



Habitat structure influences the survival and predator–prey interactions of early juvenile red king crab *Paralithodes camtschaticus*

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ABSTRACT: Highly structured nursery habitats promote the survival of juvenile stages of many species by providing foraging opportunities and refuge from predators. Through integrated laboratory and field experiments, we demonstrate that nursery habitat structure affects survival and predator-prey interactions of red king crab *Paralithodes camtschaticus*. Crabs (<1 yr old [Age 0]; 8 to 10 mm carapace length [CL]) preferred complex biogenic habitats formed by structural invertebrates and macroalgae over structural mimics and sand in the absence of predators in laboratory experiments, yet they associated with any available structural habitat when fish predators were present. Survival was higher in the presence of complex habitat for Age 0 crabs (5 to 7.5 mm CL) with Pacific cod *Gadus macrocephalus* predators in the laboratory and for Age 0 (4 to 8 mm CL) and Age 1 (16 to 28 mm CL) crabs with fish and invertebrate predators in the field. Crab activity and refuge response behavior varied with crab stage and habitat. Age 0 crabs were cryptic, avoiding predators by associating with habitat structure or remaining motionless in the absence of structure, and were less likely to respond to an attack. In contrast, Age 1 crabs were more likely to respond to an attacking predator and were less likely to remain motionless in the absence of structural refuge, suggesting an ontogenetic shift in behavior. Complex habitats, cryptic behavior, and direct defense improve juvenile red king crab survival against certain predators, including demersal fishes.

KEY WORDS: Red king crab · *Paralithodes camtschaticus* · Nursery habitat dynamics · Predator–prey interaction · Habitat complexity · Refuge · *Gadus macrocephalus*

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INTRODUCTION

Habitat structural complexity has a profound effect on the ecology of associated organisms (Crowder & Cooper 1982, Stoner & Lewis 1985, Wahle & Steneck 1991, Carr 1994, Hovel & Fonseca 2005). Structurally complex habitats have high surface area relative to their size and abundant crevices to shelter small animals (Caddy 1986, Eggleston et al. 1990). Complex habitats in aquatic environments may include aggre-

gated boulders, rock wall crevices, and biogenic habitats formed by seagrasses, macroalgae, and invertebrates, such as hydroids, corals, and sponges.

Structurally complex nursery habitats are critical for the early life stage survival of many aquatic organisms. Survival of juvenile spiny lobster *Panulirus argus* and blue crab *Callinectes sapidus* is substantially increased by small amounts of seagrass and algal structure (Lipcius et al. 1998, Hovel & Fonseca 2005). Complex habitat associations are important for

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American lobsters *Homarus americanus* from settlement until individuals outgrow the most vulnerable early juvenile stages (Wahle & Steneck 1992). Predator foraging efficiency is often decreased in complex habitats, increasing survival (Lima & Dill 1990).

Predator–prey interactions have substantial effects for early life stages beyond removal of individuals, including trade-offs between foraging and predation risk (reviewed by Werner 1992). Highly structured nursery habitats support the growth of early life stages by providing foraging opportunities (Mittelbach 1984, Marx & Herrnkind 1985). When predators are absent, prey habitat choice should maximize foraging (Werner et al. 1983). Under perceived predator threat, prey should respond with behaviors that maximize immediate survival (Stein & Magnuson 1976), including retreat to refuge structure, reduced activity, reduced foraging, and direct defense (Stein & Magnuson 1976, Gilliam & Fraser 1987, Gotceitas & Colgan 1987, Laurel & Brown 2006). This trade-off results in reduced growth rates (Werner et al. 1983, Werner 1991, 1992, Tupper & Boutilier 1995), with population-level consequences such as reduced reproductive potential. Furthermore, prey response behaviors often change with ontogeny, as foraging-risk implications are altered and individuals outgrow refuge habitat (Stein & Magnuson 1976, Werner & Hall 1988, Wahle & Steneck 1991, Sandt & Stoner 1993). Investigating predator–prey interactions, including refuge response behavior and survival relative to habitat structural complexity, will improve understanding of nursery habitat function for structure-seeking early life stages.

Red king crab *Paralithodes camtschaticus* is a large, commercially important anomuran crab (Lithodidae) distributed throughout the North Pacific. Red king crab have a multistage life cycle with dispersive larval stages (2 to 4 mo planktonic period) and benthic juveniles and adults (Marukawa 1933, Shirley & Shirley 1989). In Alaska during June and July, larval red king crab settle to nearshore habitats where crabs in the early juvenile stage (0 to 2 yr; 2 to 25 mm carapace length [CL]) (Donaldson et al. 1992, Loher & Armstrong 2000) are solitary and cryptic and live in a habitat different from that of older juveniles and adults (Karinen 1985). The early benthic stage is most abundant in complex habitats, including fractured rock, cobbles, and bivalve shells (Sundberg & Clausen 1977, Loher & Armstrong 2000), and complex biogenic habitats formed by macroalgae and structural invertebrates, including hydroids and bryozoans (Sundberg & Clausen 1977, McMurray et al. 1984, Rodin 1985). Previous studies of habitat choice

by red king crab have demonstrated that settlement-stage red king crab prefer structurally complex habitats over open sand (Stevens & Kittaka 1998) and that juveniles prefer structural invertebrates and macroalgae over sand (Stevens 2003, Pirtle & Stoner 2010). Associating with complex habitats should reduce predation of the early juvenile stage, including predation by conspecifics, because red king crabs are highly cannibalistic (Stevens & Swiney 2005). Habitat choice is also driven by foraging opportunities, particularly when biogenic habitats are present (Pirtle & Stoner 2010). After Age 2, juvenile crabs emerge from complex habitats to form 'pods', mobile aggregations of hundreds to thousands of individuals (Powell & Nickerson 1965, Dew 1990). Red king crab growth and maturity are temperature dependent, and red king crabs mature at ages ranging from 5 to 12 yr (Stevens 1990).

Red king crab supported the most valuable crustacean fishery in Alaska until a sharp decline occurred in the late 1960s followed by large-scale collapse in the early 1980s (Orensanz et al. 1998, Zheng & Kruse 2000). At present, many red king crab populations throughout Alaska remain depleted, even in areas without a commercial fishery (Woodby et al. 2005, Hebert et al. 2008). Hypotheses for recovery failure attribute low spawning stock biomass to overharvest in the directed pot fishery (Orensanz et al. 1998), female bycatch in trawl fisheries (Armstrong et al. 1993, Dew & McConnaughey 2005), North Pacific ocean-atmospheric conditions (Tyler & Kruse 1996, Zheng & Kruse 2000, 2006), loss of early benthic stage habitat (Armstrong et al. 1993), and predation by groundfish, such as Pacific cod *Gadus macrocephalus* and flatfishes (e.g. Pacific halibut *Hippoglossus stenolepis*) (Tyler & Kruse 1996, Zheng & Kruse 2006, Bechtol & Kruse 2010).

The collapse of red king crab in the North Pacific coincided with increased groundfish abundance (Bakkala 1993, Bailey 2000, Bechtol 2009), implicating groundfish as potential predators of vulnerable juvenile crab stages with population-level consequences (Tyler & Kruse 1996, Zheng & Kruse 2006). Population modeling has demonstrated a strong negative association between Pacific cod biomass and red king crab recruitment (Zheng & Kruse 2006, Bechtol 2009). However, lack of recovery of red king crab has not been directly linked to groundfish predation. If we can gain understanding of factors that support early life stage success of red king crab, then we may better understand conditions that contribute to population fluctuation for this depleted fishery resource species.

Habitat-mediated survival of early juvenile red king crab was examined in the laboratory using Pacific halibut as a fish predator. Halibut (Age 1) were efficient predators of early juvenile crabs (Age 0; <5 mm CL) and quickly consumed all crabs in sand habitat without structure (Stoner 2009). The addition of complex habitat structure increased crab survival (Stoner 2009). Whether or not complex habitat structure mediates crab survival in the presence of other predators that may have different foraging strategies is not presently known. Also unknown is how crab refuge-response behavior may change with ontogeny and how early juvenile stage crabs respond to predators *in situ*.

