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Monograph

Comparative predator-mediated habitat use in early juvenile southern Tanner crab (*Chionoecetes bairdi*), snow crab (*Chionoecetes opilio*), and red king crab (*Paralithodes camtschaticus*)

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Highlights

- Only juvenile Tanner crabs demonstrated a clear sediment association.
- Tanner and snow crabs increased burial behavior in response to a predator; red king crabs did not bury.
- Juvenile Tanner and red king crabs use of emergent structure was not affected by predator presence.

Abstract

Despite declining populations, southern Tanner crab (Chionoecetes *bairdi*), snow crab (Chionoecetes opilio) and red king crab (Paralithodes *camtschaticus*) support economically important fisheries in the Gulf of Alaska and the southeastern Bering Sea. In the southeastern <u>Bering Sea</u> these crab species have distinct although overlapping habitats. Juvenile snow crab, a stenothermic arctic species, are concentrated in waters below 2°C, in contrast to the distributions of Tanner crab and red king crab which occupy much wider thermal ranges. Other aspects of the habitat associations of early benthic stages of *Chionoecetes* spp. have not been extensively studied. We describe habitat selection and predation avoidance strategies of early benthic stages (C1-C4) of Tanner crab, snow crab, and red king crab with experiments examining (1) sediment grain size associations, (2)burial behavior and (3) use of emergent benthic habitat structure (artificial worm tubes) in response to a predator presence, and (4) effect of worm tube density on the survival of age-0 Tanner crabs in the presence of predatory juvenile Pacific cod (Gadus macrocephalus) and age-1 Tanner crab. Tanner crabs were the only species that exhibited a clear sediment association, selecting silty muds to fine sand rather than larger sands and pebbles. Tanner and snow crabs buried deeper in sandy mud than in fine sand and both species significantly increased burial behavior in response to introduction of a cod predator. Conversely, red king crabs did not exhibit burial behavior even in the presence of a predator. Early juvenile Tanner and red king crabs displayed strong affinity for emergent structure, while snow crabs were evenly distributed between emergent structure and bare sand habitats. Contrary to expectations, crab selection of emergent structure was not significantly influenced by a cod predator presence. In trials with actively foraging predators, survival of juvenile Tanner crabs was higher in worm tube habitat. Our results demonstrate that early juvenile Tanner and snow crabs use burial behavior as the first line of avoidance/defense, while red king crabs rely upon occupancy of structurally complex habitat. Tanner crab affinity for worm tube structure may facilitate foraging in addition to serving as a refuge. Snow crabs settle on organically rich, fine sediments with little to no emergent structure in the eastern Bering Sea and may benefit from reduced predation pressure in cold waters, suggesting the importance of low temperature as a critical habitat feature for this species.

Introduction

Since the 1970s, stocks of southern Tanner crab (*Chionoecetes bairdi*, hereafter "Tanner crab"), snow crab (*Chionoecetes opilio*), and red king crab (*Paralithodes camtschaticus*) have declined dramatically in the eastern Bering Sea. Overexploitation, environmental regime

shifts, and predation affecting juvenile recruitment success appear to have contributed to decreasing population levels (Orensanz et al., 1998; Orensanz et al., 2004; Lang et al., 2018). Despite these declines, commercial crab catches have continued to support an important fishery in Alaska with annual revenues of over \$200 million (Garber-Yonts and Lee, 2021). While the geographic ranges of these species vary, adult populations support overlapping fisheries in the southeastern Bering Sea (SEBS). The SEBS represents the southernmost range of snow crab, a stenothermic, arctic species that primarily inhabits deep, cold waters (-1.5 to 5°C). In contrast, the SEBS is the northernmost range of congeneric Tanner crab, a subarctic species, which also occurs in the Gulf of Alaska (GOA) and extends as far south as Puget Sound, WA with temperature tolerances of 2 to 12°C (Ryer et al., 2016; Murphy, 2020). Red king crab, an anomuran crab, is found in the Bering Sea and the GOA south to British Columbia, Canada and are known to tolerate temperatures from -1.5 to 15.0°C, depending on life history stages (Rodin, 1989; Long and Daly, 2017).

From a fisheries perspective, it is important to understand the ecological drivers that influence cohort strength and the role of juvenile nursery habitats in population productivity (Ernst et al., 2012). Warming of the SEBS is resulting in community level changes including northward shifts of arctic and subarctic species (Mueter and Litzow, 2008) including snow crab (Fedewa et al., 2020; Szuwalski et al., 2021). Another such species, Pacific cod, is expanding northward with warmer bottom temperatures resulting in increasing spatial overlap with snow crab (Orensanz et al., 2004; Zheng and Kruse, 2006; Fedewa et al., 2020). Pacific cod are primary consumers of juvenile Tanner crab and prey heavily on juvenile snow crab in this region (Livingston, 1989). Pacific cod predation, in conjunction with increasing bottom seawater temperatures, is believed to be contributing to the northward shift of snow crab distribution and limiting their recovery (Orensanz et al., 2004). Understanding nursery habitat requirements of these crab species is critical to predicting species abundances and distributions in the face of shifting thermal and biological conditions.

