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Habitat-mediated survival of newly settled red king crab in the presence of a predatory fish: Role of habitat complexity and heterogeneity

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ABSTRACT

Red king crab (RKC) (*Paralithodes camtschaticus*) are generally associated with structurally complex habitats during the first 2 years of benthic life. In this first experimental laboratory study with a fish predator, survival of newly settled juvenile RKC was tested in eight different habitat treatments with varying amounts and types of physical structure, open sand, gravel bottom, and habitat islands. Video observations provided insights on habitat-mediated interactions between Pacific halibut predators (*Hippoglossus stenolepis*) and crab prey. Survival of RKC increased with amount of physical structure and was highest in the most heterogeneous habitat and in habitats characterized by high density patches. Predator activity decreased with increasing amount of structure, and attacks on RKC were correlated with predator activity. Low survival in open sand habitat was associated with both high attack rate and high capture success (captures per attack). Lower levels of capture success did not vary among the habitats containing algae and other complex physical structures, but attack rates declined with increasing amount of structure, and encounter rate (i.e., prey detection and attack) was the primary determinant of mortality. RKC were capable of detecting predators and adjusted their behavior to avoid predation by sheltering in dense microhabitat patches. Successful stock enhancement for greatly reduced populations of RKC in the Gulf of Alaska will depend upon placing seed stock in habitats with abundant protective habitat, and high quality microhabitats may serve as well as continuous cover.

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1. Introduction

Predator–prey relationships are a crucial part of recruitment processes in the field. Survival of early-stage juveniles often determines both the year-class strength (Sissenwine, 1984; Walters and Juanes, 1993) and distribution (Gibson, 1994; Stoner, 2003a) of demersal invertebrates and fishes. Understanding predation processes is also crucial in stock enhancement programs to maximize survival of hatchery-reared seed stock. This requires using the best possible release strategies including site selection, timing, and the size and conditioning of the seed stock (Leber et al., 2004; Bell et al., 2005; Hines et al., 2008).

Valuable insights into spatial and temporal variation in predation intensity can be gained through various forms of experimentation in the field and laboratory. Tag and recovery experiments (Davis et al., 2005; Zohar et al., 2008), and tethering (Herrnkind and Butler, 1986; Heck and Wilson, 1987; Ray et al., 1994; Hines and Ruiz, 1995) have been useful field methods in both ecological studies and stock enhancement projects with invertebrates. A complementary laboratory approach can be used to control for environmental variables that affect predation rates in the field including different kinds of predators, structures, and habitat configurations (e.g., Stoner, 1982; Dittel et al., 1996; Macia et al., 2003). A laboratory approach was used in this study.

The red king crab (RKC) (*Paralithodes camtschaticus*) is a large anomuran crab that has enormous economic significance as a fishery resource in Alaska. However, populations have declined dramatically since the 1980s (Dew and McConnaughey, 2005; Stevens, 2006a), and a major effort is now underway to perfect culture of juveniles toward the goal of stock rehabilitation (Stevens, 2006b). A significant challenge for those attempting to rehabilitate invertebrate populations in the field is to reduce losses to predators (Bell et al., 2005; Hines et al., 2008). Natural mortalities on small motile invertebrates tend to be high even under the best of circumstances (Stoner and Glazer, 1998), and site selection for releases of hatchery-reared juveniles is critical (Stoner, 1994). Consequently, a clear understanding of habitat requirements and how habitats mediate the predation process will help to reduce mortality.

Newly settled juvenile RKC are distinctive with their heavy covering of spines and red color, but they are small at settlement (<2 mm carapace length) and highly cryptic; therefore, little is known about their ecology. Early benthic stage RKC are often associated with sessile invertebrates and macroalgae (Sundberg and Clausen, 1977; Dew, 1990; Loher and Armstrong, 2000). Recent laboratory experiments show that young RKC have a particularly high affinity for structurally complex habitats such as bryozoa, hydroids,

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and highly branched macroalgae (Stevens and Kittaka, 1998; Stevens, 2003), and that the presence of food mediates the response (Pirtle and Stoner, in review). Much less is known about predator–prey interactions, although cannibalism is a significant problem in the culture of RKC (Borisov et al., 2007), and Stevens and Swiney (2005) provided the first experimental investigation showing that the presence of shelter can protect glaucothoe and newly metamorphosed stages of RKC from predation by larger juveniles. Other probable predators include young fishes that are abundant in the settlement habitats of RKC such as Pacific halibut (*Hippoglossus stenolepis*), northern rock sole (*Lepidopsetta polyxystra*), and Pacific cod (*Gadus macrocephalus*) (Dean et al., 2000; Laurel et al., 2009).

This laboratory study, the first to explore fish predation on RKC, was conducted to evaluate how different forms of shelter affect the survival of early benthic stage crabs in the presence of juvenile Pacific halibut. The form, density, heterogeneity, and distributional characteristics (patchiness) of habitat structure were manipulated in laboratory experiments, and video recordings of the trials were used to determine how the interactions between predator and prey were mediated by the habitat structures.

2. Methods

2.2. Experimental animals

Red king crabs for this study were supplied by the Alutiiq Pride Shellfish Hatchery in Seward Alaska. Briefly, 12 ovigerous female RKC were collected with baited pots from Bristol Bay, Alaska, during November 2007 and maintained at the hatchery on chopped herring and squid until their larvae were released in May 2008. Larvae from each female were mixed and reared in 1200 L cylindrical tanks until the first juvenile instar (C1) was achieved. They were fed daily with *Artemia* nauplii enriched with DC DHA Selco enrichment media.

