HABITAT FUNCTION IN ALASKA NEARSHORE MARINE ECOSYSTEMS

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By

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Abstract

This research demonstrates how habitat structures subtidal communities and supports individual species in Alaska nearshore marine ecosystems. This was accomplished through a case study of southeast Alaska coastal regions, and an in-depth investigation of red king crab *Paralithodes camtschaticus* early life stage ecology and nursery habitat.

How subtidal communities reflect variation in the marine environment of southeast Alaska is poorly understood. The purpose of the first part of this body of research was to identify and compare patterns of community structure for macroalgae, invertebrate, and fish communities at shallow subtidal depths between inner coast and outer coast regions, and link patterns of community structure to environmental variability in southeast Alaska. The major hydrographic gradient of decreasing salinity and increasing temperature from the outer coast to the inner coast affected regional community structure, with greater species diversity at the outer coast. Species distribution for invertebrate communities was linked to variation in benthic habitat at local scales among sites within regions. This study improves understanding of processes that structure marine communities to better predict how environmental change will affect Alaska marine ecosystems.

Many Alaska red king crab populations have collapsed and continue to experience little recovery, even for areas without a commercial fishery. Several aspects of red king crab early life stage ecology were investigated because reasons for the lack of recovery may be related to the early life history of this species. Field experiments were conducted in southeast Alaska. Settlement timing was consistent between study years (2008-09) and with historical data for this region. Local oceanographic processes that influence larval transport may be responsible for spatial variation in larval supply. In laboratory and field experiments, early juvenile crabs (age 0 and 1) demonstrated refuge response behavior to a predator threat that changed with crab ontogeny. When predators were absent, juvenile crabs preferred highly structured biogenic habitats due to foraging opportunities, and associated with any structural habitat to improve survival when predators were present. This research shows how availability of high quality nursery habitat affects red king crab early life stage success and potential for population recovery.

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General Introduction

Understanding habitat function in marine ecosystems is integral to an ecosystem-based approach to marine resource management and conservation. Habitat in its most basic form is the place or environment where an organism naturally lives. In this sense, habitat is a suite of environmental characteristics where individuals exist within their physiological tolerances, with shelter for predator avoidance, and opportunity for successful foraging and reproduction (Rice, 2005). Essential Fish Habitat, by marine policy definition, is the combination of those waters and substrate necessary to marine species for spawning, breeding, feeding, or growth to maturity (U.S. Department of Commerce, 1996), which reflects the ecosystem integrated intention of current U.S. fishery management policy.

A variety of habitat characteristics must be considered to understand the basic structure of marine ecosystems and how these ecosystems support individual species. Habitat for marine species includes seafloor habitats that are composed of physical substrates, such as bedrock and fine sediments, and biological structures provided by macroalgae, and structure-forming invertebrates, such as corals and bryozoans. Marine habitat also includes hydrographic features of the water column such as temperature, salinity, and currents. Characteristics of marine habitat, including spatial and temporal aspects of environmental variability, influence patterns of community biogeography and individual species distribution.

This body of research demonstrates habitat function in Alaska nearshore marine ecosystems with a two-part approach. The first approach investigates how habitat structures nearshore subtidal communities, with a case study in southeast Alaska. The second approach investigates how habitat supports a single species, red king crab *Paralithodes camtschaticus*, through an in-depth study of red king crab early life stage ecology and nursery habitat function.

Chapter 1 of this research takes place in southeast Alaska, a north temperate fjord system in the eastern Gulf of Alaska. Fjord systems form transitions between terrestrial and ocean environments and are common along coastlines that were shaped by glacial ice during geologic history (Farmer & Freeland, 1983; Syvitski *et al.*, 1987). The coastline of southeast Alaska is an intricate landscape with many islands, deep inlets, and interconnected channels. This complex coastal topography leads to environmental variability, most notably between the inner and outer coast regions. For example, the inside waters near the coastal mountain range, where freshwater runoff is concentrated, have estuarine characteristics, whereas the outer coast has greater stability of salinity and temperature with direct influence by the Gulf of Alaska (Pickard, 1967; Murphy & Orsi, 1999).

There is limited quantitative information for shallow subtidal marine communities in southeast Alaska. Furthermore, environmental variability between coastal regions in southeast Alaska has not been quantitatively linked with patterns of species distribution. This study identifies and compares patterns of nearshore subtidal community structure for macroalgae, invertebrate, and fish communities between inner coast and outer coast regions in southeast Alaska, and links patterns of community structure to habitat and environmental variability, at regional and local spatial scales.

The next three chapters form an in-depth investigation of red king crab early life stage ecology and nursery habitat function. Red king crab are a commercially important species distributed throughout the North Pacific that 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 and Kruse, 2000). At present, many red king crab populations throughout Alaska remain depressed, even in areas without a commercial fishery (Woodby *et al.*, 2005; Hebert *et al.*, 2008).

Recruitment success for marine fish and crustaceans depends upon early life stage survival (Wahle and Steneck, 1991; Eggleston and Armstrong, 1995). If we can gain understanding of factors that support red king crab early life stages, then we may better understand conditions that contribute to population fluctuation and recovery for this species. Variability in the marine environment, such as water temperature, affects planktonic larval development for red king crab, and availability of structurally complex benthic habitat is important during settlement and for early juvenile stages (Powell and Nickerson, 1965; Shirley and Shirley, 1989; Stevens and Kittaka, 1998; Loher and Armstrong, 2000), similar to American lobster *Homarus americanus* (Wahle and Steneck, 1991). Ecological field studies of American lobster demonstrated that a habitat-related population bottleneck can occur during the early juvenile stage and affect fishery recruitment (Wahle and Steneck, 1991; Wahle, 2003). It is possible that similar habitat-survival relationships are functioning in Alaska red king crab populations.

Red king crab larval dynamics are poorly understood and have not been studied in southeast Alaska beyond one location during the late 1990s. For Chapter 2 of this research, red king crab larval supply, settlement timing, and settlement habitat availability were investigated during 2008 and 2009 at six locations in northern southeast Alaska. Mechanisms of red king crab habitat associations during the first year post-settlement are an important aspect of red king crab nursery habitat function. Chapter 3 includes laboratory experiments that examine the role of structural habitat complexity and foraging opportunities to drive habitat associations with two sizes of age 0 red king crab. Chapter 4 includes integrated laboratory and field experiments that investigate the effects of habitat structure on survival and refuge response behavior of early juvenile red king crab (age 0 and 1 yr) to determine whether or not habitat choice is influenced by perceived predator threat, whether survival is greatest within habitats of complex structure, and how refuge response behavior may vary between habitats with and without structure and with crab size or age. Crab survival was evaluated in the laboratory with age 1 Pacific cod *Gadus macrocephalus* as a fish predator and with a variety of potential predators at nearshore nursery locations in the field.

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Chapter 1

Comparisons of marine biogeography in a north temperate fjord: subtidal community structure and environmental variability in southeast Alaska[1]

Abstract

Aim This study defines and compares patterns of nearshore, subtidal community structure and environmental gradients between coastal regions of southeast Alaska to explore the processes that structure marine communities in fjord systems. Our research goals were: 1) identify and compare patterns of community structure for macroalgae, invertebrate, and fish communities between inner coast and outer coast regions, and 2) link patterns of community structure to environmental variability at regional and local spatial scales.

Location Northern southeast Alaska, U.S., including the inside waters of Lynn Canal near Juneau (ca. 58° 23' N, 134 ° 38' W) and Sitka Sound on the outer coast near Sitka (ca. 58° 23' N, 134 ° 38' W).

Methods Species assemblage and benthic habitat data were collected by SCUBA surveys at 6 m and 12 m depths (9 sites·region^{-1}) during summer 2007. Hydrographic data (salinity and temperature) were collected using a conductivity-temperature-depth (CTD) meter. Species diversity was compared between regions and depths. Multivariate analysis was applied to reduce the number of environmental variables to major gradients, to resolve community structure, and to relate community structure to environmental gradients of hydrography and benthic habitat at regional and local scales.

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Results The major hydrographic gradient in northern southeast Alaska of decreasing salinity and increasing temperature from the outer coast to the inner coast was associated with regional community structure, with greater species diversity at the outer coast ($p < 0.0001$) at 6 m depth ($p < 0.0001$) with range restriction and overlap for kelps, macroinvertebrates, and small epibenthic invertebrates. Local-scale species distribution for invertebrate communities was linked to variation in benthic habitat, including algae (PC1, 44.4% of algae variation) and substrate (PC2, 23.9% of substrate variation) for small epibenthic invertebrates, and crust and coralline algae on hard substrates (PC2, 23.3% of algae variation) for macroinvertebrates.

Main conclusions We demonstrate that the inner coast and outer coast regions of northern southeast Alaska represent biogeographic areas for shallow subtidal communities, based on relationships with variation in the marine environment between regions. We further demonstrate the influence of benthic habitat in structuring species distribution at the local scale among sites within regions.

1.1 Introduction

Studies that link patterns of marine community structure with environmental gradients develop testable hypotheses about mechanisms that drive ecological processes. This approach is essential for newly studied and data poor regions that lack baselines to identify and evaluate ecosystem shifts with environmental change and disturbance. In this study, we resolve variation of regional community structure and environmental gradients for southeast Alaska, a north temperate fjord system with limited quantitative information for shallow subtidal marine communities (< 20 m depth).

Fjords are the youngest of all estuaries, found in high-latitude mountainous regions worldwide (above 42° N and S latitude and above 56° N in the Scottish Isles) that presently or in the past have supported fluctuating ice fields with valley glaciers (Syvitski *et al.*, 1987). Fjord estuary systems form transitions between terrestrial and ocean environments, where salinity and circulation are due to complex interactions between freshwater input from glaciers and rivers, winds and tides, and local geomorphology, including entrance sills (Hansen & Rattray, 1966; Farmer & Freeland, 1983; Gibbs *et al.*, 2000). Common hydrographic features of fjords include a low salinity surface layer that decreases towards the entrance, saltwater intrusion at depth near the entrance, circulation fronts from colliding water masses, and strong along-shore currents that shape the local oceanographic environment (Farmer & Freeland, 1983; Syvitski *et al.*, 1987).

Spatial patterns of marine communities in fjords reflect the influence of many environmental variables, including salinity, temperature, dissolved oxygen, seafloor habitat, sedimentation, and exposure to winds and wave action (e.g., Farrow *et al.*, 1983; Buhl-Mortensen & Hoisaeter, 1993; Smith & Witman, 1999; Zacharias & Roff, 2001; Fetzer *et al.*, 2002; Josefson & Hansen, 2004). Such patterns have been observed in the fjord environments of Canada (Levings *et al.*, 1983; Leys *et al.*, 2004), the North Sea (Middelboe *et al.*, 1998; Middelboe & Sand-Jensen, 2004), Norwegian coast (Gulliksen, 1980; Jensen *et al.*, 1985), New Zealand (Kregting & Gibbs, 2006; Miller *et al.*, 2006), Patagonia (Haussermann & Forsterra, 2007), the sub-Antarctic islands (Barnes *et al.*, 2006), and the Arctic (Wlodarska-Kowalczuk *et al.*, 2005). These variables exhibit gradients that affect species interactions, including predation (Witman & Grange, 1998), competition (Menge & Sutherland, 1987), and habitat facilitation (Bertness & Callaway, 1994) to further influence patterns of community structure.

Southeast Alaska is a northern temperate region where glacial ice and erosion has created an intricate fjord landscape with many islands, deep inlets, and interconnected channels (Figure 1.1). Storms associated with the Aleutian Low collide with the high coastal mountain range providing ample precipitation throughout the year (Wilson & Overland, 1987). This precipitation is stored as snow in the winter creating an ideal environment for ice formation resulting in extensive ice fields and glaciers (Powell & Molnia, 1989; Meigs & Sauber, 2000). Glacial fluctuations that shaped this region throughout geologic history include the advance and retreat of the Wisconsin-Laurentide Ice Sheet that extended seaward to the continental shelf during the last glacial maximum (ca. 10,000-12,000 BP), and the most recent glacial advance during the Little Ice Age (ca. 1400 AD) (Goldthwait, 1963; Calkin *et al.*, 2001). Glacier Bay (Figure 1.1) was ice-covered just over 200 years ago when first surveyed in 1794 by George Vancouver (Goldthwait, 1963).

The complex coastal topography of southeast Alaska leads to environmental variability, most notably between the inner coast and outer coast regions. We refer to the interior islands and waters adjacent to the coast range as the inner coast region. The inner coast includes Lynn Canal, the deepest fjord in North America, with depths exceeding 900 m, and a fault trace that extends the length of Chatham Strait (Martin & Williams, 1924; Brew *et al.*, 1991) (Figure 1.1). The outer coast region includes the outermost islands and waters directly connected to the Gulf of Alaska, including Sitka Sound (Figure 1.1). In southeast Alaska the gradient of freshwater discharge is from the interior coastal mountain range to the outer coast (Weingartner *et al.*, 2009). Freshwater runoff is seasonally most pronounced during the spring and autumn causing water column stratification that is strongest near freshwater discharge sites (Pickard, 1967; Royer, 1982; Weingartner *et al.*, 2009). The inside coastal waters, where this runoff is concentrated, have estuarine characteristics, whereas the outer coast has greater stability of salinity and temperature, directly influenced by the Gulf of Alaska (Pickard, 1967; Murphy & Orsi, 1999).

How marine community structure reflects variation in the marine environment of southeast Alaska is poorly understood. Previous observational studies identify differences in species assemblage structure for nearshore fishes (Quast, 1968; Murphy *et al.*, 2000), rocky intertidal fauna (O'Clair & O'Clair, 1998), and algae (Lindstrom, 2006; Lindstrom, 2009) between the outer coast and the inside coast, with further separation between the northern and southern inside coast at the Kuiu-Kuprenof-Mitkoff Island complex in central southeast Alaska (Figure 1.1) and Ketchikan to the south. However, these observations are not quantitatively linked to environmental variability between coastal regions. We use a community-level multivariate approach and a variety of diversity measures to define and compare patterns of marine community structure and environmental gradients between coastal regions of northern southeast Alaska to explore the processes that structure marine communities in this fjord system. Two goals of this research are to 1) identify and compare patterns of nearshore subtidal community structure between the inside coast and outer coast regions, and 2) link patterns of community structure to environmental variables, including temperature, salinity, and benthic habitat.

1.2 Materials and Methods

1.2.1 Study Location

This study was conducted in northern southeast Alaska near Juneau (ca. 58° 23' N, 134° 38' W, North American Datum of 1983) located on the inside coast, and Sitka (ca. 57° 02' N, 135° 21' W) on the outer coast (Figure 1.1). Our locations were selected to represent maximum variation between coastal regions with terrestrial and ocean influence. Study sites were selected to maximize the variety of habitat features sampled and included protected embayments and exposed rock reefs. A total of nine study sites were established at the inner coast near Juneau and nine at the outer coast near Sitka (Table 1.1 and Figure 1.1).

1.2.2 Data Collection

SCUBA surveys were conducted at study sites along two transects (25 m x 1 m) parallel to shore at 6 m and 12 m depth, during the summer months of June-August 2007. These depths were chosen to capture the area of the shallow subtidal zone just deeper than the transition with the low intertidal zone in Alaska and shallower than depths where subtidal macroalgae are limited. These depths were also easily accessible to divers. Benthic habitat was characterized by the physical seafloor substrates as well as the percent cover and species of benthic algae. Substrate composition was characterized along transects as areas of uniform substrate type, using a two-code system with the following categories: rock with vertical relief (R); flat bedrock (F); boulder (B) (> 25.5 cm); cobble (C) (6.5-25.5 cm); pebble (P) (2-6.5 cm); gravel (G) (2-4 mm); sand (S) (grains distinguishable); and mud (M) (Stein *et al.*, 1992; Greene *et al.*, 1999). The first code represented 50-80% of the substrate composition, and the second code represented 20-50% (e.g., RS is at least 50% rock and at least 20% sand, and RR is > 80% rock). Total percent cover of algae was estimated within each area of uniform substrate type by the following groups: greens, reds, coralline, crusts, understory browns and kelps, and canopy kelps.

Community composition was quantified for macroalgae, fishes, macroinvertebrates, and small epibenthic invertebrates. Individuals were identified to species or the lowest taxonomic level possible in the field and verified with photographs or voucher specimens as necessary. All individual kelps, fishes, and macroinvertebrates were counted along transects. Quadrats (0.30 x 0.30 m) were placed at 10 random points along transects to count small epibenthic invertebrates. Both invertebrate communities included epibenthic taxa that were sessile and mobile. Macroinvertebrates could be counted along transects and were generally > 5 cm in size. Small epibenthic invertebrates were too small to be counted at the scale of the transect and were generally < 5 cm in size. We do not assert a functional difference between invertebrate groups at the size threshold of our counting methods. Rather, these groups were analyzed separately because species associations with benthic habitat features are influenced by body size (e.g., Caddy, 1986) and functional relationships may exist within the size thresholds distinguished by our methods. Counts of individual taxa along each transect were used in community analysis.

Conductivity and temperature were sampled once at each site in July 2007. We sampled the vertical dimension of the water column from the surface to 25 m depth on an outgoing tide using a Seabird SBE 25 CTD with an automated 2 s sampling interval. CTD data were processed into bins of 0.5 m depth, and conductivity was converted to salinity.

