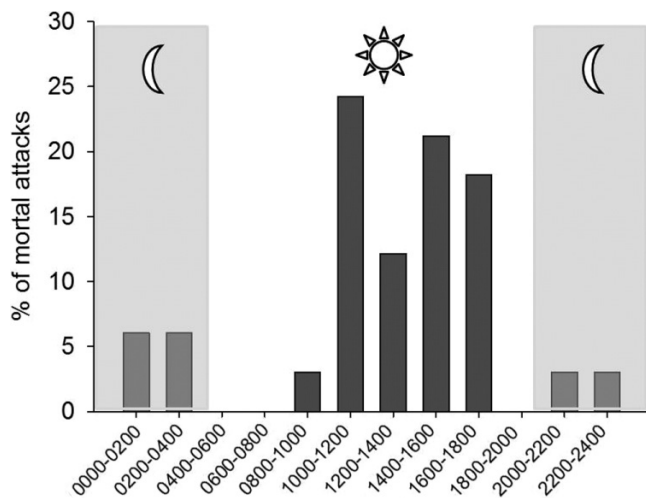
<sup>a</sup>Abundance before removal.

<sup>b</sup>Abundance after removal.

**Fig. 2.** Percentage of total mortal attacks observed in video footage by predators (hermit crabs (*Pagurus* spp.), Alaskan ronquill (*Bathymaster caeruleofasciatus*), Arctic shanny (*Sticheus punctatus*), northern rock sole (*Lepidopsetta polyxystra*), and kelp greenling (*Hexagrammos decagrammus*)) on small (open bars) and large (shaded bars) red king crabs (*Paralithodes camtschaticus*) in July and September. Of 55 crabs tethered with cameras, 33 crabs were consumed. These data represent 16 separate 24 h trials (8 in July, 8 in September).



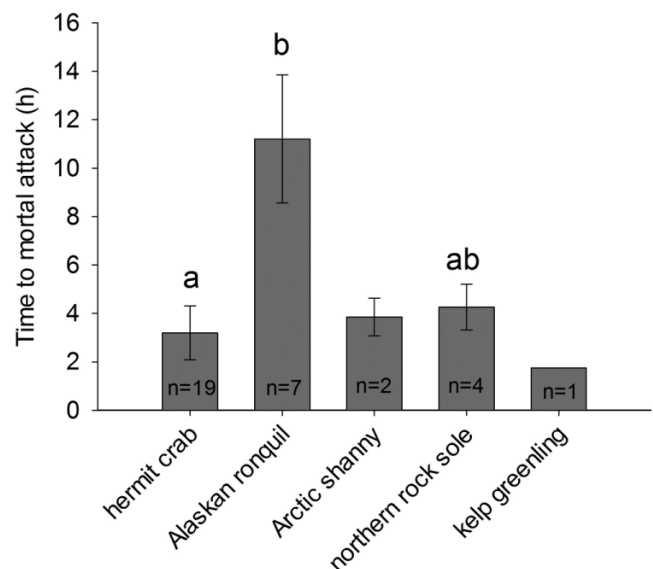
**Fig. 3.** Percentage of total mortal attacks on red king crabs (*Paralithodes camtschaticus*) observed in video footage by time of day over the 24 h trials. Of 55 crabs tethered with cameras, 33 crabs were consumed. These data represent 16 separate 24 h trials (8 in July, 8 in September). Crabs were deployed at approximately 0900–1000 h for each trial.