In the present study, we examined the effects of habitat structure on survival and refuge response behavior of early juvenile *Paralithodes camtschaticus* (ages 0 and 1 yr) using laboratory and field experiments. We tested the habitat choice of Age 0 crabs in the laboratory without predators and in habitats with and without structure as well as survival in the same habitats with Pacific cod as a predator. We then tested Age 0 and Age 1 crab survival in nearshore habitats with and without structure and identified predators and crab refuge-response behavior. We investigated the following hypotheses: (1) habitat choice is influenced by perceived predator threat; (2) survival is greatest within habitats of complex structure; and (3) refuge-response behavior differs between habitats with and without structure and according to crab size or age.

MATERIALS AND METHODS

Habitat choice experiment

We tested the habitat preference of Age 0 red king crabs in the absence of predators to determine whether crabs associate with structurally complex biogenic habitats more often than with habitats of complex physical structure or with sand (structure absent). All of the laboratory trials were conducted in the seawater facilities of the US National Marine Fisheries Service Alaska Fisheries Science Center (AFSC) in Newport, Oregon.

Three general habitat configurations were employed: (1) bare sand, (2) sand with biogenic structure and (3) sand with artificial structure. The test with biogenic structure was further subdivided into 2 treatments, the first composed solely of hydroids *Obelia* spp. and the second of a composite of hydroids and branched macroalgae *Neorhodomela larix*.

The hydroid treatment consisted of 8 branches of hydroid structure bound together at the base with 3 cm of craft pipe cleaner. The branched macroalgae treatment was composed of 8 algal fronds arranged in a clump. The biogenic treatment units were ~20 cm in length and resembled the structure formed by the hydroids and macroalgae in the field. Likewise, 2 treatments of artificial biogenic substrate were used to test the effect of structure alone on crab habitat choice. Artificial structures were constructed from synthetic yarns (Lion Brand®) that closely mimicked the structure formed by the natural habitat treatments. Hydroid mimics were constructed of fringed, polyester yarn (Fun Fur®, 2 mm diameter), and macroalgal mimics were constructed of chenille, acrylic yarn (5 mm diameter). Thus, the laboratory component was composed of 5 unique habitat treatments.

For each of the 5 habitat treatments, 3 replicates were conducted. Each replicate was conducted in a circular, flat-bottom tank (1.1 m diameter) filled to a depth of 0.3 m with continuously flowing (150 ml s⁻¹), natural, sand-filtered seawater at 7°C (±0.5°C). The substrate in all tanks was composed of 1 cm of 0.5 mm grain-diameter quartz sand. Structurally complex (i.e. hydroid and algae) habitat treatments also contained 22 pieces of the specified structural element, placed on top of the sand, interspersed throughout the tank. For treatments composed of both hydroid and macroalgae (whether natural or mimic), an even ratio (i.e. 11 pieces) of each structural element was placed on top of the sand in a mixed arrangement. Once established, 20 Age 0 crabs (8 to 10 mm CL) were selected randomly from a large laboratory population and introduced into the experimental tank. We used hatchery-reared (Alutiiq Pride Shellfish Hatchery, Seward, Alaska) crabs from wild-captured female crabs from Bristol Bay, Alaska, that were supplied to us by the Alaska King Crab Research Rehabilitation and Biology Program. Crabs were allowed to acclimate to the tank for 3 h and to associate with the habitat structures or with sand, after which the total count of crab associations on or under the habitat structure was recorded. Any molting behavior or cannibalism was also noted. The arcsine-square-root transformed proportion of crab associations with each habitat type within each treatment was compared using single-factor analysis of variance (ANOVA) ($\alpha = 0.05$), and treatment-specific differences were identified using Tukey's post-comparison tests. All analyses were performed using SAS version 9.2 (SAS® Analytics).

Laboratory predation experiment

We tested the survival of crabs in the presence of fish predators when crabs were presented with the same habitat treatments described above. Fish predators were Age 1 Pacific cod *Gadus macrocephalus* (175 to 220 mm fork length) that were collected as Age 0 fish from the waters off Kodiak Island, Alaska, and grown to this size in the Newport facility.

Predation trials were conducted in 3 circular, flat-bottomed tanks (1.4 m diameter) filled to a depth of 0.5 m with continuously flowing, natural, sand-filtered seawater. The tanks were located in a light-controlled room with a daily light cycle of 12 h light to 12 h dark and daytime light levels of $3 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. The substrate in all tanks was composed of 1 cm of sand. Complex habitat treatments were the same as those applied in the habitat choice experiment, except a greater amount of structure was used (i.e. 28 versus 22 pieces) because the tanks were larger. Pairs of cod were used in the experiment because fish predators are known to behave more naturally with social facilitation (Ryer et al. 2004, Stoner & Ottmar 2004). Pairs of cod were transferred to the tanks 2 wk prior to the first trials so that they could acclimate to their new surroundings in the tanks. At the end of Week 2, the pairs were presented with 10 Age 0 red king crabs (5 to 7.5 mm CL) on sand habitat in one preliminary trial for 24 h to ensure that the fish were motivated to forage on red king crabs in the experimental system. Before the beginning of the next preliminary trial, fish pairs were fed to satiation on krill *Euphausia pacifica* and then deprived of food for 48 h. Preliminary trials for 3 h followed. Fish were determined to be ready for experimental trials after two 3 h preliminary trials were completed during which the fish had consumed at least half of the crabs on sand habitat during the trial. Fish pairs were fed to satiation on frozen krill following the last preliminary trial and then deprived of food for 48 h prior to the first experimental trial to ensure that they were active and uniformly motivated to forage during the experiment.

Experimental trials were conducted using methods used by Stoner (2009) with some modification. For each of the 5 habitat treatments, 6 replicates were conducted. Fish pairs were introduced to each habitat treatment once. Fish were allowed to acclimate to the habitat treatment in the experimental tank for at least 12 h prior to the introduction of crabs. A total of 20 Age 0 crabs were then introduced to each tank in darkness ($1 \times 10^{-8} \mu\text{mol photons m}^{-2} \text{s}^{-1}$) and allowed to acclimate for 30 min before the lights were raised

by rheostat to daytime light levels. Fish pairs were then allowed to forage on crabs for 3 h. The tanks were monitored with overhead video cameras to record cod behavior during the trials. Surviving crabs were enumerated at the end of each trial, and their habitat associations were recorded. Habitat structure was sorted by hand to detect crabs that had attached themselves out of sight. Following each experimental trial, fish pairs remained in the tanks and were fed to satiation on krill and then deprived of food for 48 h before being used in the next trial. Experimental tanks were cleaned by removing all complex treatment structures and then by siphoning any remaining debris and waste from the sand substrate. Subsequent habitat treatments were arranged in the tanks 15 to 20 h prior to the start of the next trial. The habitat treatments were presented randomly to each fish pair so that the order in which each pair experienced the habitat treatments was unique and non-sequential. When a pair had completed all habitat treatments once, the pair was retired. A total of 6 fish pairs was tested. The number of crabs consumed by cod was compared among habitat treatments using a randomized block ANOVA ($\alpha = 0.05$) in which habitat treatment ($n = 5$) was a fixed factor and fish pair ($n = 6$) was a random blocking factor. Treatment-specific differences in relative predation rates by cod among habitats were identified using Tukey's post-comparison tests.