1.2.3 Data Analysis

We determined species richness, species diversity, and evenness as components of community structure for species with positive taxonomic classification. Taxa that could not be identified to species were not included, such as genera and undefined taxonomic groups (Appendix 1.0). Species richness (s) was calculated as the total count of species found along dive surveys for sites and regions. The Shannon-Weiner Diversity index $(H' = -\sum_{i=1}^{s} p_i \cdot \ln p_i)$ was calculated as a measure of species alpha diversity (Gray, 2000), using the proportional abundance $(p_i = \frac{n_i}{N})$ of species at sites and regions, where (n_i) is the number of individuals of a species and (N) is the total number of individuals of all species. Community evenness $(E_H = H' / H_{\max})$ was calculated from species diversity estimates as the relative abundance of species within a community, where $H_{\max} = \ln s$ (Pielou, 1969). The relative abundance and diversity of species was represented by plotting a species relative abundance against its rank in abundance (Hill, 1973). Rank-abundance curves presented differences in community structure between regions, and the slope of the curve is related to community evenness (E_H), with a steeper slope reflecting lower evenness of individual species distribution within that community. Species diversity (H') was compared between locations and depths using the Shannon t-test ($\alpha = 0.05$) (Hutcheson, 1970). The Bonferroni correction $(\alpha' = \alpha / k)$ for multiple tests was applied to adjust the experiment-wide error rate for a total of six tests (k) for each community $(\alpha' = 0.008)$.

Temperature and salinity measurements were compared between regions and depths using point measurements at the depth of dive surveys at 6 m and 12 m depth from CTD casts at each study site. Temperature was compared using a two-factor General Linear Model (GLM) ($\alpha = 0.05$). Salinity was compared using Welch's ANOVA because the assumption of equality of variances could not be met by Bartlett's or Levene's test ($p < 0.05$). Temperature and salinity measurements at the surface (0.5 m depth) were compared between regions using a single-factor GLM. Univariate analysis was conducted using SAS 9.2 (SAS Institute, Inc.).

Many potentially correlated benthic habitat variables were reduced to the most influential gradients using Principal Component Analysis (PCA). Variables were log-transformed $(\log_{10}(x+1))$ to reduce the influence of outliers and standardized (mean = 0, standard deviation = 1) to compare variables of different scale. PCA was applied separately to percent cover estimates of substrate (rock, boulder, cobble, pebble, gravel, sand, and mud) and algae (red, brown, canopy, crusts, and coralline).

Spatial variation in community structure was resolved using multivariate analysis, which is more accurate to characterize community structure than diversity measures alone (Gray, 2000). Detrended Correspondence Analysis (DCA) is an unconstrained ordination technique that provides simultaneous ordination of sites and species along multivariate dimensions to identify major gradients in ecological data (Hill & Gauch, 1980). DCA was run separately for kelps (n = 14), fishes (n = 12), macroinvertebrates (n

= 26), and small epibenthic invertebrates (*n* = 58), using log-transformed counts of species and taxonomic groups from 34 surveys. Preliminary analysis of the diversity metrics with species and taxonomic groups indicated that the results did not change when conducting the analysis with species only. For this reason, taxonomic groups were included in DCA that were not included in the species diversity analysis, as many of these groups were specific to one region or to one habitat type and were helpful to resolve community structure by ordination. Species or taxa with greater than one observation were included in DCA because rare species are problematic with ordination (Appendix 1.0). Due to the occurrence of many rare small epibenthic invertebrates from quadrat counts, only species or taxa with at least 0.1% of the total abundance of all taxa for this community were used in the analysis. DCA works well with unimodal species response curves along environmental gradients. Environmental data can be related to DCA ordination as vectors that describe significantly correlated environmental gradients with species groups (Oksanen *et al.*, 2006). Environmental vectors were fitted to DCA ordinations by permutation analysis (1000 permutations, $\alpha = 0.05$) using six environmental variables. The environmental variables were point measurements of temperature and salinity at 6 m and 12 m depth from CTD casts at the depth of dive surveys, and multivariate scores from the first and second principal components for substrate and algae that described gradients of benthic habitat. DCA scores for sites and species were summarized in ordination plots with vectors of significant environmental gradients. Multivariate analyses were conducted using R (R Development Core Team). DCA and vector permutation tests were run using the R package Vegan (Oksanen *et al.*, 2006).

1.3 Results

1.3.1 Biodiversity and Community Structure

We identified 135 species, consisting of 13 kelps, 15 fishes, 26 macroinvertebrates, and 75 small epibenthic invertebrates (Appendix 1.0). In addition, 44 taxonomic groups were identified, including 1 kelp, 10 fishes, 11 macroinvertebrates, and 22 small epibenthic invertebrates (Appendix 1.0). The diversity indices demonstrated that these communities had different species richness (s), species diversity (H'), and community evenness (E_H) between coastal regions and depths (Table 1.2). Outer coast communities in general had higher species diversity (H') than inner coast communities ($p < 0.0001$) at 6 m depth ($p < 0.0001$), except for fish where species diversity was not significantly different (Table 1.3). Macroinvertebrate diversity was greater at 12 m depth at the inner coast ($df = 3$, $t = 14.98$, $p = 0.004$). Community evenness was lower for all groups at the inner coast than the outer coast region due to relative differences in species dominance within each community in these regions (Figure 1.2). Dominance by one or more species resulted in decreased evenness within regions or depths, reflected by a steep drop in slope of the species rank abundance curve with kelps (Table 1.2). Rank abundance curves were relatively similar between regions for the other communities despite significant differences in species diversity for most communities between regions (Figure 1.2 and Table 1.3).

The inner coast macroalgae community included a total of seven kelps ($H' = 1.03$, $E_H = 0.53$), with seven observed at 6 m depth and three at 12 m depth (Table 1.2 and Appendix 1.0). The outer coast macroalgae community was composed of 12 kelps ($H' = 1.75$, $E_H = 0.70$), with nine observed at 6 m and six at 12 m depth (Table 1.2 and Appendix 1.0). The outer coast kelp community had higher species diversity ($df = 1064$, $t = 15.11$, $p < 0.0001$) than the inner coast, driven by greater diversity of kelps at the outer coast at 6 m depth ($df = 958$, $t = 10.70$, $p < 0.0001$) and dominance by three species at the inner coast that decreased relative evenness for this region (Table 1.3 and Figure

1.2 a). The three dominant inner coast kelps were *Saccharina subsimplex* (n = 631, p_i = 54.5%), *Agarum clathratum* (n = 385, p_i = 33.3%), and *Laminaria yezoensis* (n = 119, p_i = 10.3%). Kelps belonging to *Desmarestia spp.* were *D. aculeata* and *D. viridis* that could not be positively identified in the field and included a total of 106 individuals and 8.4% of individual kelps observed in this region. Kelps found exclusively at the inner coast, included *Alaria fistulosa* and *Desmarestia spp. Saccharina subsimplex* (n = 306, p_i = 46.8%) was the most abundant outer coast kelp, though the proportional abundance of kelps in this community was more evenly distributed than the inner coast community, consistent with greater observed diversity and evenness (Figure 1.2 a). Half (50%) of the kelps observed at the outer coast were from species only found in that region, including giant kelp *Macrocystis integrifolia* and *Pleurophycus gardneri.*

The inner coast fish community included 14 fishes (H' = 1.72, E_H = 0.65), with nine observed at 6 m depth and six at 12 m depth (Table 1.2 and Appendix 1.0). The outer coast fish community included 12 fishes (H' = 1.86, E_H = 0.75), with nine observed at 6 m depth and seven at 12 m depth (Table 1.2 and Appendix 1.0). The inner coast fish community was dominated by rock sole *Lepidopsetta bilineata* (n = 38, p_i = 52.1%), occurring at the deeper survey depth (12 m) at four of nine sites (Figure 1.2 b). Several sculpins (Cottidae) were observed at the inner coast, and certain species like Northern ronquil *Ronquilus jordani* and Arctic shanny *Stichaeus punctatus* were relatively common. Quillback rockfish *Sebastes maliger* was the only rockfish *Sebastes spp.* observed from inner coast surveys. Rockfishes found at outer coast shallow subtidal depths included quillback, copper *Sebastes caurinus*, and black rockfish *S. melanops*, in addition to schools of undefined juveniles (n = 78, 58.2% of observations) and many more were observed in the distance off-transect and were not counted. Several fish species were observed exclusively in one region, and many were observed only once (Figure 1.2 b, Appendix 1.0). This included nine fishes found only at the inner coast, 64.3% of observed fish species at that region, and seven species at the outer coast (58.3%). It should be noted that several fish species occur within respective regions at shallow subtidal depths, but were not observed on our dive surveys, including dark dusky rockfish *S. ciliatus* at the inner coast, and wolf eel *Anarrhichthys ocellatus* at the outer coast.

The inner coast macroinvertebrate community was composed of 18 taxa ($H' = 1.16$, $E_H = 0.40$), including 14 at 6 m depth and 11 at 12 m depth (Table 1.2 and Appendix 1.0). Outer coast macroinvertebrates included 17 taxa ($H' = 1.71$, $E_H = 0.61$), with 11 observed at 6 m depth and 13 at 12 m depth (Table 1.2 and Appendix 1.0). Higher species diversity was observed at the outer coast ($df = 608$, $t = 7.33$, $p < 0.0001$) at 6 m depth ($df = 145$, $t = 14.58$, $p < 0.0001$) (Table 1.3). However, within regions, macroinvertebrate diversity was higher at 12 m depth ($df = 3$, $t = 14.98$, $p < 0.004$) at the inner coast (Table 1.3). Dominance by green urchins *Strongylocentrotus droebachiensis* at the inner coast region at 6 m depth contributed to lower species diversity and lower evenness, as this species was an order of magnitude greater in abundance ($n = 877$, $p_i = 70.4\%$) than the second and third most abundant species, the red cucumber *Cucumaria miniata* ($n = 133$, $p_i = 10.6\%$) and the seastar *Evasterias troschelii* ($n = 93$, $p_i = 7.4\%$) (Figure 1.2 c). The outer coast community was dominated by the sand anemone *Pachycerianthus fimbriatus* ($n = 175$, $p_i = 50.7\%$), a Cerianthid that formed dense aggregations at protected sites in silty-sand habitats, followed by sunflower star *Pycnopodia helianthoides* ($n = 44$, $p_i = 12.8\%$), and giant cucumber *Parastichopus californicus* ($n = 31$, $p_i = 9\%$) (Figure 1.2 c). *Chlamys spp.* scallops, including *C. rubida* and *C. hastata*, were abundant at the outer coast ($n = 49$, 11.4% of observed macroinvertebrates) and could not be distinguished in the field due encrusting sponges and bryozoan. Macroinvertebrates found exclusively at the outer coast included 47.1% of observed species, compared to 50% of species at the inner coast. Several species of crab were observed at the inner coast, including Dungeness crab *Cancer magister*, lyre crab *Hyas lyratus*, graceful decorator crab *Oregonia gracilis*, helmet crab *Telmessus cheiragonus*, two large hermits of the genus *Elassochirus*, *E. gilli* and *E. tenuimanus*, and small undefined hermit crabs, but few were observed at the outer coast, including helmet crab and small undefined hermit crabs (Appendix 1.0). Red urchins *Strongylocentrotus franciscanus* were exclusive to the outer coast and green urchins were only observed at inner coast sites (Appendix 1.0).

The inner coast community of small epibenthic invertebrates included 45 taxa (H' = 2.46, E_H = 0.65), with 30 at 6 m depth and 29 at 12 m depth (Table 1.2 and Appendix 1.0). Outer coast small epibenthic invertebrates included 57 taxa (H' = 2.85, E_H = 0.70), with 42 at 6 m depth and 31 at 12 m depth (Table 1.2 and Appendix 1.0). Species diversity for this community was higher at the outer coast region (df = 2773, t = 8.71, p < 0.0001) at 6 m depth (df = 1364, t = 2.94, p < 0.0001) (Table 1.3). Three species comprised more than half (56.3%) of total abundance of the inner coast community, including the snail *Margarites pupillis*, the red trumpet calcareous tube-worm *Serpula columbiana*, and a nudibranch *Onchidoris muricata* that was numerous at one site (Figure 1.2 d). Four species accounted for more than half (51.5%) of the abundance of small epibenthic invertebrates at the outer coast, including the green phoronid *Phoronopsis harmeri* that was abundant at deeper depths at two sites, *S. columbiana*, *M. pupillis*, and the orange cup-coral *Balanophyllia elegans* (Appendix 1.0). It should be noted that the small difference in community evenness between regions may not be that meaningful because there was relatively little difference in the shape of the rank abundance curves between regions for this community (Figure 1.2 d). A variety of undetermined small hermit crabs comprised 13.9% of all individuals observed in this community at the outer coast. A total of 18 species (40%) were exclusively observed at inner coast sites, and 30 species were only found at the outer coast accounting for 52.6% of species richness for this community at this region (Appendix 1.0).

1.3.2 Environmental Gradients and Community Structure

Temperature and salinity varied between regions and survey depths, measured during the summer month of July. Temperature was greater at the inner coast (df = 1, F = 9.79, p = 0.004) and at the shallow 6 m survey depth (df = 1, F = 6.45, p = 0.02) (Figure 1.3 a). Inner coast temperature at 6 m depth was (mean ± SE) 10.2 °C (± 0.4) and 9.0 °C (± 0.2) at the deeper 12 m survey depth. Temperature at the outer coast was 8.7 °C (± 0.4) at 6 m depth and 7.9 °C (± 0.5) at 12 m depth. Temperature near the surface (0.5 m depth) was not significantly different between inner coast (12.5 °C ± 0.4) and outer coast (12.3 °C ± 0.3) regions, although temperature decreased more rapidly with depth at the outer coast (Figure 1.3 a). In contrast, salinity was greater at the outer coast with less variability than the estuarine waters of the inner coast ($df = 1$, $F = 76.79$, $p < 0.0001$) (Figure 1.3 b). Inner coast salinity at 6 m depth was (mean ± SE) 26.9 (± 0.5) and 29.2 (± 0.2) at 12 m depth. Outer coast salinity at 6 m depth was 31.4 (± 0.1) and 31.5 (± < 0.1) at 12 m depth. Salinity near the surface (0.5 m depth) was significantly greater at the outer coast (24.7 ± 2.1) ($df = 1$, $F = 19.33$, $p < 0.001$) and the salinity profile was much steeper with the halocline to 1.5 m depth (Figure 1.3 b). Surface stratification was present at inner coast sites where salinity near the surface (0.5 m depth) was 13.6 (± 1.5). Brackish waters (salinity of 9-17) were present from 1-6 meters depth among inner coast sites and the halocline extended to 9 m depth (Figure 1.3 b).

Benthic habitat variability was described by physical seafloor substrate and algae composition. The first and second principal components for substrate percent cover accounted for 29.7% and 23.9% of the total variability in substrate composition among benthic habitats at study sites. The first major gradient for substrate was between benthic habitats with mud and gravel and those composed of sand and other hard substrates (Table 1.4, PC1). The second gradient further separated benthic habitats composed of sand and pebble substrates from those with hard substrates dominated by rock, boulder, and cobble (Table 1.4, PC2). The first and second principal components for algae percent cover described 44.4% and 23.3% of the total variability in algae composition among benthic habitats. The first major gradient distinguished benthic habitats with little algal cover from those with extensive algal cover (Table 1.4, PC1). The second gradient was between benthic habitats with substrates predominantly covered with crustose and coralline algae (i.e., exposed hard substrates) to benthic habitats with other algae types, such as understory reds, browns and canopy kelps (Table 1.4, PC2). Major gradients of benthic habitat composition and hydrographic gradients of salinity and temperature were associated with changes in community structure (Table 1.5).

Ordination of the first and second dimensions from Detrended Correspondence Analysis (DCA1 and DCA2) for kelp community structure described 100% and 58.4% of the respective variation in kelp community structure along these dimensions. Ordination by DCA1 and DCA2 resulted in most sites and kelps clustering around the origin, so we did not use this ordination to further examine kelp community structure. However, one interesting source of variation in kelp community structure was demonstrated with DCA1 and DCA2 at two sites with associated kelps that were not observed elsewhere in this study. Sites and kelps driving this pattern included one inner coast site, a current swept boulder field dominated by bull kelp *Nereocystis luetkeana* (site 14), and one outer coast site, an exposed rocky pinnacle with bull kelp, *P. gardneri, Alaria marginata*, and *Desmarestia ligulata* (site 1) (Figure 1.1 and Appendix 1.0).

Major variation in kelp community structure, described by DCA3 and DCA4, accounted for 55.9% and 34.5% of the respective variability along those dimensions. Hydrographic gradients of salinity ($r^2 = 0.43$, $p = 0.001$) and temperature ($r^2 = 0.35$, $p = 0.02$) were significantly correlated with kelp community structure, and substrate and algae cover were not (Table 1.5). Regional variation for this community was most clearly separated along DCA3, reflecting salinity and temperature gradients (Figure 1.4). Inner coast sites and kelps occurring at those locations such as *Desmarestia spp.* and *A. clathratum* were described by negative values of DCA3, higher temperature, and lower salinity (Figure 1.4). Outer coast sites and kelps such as giant kelp and *Costaria costata* were described by positive values of DCA3, lower temperature, and higher salinity (Figure 1.4). Depth was not a major source of variation in kelp community structure at our survey sites. However, local variability with inner coast kelps was present, displayed along DCA4, though the source of this local variation was not determined (Figure 1.4).

We did not have sufficient sample size to resolve fish community structure by multivariate analysis. Many fish species identified from dive surveys were observed only once (Appendix 1.0), and many rare species are known to be problematic with ordination techniques so many fishes were excluded from the analysis. Although fish community structure was not resolved by DCA, salinity was a significant hydrographic gradient as a result of permutation analysis of species scores with environmental variables ($r^2 = 0.46$, $p < 0.01$) (Table 1.5).