**Discussion**

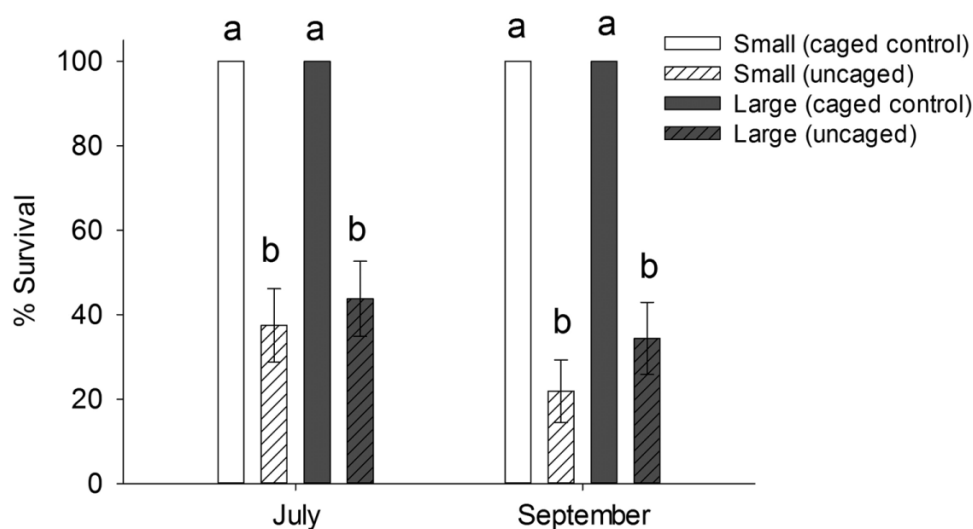
Predation will likely be the first challenge hatchery-cultured red king crabs face once released into the wild or that wild crabs face immediately after settlement. Our study is the first to deploy hatchery-cultured red king crabs in Alaskan waters and the first to assess in situ predation on red king crabs during the time period (July) and in the size range immediately following settlement (1.8–4.0 mm CW). We show that demersal fishes and crustaceans are

**Fig. 4.** Average ± SE time between when red king crabs (*Paralithodes camtschaticus*) were deployed and when they were consumed by predators. Time to mortal attack differed among predators (ANOVA,  $df = 2, F = 4.81, p = 0.016$ ). Different letters indicate statistical significance (Tukey's HSD,  $p \leq 0.05$ ). Arctic shanny and kelp greenling were excluded from analysis because of low predation frequencies.



predators of small (1.8–4.0 mm CW) juvenile red king crabs in nearshore habitats. Hermit crabs, Alaskan ronquill, and Arctic shanny consumed both small and large crabs, while northern rock sole and kelp greenling consumed only large crabs. Interestingly, Alaskan ronquill and Arctic shanny were less abundant at

**Fig. 5.** Average  $\pm$  SE survival in July and September for small and large red king crabs (*Paralithodes camtschaticus*) ( $n = 8$  for all treatments). Different letters indicate statistical significance (Tukey's HSD,  $p \leq 0.05$ ).



**Table 4.** ANOVA for survival of red king crab (*Paralithodes camtschaticus*) juveniles deployed with and without mesh enclosures (cage effect) of two size classes (small, large) and in two months (July, September).

Effect	SS	df	MS	F	p
Cage	15.642	1	15.642	241.67	<b>&lt;0.001</b>
Size	0.047	1	0.047	0.72	0.399
Month	0.133	1	0.133	2.05	0.157
Size $\times$ month	0.002	1	0.002	0.03	0.859
Residual	3.625	56	0.065		

Note: Bold indicates statistical significance ( $\alpha \leq 0.05$ ).

