Journal of Experimental Marine Biology and Ecology 464 (2015) 58–67

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Habitat, predation, growth, and coexistence: Could interactions between juvenile red and blue king crabs limit blue king crab productivity?

William Christopher Long *, Scott B. Van Sant [1], Jan A. Haaga [2]

Kodiak Laboratory, Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 301 Research Ct., Kodiak, AK 99615 USA

A R T I C L E I N F O

Article history:
Received 25 February 2014
Received in revised form 15 December 2014
Accepted 28 December 2014
Available online 14 January 2015

Keywords:
Blue king crab
Coexistence
Habitat
Intra-guild interactions
Predation
Red king crab

A B S T R A C T

Since the 1970s, dominance of the shallow water Pribilof Islands king crab populations has shifted from blue king crab (*Paralithodes platypus*) to red king crab (*Paralithodes camtschaticus*), potentially influenced by interactions at the juvenile stage. In laboratory experiments, we determined whether habitat and temperature could mediate competitive and predatory interactions between juveniles of both species. We examined how density and predator presence affect habitat choice by red and blue king crabs. Further experiments determined how temperature and habitat affect predation by year-1 red king crab on year-0 blue king crab. Finally, long-term interaction experiments examined how habitat and density affected growth, survival, and intra-guild interactions between red and blue king crab. Red king crabs had a greater affinity for complex habitat than blue king crabs and the presence of predators increased preference for complex habitat for both species. Predation on year-0 blue king crabs by year-1 red king crabs was lower in complex habitats and at colder temperatures. When reared alone, red king crab survival was higher at low densities and in complex habitats. When reared with blue king crab, survival of red king crab was higher in complex habitats and in the presence of blue king crab. Blue king crab survival was substantially lower in the presence of red king crabs regardless of habitat. In both rearing experiments, differences in changes in crab size appeared to be driven by mortality rates and size-selective predation. This demonstrates that interactions between juvenile red and blue king crabs are primarily driven by intra-guild predation and not competition for resources. These results, suggest that juvenile red king crabs have an advantage over blue king crabs which could lower productivity of the Pribilof Islands blue king crab stock since the former became dominant in that system.

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1. Introduction

Somerton (1985) commented on the disjunct distribution of red king crab, *Paralithodes camtschaticus*, and blue king crab, *Paralithodes platypus*, in Alaskan waters. At the time, overlap between the two species occurred only in a few widely spaced bays and fjords, with the major populations occupying distinctly different areas. He proposed three potential mechanisms to explain this observation: 1) differences in thermal tolerance leading to reproductive isolation, 2) competitive displacement of blue king crab by red king crab in areas of potential overlap mediated by differences in thermal tolerance, and 3) differential predation in favor of red king crab, and noted the relative strengths of each hypothesis without reaching a conclusion (Somerton, 1985). In the late 1980s, the red king crab population in the Pribilof Islands area of the Bering Sea increased dramatically (Fig. 1); this area, up till that point, had been populated almost exclusively by blue king crabs (Foy and Armistead, 2012). A period of brief overlap followed the red king crab escalation, after which the blue king crab populations crashed. Blue king crabs are currently at a historically low level of abundance (Foy and Armistead, 2012). As there is no evidence of sweeping changes in regional temperatures or community structure, the fact that red king crabs were able to become dominant in the Pribilof Islands is evidence against the first and third mechanisms proposed by Somerton, at least as they apply to the Pribilof Islands. Although temperature cannot be the mediating factor, the remaining hypothesis of competitive displacement remains as a potential explanation for both the generally disjunct distributions as well as the substantial decrease in the productivity of the Pribilof Islands blue king crab stock. Competition for resources among late juvenile and adult red and blue king crabs has been considered (NPFMC, 2011); however, observations on the foraging habitats of adults of the two species do not support this mechanism (Somerton, 1985).

Difficult to capture and assess in the field, interactions at the early juvenile stage have not been considered as a potential mechanism contributing to the disjunct distribution, but there are several reasons it could be important. Similarities between red and blue king crabs in

* Corresponding author. Tel.: +1 907 481 1715; fax: +1 907 481 1701.
E-mail address: chris.long@noaa.gov (W.C. Long).
[1] Current address: Southeast Fisheries Science Center, NOAA NMFS. C/O NC Department of Marine Fisheries, 127 Cardinal Dr. Ext., Wilmington, NC 28405, USA.
[2] Current address: 1719 Mission Road, Kodiak, AK 99615, USA.

http://dx.doi.org/10.1016/j.jembe.2014.12.011
0022-0981/Published by Elsevier B.V.

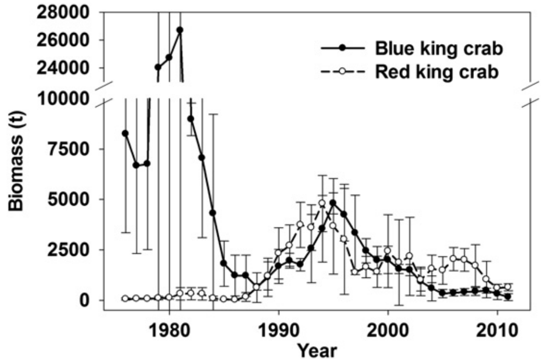

Fig. 1. Three-year running average (± SD of the annual averages) of mature female biomass for the Pribilof Islands stocks of red and blue king crabs in the Eastern Bering Sea trawl survey (data from Foy and Armistead, 2012).