Video recordings of the predation trials were reviewed for metrics of fish behavior that included fish attacks, browsing, and general activity, similar to the criteria of Stoner (2009). We analyzed the video from a selection of 15 trials that was composed of 3 randomly selected trials from each habitat treatment. We defined an attack as a fish biting a piece of substrate containing a prey target or striking at a target on open sand. When cod searched through the habitat structure, we referred to this behavior as browsing, defined as committed investigation of a single target. Because a successful attack (i.e. kill) could not always be positively identified from video, we scored all attacks and browsing events for the entire 3 h duration of a trial. The ratio of fish attacks to consumption rate (consumed attack⁻¹) was calculated for each scored trial as the proportion of known crabs consumed based on the count of crabs at the beginning of the trial minus the count at the end of each trial divided by the total attacks observed from video. A fish activity index was calculated for each selected trial by reviewing the first 5 min of each 15 min video segment to visually determine the number of instances during which an individual fish crossed from

one equal, ordinal quadrant of the circular tank to another. The ratio of fish attacks to consumption rate, total attacks, total browsing events, and activity index were separately compared among habitat types with single-factor ANOVA ($\alpha = 0.05$). Differences among habitat treatments were identified using Tukey's post-comparison tests.

Field predation experiment

We tested the effect of habitat structure on the survival of early juvenile red king crab in nearshore field

habitats from September to November 2009. Preliminary SCUBA surveys at our field site, Yankee Cove, near Juneau, Alaska (58° 35.4' N, 134° 54.4' W, North American Datum of 1983), in July to August 2008 and August to October 2009 identified diverse macrofaunal communities including juvenile red king crab and potential fish and invertebrate predators (Table 1). We used 2 stages of early juvenile red king crab to test the effect of crab size and age on predation rates, crab behavior, and predator-prey interactions. Wild Age 0 red king crab were captured from the Juneau area during June and July 2009 using larval settlement collectors (Blau & Byersdorfer 1994, Pirtle 2010)

Table 1. Behavioral interactions of potential predators of small red king crab *Paralithodes camtschaticus* at the field experiment site, including taxa that were observed in dive surveys at the site (Present), appeared in the camera field of view (Appear), interacted with the tethered crabs (a) or habitat (b) (Approach), attacked a crab (Attack), or successfully consumed a tethered crab (Consume). Crab stages (Age 0 or Age 1) are indicated for attacks and consumption, as well as time from crab deployment in the habitat treatment until successful consumption (duration, h:min)

Taxa common and scientific names	Behavioral interactions				
	Present	Appear	Approach (a, b)	Attack (stage)	Consume (stage, duration)
Pacific cod <i>Gadus macrocephalus</i>	X	X	X (a, b)	-	-
Walleye pollock <i>Theragra chalcogramma</i>	X	-	-	-	-
Kelp greenling <i>Hexagrammos decagrammus</i>	X	X	-	-	-
Whitespotted greenling <i>Hexagrammos stelleri</i>	X	X	X (a, b)	X (0, 1)	-
Copper rockfish <i>Sebastes caurinus</i>	X	-	-	-	-
Dark dusky rockfish <i>Sebastes ciliatus</i>	X	X	-	-	-
Quillback rockfish <i>Sebastes maliger</i>	X	-	-	-	-
Buffalo sculpin <i>Enophrys bison</i>	X	X	-	-	X (0, 2:36)
Great sculpin <i>Myoxocephalus polyacanthocephalus</i>	X	-	-	-	-
Crested sculpin <i>Blepsias bilobus</i>	X	X (b)	-	-	-
Silverspotted sculpin <i>Blepsias cirrhosus</i>	X	-	-	-	-
Red Irish lord <i>Hemilepidotus hemilepidotus</i>	X	-	-	-	-
Undefined sculpins <i>Artedius</i> , <i>Clinocottus</i> , or <i>Oligocottus</i> spp.	X	X	X (a, b)	X (0, 1)	X (0, 0:2)
Sturgeon poacher <i>Agonus acipenserinus</i>	X	-	-	-	-
Arctic shanny <i>Sticheus punctatus</i>	X	X	X (a, b)	-	-
Northern ronquils <i>Ronquilus jordani</i>	X	X	X (a, b)	X (0, 1)	-
Alaskan ronquil <i>Bathymaster caeruleofasciatus</i>	X	X	X (a, b)	X (0)	X (0, 7:21)
Starry flounder <i>Platichthys stellatus</i>	X	X	X (b)	-	-
English sole <i>Pleuronectes vitulus</i>	X	-	-	-	-
Yellowfin sole <i>Limada aspera</i>	X	-	-	-	-
Crescent gunnel <i>Pholis leata</i>	X	X	X (b)	-	-
Undefined moonsnails <i>Euspira</i> spp.	X	X	X (b)	-	-
Giant Pacific octopus <i>Enteroctopus dofleini</i>	X	-	-	-	-
Red king crab <i>Paralithodes camtschaticus</i>	X	-	-	-	-
Dungeness crab <i>Cancer magister</i>	X	X	X (b)	-	-
Helmet crab <i>Telmessus cheiragonus</i>	X	-	-	-	-
Pacific lyre crab <i>Hyas lyratus</i>	X	X	X (a, b)	-	-
Undefined hermit crabs <i>Pagurus</i> and <i>Elassochirus</i> spp.	X	X	X (b)	-	-
Undefined shrimps Pandalidae	X	X	X (b)	-	-
Sunflower star <i>Pycnopodia helianthoides</i>	X	X	X (a, b)	X (0, 1)	X (0, 10:49) (1, ^a)
Steller sea lion <i>Eumetopias jubatus</i>	X	X	X	-	-
Harbor seal <i>Phoca vitulina</i>	X	X	-	-	-
Pelagic cormorant <i>Phalacrocorax pelagicus</i>	X	-	-	-	-

^aTime (h:min) from crab deployment until *P. helianthoides* consumption of Age 1 crabs (14:8; 1:3; 12:12; 20:31; 0:16; 18:31)

and reared in the laboratory through at least 2 molt cycles until crabs were 4 to 8 mm CL. Wild Age 1 red king crab were captured using the same collectors in 2008 (Pirtle 2010) and reared from 2008 to 2009, when the crabs were 16 to 28 mm CL.

We tethered individual crabs (*sensu* Heck & Thoman 1981) by gluing nylon monofilament line (0.45 kg breaking strength) to the carapace of a crab using cyanoacrylate glue. Tethered crabs were monitored in the lab for 24 h prior to experimental use to ensure that crabs were active and not likely to molt during the field experiment. In the field, we attached the monofilament to an eyebolt anchored in a concrete slab (30.5 cm diameter \times 5 cm). The monofilament line length was equal to the radius of the slab (15.25 cm) and allowed the crab to move freely on the slab. Preliminary experiments conducted at the Newport laboratory with Age 1 cod and halibut predators showed that fish predators quickly consumed tethered and un-tethered crabs in laboratory tanks on sand and did not show negative effects from consuming tethered prey, such as disinterest, choking, or entanglement. Tethered Age 0 crabs moved freely through dense hydroid structure, occupying a variety of locations during 24 h trials.

Field predation habitat treatments included (1) high structure: hydroids with natural substrate (used throughout the field experiment, consisting of gravel, composed mostly of shale, and gravel-sized pieces of crushed bivalve shells [\sim 2 to 64 mm based on visual assessment, *sensu* Wentworth 1922]); (2) low structure: natural substrate; and (3) a procedural control: natural substrate covered by mesh to eliminate predation during the experiment while still subjecting crabs to handling methods. SCUBA divers deployed 3 experimental stations, 1 with each of the 3 habitat treatments, spaced 5 to 7 m apart in 8 to 12 m water depth and arranged adjacent to a rocky reef with boulders, understory macroalgae, and structural invertebrates (Fig. 1). We used high-resolution digital time-lapse video (704 \times 480 resolution at 7 images s^{-1}) with a ring of 15 LED lights (white, individual maximum intensity 2600 mcd) (Well-Vu Nature Vision, Manual Wind Color System) to record crab behavior and predator–prey interactions. Video cameras were supported by underwater cables

that ran to shore and connected to a 12 V battery bank and digital video recorder. Cameras were mounted on sand anchors 60 cm above each station for a full view of the test habitat and tethered crab. The lights were adjusted to the minimum illumination required to view the apparatus clearly during hours of darkness, which was 25% of full illumination on the rheostat (Fig. 1). Divers established the habitat treatments and crabs (1 crab per treatment) at the underwater camera stations during daylight hours, between 10:00 and 13:30 h Alaska Standard Time. Divers noted crab survival in the field after 24 h and exchanged the habitat treatments and surviving crabs for new habitat treatments and crabs. The 3 habitat treatments were replicated 5 times for both Age 0 and Age 1 crabs, which was the sample size that could be accomplished before the weather in late autumn became too inclement to continue the experiment. The location of each treatment was chosen randomly among the 3 stations for the 30 trials, with Age 0 and Age 1 crabs alternating every other day. Due to low sample size, the results are presented graphically, and a significance test to compare crab survival among treatments was not performed.