the study site than other species that were more abundant but did not consume tethered crabs. Arctic shanny observed preying on tethered crabs were relatively small ( $\sim 12$  cm total length), suggesting early benthic phase red king crabs are not necessarily precluded from small fish predators. Cannibalism is pervasive in red king crab aquaculture (Daly et al. 2009; Stoner et al. 2010), but we did not observe predation by wild conspecifics, likely because natural densities in southeast Alaska (e.g.,  $\sim 2$  crabs $\cdot$ m $^{-2}$ ) (Loher and Armstrong 2000) are much lower than hatchery conditions (i.e., 2000 crabs $\cdot$ m $^{-2}$ ) (Daly et al. 2009). Though we observed juvenile red king crabs ( $\sim 20$ – $30$  mm CW) at the study site during dive surveys, they were relatively rare and were not observed in video analysis, suggesting encounters with tethered conspecifics were uncommon. Further, recently molted crabs are at greatest risk of being preyed on because of reduced mobility and lack of defensive armor; thus, we tethered hardshell, intermolt crabs, which likely also contributed to our lack of observed cannibalism. We expected predation by sculpins (Cottoidea) (Pirtle et al. 2012) and Pacific cod (Bechtol and Kruse 2010), both of which were relatively abundant and appeared in video footage but were uninterested in tethered crabs. Sculpins consume larger tethered red king crabs (4–8 mm CL) (Pirtle et al. 2012), suggesting they may preferentially target prey items larger than crabs used in our study (1.8–4.0 mm CW). In laboratory studies, Pacific cod consume hardshell early benthic phase red king crabs in the absence of alternative prey items when deprived of food for 48 h (Daly et al. 2012a), but are less enthusiastic predators compared with Pacific halibut (Stoner 2009; Pirtle and Stoner 2010; Daly et al. 2012a). The relative disinterest in tethered crabs in the field may be a result of the Pacific cod being distracted by the abundant pelagic zooplankton swarming around the camera lights. Further, Pacific cod may preferentially consume red king crabs when they are in the softshell state,

and their spines have no antipredator effect, though it is unknown if Pacific cod consume softshell red king crabs in the size range used in our study. As such, we cannot discount the potential importance of Pacific cod predation on early benthic phase red king crabs in nearshore habitats.

The prevalence of hermit crab predation was unexpected. We assessed the possibility of a tethering artifact by placing an untethered red king crab and a hermit crab (of typical size observed in video analysis) in a laboratory tank to determine if juvenile red king crabs could escape hermit crab predation. In each of three trials, different hermit crabs easily captured and consumed untethered red king crabs, suggesting hermit crab predation was not necessarily a tethering artifact. Hermit crabs observed in video analysis were large (up to approximately 140 mm shell length) and capable of short bursts of speed, which enhances their ability to capture and consume small, wild, juvenile red king crabs. Hermit crabs are also known predators in other systems (Pechenik et al. 2010). Therefore, given their abundance and our results, hermit crabs may be significant consumers of recently settled red king crabs in nearshore habitats, and future studies could examine this relationship further.

Sunflower sea stars may affect survival of recently settled red king crabs in the wild. Though untethered age-1 juvenile red king crabs are capable of escaping sunflower sea stars in laboratory conditions (Pirtle et al. 2012), spatial separation may not be possible in areas of dense sunflower sea star aggregations. For example, crabs may have difficulty escaping persistent attacks by multiple individuals. Further, secondary predation by other species (e.g., fishes) may occur if fleeing crabs become more vulnerable when leaving interstitial refugia. As such, the presence and density of sunflower sea stars should be considered when evaluating release locations for cultured red king crabs.

Almost all predation occurred in daylight hours. Interestingly, predation by Alaskan ronquill occurred exclusively during hours of darkness, despite appearing in video footage in daylight hours. It is unclear from video footage why Alaskan ronquill predated exclusively at night, though camera light likely enabled visual detection (although survival was similar in lighted and unlighted treatments). Tethered juvenile spiny lobsters (*Jasus edwardsii*) are preyed on by fish during daylight hours and by invertebrates (crabs, octopus) during the night (Mills et al. 2008). As such, the importance of visual detection and foraging activity likely varies with predator species (Aksnes and Giske 1993). Predation was not observed during the dawn or dusk phases, suggesting these time

spans may be optimal for releases. Further, dusk releases may provide crabs additional time to establish crypsis prior to daylight hours where predation by fish can be most intense.