Despite their economic importance to the region, knowledge of juvenile habitats of *Chionoecetes* spp. is limited. In the Bering Sea, early benthic stages of Tanner crabs are found on the outer shelf at depths >100m where temperatures are generally >2°C and sediments are dominated by sand mixed with gravel (Smith and McConnaughey, 1999; McConnaughey and Smith, 2000; Ryer et al., 2016). Annual melting of sea ice on the Bering Sea results in the formation of the "cold pool" (near bottom temperatures <2°C) over the shelf at depths of 50–100m (Orensanz et al., 2004) where early juvenile snow crabs are most abundant (Zheng et al., 2001; Copeman et al., 2021). In addition, seasonal stratification and high productivity of the surface waters over the middle shelf result in organically rich sand and

mud substrates (Smith and McConnaughey, 1999; McConnaughey and Smith, 2000). Juvenile red king crab use the shallowest habitats of the three species, commonly found at depths of 20–60m in the GOA and SEBS. In coastal waters of the GOA, Tanner crabs have been associated with biogenic benthic structure (Ryer et al., 2016) and red king crabs are often associated with rocks, shell hash or a variety of biological covers (Loher and Armstrong, 2000). The availability and distribution of these emergent benthic features is not well characterized on the Bering Sea shelf and the affinity of juvenile snow crab for such habitat features is not known. As such the potential importance of benthic habitat structures to juvenile crab nursery areas in the Bering Sea remains largely unknown.

Marine benthic organisms employ a variety of related anti-predation strategies for survival including behavioral (e.g., habitat selection and sheltering) and morphological defenses (e.g., claw, shell, and spines). Many benthic crustaceans avoid predation by associating with structurally complex habitats that serve as refuges. Juvenile spiny lobster (*Panulirus argus*; Herrnkind and Butler, 1986), Dungeness crab (*Cancer magister*; Fernandez et al., 1993), and blue crab (*Callinecties sapidus*; van Montfrans et al., 2003) actively select complex habitats, providing shelter from predators. Similarly, juvenile red king crab are known to prefer structurally complex habitats such as highly branched macroalgae, bryozoans, and hydroids as a refuge from predators, relying on immobility and crypsis to further reduce predation risk (Babcock et al., 1988; Stoner, 2009; Pirtle et al., 2012). In the GOA, where early juvenile Tanner crabs inhabit worm tube habitats, it is unknown whether the crabs select this habitat to mediate predator-prey interactions or if the crabs and tube-forming *Sabellides sibirica* have shared preferences for other aspects of habitat (i.e., depth and substrate; Ryer et al., 2015).

In addition to inhabiting structurally complex habitats, benthic crustaceans can also use burial to mediate predator-prey interactions (Davis et al., 2004). Since both Tanner and snow crab lack dermal spines, they may have a tendency to bury as the first line of defense. Older Tanner crabs are known to bury in muddy and sandy substrates and both species may settle in nursery habitats consisting of organically rich fine sediments (Stevens et al., 1994; Rosenkranz et al., 1998; Moles and Stone, 2002). The literature for early juvenile snow crab habitat associations is mainly from the Gulf of Saint Lawrence and emphasizes the importance of temperature in mediating predation risk (Brethes et al., 1987; Conan et al., 1996; Dionne et al., 2003).

In the present study, we examined the behavior and habitat selection of early benthic stages (C1 – C4) of Tanner crab, snow crab, and red king crab in a series of laboratory experiments. Specifically, we examined sediment grain size associations, burial behavior (in two

sediments), and selection of worm tube habitat (using an artificial worm tube mimic). In addition, we examined the effect of predator presence (juvenile cod) on burial behavior and use of worm tube habitat. Finally, we examined the effect of artificial worm tube presence and density on the survival of age-0 Tanner crabs in the presence of predatory juvenile Pacific cod and age-1 Tanner crab. Based on observed distributions in the field, we hypothesized that Tanner and snow crabs would select finer sediments (mud-sand) and that red king crab would select larger grain sizes. We also hypothesized that Tanner and snow crabs would exhibit burial as an anti-predator behavioral response and that red king crab would exhibit an association with artificial worm tube structures. Finally, we predicted that the presence and density of worm tubes would affect crab survival in the face of both piscine and crustacean predators.

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Experimental animals

All laboratory trials were conducted at the Alaska Fisheries Science Center (AFSC) laboratory at Hatfield Marine Science Center (HMSC) in Newport, OR. All behavioral experiments were conducted between 2010 and 2016 based on the availability of each species. Experiments for each species used identical procedures and were conducted in the same experimental apparatus. All crabs used in habitat and behavior trials were post-metamorphic juveniles, with stages referring to the number molts completed...

Sediment association experiment

The distribution of crabs across sediments differed between species (G=47.52, df=12, P<0.001), with only juvenile Tanner crabs exhibiting a clear sediment association. Tanner crabs were concentrated on the three finest sediments (extrinsic G=56.19, df=6, P<0.001) and infrequently occupied the coarser sediment types (8% of observations; Fig. 1). There was a significant difference in distribution between C3 and C4 Tanner crabs (G=13.33, df=6, P=0.038), with C3 crabs most...

Discussion

Tanner crab, snow crab and red king crab display differing sediment grain size association, degree of burial in sediment, and association with emergent structural habitat features. These behavioral traits, which influence vulnerability to predators, likely reflect differences in the dominant habitat features in their overlapping but distinct distributions in the Gulf of Alaska and Bering Sea. These regions vary from substrates with structurally complex geologic and biogenic features (common to...

Conclusions

Our laboratory results show that *Chionoecetes* and *Paralithodes* spp., with overlapping distributions in the GOA and EBS, exhibited distinct suites of habitat selection and behaviors which are important in mediating predator–prey interactions. Their life histories and survival strategies reflect the patterns of variation in substrate, structure, depth, and temperature in their primary settlement habitats. Early juvenile red king crab occupy structurally complex habitat to reduce predation risk...

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper....

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