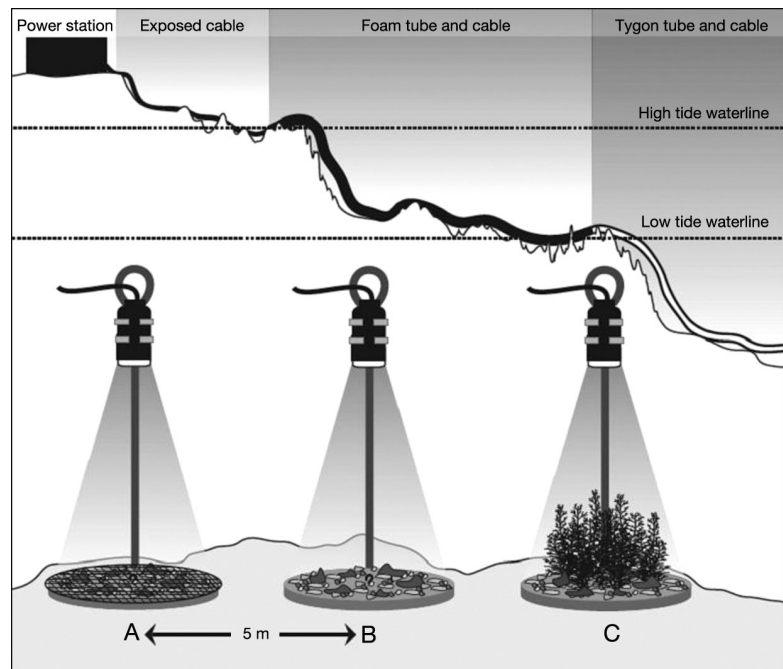


Fig. 1. Field experiment setup, illustrating the camera cable path from the shore-based power station through the intertidal zone to 3 subtidal camera stations, spaced 5 to 7 m apart at ca. 8 to 12 m depth and located at the base of a rocky reef with boulders and macroalgae. Cameras are mounted on sand anchors above concrete slabs with the location of the following habitat treatments presented at random in each trial: (A) low structure, mesh-covered procedural control; (B) low structure habitat with crushed shells and gravel; and (C) high structure habitat with hydroids

Field videos were reviewed to assess crab behavior and predator–prey interactions. For each crab mortality, the predator species and the total time from crab deployment to mortal attack were identified from video. Any animals that attacked the crab unsuccessfully, approached and interacted with the crab or habitat treatment, or passed through the camera field of view were identified. Crab behavior was quantified as the proportion of time spent during the experiment engaged in the following activities, from the time of deployment until mortal attack or recovery: (1) resting motionless (motionless); (2) sorting through the substrate with chelae (sorting); (3) moving laterally through the habitat (moving); and (4) climbing the habitat structure (climbing). The proportion of each of the following response behaviors was quantified from the total count of attack and approach events during a predation trial: (1) fleeing from a predator (flee); (2) fighting a predator with chelae (fight); (3) stopping activity upon interacting with a predator (stop); and (4) no observed response (none). Crab response behavior was quantified separately for predator attacks and direct interactions by potential predators (i.e. approach). Crab behaviors were analyzed individually due to non-independence of the observations over time. For the activity analysis, the arcsine-square-root-transformed proportion of the total time a crab was engaged in a single behavior during a trial was compared among habitat type and crab age class using 2-factor ANOVA ($\alpha = 0.05$). For the response analysis, the arcsine-transformed proportion of the events of a single behavioral response for each trial was compared among habitat type and age class using a 2-factor general linear model ($\alpha = 0.05$) due to unbalanced sample size.

The sunflower star *Pycnopodia helianthoides* was a predator of early juvenile red king crab in the field predation experiment. Seastar predation may or may not have been an artifact of tethering. To test whether or not Age 1 crabs could escape sunflower star predation in the absence of tethering, we placed 2 untethered Age 1 crabs in a laboratory tank with 2 seastars monitored by overhead video for 24 h and replicated this experiment 3 times with different crabs used in each trial.

RESULTS

Habitat choice

Early juvenile *Paralithodes camtschaticus* preferred to associate with biogenic habitats of hydroids and

macroalgae significantly more than structural mimics, and crabs preferred all structural habitats more than sand when fish predators were absent ($F_{4,29} = 84.58$, $p < 0.0001$, Fig. 2a). Crabs not associated with habitat structures were on open sand spaces or near the wall of the tank. Crabs associated more frequently with structure than sand in the biogenic habitat treatments, including (mean \pm SD) 93% \pm 7% of the time in habitat composed solely of hydroids and 83% \pm 8% of the time in hydroid and macroalgal habitat. Crabs associated less often with structural mimics of these species, including 45% \pm 16% of the time with hydroid mimics and 34% \pm 15% with hydroid and macroalgal mimics. Two crabs molted during the experiment. One crab was observed on top of hydroid structure with its exuvium at the end of the 3 h trial. The other crab molted while unsheltered on sand habitat and was consumed by other crabs.

Laboratory predation

Survival of Age 0 red king crab, when exposed to Age 1 cod predation, was greatest in structural habitat treatments. Cod consumed significantly more crabs in the sand habitat treatment (mean \pm SD: 10.5 \pm 3.3 crabs out of 20) than in all habitats with complex structure combined (5.8 \pm 2.2 crabs out of 20) ($F_{4,29} = 13.82$, $p < 0.0001$ (Table 2, Fig. 2b). A significant effect of fish pair resulted from 2 trials, wherein 1 pair consumed fewer crabs than others in the hydroid habitat (Trial 2) and 1 pair consumed fewer crabs than others in the hydroid and macroalgal habitat (Trial 4) ($F_{5,29} = 11.28$, $p < 0.0001$). These trials were excluded from the video analysis of predator foraging behavior because the fish were relatively inactive and unmotivated to forage on crabs compared to fish in all other trials. Upon recovery at the end of a trial, all surviving crabs were found associated with structural habitat or habitat mimics. These survivors were recovered from under the habitat structure or clinging to the structure with flattened bodies and limbs drawn inwards, a behavior different from an aggressive or defensive posture, with spiny walking legs extended and raised chelae. Cannibalism by crabs was not observed during the fish predation experiment. Crabs surviving predation in sand habitats were often recovered near the walls of the tank.