Survival did not vary among the size ranges of animals used in this study (1.8–4.0 mm CW). We expected to find improved survival with increasing body size, as observed for other crustacean species, including American lobsters (Wahle 1992; Wahle and Steneck 1992), spiny lobsters (*Panulirus argus*) (Smith and Herrnkind 1992), and blue crabs (Hines and Ruiz 1995; Johnson et al. 2008); however, these differences in predation vulnerability often correspond with broader size ranges than we used in our study. For example, Wahle and Steneck (1992) demonstrate increasing American lobster survival among 5–7, 15–20, and 30–40 mm CL size classes. Yet not all studies find improved survival with increasing size. Artificially reared winter flounder (*Pseudopleuronectes americanus*) do not differ in predation risk with slight increments in size or age in laboratory experiments (Bertram and Leggett 1994). Pirtle et al. (2012) failed to detect size-specific survival between tethered age-0 (4–8 mm CL) and age-1 (16–28 mm CL) red king crabs at the same study site, though sample sizes were small. Further, Pirtle et al. (2012) found that all age-1 crabs tethered in gravel and shell hash were consumed by sunflower sea stars, making survival rate comparisons with the present study inappropriate because we removed sunflower sea stars from the study site to avoid tethering artifacts. Red king crab glaucothoe and first stage juveniles (C1) are similar in size, but predation rates on juveniles are lower because of increased associations with refuge habitat (Stevens and Swiney 2005). In our study, large crabs took twice as long to be consumed as small crabs; however, behavioral differences among size classes (e.g., limb flaring, aggressive postures, crypsis) were not visible in video analysis owing to the small size of the crabs. Because all crabs in the present study are early benthic phase, we expect the same shelter-seeking behavior among size classes. Increases in predation may become more apparent at sizes where crabs can no longer effectively use refuge habitats and are less cryptic. We suggest any differences in predation risk among red king crabs within the size range in our experiment (1.8–4.0 mm CW) are subtle and potentially ecologically inconsequential.

It is generally understood that seasonal timing of release of hatchery-cultured individuals impacts survival by effects of size at release, water temperature, food availability, or related shifts in predator suites (Bertness et al. 1981; Leber et al. 1997; Stoner and Glazer 1998; van der Meeren 2000; Johnson et al. 2008). For example, European lobster (*Homarus gammarus*) and queen conch (*Strombus gigas*) survival is lowest in summer compared with spring and fall months because of higher predator densities in the summer (Stoner and Glazer 1998; van der Meeren 2000). We did not detect temporal variation in survival, likely because of minimal predator assemblage fluctuations associated with the relatively short time span between trials.

Extended hatchery rearing may not be beneficial if relative survival rates do not vary temporally or improve with body size. Cannibalism in the hatchery causes high mortality rates (e.g., 1.8% mortality-day<sup>-1</sup>) at typical rearing densities (e.g., 2000 crabs·m<sup>-2</sup>) (Daly et al. 2012b). Early postsettlement (C1 or C2 instar stage) release eliminates opportunity for cannibalistic mortality associated with high density hatchery rearing conditions. Individuals released in the wild could disperse and potentially establish crypsis, which could minimize density-dependent cannibalism and potentially allow for higher survival rates compared with hatchery conditions. Further, early postsettlement releases would reduce economic cost of hatchery culture associated with extended juvenile rearing. Thus, releasing crabs soon after settlement may be beneficial for stock enhancement efforts.

We acknowledge that the tethers and camera light create artifacts (i.e., enhanced predation) (Zimmer-Faust et al. 1994) and that our results cannot be used to measure absolute predation rates.

However, these studies are useful to identify predators and to evaluate relative predation rates. Camera lights could have impacted predator behavior or species composition; however, crab survival was similar with and without the use of cameras, indicating that the lighting did not result in increased predation.

Tethered red king crabs showed no obvious behavioral deficiencies (e.g., prolonged immobility, abnormally high activity) that may exacerbate predation. For example, hatchery-cultured European lobsters are highly susceptible to fish predation immediately after release because of abnormal swimming behavior or prolonged immobility induced by stress associated with transportation to the release site (van der Meeren 1991). The tethered red king crabs typically found crevice space soon after deployment and were highly cryptic. Substrate with adequate crevice space is likely important for survival of early benthic phase red king crabs by reducing susceptibility to predators, especially immediately after deployment. Similarly, artificially reared early benthic phase European lobsters require cobble and gravel substrate to reduce in situ predation by small benthic fishes (Ball et al. 2001).