Macroinvertebrate community structure was described by DCA1 and DCA2 that accounted for 67.6% and 55.3% of the respective variability along these dimensions. Significantly correlated environmental gradients were salinity ($r^2 = 0.63$, $p < 0.001$) and algae cover (PC2) ($r^2 = 0.25$, $p = 0.04$), but not substrate (Table 1.5). Regional-scale variation in macroinvertebrate communities between regions was represented along DCA2 and the salinity gradient, with higher salinity at the outer coast (Figure 1.5). Local-scale variation for macroinvertebrates among sites within regions was separated along DCA1 and the benthic habitat gradient of algae composition (PC2) (Figure 1.5). Local-scale community structure between 6 m and 12 m depths at the inner coast only is also reflected by DCA1 (Figure 1.5). Maximum values of the algae cover gradient represented benthic habitats with coralline and crustose algae cover on hard substrates such as rock reef, boulders, and cobbles. In the opposing direction, this gradient represented benthic habitats with little to no algae cover with mud and sand substrates. Representative outer coast macroinvertebrates included red urchins, the seastars *Orthasterias koehleri*, *Henricia spp.*, and *Mediaster spp.*, and a variety of brittle stars and tunicates (Figure 1.5 and Appendix 1.0). The inner coast macroinvertebrate community included several crabs, such as Dungeness crab, lyre crab, helmet crab, and a variety of hermit crabs (Figure 1.5 and Appendix 1.0).

Community structure for small, epibenthic invertebrates was described by DCA1 and DCA2 that accounted for 43.2% and 37.1% of the respective variation along these dimensions. Environmental variability appeared to greatly influence regional and local-scale patterns for this community. These gradients in decreasing order of correlation strength were algae cover (PC1) ($r^2 = 0.57$, $p < 0.001$), salinity ($r^2 = 0.53$, $p < 0.001$), substrate composition (PC2) ($r^2 = 0.39$, $p < 0.01$), and temperature ($r^2 = 0.31$, $p < 0.01$) (Table 1.5 and Figure 1.6). Regional-scale variation in small epibenthic invertebrate communities was best described by DCA2, and gradients of salinity and temperature, with higher salinity and lower temperatures at the outer coast (Figure 1.6). Local-scale variability with small epibenthic invertebrates was represented along DCA1 where differences among 6 m and 12 m depths were reflected for some sites at the inner coast where temperature overall was greater at 6 m than 12 m depth for this region (Figure 1.6). Local-scale patterns for this community were represented by benthic habitat gradients of algae (PC1) and substrate composition (PC2) (Figure 1.6). The algae cover gradient represented a continuum of benthic habitats with little algae cover at maximum values to extensive algae cover (Figure 1.6). The gradient of substrate composition represented benthic habitats with sand and pebble substrates at maximum values, found mainly at the outer coast, to benthic habitats with hard substrates such as rock reef, boulders, and cobbles (Figure 1.6). Small epibenthic invertebrates representative of outer coast sites with pebble and sand substrates and less algae cover were sand anemone, green phoronid, and gray brittle star *Ophiura lutkeni* (Figure 1.6 and Appendix 1.0). Outer coast sites with rock reef, boulder, and cobble substrates and extensive algae cover were inhabited by species such as red soft coral *Gersemia rubiformis*, orange cup coral, blood stars *Henricia leviuscula*, and top snails *Calliostoma spp.* (Figure 1.6 and Appendix 1.0). In comparison, inner coast sites with hard substrates and extensive algae cover were inhabited by false jingles *Pododesmus macrochisma*, a variety of lined chitons *Tonicella spp.*, dogwinkles *Nucella lamellosa*, and checkered hairy snails *Trichotropsis cancellata* (Figure 1.6 and Appendix 1.0).

1.4 Discussion

1.4.1 Processes Structuring Biodiversity

Our study defines patterns of marine biogeography in northern southeast Alaska and links those quantitatively to environmental variability at regional and local spatial scales. Salinity and temperature describe patterns of shallow subtidal community structure between the inner coast and outer coast regions. Local-scale patterns of species assemblages at our study sites are structured by benthic habitat variability that includes physical seafloor substrate and algae composition.

The high-latitude fjord regions have common hydrographic features that similarly structure biodiversity in these systems. Our study demonstrated greater salinity and lower temperature at the outer coast of northern southeast Alaska with less variability in salinity at shallow subtidal depths than the inner coast region. These hydrographic features described regional community structure with greater species richness, diversity, and community evenness at the outer coast. Our results for salinity and temperature were consistent with observations at the inner and outer coast of southeast Alaska in 1997-98 (Murphy & Orsi, 1999) and in 1964-66 (Pickard, 1967), suggesting that the major gradient of freshwater discharge from the coast to the open ocean is persistent in this fjord system. The physical oceanographic processes that influence intertidal species assemblage structure along the fjord coast of British Columbia, Canada are quite similar to southeast Alaska. The major hydrographic gradient was decreasing salinity and increasing temperature with less variability from the outer to inner coast of British Columbia, linked to greater species diversity of intertidal algae and fauna on the outer coast. Gradients of salinity and temperature, in addition to dissolved oxygen at deeper depths, influence regional patterns of algae and benthic invertebrates in the estuaries of the North Sea (Middelboe *et al.*, 1998; Josefson & Hansen, 2004; Middelboe & Sand-Jensen, 2004; Josefson, 2009), and along the fjord coasts of Norway (Gulliksen, 1980; Jensen *et al.*, 1985) and New Zealand (Wing *et al.*, 2003; Kregting & Gibbs, 2006).

Surface water stratification likely structures shallow subtidal communities between regions and may explain a large part of the variation between regional species groups related to salinity and temperature. A characteristic feature of many fjords is a low salinity surface layer that forms due to heavy precipitation and melting snow and ice. Surface stratification was present at inner coast sites during our summer surveys, where the depth of the halocline was approximately 9 m and the extent of the low salinity layer of brackish water (salinity of 9-17) was from 1-6 m depth and visible to divers as a discontinuity of water densities. Water column stratification near the surface was not present at outer coast sites where surface salinity (0.5 m depth) was much greater than inner coast sites and the halocline was to approximately 1.5 m depth.

Our results demonstrated greater species richness and diversity at the outer coast at the 6 m survey depth that was within the range of the halocline and the low salinity surface layer present at the inner coast. Certain species that occurred at the outer coast at 6 m depth may have been excluded from the inner coast due to the low surface salinities, including red soft coral, orange cup coral, sand anemone, and green phoronid. Similarly, the upper depth limit of the black coral *Antipathes fiordensis* in New Zealand fjords was determined by the lower depth of low salinities in the upper water column (Kregting & Gibbs, 2006). The low salinity layer is the primary process structuring steep, rock wall communities in New Zealand fjords where this feature is semi-permanent, fluctuating with extreme rainfall events (e.g., 0.5 $m \cdot day^{-1}$), and typically ranging from 3-5 m depth with salinities from 0-14 (Witman & Grange, 1998; Gibbs *et al.*, 2000). Distinct subtidal community zonation is present in the New Zealand fjord region to 18 m depth (Smith & Witman, 1999). The low salinity surface layer at the inner coast of southeast Alaska had similarities to New Zealand fjords, though the low salinity layer was a brackish halocline during our summer study, rather than a fresh to brackish water lens, and we did not identify such distinct vertical zonation patterns with subtidal communities.

Regional distribution patterns of Echinoderms, including seastars and urchins, likely reflected salinity thresholds that may have facilitated competitive dominance for certain species within coastal regions in southeast Alaska. Low salinity is not tolerable to many Echinoderms (e.g., Stickle & Ahokas, 1974; Watts & Lawrence, 1990). In our study, *E. troschelii* was the dominant seastar at the inner coast, potentially due to greater tolerance for lower salinity than seastars that were only observed at the outer coast. In contrast, *E. troschelii* was infrequently observed at the outer coast where other seastars may have been competitively dominant. For example, *Pisaster ochraceus* has been characterized as the dominant seastar in rocky intertidal habitats at the outer coast of northern southeast Alaska (O'Clair & O'Clair, 1998). We demonstrate that *P. ochraceus* was not present at the inner coast where *E. troschelii* was the dominant seastar. *Pisaster ochraceus* has reduced predation at lower salinities and temperatures (Sanford, 1999; Held & Harley, 2009) as a keystone species along the northwest Pacific coastline (Paine, 1966). Similarly, the upper depth limit of seastar predation was restricted by low surface salinity in New Zealand fjords (Witman & Grange, 1998).

Major gradients of benthic habitat were strongly related to species distribution patterns for macroinvertebrates and small epibenthic invertebrates that occupied a variety of benthic habitats in our study. These patterns were most clearly resolved at local spatial scales among sites within regions. Distribution patterns for small epibenthic invertebrates reflected variation in substrate composition among some outer coast sites where sand and pebbles were common, in contrast to certain inner coast sites where these substrates were replaced by mud composed of glacial silt and organic matter often mixed with other fine-grain substrates. The presence or absence of algae cover was a major source of variation linked to invertebrate distribution, and specifically crusts and coralline algae for macroinvertebrates. We found that algae cover was a more distinguishing benthic habitat attribute for invertebrates than physical seafloor substrate alone, and implicit in the significance of algae cover was the presence or absence of hard substrates to which algae and certain invertebrates were attached.

Separating the invertebrate groups in our analysis based on the potential for invertebrates of small and large sizes to occupy different habitat features, based on the size threshold of our sampling methods, resulted in habitat use patterns reflecting different sources of habitat variation. Functional differences in habitat use based on invertebrate body size were not determined by our study, but may be present for certain taxa that occupy microhabitat features where body size may influence benthic habitat use. The importance of benthic habitat in structuring marine fauna has been demonstrated for the contiguous fjords of British Columbia, Canada, where the presence of algae cover, seagrasses, and substrate type influence species distribution at intertidal and shallow subtidal habitats (Levings *et al.*, 1983).

Algae cover provided biogenic structure that was additional to the seafloor substrate to form highly structured benthic habitat for associated fauna at certain study sites. Giant kelp and sub-canopy kelps at the outer coast created biogenic habitat for black rockfish, and grazing prosobranch gastropods like *Tegula puligo* and *Lacuna vincta*, while bull kelp created similar sub-canopy and canopy structure at current-swept locations at the inner coast. Understory algae in both regions, including *Saccharina spp.*, *L. yezoensis*, and *A. clathratum* formed dense structure for associated fauna, including urchins, the snail *M. pupillis*, and fishes such as gunnels, ronquils, and pricklebacks. Other studies in southeast Alaska (Murphy *et al.*, 2000; Johnson *et al.*, 2003; Calvert-Siddon *et al.*, 2008) and in southcentral Alaska (Dean *et al.*, 2000; Hamilton & Konar, 2007) demonstrated demersal fishes, greenlings, and juveniles of Pacific cod *Gadus macrocephalus* and rockfishes were associated with understory and canopy kelps that persisted seasonally or perennially in these locations.

The most common habitat-forming kelp encountered in our study was *S. subsimplex* that demonstrated variation in blade morphology between regions where it was common in rocky habitats and protected bays at shallow transect depths (6 m). Individuals at the inner coast had round and elongated blade morphology and formed dense, upright cover as part of the understory macroalgae assemblage. Individuals at the outer coast had elongated blades that were much greater in length (> 3 m), and draped over the substrate to deeper transect depths (> 12 m) often obscuring the underlying seafloor substrates. *S. latissima* also demonstrated this form where it co-occurred with *S. subsimplex* at the outer coast. The competitive dominance by *S. subsimplex* at certain southeast Alaska sites may result from morphology and life cycle strategy (Duggins, 1980). Kelp morphology can be driven by environmental variation such as water motion, light attenuation, and nutrient availability (Gerard & Mann, 1979; Dayton, 1985; Eckman *et al.*, 1989; Dayton *et al.*, 1999). It is possible that outer coast environmental conditions resulted in the elongated blade morphology observed at these sites. Outer coast conditions may also explain the considerable presence of canopy-forming giant kelp, as *Macrocystis spp.* are adapted for exploitative resource competition (Dayton, 1985). Morphological variation of habitat-forming kelps will affect structural habitat availability and the distribution of macroalgae associated fauna. The ecological consequences of macroalgae habitats to marine communities in this north temperate fjord region remain largely unexplored.

1.4.2 Regional Biogeography

We demonstrated biogeographic distinction between the outer and inner coast regions of northern southeast Alaska for shallow subtidal macroalgae, invertebrate, and fish communities. We observed that several taxa within each community occurred in both regions, but most taxa were either more abundant in one region or observed in one region only. This was demonstrated for kelps, where most taxa observed at the inner coast also occurred at the outer coast, but half of the kelp species that were observed at the outer coast only occurred in that region, such as giant kelp. Southeast Alaska has a more diverse macroalgae community than any other Alaska region (Lindstrom, 2006; Lindstrom, 2009).

In contrast to macroalgae, there is little comparative biogeographic information for invertebrate communities inhabiting shallow subtidal habitats fringing the deeper fjord basins of southeast Alaska. We demonstrated that macroinvertebrates and small epibenthic invertebrates had overlap in species distribution between coastal regions, but several species were distinct to one region, such as the snail *T. puligo* that associates with giant kelp canopy structure. Shallow subtidal invertebrates are understudied in this region, and consequently the ecology of many species is poorly understood.

Because we encountered few fish, SCUBA surveys may not be the best approach to properly represent the fish community at shallow subtidal depths in our study area. For the fish community, more than half of the taxa observed by our study in one region were not found in the other region, including most of the rockfishes *Sebastes spp.*, and many species were observed only once at the inner coast. We found that fish assemblages in the northern inner coast region were similar to those of the inside waters of Prince William Sound in southcentral Alaska (Dean *et al.*, 2000) and southern southeast Alaska (Murphy *et al.*, 2000), with the exception of juvenile cod (Gadidae) that were present at the inner coast of southeast Alaska but not observed along transects during the summer months of our study.

Rockfishes are an assemblage of commercial and recreational importance in southeast Alaska fisheries. Schools of black rockfish were unique to certain outer coast sites in our study, commonly associated with giant kelp at semi-exposed sites, and bull kelp canopy and *P. gardneri* sub-canopy at highly exposed sites. Quillback rockfish occurred at both locations in rocky habitats with overhangs, boulders, and dense macroalgal understory and dark dusky rockfish were observed, though not on survey transects and were consequently not counted. In a previous study, quillback and dark dusky rockfishes were the most widely distributed among species assemblages at depths < 90 m in southeast Alaska (Johnson *et al.*, 2003).

We observed schools of many hundreds of juvenile rockfishes at the more sheltered outer coast sites, associated with dense understory macroalgal cover provided by elongated blades of *Saccharina spp*. We did not observe large schools of juvenile rockfishes at our inner coast sites, but individuals were observed at shallow depths associated with rock overhangs and boulders. Shallow, nearshore rocky sites with macroalgae cover and eelgrass beds are known juvenile rockfish habitat in southeast Alaska (Murphy *et al.*, 2000; Johnson *et al.*, 2003), as well as sites with similar habitats in southcentral Alaska (Dean *et al.*, 2000), and along the U.S. West Coast (Love *et al.*, 1991). We were not able to identify to species the juvenile rockfishes observed in this study as it is quite difficult to do so in the field (e.g., Love *et al.*, 2002), but individuals likely included those of adults observed at study sites, in addition to deeper species that recruit to shallow, nearshore habitats (Carlson & Haight, 1976; Carlson & Straty, 1981; Carr, 1989; Love *et al.*, 1991).

Biogeographic patterns demonstrated by our study for certain species between the inner and outer coast regions were consistent with previous studies that identified spatial separation between regions based on the distribution of macroalgae (Lindstrom, 2006; Lindstrom, 2009), rocky intertidal invertebrates (O'Clair & O'Clair, 1998), and nearshore fishes (Quast 1968, Murphy *et al.*, 2000). In addition to describing species assemblage structure for several communities, our study related species distribution to sources of variation in the marine environment that these previous studies did not.

1.4.3 Weathering the Future

Southeast Alaska is an understudied region with respect to marine ecological processes. Our research provides a baseline for shallow subtidal community structure linked to environmental variation in the southeast Alaska fjord system.

Improved understanding of relationships between marine communities and fjord environments is necessary to understand the consequences of environmental change to fjord ecosystems. Marine ecosystems shifts are expected for coastal regions of the Gulf of Alaska as a consequence of ocean warming and increased freshwater input to the North Pacific marine environment (Royer, 1989; Royer *et al.*, 2001; Weingartner *et al.*, 2005; Royer & Grosch, 2006). Long-term studies that track community shifts over time have linked changes in marine communities at stations on the U.S. West Coast (e.g., Barry *et al.*, 1995) and arctic fjords (e.g., Beuchel *et al.*, 2006; Renaud *et al.*, 2007; Berge *et al.*, 2009) to elevated sea surface temperature and ocean freshening. We encourage future efforts to establish permanent stations along the fjord coast of southeast Alaska, especially at biogeographic transition zones, to track community shifts over time with environmental change in the North Pacific. Future study of the ecological mechanisms behind the patterns observed by this study will improve understanding of marine ecological processes in this region, including studies of the ecological effects of regional environmental variability on species interactions, and community response to environmental change.

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Table 1.1. Northern southeast Alaska study sites at outer coast and inner coast regions with site number and geographic location (North American Datum of 1983).

Outer Coast Site	Site Num.	Latitude N	Longitude W
Calming Island	1	56° 57' 45"	135° 24' 56"
Camp Cougan Cove	2	57° 0' 33"	135° 14' 54"
No Thorofare Bay	3	57° 1' 11"	135° 14' 45"
Echolms Islands	4	57° 0' 30"	135° 21' 9"
Middle Island	5	57° 6' 58"	135° 27' 51"
Lisianski Point	6	57° 9' 3"	135° 23' 20"
Alan Point	7	57° 14' 9"	135° 23' 51"
Kita Island	8	56° 56' 0"	135° 25' 56"
Vitskari Rocks	9	57° 0' 5"	135° 32' 40"
Inner Coast Site	**Site Num.**	**Latitude N**	**Longitude W**
Colt Island	10	58° 16' 31"	134° 44' 15"
Shamen Island	11	58° 18' 21"	134° 41' 14"
Portland Island	12	58° 19' 44"	134° 43' 54"
Point Louisa	13	58° 22' 15"	134° 43' 27"
Symonds Point	14	58° 20' 43"	134° 50' 31"
Aaron Island	15	58° 25' 50"	134° 49' 12"
Shrine Point	16	58° 28' 20"	134° 47' 19"
Adlershiem	17	58° 35' 22"	134° 54' 24"
Sunshine Cove	18	58° 36' 25"	134° 55' 45"

Table 1.2. Species richness (s), species diversity (H'), and evenness (E_H) of kelp, fish, macroinvertebrate, and small epibenthic invertebrate communities at inner coast and outer coast regions and 6 m and 12 m depths.