Video observation indicated that cod often made several attacks on red king crab prey before successful consumption and consumed significantly more crabs per attack on sand habitat (mean \pm SD: 0.66 \pm 0.1, i.e. a single attack resulted in consumption 66%

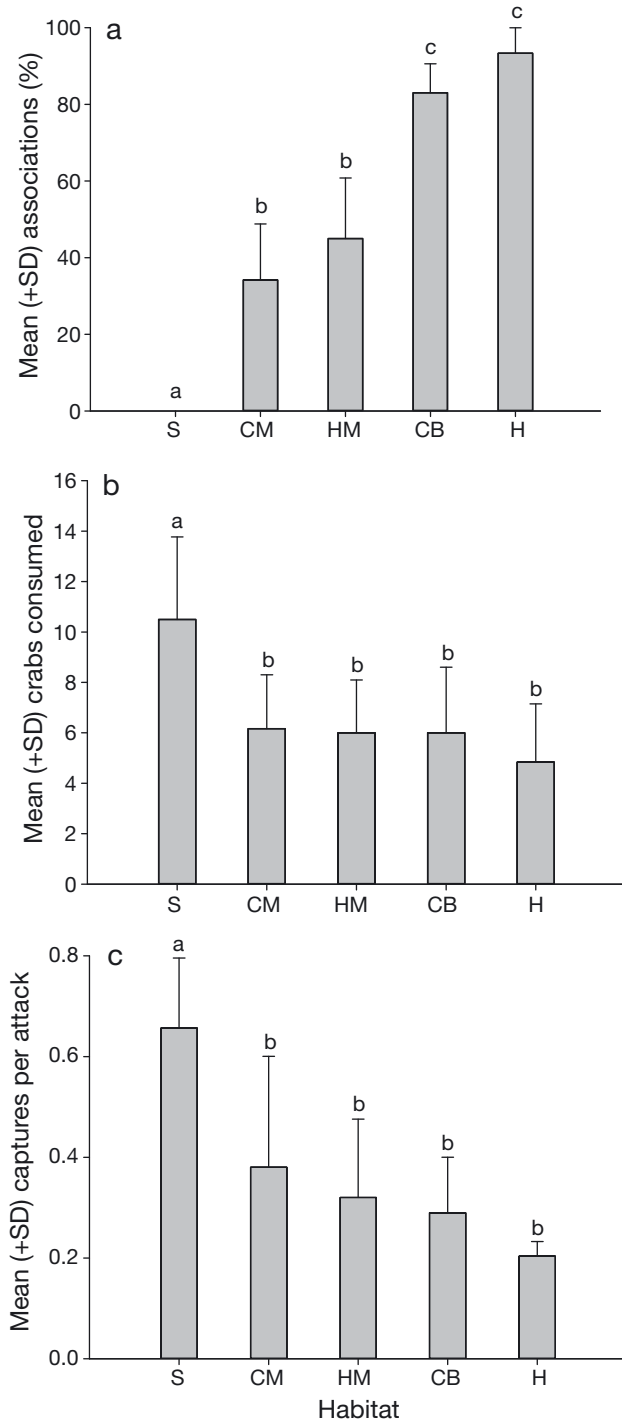


Fig. 2. *Paralithodes camtschaticus*. Results of laboratory trials. (a) Percentage of Age 0 red king crab that were associated with habitat treatments when no fish predator was present; (b) number of Age 0 crabs ($n = 20$ available per treatment) consumed by Pacific cod *Gadus macrocephalus*; and (c) proportion of Age 0 red king crab consumed per attack by Pacific cod. Habitats — (S) sand; (CM) complex biogenic mimics; (HM) hydroid mimics; (CB) live complex biogenic habitat of algae and hydroids; and (H) hydroids. Shared letters indicate groups with similar means (Tukey's HSD)

Table 2. Results of ANOVA with randomized block design for the cod laboratory predation experiment with Age 0 red king crabs. Habitat treatment was a fixed effect, and fish pair was the random blocking factor

Source	df	SS	MS	F	p
Habitat	4	115.13	28.78	13.82	<0.0001
Block	5	117.50	23.50	11.28	<0.0001
Error	20	41.67	2.08		
Total	29	274.30			

of the time) than in all complex structural habitat treatments combined (0.30 ± 0.1) ($F_{4,14} = 3.94$, $p = 0.04$) (Fig. 2c). Total numbers of attacks (22.9 ± 7.7) ($F_{4,14} = 1.31$, $p = 0.30$) and browsing events (43.8 ± 22.8) ($F_{3,11} = 0.99$, $p = 0.45$) were not significantly different among habitat treatments (Fig. 3a). Cod pairs made 8 to 35 attacks and conducted 17 to 91 browses in structural habitats (Fig. 3a). The first attack occurred within the first 5 min after raising the lights within a variety of habitat types in 10 out of the 15 trials reviewed. The first attacks observed in 4 of the remaining trials occurred within the first 30 min, and the first attack in a single trial with hydroid and algae mimics did not occur until after 78 min. Cod activity was not significantly different among habitat treatments ($F_{4,14} = 1.71$, $p = 0.22$) (Fig. 3b). Cod spent most of the trial duration browsing through the habitat structure or investigating crab targets on sand.

Field predation

Survival of tethered early juvenile red king crab exposed to predators in the field was greater in the presence of highly structured habitat than in low structure habitat (Fig. 4). All Age 0 crabs ($n = 5$) survived the high structure habitat treatment, and 20% (1 of 5 crabs) survived the low structure habitat. A total of 60% of Age 1 crabs (3 of 5 crabs) survived the high structure habitat treatment, and none survived in low structure habitat. Although a significance test to compare crab survival among treatments was not performed, the difference among treatments was clear and compelling with the caveat that a small number of crabs were used. All crabs were recovered from the mesh-covered procedural control.

Predators that consumed Age 0 crabs were small sculpin (Cottidae) (Genus *Artemius*, *Clinocottus*, or *Oligocottus*), Alaska ronquil *Bathymaster caeruleofasciatus*, and sunflower star (Table 1). The ronquil and sunflower star attacked during evening hours.

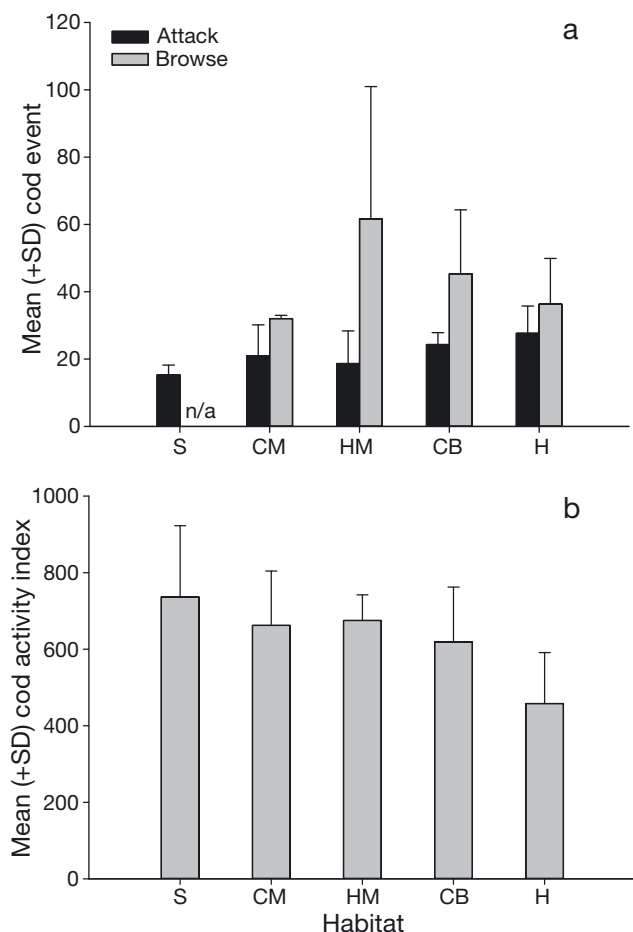


Fig. 3. (a) Number of attacks and browsing events and (b) activity index of Pacific cod in laboratory predation trials with Age 0 red king crab. Habitat abbreviations as in Fig. 2

One predator could not be determined because the video was corrupt. Time from crab deployment to consumption varied from 2 min to 10 h 49 min among crabs in the low structure treatment (Table 1). The attack leading to consumption by the small sculpin (length ~8 cm) occurred within 2 min of deployment. The small sculpin remained tethered following difficulty breaking the monofilament and was consumed by a larger buffalo sculpin *Enophrys bison* (length ~30 cm) after 2 h 36 min (Table 1). Only 1 Age 0 crab survived in the low structure treatment. The crab had burrowed under a larger piece of shale gravel where it intermittently remained for 19 h 2 min of the 24 h trial.