Our study lays groundwork for developing red king crab release strategies. We show that hatchery-cultured red king crabs can survive in the wild, at least for 24 h, and suggest that differences in predation susceptibility are minimal for the first few months after settlement. Early benthic phase red king crabs are consumed by a range of fishes and invertebrates, including hermit crabs, Alaskan ronquill, Arctic shanny, northern rock sole, and kelp greenling; thus, predator assemblages and the timing of predation should be considered when selecting release sites and time of release. Future studies should examine spatial variation in predation pressure at multiple locations on broad temporal scales to understand population-level effects. Benefits of larger size increments associated with extended (i.e., >1 year) hatchery grow-out and benefits of in situ acclimation or hatchery conditioning should also be explored. Further, a fundamental understanding of mechanisms causing low natural population abundances is necessary for stock enhancement to succeed. For example, additions of juveniles will likely be unsuccessful if recruitment limitation is caused by predation mortality; however, if recruitment limitation is caused by an inadequate supply of settling larvae from depressed spawning stocks or low reproductive success, stock enhancement could facilitate rehabilitation of depressed stocks.

## Acknowledgements

Funding for this project was provided by a Sea Grant Aquaculture grant awarded to the University of Alaska Fairbanks and a NSF REU fellowship to T.D.W. (NSF No. 0852111 to the University of Alaska Southeast). The authors thank the Alaska Department of Fish and Game for collecting ovigerous females, J. Swingle for hatchery rearing assistance, J. Hetrick for hatchery logistical support, J. Pirtle for advice on field logistics, and J. Sylvan for crab care and field support. B. Konar, G. Kruse, and A. Stoner provided helpful comments that greatly improved the manuscript.

## References

- Aksnes, D.L., and Giske, J. 1993. A theoretical model of aquatic visual feeding. *Ecol. Modell.* **67**: 233–250. doi:10.1016/0304-3800(93)90007-F.
- Ball, B., Linnane, A., Munday, B., Browne, R., and Mercer, J.P. 2001. The effect of cover on *in situ* predation in early benthic phase European lobster *Homarus gammarus*. *J. Mar. Biol. Assoc. U.K.* **81**: 639–642.
- Bannister, R.C.A., and Addison, J.T. 1998. Enhancing lobster stocks: a review of recent European methods, results, and future prospects. *Bull. Mar. Sci.* **62**: 369–387.
- Bechtol, W.R., and Kruse, G.H. 2009. Reconstruction of historical abundance and recruitment of red king crab during 1960–2004 around Kodiak, Alaska. *Fish. Res.* **100**: 86–98. doi:10.1016/j.fishres.2008.09.003.
- Bechtol, W.R., and Kruse, G.H. 2010. Factors affecting historical red king crab recruitment around Kodiak Island, Alaska. *In* *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, University of Alaska Fairbanks. pp. 413–432.
- Bell, J.D., Rothlisberg, P.C., Munro, J.L., Loneragan, N.R., Nash, W.J., Ward, R.D.,