	Inner Coast			Outer Coast		
Community	s	H'	E_H	s	H'	E_H
Kelp	7	1.03	0.53	12	1.75	0.70
Fish	14	1.72	0.65	12	1.86	0.75
Macroinvertebrate	18	1.16	0.40	17	1.71	0.61
Epibenthos	45	2.46	0.65	57	2.85	0.70

	6 m depth			12 m depth		
Community	s	H'	E_H	s	H'	E_H
Kelp	13	1.57	0.61	6	1.12	0.62
Fish	14	2.17	0.82	12	1.44	0.58
Macroinvertebrate	20	1.13	0.38	19	1.90	0.65
Epibenthos	56	2.80	0.69	46	2.95	0.77

Inner Coast	6 m depth			12 m depth		
Community	s	H'	E_H	s	H'	E_H
Kelp	7	1.07	0.55	3	0.84	0.77
Fish	9	1.76	0.80	6	0.78	0.43
Macroinvertebrate	14	0.85	0.32	11	2.01	0.84
Epibenthos	30	2.29	0.67	29	2.31	0.69

Outer Coast	6 m depth			12 m depth		
Community	s	H'	E_H	s	H'	E_H
Kelp	9	1.59	0.72	6	1.36	0.76
Fish	9	1.57	0.71	7	1.78	0.91
Macroinvertebrate	11	1.99	0.83	13	1.27	0.49
Epibenthos	43	2.51	0.67	31	2.49	0.72

Table 1.3. Shannon t-test results comparing species diversity (H') of kelp, fish, macroinvertebrate (Macroinv), and small epibenthic invertebrate (Epiinv) communities sampled at inner coast (IC) and outer coast (OC) regions at 6 m and 12 m depths with H' compared (a, b) and *p*-value two-tailed distribution (Bonferroni correction $\alpha' = 0.008$, *k* tests = 6), *df*, and *t*-statistic. Significant results are in bold text with a subscript (a, or b) for the significant community comparison.

Community Comparison	Kelp	Fish	Macroinv	Epiinv
$IC_{(a)}$, **$OC_{(b)}$**	**<0.0001**$_{b}$ 1064, 15.11	0.47 128, 0.73	**<0.0001**$_{b}$ 608, 7.33	**<0.0001**$_{b}$ 2773, 8.71
6, 12	0.01 2, 8.65	0.07 2, 3.63	0.01 3, 9.98	0.03 6, 2.90
IC.6, **OC.6**	**<0.0001**$_{b}$ 958, 10.70	0.37 65, 0.89	**<0.0001**$_{b}$ 145, 14.58	**<0.0001**$_{b}$ 1364, 2.94
IC.12, OC.12	0.02 2, 7.47	0.11 1, 5.54	0.02 3, 6.93	0.08 5, 2.30
IC.6, **IC.12**	0.13 1, 4.76	0.05 2, 4.48	**0.004**$_{b}$ 3, 14.98	0.78 4, 0.30
OC.6, OC.12	0.08 3, 3.28	0.35 2, 1.20	0.02 3, 6.73	0.04 5, 0.26

Table 1.4. Results of the principal component analysis of benthic habitat conditions at study sites, based on percent area of substrate and algae composition along dive transects. Component loadings are eigenvectors, variance explained by the components are eigenvalues.

Component Loadings		PC1	PC2
Substrate Composition			
	Rock	-0.28	-0.43
	Boulder	-0.34	-0.40
	Cobble	-0.28	-0.16
	Pebble	-0.13	0.65
	Gravel	0.50	-0.03
	Sand	-0.35	0.46
	Mud	0.58	-0.08
Variance explained by components		2.07	1.67
Percentage of total variance explained		29.6%	23.9%
Algae Composition			
	Red	-0.39	-0.47
	Brown	-0.27	-0.61
	Canopy	-0.37	-0.30
	Crustose	-0.55	0.44
	Coralline	-0.59	0.36
Variance explained by components		2.21	1.16
Percentage of total variance explained		44.4%	23.3%

Table 1.5. Results of permutation analysis of environmental gradients with ordination by Detrended Correspondence Analysis (DCA) of kelp, fish, macroinvertebrate (Macroinv), and small epibenthic invertebrate (Epiinv) communities (1000 permutations, $\alpha = 0.05$). Environmental gradients were multivariate scores from PC1 and PC2 from the substrate and algae PCA (Table 1.4), and temperature and salinity measurements from survey depths (6 m and 12 m) at inner coast and outer coast sites. Environmental gradients significantly correlated with community ordination are indicated in bold text by the squared correlation coefficient (r^2) and $p < 0.05$. Dimensions one and two from DCA were used for all communities except kelp, where ordination was by dimensions three and four.

Environmental	Kelp		Fish		Macroinv		Epiinv	
Gradient	r^2	*p*	r^2	*p*	r^2	*p*	r^2	*p*
Substrate PC1	0.07	0.47	0.15	0.22	0.18	0.14	0.06	0.36
Substrate PC2	0.03	0.75	0.24	0.11	0.10	0.36	**0.39**	**<0.01**
Algae PC1	0.15	0.20	0.29	0.05	0.07	0.48	**0.57**	**<0.001**
Algae PC2	0.08	0.45	0.04	0.70	**0.25**	**0.04**	0.02	0.74
Temperature	**0.35**	**0.02**	0.27	0.08	0.25	0.06	**0.31**	**<0.01**
Salinity	**0.43**	**0.001**	**0.46**	**<0.01**	**0.63**	**<0.001**	**0.53**	**<0.001**

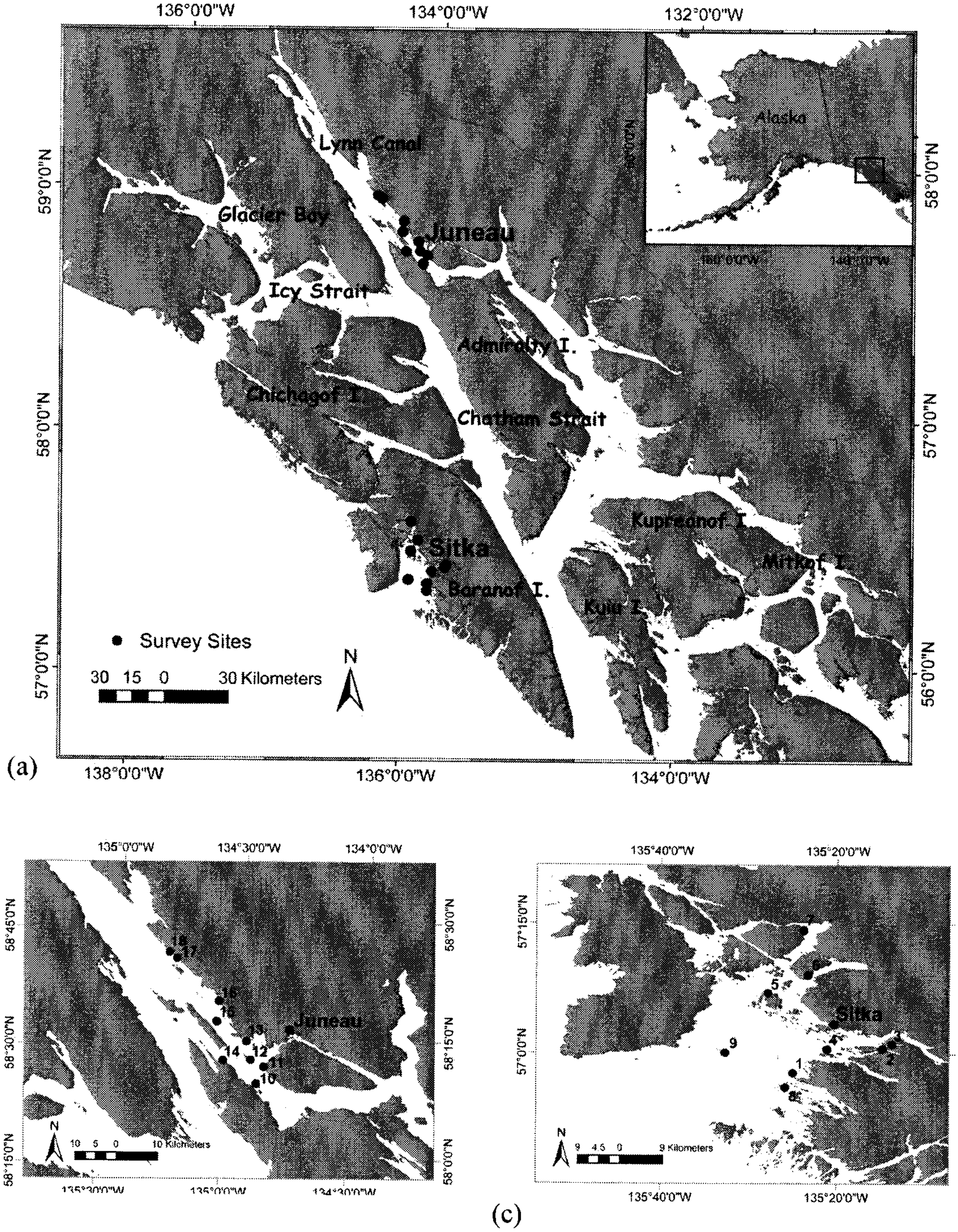

Figure 1.1. Northern southeast Alaska study location (a) and sites at the inner coast (b) and the outer coast (c) regions.

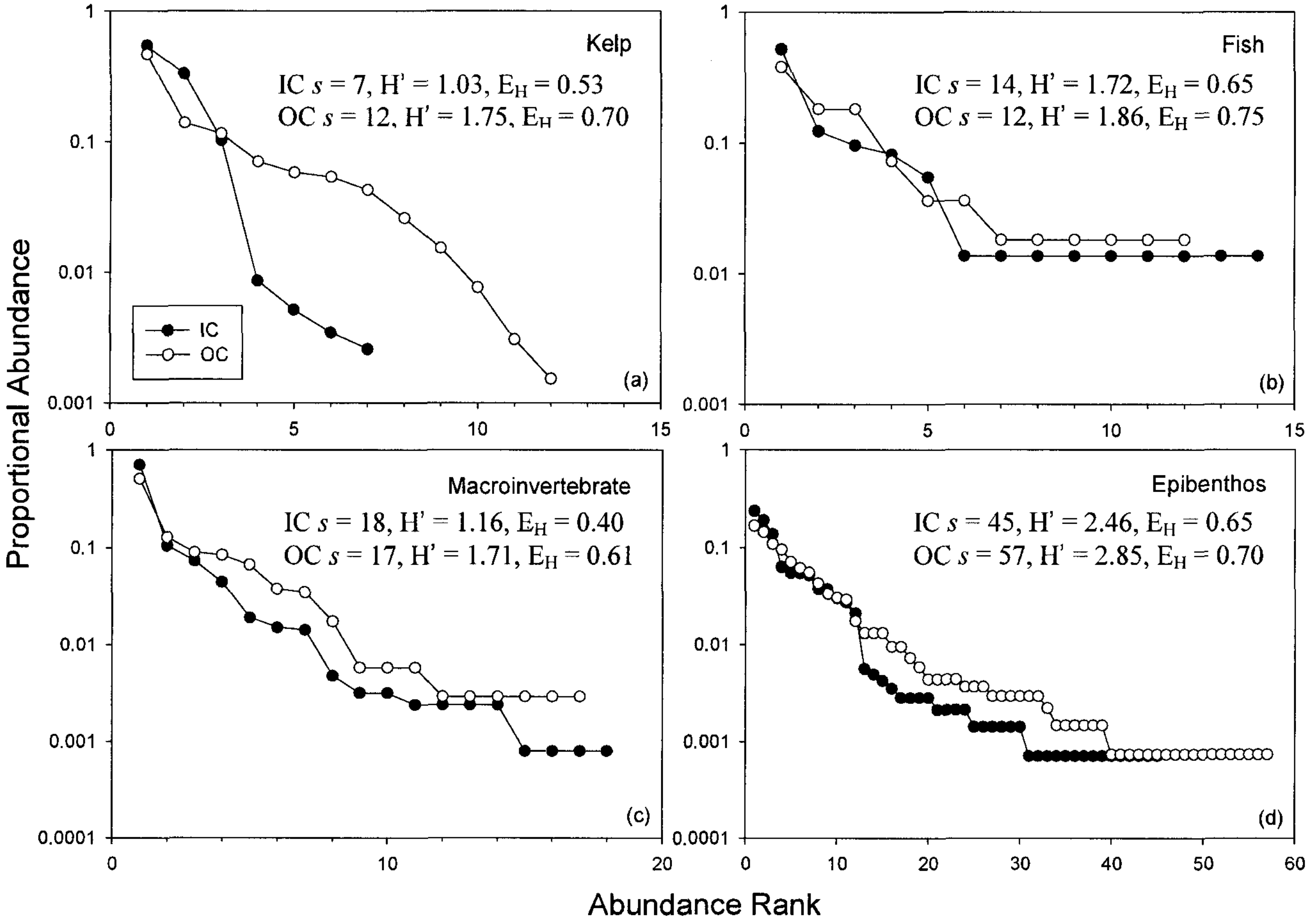

Figure 1.2. Species rank-abundance curves for subtidal communities at inner coast (IC) (closed circles) and outer coast (OC) (open circles) regions, including (a) kelp, (b) fish, (c) macroinvertebrate, and (d) small epibenthic invertebrate, with species richness (s), species diversity (H'), and evenness (E_H) for combined 6 m and 12 m depths.

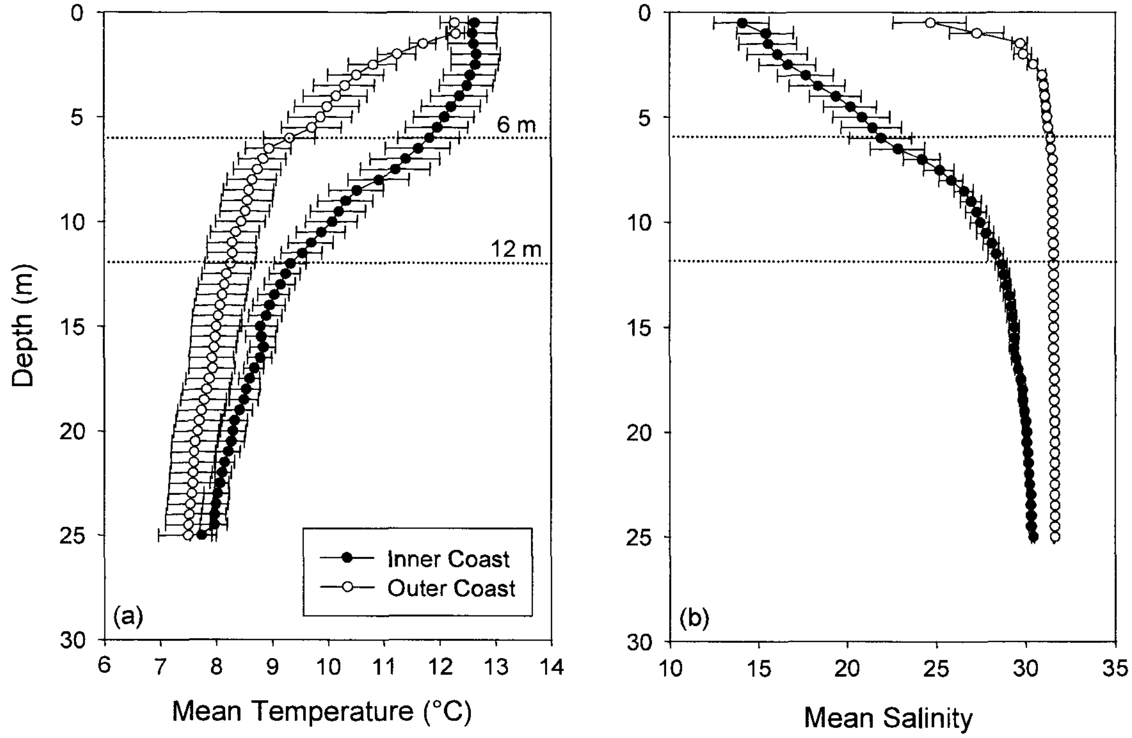

Figure 1.3. Mean temperature (°C) (a) and salinity (b) profiles of inner coast and outer coast regions measured in July 2007 from the surface (0.5 m) to 25 m depth at study sites (9 sites·region^{-1}) with standard error bars. Dive survey depths at 6 m and 12 m are indicated.