All predation observed on Age 1 crabs was by the sunflower star, with 4 out of 6 mortal seastar attacks occurring during the evening or early morning hours of darkness (Table 1). Seastars consumed 4 crabs in the low structure habitat and 2 crabs in the high structure habitat. One predator in low structure habi-

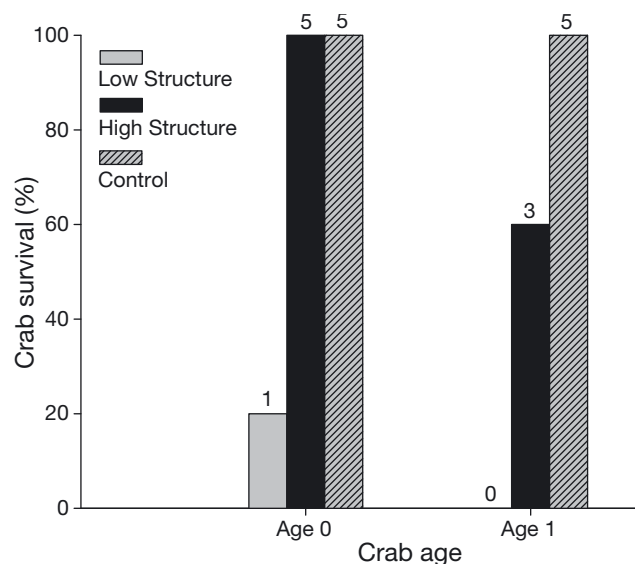


Fig. 4. *Paralithodes camtschaticus*. Percent survival of tethered red king crab (Age 0 and Age 1) in the field predation study. Habitat treatments included low structure, high structure, and a control. Numbers above bars indicate the number of crabs surviving in that habitat

tat was not identified because the video was corrupt. Predation by seastars in the field is likely an artifact of tethering. All Age 1 crabs killed by seastars attempted to flee or fight but were restrained by the tether. In laboratory tethering-artifact trials that followed the field predation experiment, un-tethered crabs fled from approaching seastars and easily escaped physical contact, and none of the crabs were consumed.

A variety of taxa passed through the camera's field of view, approached the experimental apparatus to interact with the habitat treatment or the crab, and attacked crabs unsuccessfully (Table 1). Juvenile cod, similar in size to those used in the laboratory fish predator experiment, were frequently observed near the experimental apparatus every evening, feeding on pelagic zooplankton. These zooplankton were attracted to the camera lights during hours of darkness generally from 16:00 to 08:00 h, with peak cod activity from midnight until 02:00 h. Typically, these cod did not respond to the tethered crabs. Cod interacted with crabs on only 7 occasions, although they did browse the habitat structure on 91 total occasions during the evening (mean browses in each trial \pm SD: 11.4 ± 12.4) out of hundreds of sightings near the camera lights.

Crab activity during field predation trials varied by habitat and age, with a significant interaction among these factors when crabs were moving ($F_{1,7} = 14.41$, $p < 0.05$) and sorting through the substrate ($F_{1,7} =$

10.98, $p < 0.05$). Age 1 crabs were most often moving in low structure habitat (mean percent time \pm SD: $69 \pm 13\%$) and were often motionless ($62 \pm 41\%$) in high structure habitat, resting under the hydroids. In contrast, Age 0 crabs were most often motionless in low structure habitat ($85 \pm <0.1\%$) with bursts of movement for short duration (Fig. 5). Although crabs were often motionless, habitat and age were not significant factors describing variation in this activity ($F_{1,7} = 6.47$, $p = 0.06$). Sorting was observed in low structure habitat more often with Age 0 crabs ($7 \pm 2\%$) than with Age 1 crabs ($1 \pm 1\%$) (Fig. 5). Although age was not a significant factor for the activity climbing ($F_{1,7} = 1.27$, $p = 0.30$), Age 0 crabs were often climbing in high structure habitat ($66 \pm 15\%$), foraging on hydroids (Fig. 5).

Crabs demonstrated a variety of response behaviors when attacked by a predator among 45 events.

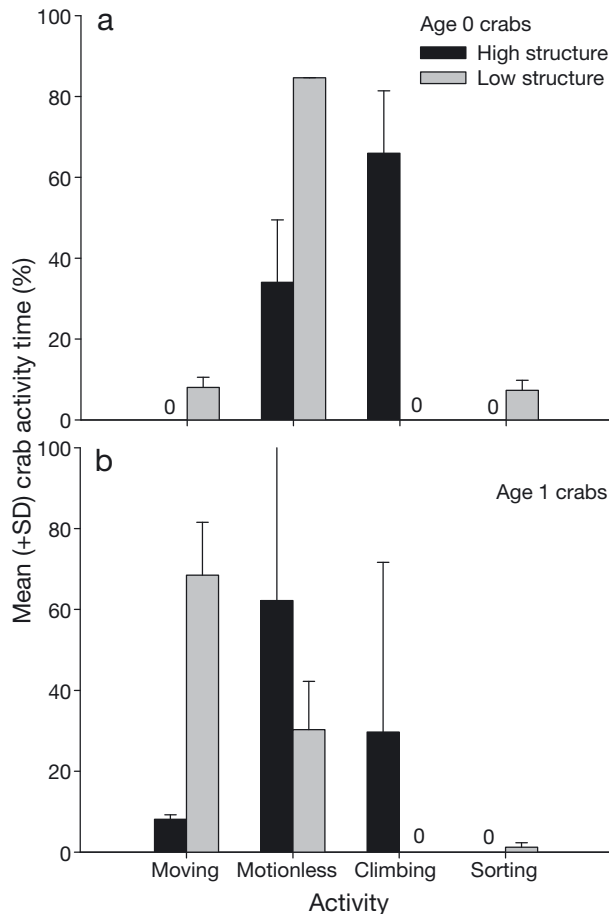


Fig. 5. *Paralithodes camtschaticus*. Mean (+SD) crab activity patterns for (a) Age 0 and (b) Age 1 crabs in the field predation study by habitat type (high or low structure), expressed as the percentage of time spent in each activity over the duration of a trial (maximum 24 h), including moving, remaining motionless, climbing, and sorting through the gravel and shell substrate

Crab response to a predator attack varied by age when the response was to fight ($F_{1,13} = 5.27$, $p < 0.05$) or flee ($F_{1,13} = 6.0$, $p < 0.05$). When Age 1 crabs were attacked in either habitat, they most often responded by fighting a predator directly (mean percent response \pm SD: high structure $54 \pm 12\%$, low structure $43 \pm 51\%$) or by attempting to flee (high structure $36 \pm 13\%$, low structure $40 \pm 43\%$). In contrast, Age 0 crabs only occasionally attempted to flee or fight when attacked (Fig. 6). Age 0 crabs most often had no observed response when attacked in either habitat (high structure $50 \pm 71\%$, low structure $56 \pm 51\%$). Age 0 crabs would also stop activity and remain motionless in habitats of high structure ($50 \pm 71\%$) and low structure ($19 \pm 38\%$) (Fig. 6). Habitat structure and crab age were not significant factors describing variation in crab response to an attack when crabs did not respond or stopped their activity ($p > 0.05$).

Habitat structure and crab age were not significant factors in crab response behavior when approached by a potential predator ($p > 0.05$). Crabs of both age classes most often did not respond in either habitat among 58 events (Fig. 6). Crabs also engaged in other response behaviors. Age 0 crabs would stop their current activity and remain motionless in response to an approach in either habitat ($13 \pm 17\%$). Age 0 crabs would also flee from a predator (high structure $8 \pm 12\%$, low structure $13 \pm 17\%$) but did not respond by fighting (Fig. 6). Age 1 crabs would flee from an interaction in either habitat (high structure $16 \pm 19\%$, low structure $11 \pm 19\%$) and would fight in habitat with low structure ($3 \pm 5\%$) but did not stop their activity and remain motionless like Age 0 crabs (Fig. 6).