- and Andrew, N.L. 2005. Restocking and stock enhancement of marine invertebrate fisheries. *Adv. Mar. Biol.* **49**: 1–370. doi:10.1016/S0065-2881(05)49001-X.
- Bell, J.D., Bartley, D.M., Lorenzen, K., and Loneragan, N.R. 2006. Stock enhancement and stock enhancement of coastal fisheries: potential, problems and progress. *Fish. Res.* **80**: 1–8. doi:10.1016/j.fishres.2006.03.008.
- Bell, J.D., Leber, K.M., Blankenship, H.L., Loneragan, N.R., Masuda, R., and Vanderhaegen, G. 2008. A new era for restocking, stock enhancement and sea ranching of coastal fisheries resources. *Rev. Fish. Sci.* **16**(1–3): 1–9. doi:10.1080/10641260701776951.
- Bertness, M.D., Garrity, S.D., and Levings, S.C. 1981. Predation pressure and gastropod foraging: a tropical–temperate comparison. *Evolution*, **35**: 995–1007. doi:10.2307/2407870.
- Bertram, D.F., and Leggett, W.C. 1994. Predation risk during the early life history periods of fishes: separating the effects of size and age. *Mar. Ecol. Prog. Ser.* **109**: 105–114. doi:10.3354/meps109105.
- Blankenship, H.L., and Leber, K.M. 1995. A responsible approach to marine stock enhancement. *Am. Fish. Soc. Symp.* **15**: 167–175.
- Blau, S.F. 1986. Recent declines of red king crab (*Paralithodes camtschatica*) 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.* **92**. pp. 360–369.
- Brewer, R., and Konar, B. 2005. Chemosensory responses and foraging behavior of the seastar *Pycnopodia helianthoides*. *Mar. Biol.* **147**: 789–795. doi:10.1007/s00227-005-1608-7.
- Castro, K.M., Cobb, J.S., Wahle, R.A., and Catena, J. 2001. Habitat addition and stock enhancement for American lobsters, *Homarus americanus*. *Mar. Freshw. Res.* **52**: 1253–1261. doi:10.1071/MF01095.
- Daly, B., Swingle, J.S., and Eckert, G.L. 2009. Effects of diet, stocking density, and substrate on survival and growth of hatchery-cultured red king crab (*Paralithodes camtschaticus*) juveniles in Alaska, U.S.A. *Aquaculture*, **293**: 68–73.
- Daly, B., Stoner, A.W., and Eckert, G.L. 2012a. 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., Swingle, J.S., and Eckert, G.L. 2012b. Dietary astaxanthin supplementation for hatchery-cultured red king crab (*Paralithodes camtschaticus*) juveniles. *Aquacult. Nutr.* doi:10.1111/j.1365-2095.2012.00963.x.
- Davis, J.L.D., Young-Williams, A.C., Hines, A.H., and Zohar, Y. 2005. Assessing the potential for stock enhancement in the case of the Chesapeake Bay blue crab (*Callinectes sapidus*). *Can. J. Fish. Aquat. Sci.* **62**(1): 109–122. doi:10.1139/f04-150.
- Dew, B. 1991. Characterization of preferred habitat for juvenile red king crab in three Kodiak Bays, Kodiak Island Borough Project. National Marine Fisheries Service. Alaska Fisheries Science Center, Kodiak.
- Dew, C.B. 1990. Behavioral ecology of podding red king crab, *Paralithodes camtschatica*. *Can. J. Fish. Aquat. Sci.* **47**(10): 1944–1958. doi:10.1139/f90-219.
- Donaldson, W., Byersdorfer, S., Pengilly, D., and Blau, S. 1992. Growth of red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), in artificial habitat collectors at Kodiak, Alaska. *J. Shellfish Res.* **11**: 85–89.
- Glazer, R.A., and Jones, R. 1997. Temporal factors influencing survival of queen conch outplants. Final report. US Fish and Wildlife Service Project.
- Heck, K.L., and Thoman, T.A. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.* **53**: 125–134. doi:10.1016/0022-0981(81)90014-9.
- Hines, A.H., and Ruiz, G.M. 1995. Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. *Bull. Mar. Sci.* **57**: 884–901.
- 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**: 175–185. doi:10.1080/10641260701678090.
- 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**: 243–253. doi:10.1080/10641260701696837.
- Kitada, S., and Kishino, H. 2006. Lessons learned from Japanese marine finfish stock enhancement programmes. *Fish. Res.* **80**(1): 101–112. doi:10.1016/j.fishres.2006.03.019.
- Leber, K.M. 1995. Significance of fish size-at-release on enhancement of striped mullet fisheries in Hawaii. *J. World Aquacult. Soc.* **26**: 143–153. doi:10.1111/j.1749-7345.1995.tb00237.x.
- Leber, K.M., Blankenship, H.L., Arce, S.M., and Brennan, N.P. 1997. Influence of release season on size-dependent survival of cultured striped mullet, *Mugil cephalus*, in a Hawaiian estuary. *Fish. Bull.* **95**: 267–279.
- Leber, K.M., Kitada, S., Blankenship, H.L., and Svåsand, T. (Editors). 2004. Stock enhancement and sea ranching: developments, pitfalls and opportunities. Blackwell, Oxford.