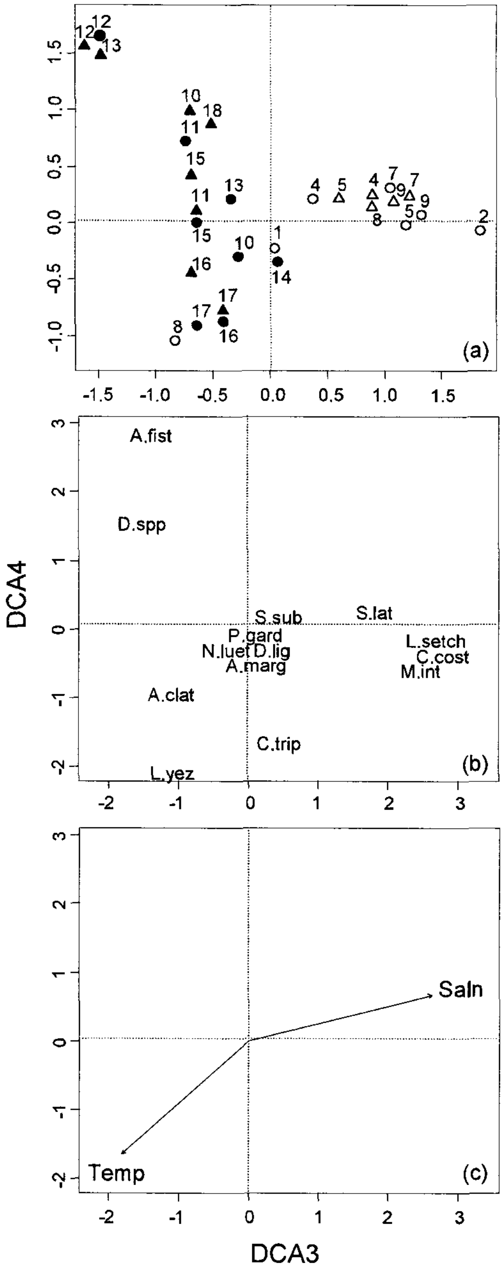

Figure 1.4. Kelp community ordination by dimensions 3 and 4 from Detrended Correspondence Analysis (DCA) that described 55.9% and 34.5% of the respective variability along those dimensions, including (a) sites at the outer coast (open) and inner coast (solid) at 6 m (circles) and 12 m depths (triangles), (b) species, and (c) significant environmental gradients of salinity ($r^2 = 0.43, p = 0.001$) and temperature ($r^2 = 0.35, p = 0.02$). Directional vectors indicate maximum values of environmental gradients. Species codes are listed in Appendix 1.0.

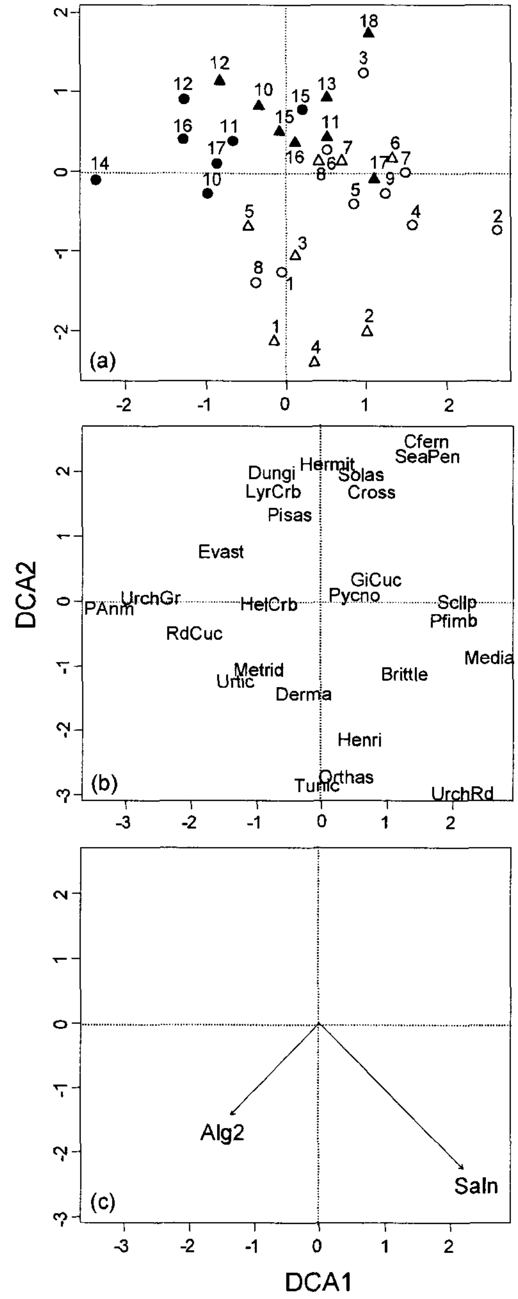

Figure 1.5. Macroinvertebrate community ordination by dimensions 1 and 2 from DCA that described 67.6% and 55.3% of the respective variability along those dimensions, including (a) sites at the outer coast (open) and inner coast (solid) at 6 m (circles) and 12 m depths (triangles), (b) species, and (c) significant environmental gradients of salinity ($r^2 = 0.63$, $p < 0.001$) and Algae PC2 (Alg2) ($r^2 = 0.25$, $p = 0.04$). Species codes are listed in Appendix 1.0.

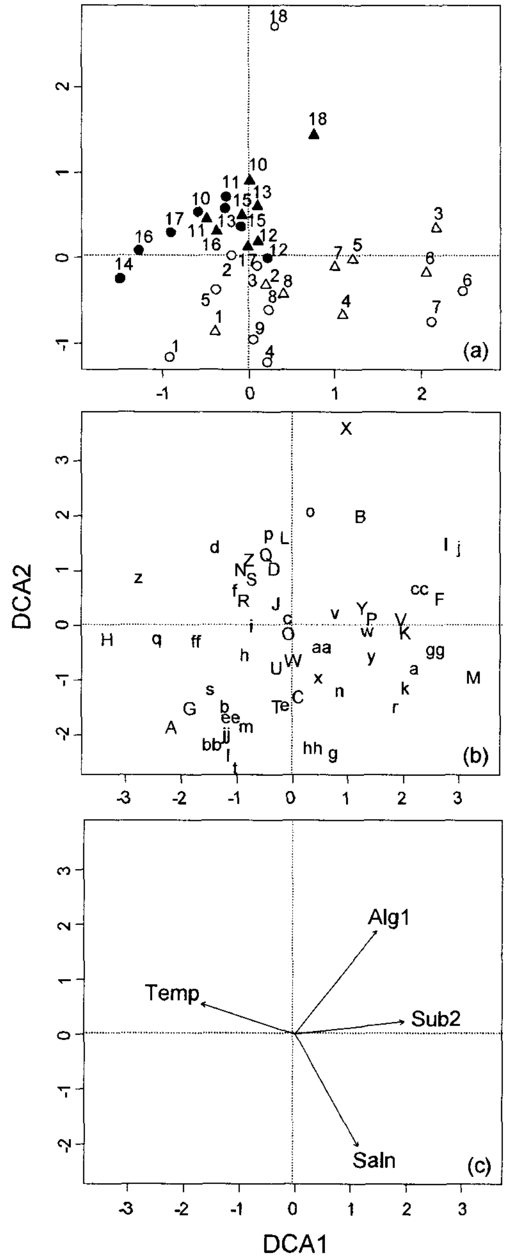

Figure 1.6. Ordination of small epibenthic invertebrates by dimensions 1 and 2 from DCA that described 43.2% and 37.1% of the respective variability along those dimensions, including (a) sites at the outer coast (open) and inner coast (solid) at 6 m (circles) and 12 m depths (triangles), (b) species, and (c) significant environmental gradients of the Algae PC1 (Alg1) ($r^2 = 0.57$, $p < 0.001$), salinity ($r^2 = 0.53$, $p < 0.001$), Substrate PC2 (Sub2) ($r^2 = 0.39$, $p = 0.002$), and temperature ($r^2 = 0.31$, $p = 0.002$). Species codes are listed in Appendix 1.0.

Appendix 1.0. Counts (*n*) and proportional abundance (p_i) of taxa from survey transects (25 m x 1 m) at inner coast and outer coast study sites organized by community. Ordination codes are provided for taxa that were included in multivariate analysis (taxa with > 1 observation and small epibenthic invertebrates at least 0.1% of community proportional abundance). Species included in diversity analysis are indicated by subscript +. Kelps and fish are listed by taxonomic Family and invertebrates are listed by taxonomic Class. Encrusting taxa are listed that were present but not individually quantified.

Taxa	Inner Coast		Outer Coast		DCA Code
	n	p_i	*n*	p_i	
Kelps					
Alariaceae					
Alaria marginata$_+$	-	-	75	0.11	*A.marg*
Alaria fistulosa$_+$	10	0.01	-	-	*A.fist*
Pleurophycus gardneri$_+$	-	-	28	0.04	*P.gard*
Costariaceae					
Agarum clathratum$_+$	385	0.31	38	0.06	*A.clat*
Costaria costata$_+$	-	-	5	0.01	*C.cost*
Laminariaceae					
Cymathaere triplicata$_+$	3	< 0.01	1	< 0.01	*C.trip*
Laminaria yezoensis$_+$	119	0.09	10	0.02	*L.yez*
Laminaria setchellii$_+$	-	-	35	0.05	*L.setch*
Macrocystis integrifolia$_+$	-	-	17	0.03	*M.int*
Nereocystis luetkeana$_+$	6	< 0.01	2	< 0.01	*N.leut*
Saccharina latissima$_+$	4	< 0.01	91	0.14	*S.lat*
Saccharina subsimplex$_+$	631	0.50	306	0.47	*S.sub*
Desmarestiaceae					
Desmarestia ligulata$_+$	-	-	46	0.07	*D.lig*
Desmarestia spp.	106	0.08	-	-	*D.spp*

Appendix 1.0. Continued.

Taxa	Inner Coast		Outer Coast		DCA Code
	n	p_i	*n*	p_i	
Fishes					
Anahichididae					
Anarrhichthys ocellatus$_+$	1	0.01	-	-	
Bathymasteridae					
Bathymaster caeruleofasciatus$_+$	-	-	1	0.01	
Ronquilus jordani$_+$	6	0.08	-	-	NoRnq
Cottidae					
Blepsias cirrhosus$_+$	1	0.01	-	-	
Hemilepidotus hemilepidotus$_+$	1	0.01	-	-	
Myoxocephalus polyacanthocephalus$_+$	4	0.05	-	-	GrScl
Scorpaenichthys marmoratus$_+$	1	0.01	-	-	
Undefined sculpin a	1	0.01	-	-	
Undefined sculpin	1	0.01	1	0.01	UnScl
Hexagrammidae					
Hexagrammos decagrammus$_+$	1	0.01	10	0.07	KGlng
Ophiodon elongates$_+$	-	-	1	0.01	
Oxylebius pictus$_+$	-	-	2	0.01	PGlng
Pholidae					
Pholis laeta$_+$	9	0.11	2	0.01	CrGun
Apodichthys flavidus$_+$	1	0.01	1	0.01	PnGun
Pleuronectidae					
Lepidopsetta bilineata$_+$	38	0.48	1	0.01	RSol
Platichthys stellatus$_+$	1	0.01	-	-	
Pleuronichthys coenosus$_+$	-	-	1	0.01	
Undefined juvenile flatfish	4	0.05	-	-	JvFlat

Appendix 1.0. Continued.

Taxa	Inner Coast		Outer Coast		DCA Code
	n	p_i	*n*	p_i	
Fishes (continued)					
Scorpaenidae					
Sebastes caurinus$_+$	-	-	1	0.01	
Sebastes maliger$_+$	1	0.01	4	0.03	QulRf
Sebastes melanops$_+$	-	-	21	0.16	BkRf
Undefined juvenile rockfish	-	-	78	0.58	JvRf
Stichaeidae					
Lumpenus sagitta$_+$	1	0.01	-	-	
Stichaeus punctatus$_+$	7	0.09	-	-	ArShn
Zoarcidae					
Rhinogobiops nicholsii$_+$	-	-	10	0.07	BlGby
Macroinvertebrates					
Anthozoa					
Ptilosarcus gurneyi$_+$	19	0.01	2	< 0.01	SeaPen
Cribrinopsis fernaldi$_+$	4	< 0.01	-	-	Cfern
Metridium spp.	58	0.04	16	0.04	Metrid
Pachycerianthus fimbriatus$_+$	-	-	175	0.41	Pfimb
Urticina spp.	4	< 0.01	2	< 0.01	Urtic
Undefined anemone a	53	0.04	-	-	PAnm
Malacostraca					
Cancer magister$_+$	3	< 0.01	-	-	Dungi
Hyas lyratus$_+$	6	< 0.01	-	-	LyrCrb
Oregonia gracilis$_+$	1	< 0.01	-	-	
Telmessus cheiragonus$_+$	3	< 0.01	1	< 0.01	HelCrb
Elassochirus gilli$_+$	1	< 0.01	-	-	

Appendix 1.0. Continued.

Taxa	Inner Coast		Outer Coast		DCA Code
	n	p_i	n	p_i	
Macroinvertebrates (continued)					
Malacostraca (continued)					
Elassochirus tenuimanus$_{+}$	1	< 0.01	-	-	
Undefined hermit crab	3	< 0.01	-	-	Hermit
Undefined shrimp	1	< 0.01	-	-	
Bivalvia					
Chlamys spp.	13	0.01	49	0.11	Scllp
Gastropoda					
Doris odhneri$_{+}$	-	-	1	< 0.01	
Flabellina triophina$_{+}$	-	-	1	< 0.01	
Triopha catalinae$_{+}$	-	-	1	< 0.01	
Undefined nudibranch	-	-	1	< 0.01	
Asteroidea					
Crossaster papposus$_{+}$	4	< 0.01	1	< 0.01	Cross
Dermasterias imbricata$_{+}$	1	< 0.01	13	0.03	Derma
Evasterias troschelii$_{+}$	93	0.07	-	-	Evast
Henricia spp.	3	< 0.01	9	0.02	Henri
Mediaster aequalis$_{+}$	-	-	29	0.07	Media
Orthasterias koehleri$_{+}$	-	-	12	0.03	Orthas
Pisaster brevispinus$_{+}$	18	0.01	2	< 0.01	Pisas
Pycnopodia helianthoides$_{+}$	56	0.04	44	0.10	Pycno
Solaster dawsoni$_{+}$	3	< 0.01	-	-	Solas
Echinoidea					
Strongylocentrotus droebachiensis$_{+}$	887	0.64	-	-	UrchGr
Strongylocentrotus franciscanus$_{+}$	-	-	23	0.05	UrchRd

Appendix 1.0. Continued.

Taxa	Inner Coast		Outer Coast		DCA Code
	n	p_i	n	p_i	
Macroinvertebrates (continued)					
Holothuroidea					
Cucumaria miniata$_{+}$	133	0.10	6	0.01	RdCuc
Parastichopus californicus$_{+}$	24	0.02	31	0.07	GiCuc
Psolus chitonoides$_{+}$	-	-	1	< 0.01	
Ophiuroidea					
Undefined brittle star	-	-	8	0.02	Brittle
Ascidiacea					
Halocynthia aurantium$_{+}$	1	< 0.01	2	< 0.01	Tunic
Small Epibenthic Invertebrates					
Porifera					
Undefined sponge	2	< 0.01	-	-	
Anthozoa					
Ptilosarcus gurneyi$_{+}$	3	< 0.01	1	< 0.01	B
Balanophyllia elegans$_{+}$	-	-	130	0.07	I
Gersemia rubiformis$_{+}$	-	-	24	0.01	A
Anthopleura artemisia$_{+}$	1	< 0.01	-	-	
Halcampa decemtentaculata$_{+}$	-	-	3	< 0.01	
Metridium senile$_{+}$	3	< 0.01	97	0.05	C
Pachycerianthus fimbriatus$_{+}$	-	-	42	0.02	F
Stomphia coccinea$_{+}$	4	< 0.01	-	-	D
Urticina lofotensis$_{+}$	-	-	1	< 0.01	
Undefined anemone a	13	0.01	-	-	H
Undefined anemone	5	< 0.01	12	0.01	G

Appendix 1.0. Continued.

Taxa	Inner Coast		Outer Coast		DCA Code
	n	p_i	n	p_i	
Epibenthic Invertebrates (continued)					
Polychaeta					
Eudistylia spp.	104	0.06	1	< 0.01	L
Serpula columbiana$_+$	268	0.14	196	0.10	J
Myxicola infundibulum$_+$	4	< 0.01	18	0.01	K
Undefined spaghetti worm	1	< 0.01	-	-	
Phoronida					
Phoronopsis harmeri$_+$	-	-	227	0.12	M
Maxillopoda					
Balanus crenatus$_+$	43	0.02	2	< 0.01	v
Malacostraca					
Cryptolithodes sitchensis$_+$	-	-	1	< 0.01	
Scyra acutifrons$_+$	1	< 0.01	-	-	
Elassochirus tenuimanus$_+$	2	< 0.01	-	-	
Undefined hermit crab	54	0.03	273	0.14	y
Pagurus hemphilli$_+$	1	< 0.01	-	-	
Pandalus danae$_+$	7	< 0.01	18	0.01	w
Hippolyte clarki$_+$	1	< 0.01	1	< 0.01	
Undefined shrimp	2	< 0.01	7	< 0.01	x
Polyplacophora					
Cryptochiton stelleri$_+$	2	< 0.01	1	< 0.01	
Mopalia muscosa$_+$	3	< 0.01	5	< 0.01	U
Tonicella insignis$_+$	78	0.04	13	0.01	S
Tonicella lineata$_+$	74	0.04	18	0.01	R
Tonicella undocaerulea$_+$	2	< 0.01	6	< 0.01	T

Appendix 1.0. Continued.

Taxa	Inner Coast		Outer Coast		DCA Code
	n	p_i	*n*	p_i	
Epibenthic Invertebrates (continued)					
Polyplacophora (continued)					
Mopalia spp.	-	-	1	< 0.01	
Leipdozona spp.	2	< 0.01	5	< 0.01	V
Undefined chiton	9	< 0.01	13	0.01	W
Bivalvia					
Chlamys spp.	4	< 0.01	10	0.01	Y
Mytilus trossulus$_+$	4	< 0.01	-	-	X
Pododesmus macrochisma$_+$	6	< 0.01	-	-	Z
Undefined clam	4	< 0.01	15	0.01	a
Gastropoda					
Acmaea mitra$_+$	2	< 0.01	4	< 0.01	b
Undefined limpet	215	0.12	76	0.04	c
Acteocina culcitella$_+$	-	-	1	< 0.01	
Balcis micans$_+$	1	< 0.01	84	0.04	l
Bittium attenuatum$_+$	-	-	1	< 0.01	
Ceratostoma foliatum$_+$	2	< 0.01	4	< 0.01	e
Epitonium indianorum$_+$	-	-	5	< 0.01	j
Lacuna vincta$_+$	4	< 0.01	4	< 0.01	h
Margarites pupillis$_+$	333	0.18	149	0.08	f
Nassarius mendicus$_+$	-	-	2	< 0.01	
Nucella lamellosa$_+$	30	0.02	-	-	d
Olivella baetica$_+$	-	-	6	< 0.01	k
Tegula puligo$_+$	-	-	46	0.02	g
Trichotropsis cancellata$_+$	90	0.05	76	0.04	i
Amphissa spp.	4	< 0.01	32	0.02	n

Appendix 1.0. Continued.