terms of size and chela morphology make it likely that they feed on similar items (Somerton, 1985) and field data show that adults do have similar diets (Chuchukalo et al., 2011). If juveniles also have similar diets, this could drive competitive displacement (Brenchley and Carlton, 1983), however, post-settlement, juvenile crabs are likely not limited by bottom-up processes as their dietary requirements are low and food is generally abundant (Long et al., 2011; Seitz et al., 2008). More likely, however, is the effect of intra-guild predation between the species. In the laboratory, red king crabs are cannibalistic both within a cohort (Borisov et al., 2007; Daly et al., 2009, 2012a) and among cohorts (Long et al., 2012a; Stoner et al., 2010), to the extent that rearing crab individually is a viable option to reduce cannibalism (Swiney et al., 2013). Blue king crabs are also cannibalistic but intra-cohort cannibalism may be less intense for them than it is for the red king crab (Daly and Long, 2014a; Daly and Swingle, 2013). Although untested, given their morphometric similarities, it is likely that both species would prey on each other if present in the same habitat. In the laboratory, red king crab will prey on blue king crab (Daly and Long, 2014b) and field data, though limited, show that blue king crab will prey on red king crab in the wild (Chuchukalo et al., 2011). As such, more effective predation by one species could lead to displacement (e.g., Dick et al., 1990, 1999; Race, 1982).

Both competition for resources and intra-guild predation as mechanisms for displacement are predicated on the assumption that the juveniles occupy similar habitats in the absence of the other species; habitat partitioning can lead to coexistence for similar species (e.g., Hines, 1982; Meyer, 1994). There is indirect evidence both for and against habitat partitioning between red and blue king crabs in the Pribilof Islands. Both species release their larvae in the spring (Armstrong et al., 1981; Shirley and Shirley, 1989). After four pelagic, zoeal stages, the larvae molt to the settling post-larval or glaucothoe stage and continue to swim until they find a complex habitat, even delaying their molt to the first juvenile instar stage (C1) in order to increase their chances of finding a complex habitat (Stevens and Kittaka, 1998). While both species demonstrate a strong preference for complex habitats, neither demonstrates a high degree of preference among different types of complex habitats such as hydroids, cobble, shell hash, or macro-algae (Palacios and Armstrong, 1985; Stevens, 2003). Habitat choice at the glaucothoe stage is likely important in determining the distribution of C1 crabs in the field (Loher and Armstrong, 2000; Sundberg and Clausen, 1977), but post-settlement movement among habitats may also play a role (Palacios and Armstrong, 1985). The non-discriminatory settling behavior (among complex habitats) of both species supports the idea that they may occupy similar habitats as juveniles; however, field surveys that included both shell and cobble, suggest that red king crab juveniles prefer cobble habitat (Loher and Armstrong, 2000) and blue king crab juveniles prefer shell hash, which is common around the Pribilof Islands (Armstrong et al., 1987), supporting the habitat partitioning hypothesis.

In this study, we examined whether post-settlement interactions between red and blue king crabs could cause decreased production of blue king crabs around the Pribilof Islands, or whether habitat type could mediate interactions between species through habitat partitioning. In particular, we determined how density and predator presence alter habitat choice of year-0 red and blue king crabs, how habitat type and temperature affect predation of blue king crabs by red king crabs, how habitat type affects intra- and inter-specific interactions, and which types of interactions dominate in both species.

2. Methods

2.1. Crab rearing and holding conditions

Red and blue king crabs for these experiments were all laboratory- or hatchery-reared. Red king crab broodstock were captured using baited commercial pots in Bristol Bay in the winters of 2008, 2009, and 2010, and transported to the Kodiak Laboratory. In 2008 and 2009, crabs were flown to the Alutiiq Pride Shellfish Hatchery, Seward, Alaska, in coolers with wet burlap and ice blocks. Blue king crab broodstock were also captured near St. Matthew Island in the winter of 2010 and flown to the Kodiak Laboratory in coolers. Broodstock crabs were held in flowing ambient seawater and fed a diet of frozen squid and herring. Larvae were collected after hatching and reared to the C1 stage (Swingle et al., 2013). Larvae were fed a diet of DC DHA Selco (INVE Aquaculture, UT, USA[3]) enriched *Artemia* nauplii. In 2009 and 2010, juvenile crabs were flown to Kodiak in insulated bottles. Juveniles were held in tanks with flowing, raw seawater at ambient temperature (typically varies between ~3 and 9 °C throughout the year, personal observation) and salinity. Whenever juveniles were held together they were given structure in the form of gill netting or artificial macro-algae in order to reduce cannibalism (Daly et al., 2009). Year-0 juvenile crabs 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 per week to excess. Older juvenile crabs were gradually shifted to a diet of chopped frozen fish and squid, and were held in individual containers to eliminate cannibalism.

2.2. Effects of density and predator presence on habitat choice

We examined the effects of density and predator presence on habitat choice by year-0 red and blue king crabs. Identical experimental procedures were followed for red king crabs in December 2010 and blue king crabs in December 2011. Trials were performed in plastic containers 31 × 20 × 24 cm (L × W × H) held inside a larger tank 170 × 90 × 30 cm (L × W × H) with flow-through ambient seawater. Plastic containers had holes covered with mesh screen on either side to allow for water exchange between the containers and the large tank. Two densities of year-0 crabs, 5 and 20 per container, were used. Three habitat types were used: sand, cobble (a preferred habitat type for red king crab in the wild) (Loher and Armstrong, 2000), and shell hash (a preferred habitat type for blue king crab in the wild) (Armstrong et al., 1987). In each trial, crabs were given a choice of 2 habitat types for a total of three treatments (sand:cobble, sand:shell, cobble:shell) and habitats were randomly assigned to different sides of the containers. In the red king crab experiments, year-0 red king crab had an average CW (±SD) of 6.6 ± 1.4 mm, predators had an

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