- Livingston, P.A. 1989. Interannual trends in Pacific Cod, *Gadus macrocephalus*, predation on three commercially important crab species in the eastern Bering Sea. *Fish. Bull.* **87**: 807–827.
- Livingston, P.A. 1991. Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1984 to 1986. NOAA Tech. Memo. NMFS F/NWC 207, Seattle, Wash.
- Livingston, P.A., Ward, A., Lang, G.M., and Yang, M.S. 1993. Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1987 to 1989. NOAA Tech. Memo. NMFS AFSC-11, Seattle, Wash.
- 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**: 83–109. doi:10.1016/S0022-0981(99)00157-4.
- Loher, T., and Armstrong, D.A. 2001. Growth of juvenile red king crab (*Paralithodes camtschaticus*) in Bristol Bay (Alaska) elucidated from field sampling and analysis of trawl-survey data. *Fish. Bull.* **99**: 572–587.
- Loher, T., and Armstrong, D.A. 2005. Historical changes in the abundance and distribution of ovigerous red king crabs (*Paralithodes camtschaticus*) in Bristol Bay (Alaska), and potential relationship with bottom temperature. *Fish. Oceanogr.* **14**: 292–306. doi:10.1111/j.1365-2419.2005.00337.x.
- Lorenzen, K. 2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* **260**: 171–189. doi:10.1098/rstb.2004.1570.
- Lorenzen, K., Leber, K.M., and Blankenship, H.L. 2010. Responsible approach to marine stock enhancement: an update. *Rev. Fish. Sci.* **18**: 189–210. doi:10.1080/10641262.2010.491564.
- Lysenko, V.N., and Gaidaev, V.E. 2005. Growth of red king crab *Paralithodes camtschaticus* in the northern part of the West Kamchatka shelf. *Izv. TINRO*, **143**: 119–127.
- Marukawa, H. 1933. Biological and fishery research on Japanese king crab, *Paralithodes camtschatica* (Tilesius). *J. Imp. Fish. Exp. St. (Tokyo)*, **37**: 1–152.
- Mills, D.J., Johnson, C.R., and Gardner, C. 2008. Bias in lobster tethering experiments conducted for selecting low-predation release sites. *Mar. Ecol. Prog. Ser.* **364**: 1–13. doi:10.3354/meps07527.
- Orensanz, J.M.L., 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**: 117–176. doi:10.1023/A:1008891412756.
- Pechenik, J.A., Ambrogio, O.V., and Untersee, S. 2010. Predation on juveniles of *Crepidula fornicata* by two crustaceans and two gastropods. *J. Exp. Mar. Biol. Ecol.* **384**: 91–98. doi:10.1016/j.jembe.2009.12.011.
- 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**: 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.
- Secor, D.H., Hines, A.H., and Place, A.R. 2002. Japanese hatchery based stock enhancement: lessons for the Chesapeake Bay blue crab. Maryland Sea Grant Rep. No. UM-SG-TS-2002-02, College Park, Md.
- Smith, K.N., and Herrnkind, W.F. 1992. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. *J. Exp. Mar. Biol. Ecol.* **157**(1): 3–18. doi:10.1016/0022-0981(92)90070-Q.
- Stevens, B.G. 1990. Temperature-dependent growth of juvenile red king crab (*Paralithodes camtschaticus*) and its effects on size-at-age and subsequent recruitment in the eastern Bering Sea. *Can. J. Fish. Aquat. Sci.* **47**(7): 1307–1317. doi:10.1139/f90-150.
- Stevens, B.G. (Editor). 2006a. King crab cultivation and stock enhancement in Japan and the United States: a brief history. In *Alaska Crab Stock Enhancement and Rehabilitation: Workshop Proceedings*. Alaska Sea Grant College Program AKSG-06-04. pp. 23–31.
- Stevens, B.G. (Editor). 2006b. Alaska crab stock enhancement and rehabilitation: an introduction. In *Alaska Crab Stock Enhancement and Rehabilitation: Workshop Proceedings*. Alaska Sea Grant College Program AKSG-06-04. pp. 5–8.
- 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**: 1–11. doi:10.1016/j.jembe.2004.12.026.
- Stone, R.P., O'Clair, C.E., and Shirley, T.C. 1993. Aggregating behavior of ovigerous female red king crab, *Paralithodes camtschaticus*, in Auke Bay, Alaska. *Can. J. Fish. Aquat. Sci.* **50**(4): 750–758. doi:10.1139/f93-086.
- Stoner, A.W. 2009. Habitat-mediated survival of newly settled red king crab in the presence of a predatory fish: role of habitat complexity and heterogeneity. *J. Exp. Mar. Biol. Ecol.* **382**: 54–60. doi:10.1016/j.jembe.2009.10.003.
- Stoner, A.W., and Davis, M. 1994. Experimental outplanting of juvenile queen conch, *Strombus gigas*: comparison of wild and hatchery-reared stocks. *Fish. Bull.* **92**: 390–411.
- Stoner, A.W., and Glazer, R.A. 1998. Variation in natural mortality: implications for queen conch stock enhancement. *Bull. Mar. Sci.* **62**: 427–442.
- 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**: 1005–1012. doi:10.2983/035.029.0401.
- Stratman, J., Messmer, A., Bishop, B., Siddon, C., and Olson, A. 2011. 2012 Report to the Board of Fisheries on Southeast Alaska/Yakutat King Crab Fisheries.