Taxa	Inner Coast		Outer Coast		DCA Code
	n	p_i	*n*	p_i	
Epibenthic Invertebrates (continued)					
Gastropoda (continued)					
Calliostoma spp.	-	-	66	0.03	m
Euspira spp.	1	< 0.01	1	< 0.01	
Onepota spp.	13	0.01	1	< 0.01	o
Undefined snail	7	< 0.01	14	0.01	p
Acanthodoris hudsoni$_{+}$	-	-	1	< 0.01	
Dendronotus frondosus$_{+}$	-	-	1	< 0.01	
Flabellina trilineata	-	-	1	< 0.01	
Hermissenda crassicornis$_{+}$	1	< 0.01	59	0.03	r
Janolus fuscus$_{+}$	1	< 0.01	-	-	
Onchidoris muricata$_{+}$	195	0.11	8	< 0.01	q
Rostanga pulchra$_{+}$	-	-	1	< 0.01	
Undefined nudibranch	3	< 0.01	8	< 0.01	s
Undefined aeolid	-	-	15	0.01	t
Rhynchonellata					
Hemithyris psittacea$_{+}$	77	0.04	-	-	Q
Laques californicus$_{+}$	8	< 0.01	2	< 0.01	O
Terebratalia transversa$_{+}$	53	0.03	6	< 0.01	N
Terebratulina unguicula$_{+}$	5	< 0.01	6	< 0.01	P
Asteroidea					
Crossaster papposus$_{+}$	-	-	1	< 0.01	
Evasterias troschelii$_{+}$	39	0.02	-	-	z
Henricia leviuscula$_{+}$	-	-	10	0.01	bb
Leptasterias hexactis$_{+}$	1	< 0.01	-	-	
Orthasterias koehleri$_{+}$	1	< 0.01	-	-	

Appendix 1.0. Continued.

Taxa	Inner Coast		Outer Coast		DCA Code
	n	p_i	*n*	p_i	
Epibenthic Invertebrates (continued)					
Asteroidea (continued)					
Mediaster aequalis$_+$	-	-	4	< 0.01	aa
Pycnopodia helianthoides$_+$	1	< 0.01	2	< 0.01	
Echinoidea					
Strongylocentrotus droebachiensis$_+$	53	0.03	40	0.02	ff
Holothuroidea					
Cucumaria miniata$_+$	3	< 0.01	-	-	
Psolus squamatus$_+$	1	< 0.01	-	-	
Ophiuroidea					
Amphipholis squamata$_+$	-	-	1	< 0.01	
Ophiura lutkeni$_+$	-	-	5	< 0.01	cc
Ophiopholis aculeata$_+$	1	< 0.01	-	-	
Undefined brittle star	4	< 0.01	42	0.02	ee
Ascidiacea					
Ascidia paratropa$_+$	-	-	2	< 0.01	
Boltenia villosa$_+$	-	-	4	< 0.01	hh
Corella inflata$_+$	-	-	1	< 0.01	
Corella willmeriana$_+$	-	-	13	0.01	gg
Metandrocarpa taylori$_+$	-	-	4	< 0.01	jj
Encrusting Taxa (presence/absence)					
Porifera					
Cliona californiana	-	-	+	+	
Undefined sponge	+	+	+	+	

Appendix 1.0. Continued.

Taxa	Inner Coast		Outer Coast		DCA Code
	n	p_i	*n*	p_i	
Encrusting Taxa (presence/absence) (continued)					
Ascidiacea					
Didemnum carnulentum	-	-	+	+	
Undefined ascidian	+	+	+	+	
Polychaeta					
Dodecaceria concharum	-	-	+	+	
Dodecaceria fewkesi	-	-	+	+	
Spiochaetopterus costarum	-	-	+	+	

Chapter 2

Red king crab (*Paralithodes camtschaticus*) larval supply, settlement timing, and benthic habitat structure[1]

Abstract

Early life history information is needed to benefit management of depleted red king crab populations in Alaska. Red king crab (*Paralithodes camtschaticus*) larval supply and settlement timing were quantified at six sites (Indian Cove, Barlow Cove, St. James Bay, Portland Island, Horse Island, and the Couverden Islands) in southeast Alaska during summer 2008 and at two sites (Indian Cove and the Couverden Islands) in 2009. Supply varied spatially among sites and depths in 2008 and 2009. Local oceanographic processes that influence larval transport from hatching to settlement locations are poorly understood and may be responsible for spatial variation in larval supply. Settlement timing for red king crab was consistent between 2008 and 2009 and with historical data from the 1980s and 1990s. Benthic habitat was characterized in 2008 and sites with similar structural complexity grouped together. Sites with both high larval supply and complex habitat have potential to serve as red king crab nurseries. Further study of processes that influence larval transport to nursery locations will advance understanding red king crab population dynamics in Alaska.

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[1] Pirtle, J.L., and Eckert, G.L. Red king crab (*Paralithodes camtschaticus*) larval supply, settlement timing, and benthic habitat structure. Prepared for submission in Canadian Journal of Fisheries and Aquatic Sciences.

2.1 Introduction

Red king crab (*Paralithodes camtschaticus*) is a large, commercially harvested anomuran crab (Lithodidae) that once supported the most economically valuable crustacean fishery in Alaska. The U.S. commercial fishery began in the Western Gulf of Alaska in the 1930s and was established by the 1950s (Kimker et al. 1993; Spalinger and Jackson 1994). Red king crab populations peaked and then sharply declined in the late 1960s followed by large-scale collapse of the major harvest areas by the early 1980s (Orensanz et al. 1998; Zheng and Kruse 2000). At present, many red king crab populations throughout Alaska remain depressed, even in areas without a commercial fishery.

A combination of factors likely contributed to the decline of red king crab statewide. Anthropogenic factors include recruitment overfishing of spawning stock biomass in the directed pot fishery (Orensanz et al. 1998) and possibly bycatch in trawl fisheries, particularly of females (Dew and McConnaughey 2005). Natural factors were also important. North Pacific ocean-atmospheric conditions of warmer ocean temperatures and a strengthened Aleutian Low pressure system are negatively correlated with red king crab year-class strength (Tyler and Kruse 1996; Zheng and Kruse 2000), though the reason for this correlation is not clear. Understanding processes affecting red king crab early life stages may reveal bottlenecks that could explain long-term population decline and lack of recovery.

Most commercially harvested crustaceans have complex life cycles with dispersive larval stages and benthic juveniles and adults. Pre-settlement processes that influence the distribution and abundance of commercially important crab planktonic larval stages include adult distribution (Lipcius et al. 1997), large-scale atmospheric forcing (Shanks and Roegner 2007), local advective processes (Hudon and Fradette 1993; Eggleston and Armstrong 1995), water-quality attributes (Shirley and Shirley 1989), and food availability (Paul and Paul 1980). Each of these processes individually and synchronously affects larval dispersal and spatial and temporal patterns of settlement. For several commercially harvested crustaceans, the abundance of the planktonic settlement stage is strongly tied to the abundance of early post-settlement stages. This is true of American lobster (*Homarus americanus*) (Incze et al. 1997; Incze et al. 2000), spiny lobster (*Paulirus argus*) (Lipcius et al. 1997), and Dungeness crab (*Cancer magister*) (Eggleston and Armstrong 1995). Post-settlement processes that influence early benthic stages include habitat availability, food availability, and predation. Benthic habitat provides refuge from predation for shelter-seeking early post-settlement stages (Crowder and Cooper 1982; Caddy 1986), with demonstrated effects of habitat on survival and growth (Herrnkind and Butler 1986; Eggleston et al. 1990; Lipcius et al. 1998; Hovel and Fonseca 2005; Mai and Hovel 2007; Stoner 2009). A limited availability of habitat post-settlement can lead to a demographic bottleneck, as documented for American lobster (Wahle and Steneck 1991) and spiny lobster (Butler et al. 2001).

Compared to the multi-year time series of early life stage population dynamics known for some commercially harvested crustaceans, we are just beginning to understand red king crab early life stage ecology, particularly the role of larval supply to settlement locations and post-settlement habitat. Red king crab have five larval stages, including four zoeae and one non-feeding settlement stage, called glaucothoe (Marukawa 1933). In southeast Alaska, red king crab larvae hatch in late spring and larvae are found in the plankton over a period ranging from 55-115 days (March to July) (Shirley and Shirley 1988; 1989; 1990). Glaucothoe settle to nearshore habitats in the Gulf of Alaska during June-July and molt to become first stage juvenile crabs (instars) (Freese and Babcock 1989; Donaldson et al. 1992; Blau and Byersdorfer 1994; Loher and Armstrong 2000). Settlement is greatest in high-complexity habitats that accommodate the body size of early post-settlement stages (to 1 year, 2-12 mm carapace length (CL), Donaldson et al., 1992), including fragmented rock, cobble, and crushed shells, macroalgae and structural invertebrates (Powell and Nickerson 1965; Sundberg and Clausen 1977; McMurray et al. 1984; Rodin 1985; Dew 1991; Loher and Armstrong 2000), while larvae actively avoid settling in low complexity habitats of mud and sand (Stevens and Kittaka 1998; Loher and Armstrong 2000). We consider red king crab nursery locations to be habitats where young crabs can forage, grow, and avoid excessive predation from settlement through the early post-settlement phase. Red king crab are solitary and cryptic in post-settlement habitat (Karinen 1985) until around age 2 when they join juvenile pods of many individuals (Powell and Nickerson 1965; Dew 1990; Zhou and Shirley 1998). Crabs are reproductively mature around age 7 and enter the Alaska fishery at ages 8 and 9 (McCaughran and Powell 1977).

We examined spatial and temporal patterns of red king crab larval supply, settlement to benthic habitat, and benthic habitat composition in southeast Alaska to increase understanding of early life stage population dynamics for this depleted fishery resource species. We included an Auke Bay site sampled by Loher and Armstrong (2000), to identify potential shifts in red king crab larval dynamics at that site since their investigation. More broadly, we extended spatial coverage to sites beyond Auke Bay with the following three objectives: 1) identify spatial and temporal variability in larval supply and settlement; 2) explore relationships between larval supply and settlement to benthic habitats; and 3) characterize benthic habitat at nearshore locations and examine spatial variability of those habitats among sites and depths.

2.2 Materials and Methods

2.2.1 Study Location and Site Selection

We sampled six sites, selected as potential red king crab nurseries, in northern southeast Alaska near Juneau (ca. 58°18' N, 134°25' W, North American Datum of 1983) (Fig. 2.1). Our Indian Cove (58°22.3' N, 134°41.6' W) site located inside Auke Bay was studied by Loher and Armstrong (2000). Sampled sites outside Auke Bay included Barlow Cove (58°19.9' N, 134°53.5' W), Saint (St.) James Bay (58°22.0' N, 135°6.4' W), Portland Island (58°19.8' N, 134°43.9' W), Horse Island (58°15.6' N, 134°47.0' W), and the Couverden Islands (58°9.1' N, 135°2.8' W). Our study sites were encompassed by Alaska Department of Fish and Game (ADF&G) red king crab harvest areas (Fig. 2.1). We had previously observed small juvenile crabs (12-23 mm CL, ages 1-3) in complex nearshore habitats at the Indian Cove site and several locations in our study area. All six sites were sampled in 2008. Sampling was repeated in 2009 at Indian Cove and the Couverden Islands to examine interannual variation at a subset of sites.

2.2.2 Larval Supply and Settlement Timing

Two collection methods were used to capture settling red king crab larvae. 1) Larval collectors were used to quantify the relative supply of settling larvae at sites and settlement timing during 2008 and 2009. 2) Settlement pails were used to examine relationships between larval settlement and benthic habitat at a subset of sites in 2008, including Indian Cove, Barlow Cove, and St. James Bay. Larval collectors were based on previous designs specifically developed to effectively collect and retain settling red king crab larvae (Donaldson et al. 1992; Blau and Byersdorfer 1994; Loher and Armstrong 2000). Our larval collectors (18 cm diameter and 60 cm length) were constructed of diamond polyethylene stretch mesh (1.5 cm aperture), stuffed with multifilament commercial salmon gill net as a complex settlement matrix, with a small doughnut float placed inside near the top of the collector to facilitate upright floating orientation. Collectors were clipped to a weighted groundline in series with 3 m spacing between collectors and 5 m of line on each end attached to anchors with a float line. Nine collectors per site were used at Indian Cove, Barlow Cove, and St. James Bay, and six collectors per site were used at the Couverden Islands, Horse Island, and Portland Island. The resulting groundlines were 34 m long with nine collectors and 25 m long with six collectors. Settlement pails were plastic containers (33 x 18 x 12 cm) filled with substrate and slightly recessed in the seafloor (*sensu* Loher and Armstrong 2000). Settlement pails presented larvae with natural substrates from those study sites in a contained space to assess relative settlement across sites. Because pails required large sampling and processing effort, they were only deployed at Indian Cove, Barlow Cove, and St. James Bay in 2008.

Collectors and pails were deployed by boat and SCUBA divers in April and May (Table 2.1) before the settlement pulse to allow for natural fouling, which should make them more attractive as settlement substrate. A total of 72 collectors and 54 pails were deployed in 2008 and 42 collectors were deployed in 2009. Collectors and pails were retrieved by divers during three sampling periods in 2008 at the anticipated beginning, peak, and end of the settlement pulse from early June to August. In 2008, Indian Cove, Barlow Cove, and St. James Bay were visited during all three sampling periods as high sampling intensity sites, and the Couverden Islands, Horse Island, and Portland Island were sampled during the last two periods as low sampling intensity sites. Collectors were deployed in May and retrieved in June and July in 2009.

On retrieval, individual collectors were placed in plastic bags at depth, and pails were sealed with lids to prevent loss of contents. Collectors were returned to the lab and washed with ambient running seawater to remove settlement stage larvae and juvenile crabs from the mesh. Individual red king crab larvae and crabs were counted, a subset were measured to carapace length (mm) using microscopy, and all were maintained in laboratory aquariums with flow-through seawater for subsequent laboratory and field experiments. Of the 54 settlement pails deployed in 2008, 46 were recovered and eight were lost or damaged. Recovered pails were frozen and the contents sorted in summer 2009 for larvae and juveniles and substrate composition. Substrates available to settling larvae, defined as the top 3 cm of substrate in the pails, were identified and counted once based on the presence of that substrate. These included fine substrates, such as sand and mud, and unconsolidated hard substrates, such as cobbles (6.5-25.5 cm), pebbles (2-6.5 cm), and gravel (2-4 mm) (Stein et al. 1992; Greene et al. 1999), in addition to crushed shells, bivalve shells, macroalgae, and structural invertebrates. An index of habitat structural complexity for settlement pails was determined as the sum of the scores for the following substrate types: structural invertebrate (score = 0.5); macroalgae (0.5); bivalve shell (0.5); cobble (0.5); pebble/gravel/crushed shell (0.25), and sand/mud (0). The presence of pebble, gravel, and crushed shell were counted together, because combinations of these substrates, with fine sediments, represent a common low structure seafloor habitat in the Juneau area. The maximum score for a pail containing all substrate types was 2.25.

2.2.3 Larval Supply and Settlement Analysis

Counts of individual larvae and post-settlement stage crabs were standardized to crabs·collector^{-1}·day^{-1} for all analyses. Hypotheses were tested for red king crab larval supply and settlement, including null hypotheses of 1) no difference of larval supply among sites, years, and depths; and 2) no temporal structure of settlement timing across sampling periods. The General Linear Model (GLM) was applied ($\alpha = 0.05$) for significance tests using SAS 9.2 (SAS Institute, Inc.). A one-factor GLM with Tukey's (HSD) post-comparisons test was used to test for differences in larval supply at all sites and years sampled at 6 m depth. A two-factor GLM was applied where multiple depths were sampled, at Indian Cove, Barlow Cove, and St. James Bay in 2008 and Indian Cove in 2009, to test for differences in larval supply among sites and depths (6 and 9 m). A mixed-effects linear model, with fixed factor stage (larvae and instars) and the repeated measure sampling period (Table 2.1), was applied to test for differences in temporal structure of settlement timing, pooled across all sites and depths sampled in 2008.

2.2.4 Benthic Habitat

Divers conducted video transects along settlement groundlines to characterize benthic habitat availability at study sites. A diver swam from the anchor near the first larval collector to the opposite anchor, maintaining an approximate distance of 1 m from the seafloor and an approximate transect width of 0.5 m with the groundline at the edge of the field of view. Videos were recorded with a Fuji 6.3 megapixel digital video camera in an underwater housing. One transect was completed along each groundline at 6 and 9 m depths (0.5 m x 34 m) at Indian Cove, Barlow Cove, and St. James Bay, and at 6 m depth (0.5 m x 25 m) at the Couverden Islands, Horse Island, and Portland Island for a total of nine transects.