DISCUSSION

Habitat structural complexity and crab survival

The presence of highly structured, complex habitat increased *Paralithodes camtschaticus* survival when very small (<8 mm CL) juvenile crabs were exposed to a variety of predators in laboratory and field experiments, which demonstrates that habitat complexity is likely an integral part of early juvenile red king crab survival. Habitats with complex vertical structure and crevice space, both biogenic and non-biogenic, provided young red king crab adequate cover to facilitate crypsis as a survival strategy. In relatively low-structure gravel-shell habitat in the field experiment, only one Age 0 crab survived, and this crab

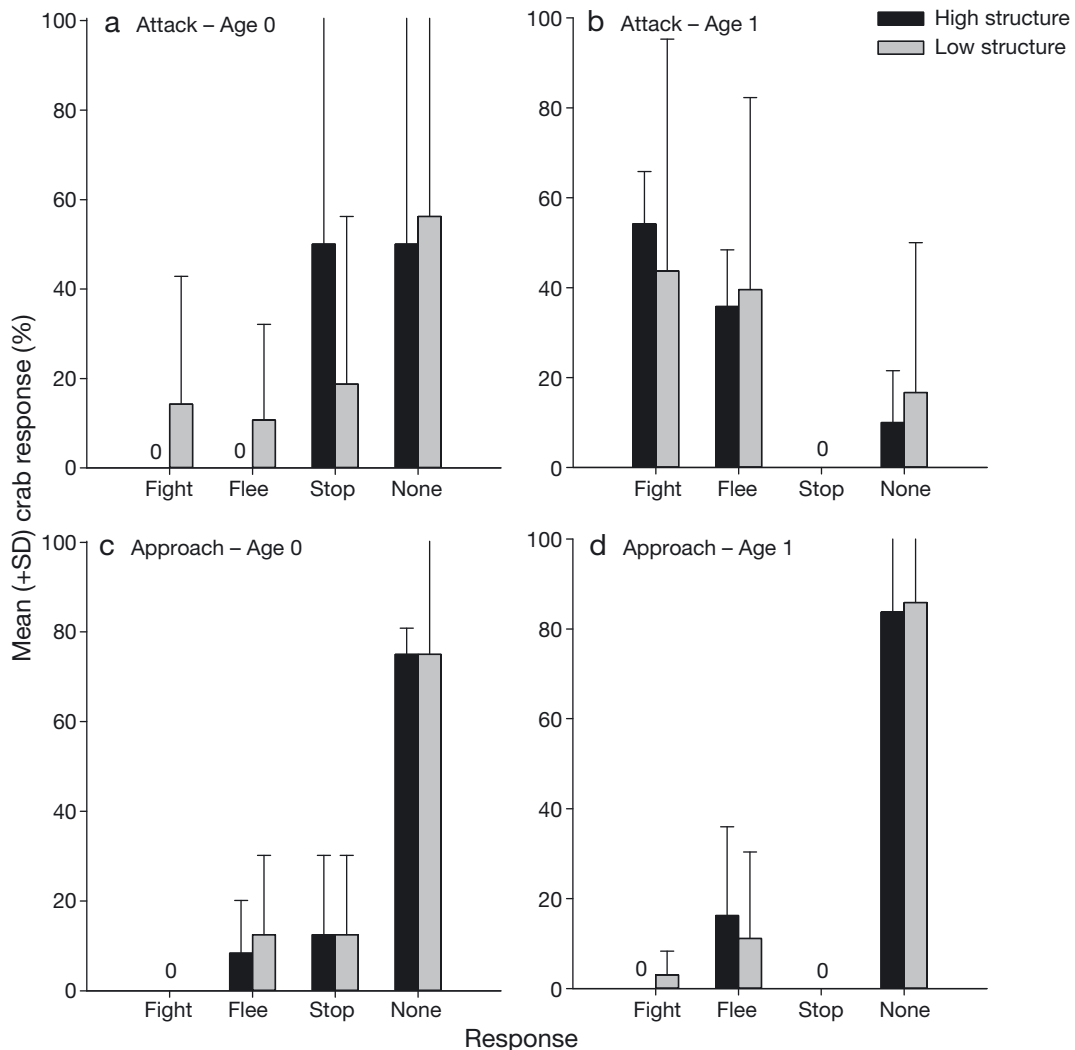


Fig. 6. *Paralithodes camtschaticus*. Mean (+SD) crab response behavior to (a,b) a predator attack or (c,d) an approach with a direct interaction for (a,c) Age 0 and (b,d) Age 1 crabs in the field predation study by habitat type (high or low structure), expressed as the percentage of each response type observed, including fighting, fleeing, stopping activity, and no response

found sufficient crevice space in which to hide. Cryptic behavior likely increases crab survival in complex habitat because detection by predators is reduced by the habitat structure (Lima & Dill 1990), compared to exposed habitats where small crabs are quite vulnerable. The association of early juvenile red king crab with complex habitat was first documented in the field (e.g. Powell & Nickerson 1965, Sundberg & Clausen 1977) and only recently demonstrated by laboratory studies to be the result of active habitat selection (Stevens & Kittaka 1998, Stevens 2003), foraging opportunities (Pirtle & Stoner 2010), and predator avoidance (Stevens & Swiney 2005, Stoner 2009).

Habitat structural complexity increased crab survival by modifying interactions between fish (predator) and red king crab (prey). In laboratory experi-

ments, the foraging efficiency of Age 1 Pacific cod was reduced by habitat structural complexity, as evidenced by repeated attacks on Age 0 red king crab with reduced capture success in complex habitats. Our results for cod were similar to those observed for Age 1 Pacific halibut, wherein prey encounter rate and capture success diminished when foraging on Age 0 red king crab was associated with complex habitats (Stoner 2009). Complex habitat structure has a similar effect on predator-prey interactions in other aquatic systems. For example, the foraging efficiency of smallmouth bass *Micropterus dolomieu* was greatly reduced when juvenile crayfish *Orconectes propinquus* associated with macrophyte habitats (Stein & Magnuson 1976), and a similar pattern was observed for bluegill sunfish *Lepomis macro-*

chirus consuming various prey items in habitats of high macrophyte densities (Crowder & Cooper 1982).

Cod and halibut have different foraging strategies as predators of early juvenile red king crab. Cod in our laboratory experiment actively searched the tank for crabs in open spaces and browsed through structural habitat to locate and attack crabs. In contrast, halibut did not attack crabs associated with structure and instead ambushed crabs in open spaces and at the edge of structures (Stoner 2009). Activity levels were also different between these 2 predators. Cod in our experiment did not alter activity levels between habitats with and without complex structure. However, halibut were less active in habitats with complex structure.

Crab habitat choice and predation risk

Our experiments demonstrated that the habitat choice of early juvenile red king crab reduces predation risk. Crabs were strongly attracted to structurally complex biogenic habitats formed by hydroids and macroalgae when fish predators were absent. This result was not surprising since young red king crab have been observed in biogenic habitats in the field (e.g. Sundberg & Clausen 1977) and prefer those habitats over non-biogenic structure (Stevens 2003) due to foraging opportunities provided by those habitats (Pirtle & Stoner 2010). Prey habitat choice in the absence of predators should maximize foraging (Werner et al. 1983). When threatened, however, prey should respond with behaviors that maximize immediate survival (Stein & Magnuson 1976). Red king crab responded to Age 1 cod predators by associating with any available structure in our laboratory experiment, even if the habitat was not preferred. A similar response was demonstrated for Age 0 red king crab with halibut (Stoner 2009) and larger juvenile conspecifics as predators (Stevens & Swiney 2005, Stoner et al. 2010). Refuge-seeking behavior in response to predation pressure influences the distribution of structure-seeking early life stages of a variety of aquatic animals, including American lobster (Wahle & Steneck 1992) and spiny lobster (Herrnkind & Butler 1986). This behavioral response has implications for the distribution of early juvenile red king crabs among available habitats at nursery locations.