- Alaska Department of Fish and Game, Fishery Management Report No. 11-68. pp. 1-94.
- 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.
- Tyler, A.V., and Kruse, G.H. 1996. Conceptual modeling of brood strength of red king crabs on the Bristol Bay region of the Bering Sea. In *High latitude crabs: biology, management, and economics*. Alaska Sea Grant College Program, AK-SG-96-02.
- Urban, J.D. 2010. Pacific cod predation on Tanner crab in Marmot Bay, Alaska. In *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, University of Alaska Fairbanks. pp. 341-358.
- van der Meeren, G.I. 1991. Out-of-water transportation effects on behavior of newly released juvenile Atlantic lobsters (*Homarus gammarus*). *Aquac. Eng.* 10(1): 55-64. doi:10.1016/0144-8609(91)90010-H.
- 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.
- Wahle, R.A. 1992. Body-size dependent anti-predator mechanisms of the American lobster. *Oikos*, 65: 52-60. doi:10.2307/3544887.
- Wahle, R.A., and Steneck, R.S. 1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? *Mar. Ecol. Prog. Ser.* 69: 231-243. doi:10.3354/meps069231.
- Wahle, R.A., and Steneck, R.S. 1992. Habitat restrictions in early benthic life: experiments on habitat selection and *in situ* predation with the American lobster. *J. Exp. Mar. Biol. Ecol.* 157: 91-114. doi:10.1016/0022-0981(92)90077-N.
- Willis, S.A., Falls, W.W., Dennis, C.W., Roberts, D.E., and Whitchurch, P.G. 1995. Assessment of season of release and size at release on recapture rates of hatchery-reared red drum. *Am. Fish. Soc. Symp.* 15: 354-365.
- Zheng, J., and Kruse, G.H. 2006. Recruitment variation of eastern Bering Sea crabs: climate-forcing or top-down effects? *Prog. Oceanogr.* 68: 184-204. doi:10.1016/j.pocean.2006.02.002.
- Zimmer-Faust, R.K., Fielder, D.R., Heck, K.L., Coen, L.D., and Morgan, S.G. 1994. Effects of tethering on predatory escape by juvenile blue crabs. *Mar. Ecol. Prog. Ser.* 111: 299-303. doi:10.3354/meps111299.
- Zohar, Y., Hines, A.H., Zmora, O., Johnson, E.G., Lipcius, R.N., Seitz, R.D., Eggleston, D.B., Place, A.R., Schott, E.J., Stubblefield, J.D., and Chung, J.S. 2008. The Chesapeake Bay blue crab (*Callinectes sapidus*): a multidisciplinary approach to responsible stock replenishment. *Rev. Fish. Sci.* 16(1-3): 25-35.