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Cannibalism in red king crab: Habitat, ontogeny, and the predator functional response

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ABSTRACT

The red king crab, *Paralithodes camtschaticus*, stock in the Gulf of Alaska crashed in the early 1980s. Stock enhancement has been proposed as a potential means of restoration. As predation is likely the most important source of mortality for juvenile crabs, understanding the predator–prey dynamics of the system is an essential consideration when designing release strategies to maximize survival. In this study, we determined the predator functional response of year-1 and year-2 juvenile red king crabs feeding on newly settled year-0 crabs in sand habitat and macroalgae mimic habitat. The predator functional response describes how the predation rate varies with prey density and can be linear and partially destabilizing (Type I), inversely density-dependent and destabilizing (Type II), or density-dependent and stabilizing (Type III). Year-1 predators exhibited a Type II functional response in sand and Type I in macroalgae mimic. Year-2 predators exhibited a Type I functional response in sand and Type III in macroalgae mimic. Predation rates were generally lower for year-1 predators and lower in macroalgae mimic habitats. Year-2 crabs were highly efficient predators in sand, but the reduction in predation with the addition of structure was much greater than for year-1 crabs, indicating that the smaller predators are less inhibited than larger crabs by structured habitat when foraging. Prey crabs in the macroalgae mimic habitat exhibit no net movement from sand onto macroalgae in response to predation pressure. Prey use of macroalgae mimic was highest at intermediate prey densities. This work shows that the functional response can vary both quantitatively and qualitatively, with habitat type and predator size indicating ontogenetic changes in foraging efficiency in different habitats. Further, it suggests that stock-enhancement releases should be at low densities in complex habitat, and possibly should occur every other year to minimize loss to predation.

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1. Introduction

The red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), is an important fishery species in Alaska. In the 1960s, there was a substantial fishery in both the Gulf of Alaska and Bering Sea; however, in the early 1980s the stocks supporting these fisheries declined precipitously. Although the Bering Sea stock has recovered, albeit to lower levels than occurred in the 1960s and 70s, and is again being commercially fished, the Gulf of Alaska stock has not recovered despite the closure of the fishery (Bechtol and Kruse, 2009). Possible reasons for the crash and the lack of a recovery include overfishing (Orensanz et al., 1998), poor recruitment (Blau, 1986), climatic shifts (Zheng and Kruse, 2000), or a combination of these factors (Bechtol and Kruse, 2009). Stock enhancement of red king crabs using hatchery reared juveniles was used in Japan for 14 years (Stevens, 2006c) and has been proposed as a potential avenue to increase recruitment in local stocks of red king crabs (Stevens, 2006b).

For stock enhancement to be successful, survival of released juveniles to maturity must be high enough to offset the costs of juvenile production (Stevens, 2006a) so release strategies that maximize survival and growth are necessary. For juvenile red king crabs, predation is likely the most important factor in determining success, similar to other species, such as the blue crabs, *Callinectes sapidus* (Hines and Ruiz, 1995). For example, although juvenile blue crab growth may vary by a factor of 2 among habitat types (Seitz et al., 2005), predation risk can vary by a factor of 5 among habitat types without any significant change in growth (Long et al., 2011). It is therefore important to understand the predator–prey dynamics of a system in order to release crabs in the optimal habitat and at the best time, density, and size to minimize predation and maximize enhancement success (Hines et al., 2008; Johnson et al., 2008).

One of the most important aspects of predator–prey dynamics is the functional response, or the effect of prey density on predation rates (Hassell et al., 1977; Holling, 1959), because the shape of the functional response is an important determinant of prey persistence. In a Type I functional response, predation rate is independent of prey density and

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can be destabilizing. In a Type II functional response, predation risk is highest at low prey densities, which is destabilizing and can lead to localized extinction of prey populations. In a Type III functional response, predation risk is highest at intermediate densities, thus giving preys a low-density refuge from predation and stabilizing the predator–prey interactions (Seitz et al., 2001). The functional response of predators can be changed both quantitatively and qualitatively by a number of factors, including habitat (Dittel et al., 1995; Lipcius and Hines, 1986; Long et al., 2012a), predator size (Alexander et al., 2013; González-Suárez et al., 2011), the spatial arrangement of preys (Hines et al., 2009; Long and Hines, 2012), and the presence of alternative preys (Chesson, 1989).

In this study, we examine aspects of the cannibalistic predator functional response in red king crabs. Because year-0 crabs use the same habitat types as year-1 and year-2 red king crabs (Dew, 1990) and because red king crabs are cannibalistic (Stoner et al., 2010), understanding the effect of cannibalism on the survival of new recruits is critical to designing the most effective release strategy in an enhancement effort. Red king crabs are known to preferentially settle in complex habitat (Loher and Armstrong, 2000; Stevens, 2003), probably because such habitats are associated with lower predation rates (Pirtle et al., 2012; Stoner, 2009; Stoner et al., 2010). Previous work indicates that the functional response of year-1 red king crabs to year-0 red king crabs in complex non-biogenic habitats is a Type II (Long et al., 2012a), despite evidence that they settle in such habitats in the field (Loher and Armstrong, 2000). However, the functional response in biogenic habitats, which are also high settling areas (Sundberg and Clausen, 1977), is unknown. In addition, how the size of predator red king crabs affects their functional response to year-0 prey crabs is unknown. Predator size can have a substantial effect on the predation rate (González-Suárez et al., 2011) and the effect can interact with habitat complexity (Bartholomew et al., 2000; Gotceitas and Colgan, 1989). As high rates of cannibalism may reduce stock enhancement success, it may be advisable to wait until the threat from previously released cohorts has passed before releasing again in the same area (Long et al., 2012a). Therefore, understanding how long a cohort remains a threat to subsequently released juveniles will allow for optimal timing of release. In this paper we consider the interactive effects of habitat and predator size on the cannibalistic functional response of red king crabs.