Refuge-seeking behaviors that promote early life stage survival have been associated with trade-offs between predation risk and energetic return or growth. The tendency of early juvenile red king crab to shelter with the closest structural habitat and alter

or reduce activity levels may lead to decreased energy intake when associating with suboptimal food sources under high predation pressure or for long duration. For example, crabs did not leave refuge habitats to forage for 3 to 19 h when associated with non-biogenic structures in the laboratory with cod predators, or when associated with gravel crevice space in the field with a variety of predators. This behavior was different than that of Age 0 crabs that actively foraged when associated with hydroids during the field experiment. Several studies have established that aquatic prey reduce foraging and other activity levels in the presence of predators at the expense of energetic return, including juvenile crayfish (Stein & Magnuson 1976), anuran tadpoles (Werner 1991), salmonids (Dill & Fraser 1984), and sunfish (Werner et al. 1983). Small bluegill sunfish, for example, have lower growth rates under high predation pressure when confined to suboptimal foraging habitats by largemouth bass *Micropterus salmoides* (Werner et al. 1983). Red king crab may have a similar response if confined to refuge habitats where food is not optimal for growth. Delayed growth could ultimately affect time to maturity, with population-level consequences, such as reduced reproductive potential.

Crab activity and refuge response with ontogeny

Crab activity in the present study was dependent on crab size or age and habitat complexity. Our field experiments demonstrated that Age 0 crabs were consistently cryptic, associating with complex structure at any opportunity and often remaining motionless in exposed habitat. By comparison, Age 1 crabs were less active in complex structure provided by hydroids, until provoked into an attack or flight response, and very active in exposed habitat, often moving around at the farthest reach of the tether, perhaps attempting to seek habitats with greater cover. Lima & Dill (1990) proposed that prey activity should depend on the perceived security of an animal against its background when predators are nearby, such that more conspicuous animals may increase spontaneous activity levels in an attempt to seek refuge in other surroundings. Our results suggest that the Age 1 crabs were more conspicuous than the smaller, cryptic Age 0 crabs and, as a result, have different behaviors.

An unsuccessful flight response by red king crab to seastar attack during the field predation experiment was likely an artifact of tethering. We expect that

crabs would successfully flee when threatened, as evidenced by the ability of untethered Age 1 crabs to avoid seastar predators in the lab. Although this tethering artifact was examined with only 1 species of predator, we speculate whether or not early juvenile stage crabs can successfully flee from other predators in the field with different foraging strategies. It would be insightful to investigate predator avoidance behavior of untethered early juvenile stage red king crab with other predators.

Behavioral differences in activity and refuge response suggest that size drives ontogenetic shifts for juvenile red king crab. We hypothesize 2 potential drivers of ontogenetic shifts, including breakdown of crypsis as a refuge strategy and energetic demands for growth. Red king crab associate less frequently with highly structured habitats as crabs reach larger sizes (Pirtle & Stoner 2010). Our Age 1 crabs were 16 to 28 mm CL, within the range of the approximate size when cryptic behavior may end and social behavior begins, around 25 mm CL or Age 2 (Powell & Nickerson 1965, Dew 1990). If the adaptive significance of aggregation for red king crab is increased vigilance or safety in numbers (reviewed by Lima & Dill 1990), the social podding behavior observed with older juveniles may be necessary when crypsis becomes less dependable as crabs outgrow refuge habitats. It is further possible that cryptic behaviors are no longer needed when red king crab outgrow their most vulnerable sizes, as has been shown for lobsters (Wahle & Steneck 1992) and crayfish (Stein & Magnuson 1976). However, aggregation of many individual crabs may also benefit efficient foraging by larger juveniles that likely require different food sources due to energetic demands for growth. In the case of foraging, aggregation would increase encounter rates with resources for individuals (reviewed by Werner 1992). Associating with structurally complex biogenic habitats as refuge confers an additional survival advantage to small red king crab due to foraging opportunities provided by those habitats (Pirtle & Stoner 2010). We suggest this advantage may be lost for larger individuals, perhaps as early as Age 1.

Predators of early juvenile red king crab

Our laboratory and field experiments suggest that Pacific cod may not be major predators of early juvenile red king crab. Cod were willing to consume crabs. However, cod in 2 trials in complex habitat were less motivated predators and consumed signifi-

cantly less crabs than all other trials, and cod consumed on average only half of the available unsheltered crabs in sand habitat. This behavior is in contrast to halibut that consumed all available, unsheltered crabs in shorter trials (Stoner 2009). Cod may be deterred from consuming red king crab by the crabs' spiny body armor, which may have contributed to the tentative predation behavior observed during the laboratory experiment. For example, a cod predator would bite a crab and drop it, or attack a crab and reject it repeatedly before consuming the crab or moving on. Although juvenile and smaller adult cod inhabit shallow inshore locations (Dean et al. 2000, Laurel et al. 2007) in habitats where they co-occur with juvenile red king crab (Loher & Armstrong 2000, Pirtle 2010), including our field experiment site, we observed no cod predation on tethered crabs during the field experiment.

The positive response by cod to the camera lights and relative disinterest in tethered red king crab during the field experiment may have been an experimental artifact due to the lights attracting pelagic zooplankton as an easy to obtain food source. We did not control for the effect of artificial light used in the field experiment on crab survival and predator/crab behavior. However, a subsequent study at our field location found no difference in crab survival in low structure habitat with and without artificial lights and cameras (Daly 2012). It remains unresolved whether or not cod were interested in red king crab as prey when the cameras and light source were not present.

Potential fish predators of early juvenile stage red king crab include sculpins, certain flatfishes, and other demersal fishes. Sculpins and Alaskan ronquil consumed Age 0 crabs in our field experiment and were apparently not deterred by red king crab spiny body armor. These fishes inhabit inshore locations where they co-occur with early juvenile red king crab (Dean et al. 2000, Loher & Armstrong 2000, Pirtle 2010). Halibut are efficient predators of early juvenile stage red king crab (Stoner 2009) but were not observed at our field predation site; however, halibut nursery grounds (Norcross & Mueter 1999, Stoner & Titgen 2003) potentially overlap with red king crab nursery locations (Pirtle 2010).

Red king crabs were not a major diet component for any predator fish species based on groundfish diet analysis from fishery resource surveys conducted in the Gulf of Alaska and Bering Sea. In those studies, softshell adult red king crab were found sporadically in the stomach contents of Pacific cod (Jewett 1978, Livingston 1989, Livingston et al. 1993,

Livingston & deReynier 1996, Lang et al. 2005) and Pacific halibut (Gray 1964, Livingston & deReynier 1996, Lang et al. 2005), but juvenile stage crabs were not. However, yellowfin sole *Pleuronectes asper* (Haflinger & McRoy 1983, Livingston et al. 1993) and walleye pollock *Theragra chalcogramma* (Livingston et al. 1993, Livingston & deReynier 1996, Lang et al. 2005) consumed settlement stage larvae and early juvenile stage crabs. Sculpins (Cottidae), which are not commercially targeted but commonly caught as bycatch, also consumed early juvenile stage crabs (Jewett & Powell 1979).

We do not fully understand the effect of predation on red king crab early juvenile stages and the recovery of depleted red king crab stocks. Further study is needed to improve understanding of the role of predation and complex habitat availability in red king crab early life stage success. We acknowledge that both the present field and lab experiments are unnatural and not intended to simulate natural events. For example, to acclimatize fish and minimize handling, fish were maintained in experimental tanks to which crabs were added. In the field in a natural setting, fish might be expected to encounter crabs while moving, and thus the field experiment is closer to a natural predator–prey encounter despite the tethering. The predation rates observed here are likely inflated, but ultimately, the main point remains the same: habitats with greater complexity are better for crab survival, and crabs ‘know’ that from a mechanistic sense, as evidenced by the fact that they seek shelter even when fish are absent. Our field study was the first to investigate early juvenile red king crab behavior, survival, and predators at a nursery location using video to record *in situ* observations. Although considerable new insight about red king crab early life stages has been gained from the present field study, this insight may be expanded with a similar or improved approach that can accomplish greater replication. Further studies may also include diet analysis of potential predators of early juvenile stage crabs in nursery locations and investigation of the extent to which cannibalism occurs, using integrated laboratory and field studies.

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