The major habitat categories encountered were substrate, macroalgae, and macroinvertebrates. The substrate category was classified into the following eight subcategories: a) silty mud; b) silty sand; c) small unconsolidated (gravel and pebble ($\geq$ 5 mm and < 7 cm); d) large unconsolidated (cobble and small boulders ($\geq$ 7 cm and < 30 cm) (after, Stein et al. 1992; Greene et al. 1999); and e) bivalve shells; f) crushed shells; g) diatom mat; and h) terrestrial organic debris. Fine sediment groundtruthing from settlement pails and diver observations was helpful to distinguish between silty sand and mud, in addition to crushed shells that were intermixed with fine sediments. The category macroalgae was classified into the following most common five subcategories: a) understory kelp (*Saccharina spp.* and *Laminaria spp.*); b) shotgun kelp (*Agarum clathratum*); c) acid kelp (*Desmarestia spp.*); d) drift algae (unattached or entrained on groundlines); and e) algae other (e.g., unidentifiable red algae). Macroinvertebrates included the following seven subcategories: a) parchment tubeworm (*Eudistylia spp.*); b) plumose anemone (*Metridium farcimen*); c) orange cucumber (*Cucumaria miniata*); d) giant cucumber (*Parastichopus californicus*); e) mottled seastar (*Evasterias troschelii*); f) sunflower star (*Pycnopodia helianthoides*); and g) dungeness crab (*C. magister*). Tubeworms, anemones, and orange cucumbers were structure-forming macroinvertebrates that increased benthic habitat complexity.

2.2.5 Benthic Habitat Analysis

Videos were processed to create a sequence of non-overlapping frames for the total length of each transect. Habitats were relatively homogenous along groundlines, so a stratified sample of every fourth frame was selected for image analysis to avoid spatial correlation (Thompson 2002). We used the program Coral Point Count with Excel extensions (CPCe) (Kohler and Gill 2006) to quantify percent cover of habitat attributes using a stratified random overlay of 25 points per frame. The number of random points was selected using Pearson product-moment correlation (Zar 1999). The habitats underlying points on an individual frame were classified into habitat subcategories.

Multivariate analysis was conducted to compare benthic habitat composition among sampling locations at study sites, using PRIMER 6.0 (PRIMER-E Ltd, Plymouth, UK). Percent cover estimates (e) were log-transformed as proportions $\left(\varepsilon' = 0.5 \times \log_{10}\left(1 + e\right)\right)$ (Aitchison 1986) prior to analysis to reduce the influence of high percent cover values. Similarities in habitat composition among sampling locations (n = 9) were tested using the Bray-Curtis group-average method with log-percent cover estimates of habitat subcategories. Non-metric multi-dimensional scaling (nMDS) ordination was constructed from the similarity matrix for two and three-dimensional solutions, using 30 iterations, and hierarchical clustering was performed with similarity profile (SIMPROF) permutation tests (1000 permutations). The null hypothesis of no difference in multivariate structure of habitat attributes among groups was tested ($\alpha = 0.05$), with site.depth as the lowest level of group structure (Clarke and Warwick 2001).

2.2.6 Adult Abundance and Distribution

Red king crab stock assessment survey data, provided by the Alaska Department of Fish and Game (ADF&G), have been analyzed to examine the abundance and spatial distribution of red king crab in southeast Alaska relative to our study area. The ADF&G red king crab pot survey is conducted to obtain a relative measure of abundance of red king crab in locations where red king crab are harvested by personal use and commercial fisheries, evaluate the overall health and condition of the resource, and determine guideline harvest levels (Clark et al. 2003). The survey is conducted annually in June-July in eight areas defined as a single bay or a collection of nearby bays and adjacent shorelines of straits and sounds (Clark et al. 2003). These areas are divided into strata where random pot locations are sampled each year (mean pots·area^{-1} ± SE, 48 ± 2; mean pots·year^{-1} ± SE, 386 ± 30). Pots are generally set at depths greater than 37 m and less than 183 m and are recovered after 16-24 hours. Data are recorded for sex, carapace length (mm), shell condition, reproductive status, and the presence of parasites (Clark et al. 2003).

We examined the distribution and abundance of adult and older juvenile red king crab relative to our southeast Alaska study sites in survey years 2008-09. Years were pooled for this analysis to generate the overall trend in red king crab abundance for the years sampled by our study. Abundance of juvenile males (fishery pre-recruits, < 129 mm CL) and mature females were mapped separately to examine nursery habitat potential and female reproductive potential near our study sites. We included large female crab that were $\geq$ 114 mm CL, a size threshold of female maturity (error probability 0.01%), and small female crab (< 114 mm CL) judged mature by the presence of eggs and egg development stage. An abundance index was estimated using the nearest five pots sampled in 2008-09. The nearest five pots to each site were identified by the linear distance from the pot to the site using ArcGIS 9 (Esri Institute). The estimated index of abundance was calculated as mean crabs·pot^{-1} with standard error as measure of variability. The Couverden Islands site was not included because the nearest station in 2008-09 was 24 km to the northwest in Excursion Inlet. Abundance was also estimated near Indian Cove from 1997-98 when Loher and Armstrong (2000) conducted their study of larval supply and settlement. The mean distance required to account for the nearest five pots to our study sites, for both mature female and juvenile male crabs, was 2 km ± 0.8 km SE. The smallest distance to the nearest pot for both females and males was 0.2 km near the head of Barlow Cove. The greatest distance was 8.8 km to a pot containing juvenile male crab near our Horse Island site, whereas the distance to the nearest pot with mature females near this site was 6.5 km.

Biomass estimates of mature ($\geq$ 129 mm CL) and legal ($\geq$ 145 mm CL) male crab were also provided by ADF&G for southeast Alaska from 1979-2009, and from 1993-2009 for the following survey areas: Juneau (inclusive harvest area 11A); Lynn Canal (15C and 12B); and Excursion Inlet (14C) (Fig. 2.1). Biomass estimates were calculated by ADF&G from stock assessment survey catch estimates and biological data, commercial and personal use fishery catch, and estimates for natural mortality and growth (Clark et al. 2003). Southeast Alaska commercial catch history data from 1970-2009 were obtained from ADF&G.

2.3 Results

2.3.1 Larval Supply and Settlement

A total of 24 red king crab glaucothoe and 154 instars were captured in floating larval collectors at our southeast Alaska study sites in 2008 (Table 2.1). A subset of these larvae ($n = 7$) and instars ($n = 46$) were measured to carapace length (CL). The mean size of the larvae was 2.6 mm CL ± 0.2 SE (min = 2.0 mm, max = 3.1 mm) and the instars were 2.2 mm CL ± 0.1 (min = 1.7 mm, max = 3.3 mm). A total of 15 larvae and 64 instars were captured in floating collectors at Indian Cove and the Couverden Islands in 2009. The larvae and instars of other crab species, including lithodids other than red king crab, were also captured in 2008 and 2009. In 2008 these included five helmet crab (*Telmessus cheiragonus*) megalopae and 193 instars, six instars of unknown decorator crabs, and two instars of other lithodids, including one *Hapalogaster cavicauda* and one undetermined lithodid. In 2009, six helmet crab larvae and 102 instars were captured along with one unknown decorator crab instar, and six other lithodid instars, including three *H. cavicauda*, two *Cryptolithodes typica*, and one undetermined lithodid. The other lithodid instars, with the exception of *C. typica*, were morphologically similar in appearance to first or second stage red king crab instars, but with distinguishing variations in color, spination, and limb length.

Larval supply at 6 m depth varied spatially (df effect/total = 7/70, $F = 7.61$, $p < 0.0001$) (Fig. 2.2). The Couverden Islands in 2008 (mean crabs·collector^{-1}·day^{-1} ± SE, 0.07 ± 0.01) and 2009 (0.06 ± 0.01) had the greatest supply of settling larvae at 6 m depth, significantly more than at Horse Island (0.02 ± < 0.01), Indian Cove 2009 (< 0.01 ± < 0.01), and Barlow Cove (0). Indian Cove 2008 (0.05 ± 0.01) had significantly greater larval supply than Barlow Cove, but not Horse Island. Further, differences were not detected among St. James Bay (0.03 ± 0.01), Portland Island (0.02 ± 0.01), and other sites.

Patterns of larval supply at 6 m versus 9 m were not consistent across sites in 2008 (Table 2.1 and Fig. 2.3). A significant interaction between site and depth (df effect/total = 3/70, $F = 3.50$, $p = 0.02$) occurred because more larvae and benthic stage crabs were captured at 9 m than at 6 m depth at St. James Bay, Barlow Cove, and Indian Cove 2009, but larval supply was similar between depths at Indian Cove 2008 (Fig. 2.3). The difference in larval supply at 6 m and 9 m depths was greatest at St. James Bay, where mean captures at 9 m depth were 0.10 crabs·collector^{-1}·day^{-1} ± 0.06 SE, compared to 0.03

± 0.04 at 6 m depth. St. James Bay at 9 m depth had greater supply of settling larvae than all sites and depths sampled in 2008. Individually, site (df = 3/70, F = 10.66, $p < 0.0001$) and depth (df = 1/70, F = 9.84, $p < 0.01$) were significant sources of variation in larval supply.

A consistent temporal pattern of larval settlement was evident across sites in 2008 (Fig. 2.4). A significant interaction occurred between settlement stage and sampling period (df effect/total = 2/60, F = 15.54, $p < 0.0001$), due to more larvae captured during period 08-1 (June 10-20) than period 08-2 (June 27-July 2) or 08-3 (July 25-August 8), and more benthic stage instars captured during periods 08-2 and 08-3 than period 08-1 (Table 2.1 and Fig. 2.4). Settlement stage alone was a significant source of variation in temporal settlement patterns (df = 1/40, F = 8.29, $p < 0.01$), but sampling period was not significant (df = 2/60, F = 0.91, $p = 0.41$). The last date of capture of larvae in 2008 was June 14 at St. James Bay, even though sampling continued until June 20, and the first date of capture of juveniles was June 27, the first day of our second 2008 sample period. This temporal pattern was evident across all sites (Fig. 2.4). Settlement timing in 2009 was largely consistent across sites. In contrast to 2008, two larvae were captured on July 14, 2009 at Indian Cove at 9 m depth, extending the 2009 settlement window into July (Table 2.1 and Fig. 2.4).

Few settling red king crab larvae and benthic stage crabs were captured in settlement pails at Indian Cove, Barlow Cove, and St. James Bay (Table 2.1). Five pails returned larvae or instars, and four of those five pails were from Indian Cove. Larvae and instars were found at 6 and 9 m depth at Indian Cove during period 08-1, and larvae were found at 6 m depth during period 08-2. One pail from St. James Bay returned larvae and instars during period 08-1. Larvae or instars were not found in benthic pails during period 08-3. Barlow Cove, the site with the lowest larval supply from floating collectors, returned no settling red king crab from benthic pails.

Settlement pail substrates available to settling larvae varied among sites, reflecting seafloor substrate composition at those sites. Substrates in pails at Barlow Cove were overall less structurally complex (mean HCI ± SE, 0.67 ± 0.06) than St. James Bay (1.16

± 0.16) and Indian Cove (1.38 ± 0.16). Most pails at Barlow Cove contained only small parchment tubeworms and some contained small pieces of macroalgae that added structural complexity to otherwise low-complexity sand. The pails from Indian Cove with red king crab settlers contained combinations of structurally complex substrates (1.75 ± 0.20), including parchment tubeworms, macroalgae, bivalve shells, and cobbles. The one pail from St. James Bay with four settlers contained one large cobble with attached macroalgae and small encrusting tubeworms (HCI = 1.75). The presence of infrequent parchment tubeworms and macroalgae in pails at St. James Bay added structural complexity to otherwise low complexity silty mud substrate. Substrates available to settling larvae also varied among pails within sites. Pails without settlers at Indian Cove (1.25 ± 0.19) and St. James Bay (1.19 ± 0.15) contained substrates that were generally less structurally complex than pails with settlers.

Helmet crab larvae and instars were also found in settlement pails. These included one pail from St. James Bay with a low complexity substrate (HCI = 0.25), and three pails from Barlow Cove containing parchment tubeworms and small pieces of macroalgae (mean HCI ± SE) 0.83 ± 0.29. Pails from Indian Cove did not capture settlers of other crab species.

2.3.2 Benthic Habitat

Benthic habitats varied among sites (Table 2.2 and Fig. 2.5). Indian Cove, the Couverden Islands, and Portland Island had a variety of unconsolidated hard substrates (small boulders, cobbles, pebbles, and gravel). These were on or embedded in fine sediments, such as silty sand, with a dense variety of macroalgae cover and structural invertebrates including parchment tubeworms, red cucumbers, and plumose anemones. In contrast, Horse Island habitats contained more silty mud than unconsolidated hard substrates, less variety of macroalgae, and no structural invertebrates. Habitats at Barlow Cove and St. James Bay were mainly composed of fine substrates with crushed shells and drift algae entrained on the groundlines. Parchment tubeworms occurred in small, patchy clumps at Barlow Cove creating small islands of biogenic habitat. However, sessile habitat-forming invertebrates were not identified from video at St. James Bay.

Similarities and differences in habitat composition among sites were illustrated by nMDS ordination with distinct groupings and a low stress value (three-dimensional stress = 0.01, two-dimensional stress = 0.03) (Clarke and Warwick 2001) (Fig. 2.6). Hierarchical cluster analysis with SIMPROF tests of Bray-Curtis similarities demonstrated statistically significant groups ($p < 0.0001$). Ordination contours were drawn to encompass sites and depths that were at least 70%, 60%, and 40% similar in habitat composition. Indian Cove habitats were 79% similar between 6 and 9 m depths, indicating little within site variation. Habitats at the Couverden Islands and Portland Island were 86% similar at 6 m depth. Indian Cove, the Couverden Islands, and Portland Island habitats were 66% similar (Fig. 2.5 and 2.6). These sites were 48% similar to Horse Island habitats, which had more silty mud like habitats at St. James Bay. Habitats at Barlow Cove and St. James Bay were 43% similar in composition, largely due to high proportions of fine sediments, and had little within-site variation among depths. Barlow Cove habitats were 68% similar at 6 and 9 m depths with high proportions of silty sand and drift algae. Habitats at St. James Bay were 63% similar at 6 and 9 m depths but contrasted with Barlow Cove by having silty mud with benthic diatom cover rather than silty sand.

2.3.3 Adult Abundance and Distribution

Red king crab were distributed throughout the ADF&G stock assessment survey area in northern southeast Alaska during June-July in 2008-09 (Fig. 2.7). Mature female crab (84-169 mm CL) were most abundant near the head of bays, including Barlow Cove and Excursion Inlet, and inside Auke Bay and at locations near N. Douglas Island and S. Stephens Passage (Fig. 2.8). Both mature females and juvenile male crab (fishery pre-recruits, < 129 mm CL) were concentrated near the head of bays and absent from the entrance to these bays and from pots sampled in the central channels of Stephens Passage and Lynn Canal (Fig. 2.9). Juvenile males were not as widely distributed as mature female crab in 2008-09.

Among our study sites, mature female crab were most abundant near Barlow Cove at the head of the bay (mean crabs·pot^{-1} ± SE, 35.6 ± 9.9) and the next highest local abundance was near Indian Cove (9.0 ± 3.5) (Fig. 2.10). Juvenile males were most abundant near Indian Cove (8.2 ± 2.3) and the next highest local abundance was at the head of Barlow Cove (5.0 ± 1.1). Mature female and juvenile male crab had relatively low abundance near our site in St. James Bay (1.6 ± 0.2, 1.6 ± 0.4), and near Horse Island (3.6 ± 1.1, 4.0 ± 2.3), and Portland Island (6.8 ± 4.6, 1.4 ± 0.4). Abundance of mature female crabs and juvenile males at Indian Cove in 1997-98 during the study by Loher and Armstrong (2000) (39.8 ± 22.0, 29.0 ± 12.9) was relatively greater than 2008-09 estimates at this site, though relatively similar to Barlow Cove in 2008-09.

Commercial catch of southeast Alaska red king crab has declined overall since the early 1970s, with slight increase in the 1980s followed by continued decline with fishery closures in 1986-1992 (Fig. 2.11). The fishery was re-opened in 1993-1997, closed 1998, open in 1999, 2001-2003, and 2005, and has been closed since 2006. Biomass of mature and legal male crabs steadily declined from 1979 through the 1980s with historic low estimates of < 300 mt of mature male crab in the late 1980s. Rebuilding began by 1990 and reached a peak of 753 mt of mature male crab in 1995. The population has generally declined since 1995 and was < 300 mt in 2009, approaching the historic lows of the late 1980s.

The Juneau survey area, encompassing our Indian Cove, Barlow Cove, Portland Island, and Horse Island study sites, has relatively high local biomass of mature male crabs, though biomass has steadily declined since 2000 (Fig. 2.12 a). Our St. James Bay study site is located in the Lynn Canal survey area where mature male biomass has recently increased (Fig. 2.12 b). Mature male biomass has declined since 2002 and is relatively low in the Excursion Inlet survey area that is located northwest of our Couverden Islands study site near Icy Strait (Fig. 2.12 c).

2.4 Discussion

2.4.1 Current Status of Red King Crab Larval Biology

Red king crab larval biology is less well-known than that of other commercially harvested crustaceans, including Dungeness crab, and American and spiny lobsters. Knowledge gaps include adult female distribution, hatch timing, larval behavior, transport mechanisms, settlement locations, and population connectivity.

Adult female red king crab make a seasonal migration to shallow depths, where egg-bearing females release developed larvae prior to molting and mating. This reproductive movement pattern was documented in the Gulf of Alaska by Powell and Nickerson (1965) and later by Stone et al. (1992, 1993) who investigated distribution, aggregative behavior, and movement in Auke Bay in the southeast Alaska study area. Stone et al. (1992, 1993) found that female depth distribution and aggregative behavior changed seasonally. Females were highly aggregated at shallow depths (< 25 m depth) in groups of more than 300 individuals during late November-March when hatching, molting, and mating occurred. These activities were followed by female migration as loose aggregations to intermediate depths (> 25 and < 40 m) in April and to deeper depths (> 40 m) in late May where females remained through summer to mid-fall in less aggregated groups that occupied non-random locations. Hatch timing for females may be bimodal, as smaller, first time spawning females occupied shallow waters earlier than larger multi-year spawning females (Stone et al. 1992). Two hatching periods were also documented in Auke Bay in southeast Alaska in 1986 and 1988, but not 1987, based on larval timing and density in the plankton (Shirley and Shirley 1989). The movement patterns of egg-bearing females have implications for understanding larval release timing and location and the subsequent transport of larvae.