2. Materials and methods

2.1. Experimental animals

We used three year classes of red king crabs in this experiment. Year-0 crabs were the preys in all experiments and year-1 and year-2 crabs were the predators. All crabs were reared in a hatchery or laboratory; the year-0 crabs were reared at the Kodiak Laboratory, Kodiak, Alaska, and the year-1 and year-2 crabs were reared to the C1 stage at the Alutiiq Pride Shellfish Hatchery, Seward, Alaska, before being transported to the Kodiak Laboratory. Similar rearing techniques were used in both facilities. Ovigerous red king crab females were captured in commercial fishing pots in Bristol Bay, Alaska, during the winter fishing seasons in 2008, 2009, and 2010. They were transported to Kodiak in the live well of a commercial fishing vessel, and in 2008 and 2009 they were transported to the Alutiiq Pride Shellfish Hatchery in coolers with damp burlap and ice packs. Upon arrival, the crabs were held in flowing ambient seawater and fed a diet of frozen fish and squid. At hatching, larvae were collected and reared to the first crab stage (C1) on a diet of DC DHA Selco (INVE Aquaculture, UT, USA[2]) enriched *Artemia* nauplii. In 2008 and 2009, year-0 crabs were transported to Kodiak in insulated thermoses. Year-0 crabs were reared in a communal tank and were fed frozen *Artemia* (Brine Shrimp Direct, Ogden, Utah, USA), frozen bloodworms (Brine Shrimp Direct, Ogden, Utah, USA), frozen Cyclop-eeze (Argent Laboratories, Redmond, Washington, USA), Cyclop-eeze flakes, and Gelly Belly mixed with Cyclop-eeze powder and walleye pollock (*Theragra chalcogramma*) bone powder (U.S. Department of Agriculture, Agricultural Research Service, Kodiak, Alaska, USA) twice a week. As the crabs grew, they were transitioned gradually to a diet of chopped frozen fish and squid. Year-1 and year-2 crabs were reared in individual holding cells to reduce cannibalism.

2.2. Predation trials

The experiment was a fully-crossed three-way design with five replicates of each combination. We crossed predator age (year-1 and year-2 crabs), habitat (bare sand and macroalgae mimic), and prey density (2, 5, 12, 25, 35, and 50 preys per trial), and ran one control replicate with no predator at each habitat–prey density combination, for a total of 132 trials. Trials were performed in plastic containers 31 × 20 × 24 cm (L × W × H) placed in a larger tank 170 × 90 × 30 cm (L × W × H), with flow-through seawater at ambient temperature and salinity. Each container had two mesh-covered holes on opposite sides to allow water to flow through. Year-0 prey crabs had carapace widths (including spines) of 2–3 mm (~3–4 mm carapace length). Year-1 predators were 15–25 mm carapace length (CL), had to have both chelae, and could not be missing or regenerating more than two periopods. Year-2 predators were 30–40 mm CL, had to have at least one chela (preliminary trials indicated that year-2 crabs had no difficulty in capturing preys with a single chela), and could not be missing or regenerating more than two periopods. Predators that molted were not used in trials for one week, and trials in which the predator molted during or soon after the trial were excluded from analysis and re-run. Predators were randomly assigned to trials and were reused. One predator consistently refused to feed in any trial, so the trials with that crab were excluded from analysis and re-run with different predators, and the predator was not subsequently used. Predators were starved for 24 h prior to a trial to standardize hunger levels (Long et al., 2012a). Sand habitat consisted of a 2 cm layer of sand spread evenly along the bottom of the container. Sand was collected from a local beach and passed through a 1 mm mesh screen to remove all macrofauna prior to use. Macroalgae mimic habitat consisted of a 2 cm layer of sand and two pieces of macroalgae mimic affixed to flat rocks placed on the bottom (Fig. 1). The macroalgae mimic consisted of a central strand 12 cm long with plastic 'blades' extending out 13 cm on either side.

The experiment was conducted from June 14 through July 21, 2011. Trials were run in a random order and usually six trials were run each day. At 3:00 pm the day before a trial, the appropriate habitat was established in each experimental container. Prey crabs were removed from the holding tank and the appropriate number counted out for each trial. Then the prey crabs were placed in the trial containers and allowed to acclimate overnight. The next morning, before the beginning of the trials, predators were removed from their holding cells and had their CL measured. Just prior to beginning the trials, the number of preys on the sand was counted in all trials with macroalgae. Although it was impossible to count the crabs on the macroalgae mimic without disturbing them, they were easily counted on the sand and we assumed that any crab not on the sand were in the macroalgae. Occasionally, a few preys on the screen on the sides of the containers were noted. Trials were started by placing the predators in the containers at 9:00 am, where they were allowed to feed for 2 h. At the end of the trial, the predators were removed and the number of preys on the sand counted as above. Then all the preys were carefully removed from the container and counted. We calculated predation as the change in prey number in the containers.

[2] Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.