Stage C1 crabs were shipped in insulated containers to the Hatfield Marine Science Center (Newport, Oregon) in June 2008. Little mortality occurred and the crab began feeding almost immediately when transferred to polyethylene tanks (45 by 65 cm) supplied with flow-through seawater (8 °C). The crabs were fed daily on a diet of frozen Cyclop-Eeze and high-protein shrimp diet (Otohime B), and food was always present both in the form of these prepared foods and algae that grew inside the holding tanks. Initial densities were ~500 crabs/m^2 of tank bottom, with clumps of PVC ribbon (4 mm wide) (Bio-Fill filter medium) added for vertical structure.

Pacific halibut for the experiments were collected with small trawls in Chiniak Bay, Kodiak Island, Alaska, and shipped in seawater and insulated boxes to the Hatfield Marine Sciences Center. These fish were fed primarily gel food prepared from squid and herring, and maintained in flow-through seawater in large circular tanks for ~6 months before being used in the crab predation experiments. Six pairs of fish, 125 to 135 mm total length, were used for all of the experiments in a randomized block design (see below).

2.2. Experimental apparatus and substrata

Predation trials were conducted in three identical circular, flat-bottomed tanks (103 cm diameter) and supplied with continuous flows (150 ml s^{-1}) of sand-filtered seawater at 8 °C (±0.5 °C). The bottom of each tank was covered with either 1 cm of medium-grained quartz sand (0.5 mm mean diameter) or 1.5 cm of pea gravel (7 to 12 mm) (see below). The tanks were in a light-controlled room with a daily light cycle of 12 h light and 12 h dark (0700 to 1900 h). The daytime light level was 3 µmol photons $m^{-2}s^{-1}$ provided by a bank of fluorescent lamps around the upper periphery of the room, and an independent bank of light-emitting diode (LED) bulbs (555 nm wavelength) that was controlled by a rheostat. This allowed light levels to be lowered to darkness ($<1\times10^{-8}$ µmol photons $m^{-2}s^{-1}$) then raised slowly during experimental trials to prevent startling the predators. Each tank was equipped with an overhead video camera monitored from an adjacent room so that the tanks were undisturbed during trials.

Three different kinds of physical structures were placed on top of the sand to provide habitat for RKC. The most frequently used was a mimic for the macroalga *Neorhodomela larix*, a dark green chenille yarn (5 mm diameter) that, when allowed to foul in flowing seawater for at least 2 weeks, is a highly preferred substratum for RKC (Pirtle and Stoner, in review). This mimic, used in 20 cm strands, facilitated the creation of standard habitats with different complexities and heterogeneities (see below). Empty mussel shells (*Mytilus edulis*) (4 to 7 cm length), an assortment of smooth stones (25 to 50 mm diameter), and pea gravel (7 to 12 mm diameter) were also employed to create different structures.

Predator–prey interactions were tested in eight experimental habitats using the aforementioned materials. The influence of physical structure upon crab survival was tested with four basic habitat treatments: 1) bare sand, 2) 84 strands of algal mimic (~100 strands m^{-2}) evenly dispersed over the tank bottom, 3) 168 dispersed strands of algal mimic (~200 strands m^{-2}), and 4) 336 dispersed strands (~400 strands m^{-2}). These densities of algal mimics were made for direct comparison with habitat preference experiments made for newly settled RKC (Pirtle and Stoner, in review). Two other habitat preparations were created with algal mimics to explore the role of habitat dispersion or patchiness: 5) 168 strands loosely bundled into four clumps (~15 cm diameter each at ~2400 strands m^{-2}), and 6) 168 strands bundled into one island (~25 cm diameter at ~3400 strands m^{-2}). The large island was placed in the center of the sand-covered tank bottom, and the four smaller islands were placed evenly around the tank, each ~20 cm from the tank wall. 7) For increased habitat heterogeneity and direct comparison with high density algal mimics (336 strands), a treatment was created with a combination of 168 strands of algal mimic, 84 mussel shells, and 84 stones (yielding ~400 structures m^{-2}) evenly dispersed over the tank bottom. 8) A highly complex, but even distribution of structure was provided by a layer of pea gravel (1.5 cm thick) on the tank bottom instead of sand. Crabs could easily descend into crevices created by the gravel.

2.3. Experimental protocol

Pairs of Pacific halibut were transferred to the experimental tanks 2 weeks prior to the first trials with live crabs so that they could acclimate to the new surroundings. Pairs were used because they are known to perform more consistently as predators with social facilitation (Stoner and Ottmar, 2004; Ryer et al., 2004). The fish were fed frozen krill (*Euphausia pacifica*) both before and after trials to standardize hunger levels. Before the formal trials were begun, each pair of fish was presented with 25 RKC in the standard manner (see below) in bare sand habitat. Invariably, all of the crabs were consumed, confirming that the fish were sufficiently acclimated to the experimental systems and the prey.

Fish were prepared for predation trials with 48 h of food deprivation following feeding to satiation on krill. This insured that the fish were active and uniformly motivated to feed. Sixteen to 20 h before a trial the experimental tanks, already holding the fish, were prepared with the test substrata. The sand-only and gravel-bottomed tanks were smoothed but left in place. Then, on the morning of a predation trial the following procedure was followed: at 0900 h the overhead lighting in the room was slowly reduced to total darkness and 25 pre-sorted RKC (3.5 to 5 mm CL), were dispersed over the middle half of each tank. This approach allowed the prey to settle into preferred microhabitats before the visual predators began searching for crabs. For treatments with habitat islands the crabs were confined for a short period with acrylic columns (15 or 28 cm diameter) placed over the islands. This insured that the crabs would quickly find the