The two to four month larval period of red king crab (Shirley and Shirley 1988; 1989; 1990) provides great potential for long-distance dispersal (Shanks et al. 2003) away from hatching locations. This pattern has been observed with planktonic larval stages of other commercially important crustaceans, including Dungeness crab (Eggleston and

Armstrong 1995; Shanks and Roegner 2007), snow crab (*Chionocetes opilio*) (Orensanz et al. 2004; Parada et al. in press), and lobsters (Incze and Wahle 1991; Cobb and Wahle 1994). Larval transport distance in the southeastern Bering Sea was estimated to be 28-264 km, assuming passive movement (Hsu and Armstrong 1988). These estimates were from models for red king crab from 1973-1985 that incorporated larval size, sinking rate, and larval duration based on water temperature. Red king crab larval release timing and duration are linked to water temperature (Shirley and Shirley 1989), with known variation in timing and duration for Dungeness crab between southeast Alaska (Fisher 2006) and the Pacific coast of Canada and the U.S. (Lough 1976; Jamieson and Phillips 1988). Red king crab larval transport distance from known hatching locations has not been measured in the field.

Larval red king crab will encounter a variety of oceanographic processes that affect transport and settlement. The fjord coast of southeast Alaska is complex, with many islands, deep inlets and channels, and submerged topographic features remnant of glacial ice cover. Oceanographic processes that may influence larval transport along complex fjord coastlines include wind-driven advection, tidal currents, and currents driven by water density gradients from freshwater runoff (Asplin et al. 1999; Gibbs et al. 2000; Hill et al. 2009; Weingartner et al. 2009). Dungeness crab larval transport has been studied in British Columbia, Canada, and in Glacier Bay, southeast Alaska, demonstrating that zoea use vertical migration and transport by tides and winds in these areas with complex coastlines (Jamieson and Phillips 1988; Fisher 2005; Herter and Eckert 2008). In Glacier Bay, Dungeness crab zoea are transported out of the bay and return as megalopae by selective tidal stream transport where larvae migrate into inward-flowing currents and avoid outward-flowing currents, resulting in little or no net exchange of larvae from the bay (Fisher 2005). In contrast, *Cancer oregonensis*, a congener of Dungeness crab, uses vertical migration in selective tidal streams as a retention mechanism near coastal locations in British Columbia and Glacier Bay (Jamieson and Phillips 1988; Fisher 2005).

The transport processes of red king crab are not well known. Red king crab zoeae have a strong phototactic response to light that diminishes ontogenetically and is not present for glaucothoe (Epelbaum et al. 2007). Glaucothoe are highly thigmotactic, responding by touch upon contact with complex settlement substrates (Stevens and Kittaka 1998), also a behavior of European green crab (*Carcinus maenas*) megalopae (Paula et al. 2006). Red king crab larval behavior may interact with transport processes and coastal topography to influence transport and settlement location. Phototactic behavior suggests that red king crab zoea may have near surface position in the water column, with potential for transport by near surface currents and winds (Asplin et al. 1999), and the behavior of glaucothoe suggests near bottom retention at settlement locations.

Although we do not have a good understanding of the distribution of red king crab larval stages in the field, zoea have been captured in the top 30 m of the water column in southeast Alaska (Shirley and Shirley 1989) and glaucothoe have been captured in complex substrates inshore (Donaldson et al. 1992; Loher and Armstrong 2000; this study). Larval sampling to 200 m depth in the Sea of Japan near Russia found red king crab zoea I and II distributed from the coast to the 100-m isobath offshore and zoea III and IV were inshore of the 50-m isobath (Sherbakova et al. 2008). This demonstrates the potential for offshore transport of red king crab early larval stages and inshore transport or retention at late stages in open coast locations. In contrast, models of red king crab larval transport along the fjord coast of Norway predicted that larvae released along the coast were transported in the direction of the Norwegian coastal current and tended to settle on the west side of fjords at points and capes, and that larvae released inside fjords tended to be retained in those locations (Pedersen et al. 2006).

Recent genetic analysis of several nuclear loci from adult red king crab from the inside waters of southeast Alaska demonstrated heterogeneity among populations in semi-enclosed bays separated by distances less than 100 km (S. Vulstek and D. Tallmon, University of Alaska Southeast (UAS), personal communication). Differentiation among southeast Alaska populations was greater than populations in the Bering Sea and Gulf of Alaska (S. Vulstek and D. Tallmon, UAS, personal communication). Because red king crab larvae have long-distance dispersal potential, we would expect that populations would be relatively homogenous genetically, compared to marine species with low dispersal potential (Kelly and Palumbi 2010). The observed higher level of genetic differentiation among southeast Alaska populations suggests the presence of an oceanographic mechanism to enable local larval retention. Larval retention is occurring within southeast Alaska red king crab populations, but the scale of larval retention is presently not known.

2.4.2 Spatial Variation in Larval Supply

Spatial variation of red king crab larval supply was likely due to several processes that may influence larval transport and retention in southeast Alaska, including hydrographic features that typically occur along complex coastlines in fjord-estuary systems (Asplin et al. 1999; Gibbs et al. 2000). High larval supply at Indian Cove, St. James Bay, and the Couverden Islands, suggests that larvae were transported to those areas and retained. Sites located inside bays or near headlands, like the Couverden Islands, have the potential to retain larvae transported to those sites, as predicted along the fjord coast of Norway (Pedersen et al. 2006) and observed in our study. In contrast, low larval supply, at sites including Horse Island, Portland Island, and Barlow Cove, suggests that larvae were not transported to or retained at those locations, although Barlow Cove is a deep, narrow bay. Hydrographic models of particle movement at the intersection of Glacier Bay and Icy Strait demonstrated high potential for dispersal barriers formed by interacting tidal streams and fronts in this area (Hill et al. 2009). Although the larval duration of red king crab suggests potential for long-distance dispersal, hydrographic features interacting with the coastal topography (Pickard 1967; Weingartner et al. 2009) may limit dispersal distance in this region, as demonstrated by genetic differentiation among some bays (S. Vulstek and D. Tallmon, UAS, personal communication).

Barlow Cove had the lowest supply of larvae in our study area and the highest local population of mature female crab. Our study site in Barlow Cove was located near the head of this deep, narrow bay where juvenile and adult red king crab occur in high abundance in deeper habitats, observed from submersible dives (Zhou and Shirley 1998) and stock assessment surveys (Clark 2008). Our result for Barlow Cove was unexpected, because models of larval dispersal along complex coastlines predicted retention for red king crab larvae originating in bays and fjords (Pedersen et al. 2006) like Barlow Cove. Similarly, population heterogeneity for urchins (Mladenov et al. 1997) and seastars (Perrin et al. 2004) demonstrated larval retention on the local-scale of New Zealand fjords (Wing et al. 2003), despite long-distance dispersal and population homogeneity for these species along the coast. Because so few larvae were captured at our sampling sites in Barlow Cove, it is likely that larvae were transported to other locations within the bay, or were not retained at the scale of this bay. High female abundance in Barlow Cove may not contribute to larval supply at this site, but may be an important source of larvae for other sites in this region of southeast Alaska.

2.4.3 Temporal Variation and Settlement Timing

Our study revisited sites in Auke Bay (Indian Cove) more than ten years after Loher and Armstrong (2000) investigated red king crab larval dynamics and settlement habitat. Our 2008-09 results for Indian Cove larval supply were consistent with this earlier study, as the ranges of larvae and crabs captured in floating larval collectors in our study and by Loher and Armstrong (2000) were similar. We captured between 0-9 individuals·collector^{-1} at 6 and 9 m depth at Indian Cove during June-July 2008-09, and Loher and Armstrong (2000) captured between 0-8 individuals·collector^{1} at 12 m depth during June-July 1997. Consistent larval supply to the area of Indian Cove suggests that processes influencing larval transport and retention with respect to this location have remained consistent over time.

Settlement timing was also consistent among study sites in 2008 and between years in 2008-09, with settlement completed by mid-June in 2008 and mid-July in 2009. Historical patterns of settlement timing in Auke Bay were largely consistent with our results. Settlement extended into mid-July in 1997 (Loher and Armstrong 2000) and was completed by late-June in 1988 and 1989 (Freese and Babcock 1989).

Glaucothoe were present in the plankton earlier, by mid-May, during warmer years (1987-1989) and were not present until late-May and mid-June during the coldest years (1985 and 1986) from previous studies in Auke Bay during the 1980s (Shirley and Shirley 1989; 1990). In all years (1985-1989), glaucothoe were last observed in plankton samples in mid-to late-June (Shirley and Shirley 1989; 1990). Sea surface temperature measured in Auke Bay from March-July in 1985-1989 and 2008-2009, demonstrated cooler than average temperatures in 2008 and warmer than average temperatures in 2009. Variability in settlement timing among the years of our study and these historic studies was about one month, and may reflect differences in hatch timing and larval duration from year to year due to differences in annual mean water temperature during the months that larvae are present in the water column (Shirley and Shirley 1989).

2.4.4 Benthic Habitat and Settlement Potential

In our field study, we identified two sites with both high larval supply and complex benthic habitats, Indian Cove and the Couverden Islands. These two sites were grouped by benthic habitat analysis based on similar attributes that form high structural complexity. Habitats at these sites were composed of a variety of unconsolidated hard substrates, shells, macroalgae, and structural invertebrates. Benthic habitat availability likely influences red king crab early life stage success because structurally complex habitats provide crevice space and vertical structure that function as food (Pirtle and Stoner 2010) and refuge (Stevens and Swiney 2005; Stoner 2009; Pirtle 2010). Indeed, red king crab glaucothoe settle on highly structured habitats and do not settle on sand habitat without structure (Stevens and Kittaka 1998). Because of high larval supply at Indian Cove and the Couverden Islands and the presence of complex benthic habitats that can support settling larvae and early benthic stages, we suggest that these locations could serve as red king crab nurseries.

Our study in 2008 used benthic settlement pails to quantify settlement abundance at Indian Cove, St. James Bay, and Barlow Cove. Our results suggested that habitat should not have been limiting to settling larvae at Indian Cove, where we observed half of our total observed settlement in pails that contained structurally complex substrates representative of the complex benthic habitat at this site. We also found early benthic stage crabs (ages 0 and 1) in the low intertidal zone in the vicinity of Indian Cove on the lowest tides from early spring through summer at densities up to 3 $\text{crabs}\cdot\text{m}^{-2}$, demonstrating that larvae not only settle to benthic habitats at this site, but that this site functions as a nursery location. Loher and Armstrong (2000) used a variety of methods to examine settlement habitat and post-larval stage habitat use in the vicinity of Indian Cove in 1997-98, including dive transects, suction dredge sampling, and benthic settlement pails. They found newly settled larvae and post-settlement stage crabs in complex benthic habitats, and none in the silty mud habitat of a neighboring cove, demonstrating that the spatial distribution of settlement in this area was related to complex habitat availability (Loher and Armstrong 2000). Because the Couverden Islands and Indian Cove have similarities in benthic habitat composition and high larval supply, we expect a similar relationship between larval settlement and benthic habitat at the Couverden Islands.

We found high larval supply and half of our total observed settlement in St. James Bay, a relatively protected embayment with silty mud habitat and patchy occurrence of complex benthic habitat in the form of drift algae and parchment tubeworms. St. James Bay has the potential to be a nursery location, where patchy habitats could be functionally similar to continuous habitats at other locations for settlement and early post-settlement stages. Settlement observed in St. James Bay was in one pail that contained complex habitat, although more than half of the pails at this site contained some structural features in addition to silty mud. Benthic habitat analysis grouped St. James Bay with Barlow Cove based on similarities in low complexity habitat composition at these sites. Substrates in pails at Barlow Cove were overall less structurally complex than St. James Bay, because pails at Barlow Cove were dominated by sand with less variety of other substrates mixed with this low-complexity habitat. Barlow Cove also has patchy distribution of small parchment worm tubes, but this habitat feature was more frequently encountered than at St. James Bay, visible on habitat transect videos and present in all settlement pails at this site (10-100 individuals·pail^{-1}) with the occasional piece of macroalgae. Red king crab larval supply may have been limiting at Barlow Cove, because we observed low larval supply in floating collectors and did not observe settlement in the pails, although helmet crab megalopae settled in three pails that contained worm tubes and macroalgae. Worm tubes form complex biogenic habitat that early juvenile red king crab find highly attractive (Pirtle and Stoner 2010), and early juvenile tanner crab (*Chionocetes bairdi*) have been observed associating with worm tubes in habitats around Kodiak Island, Alaska (C. Ryer, Alaska Fisheries Science Center, personal communication). In laboratory experiments with fish predators, patchy habitat islands were nearly as effective as continuous, complex habitat in providing structural refuge for age 0 (3-5 mm CL) red king crab (Stoner 2009).

2.4.5 Adult Distribution and Abundance

The distribution of adult and older juvenile red king crab at the time of the ADF&G stock assessment survey, during June-July, demonstrated the spatial structure of crabs sampled by the survey in our southeast Alaska study area. Mature females and juvenile male crab were more limited in spatial distribution than mature male crab, the main component of crabs sampled by the survey in this area (Fig. 2.7, 2.8, 2.9). Adult females and juvenile male crab were concentrated near the head of bays and absent from the entrance to these bays and open channels. The distribution of mature females encountered by the survey suggests that they occupied deeper, summer locations at the head of bays, as proposed by Stone et al. (1992; 1993), including Barlow Cove and Auke Bay. From the work of Stone et al. (1992, 1993) on the seasonal movement of crabs in Auke Bay, we expect that females in the areas of high density during the survey would migrate inshore at those locations during the late-winter and early-spring when hatching occurs. Whether or not larval hatching at locations of high female density leads to retention at these sites, or transport to other locations instead, remains to be determined.

The biomass of mature male red king crab in southeast Alaska declined from 533 mt 1997, at the time of Loher and Armstrong's (2000) field work in Auke Bay, to 334 mt at the time of our study in 2008 (Figure 2.11). In the Juneau survey area that included Auke Bay, mature male biomass was 230 mt in 1997, increased to 292 mt by 2001, and declined to 107 mt by 2008. Considerable fluctuation in biomass of mature male red king crab in southeast Alaska between the late 1990s and our present study does not seem to have affected larval supply to Auke Bay. Whether or not larval supply has diminished with depleted adult populations in the southeast Alaska region as a whole is not clear.

2.4.6 Directions for Further Study

Our research provides new information about red king crab early life stage ecology with practical potential to understand mechanisms behind depleted red king crab populations in Alaska. We have learned that the supply of larvae varies spatially among locations and depths, and that settlement timing is generally consistent from year to year in our southeast Alaska study area. Benthic habitat availability for settling larvae and early benthic stages varies spatially among locations in this area and may affect the potential of certain sites to serve as nurseries. To improve understanding of red king crab early life history and population dynamics we identify several areas of further study.

The relationship between local adult populations and larval supply should be further investigated. For example, the truncation of adult female red king crab distribution in the eastern Bering Sea and subsequent shrinking of optimal hatching habitat may have shifted the transport of larvae from traditional nursery locations, to the detriment of local population strength (Loher and Armstrong 2005; Kruse et al. in press), and a similar trend is likely occurring with Bering Sea snow crab (Orensanz et al. 2004; Parada et al. in press). Snow crab spatial population dynamics were recently investigated for the Bering Sea, Alaska, using a coupled biophysical modeling approach that included the spatial distribution of juveniles and adults, results of an individual based model for snow crab early life history, and a hydrodynamic model of circulation and bottom temperature (Parada et al. in press). Given that the range of spawning female snow crab has contracted to the north with increased near bottom temperature (Orensanz et al. 2004), this model demonstrated the major role of climate in regulating snow crab spatial ecology in the Bering Sea. To accomplish this level of population modeling for red king crab in southeast Alaska, we require time-series for larval supply from spawning locations to settlement, greater knowledge of the spatial extent of nursery locations, and basic understanding of the physical oceanographic processes in the region.

Further study is needed on physical oceanographic processes in southeast Alaska and on red king crab larval behavior to better understand larval transport and population connectivity for red king crab. We have at present a rudimentary understanding of the physical oceanography of southeast Alaska (Weingartner et al. 2009). Patterns of larval supply in southeast Alaska suggest that transport and retention in this region may be similar to other fjord coast locations, including Norway (Pedersen et al. 2006) and New Zealand (Wing et al. 2003), and much different than open coastal locations such as the southeastern Bering Sea (Hsu and Armstrong 1988, Loher and Armstrong 2005).

Furthermore, red king crab larval dynamics cannot be generalized from well-studied species like Dungeness crab. Behavioral differences between Dungeness crab (Fisher 2005; Herter and Eckert 2008) and red king crab larvae in southeast Alaska could indicate that populations of these co-occurring species respond differently to environmental drivers of marine population regulation. Process-driven studies of red king crab larval dynamics are fundamental to better understand this critical life stage, including connections between larval transport and nursery locations.

To better understand nursery habitat function for red king crab, field studies are needed that examine growth and survival of early post-settlement stages in a variety of habitats, including spatially explicit knowledge of nursery habitat suitability. Nursery habitat is a complex function of conditions that optimize growth and survival of early life stages. Recent studies have investigated habitat preferences for red king crab during settlement (Stevens and Kittaka 1998), and habitat preference of early juvenile stages (Stevens 2003; Pirtle and Stoner 2010), their foraging behavior (Pirtle and Stoner 2010), and habitat-specific survival and refuge response behavior with predators in the laboratory (Stevens and Swiney 2005; Stoner 2009) and the field (Pirtle 2010). Further study of mechanisms behind habitat associations relative to early benthic stage survival in various habitat types and locations, including the suitability of contiguous versus patchy habitat and the importance of predator-prey interactions, will improve understanding of nursery habitat function for red king crab.

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Table 2.1. Larval and juvenile abundance in collectors by site and sampling period, with the number of soak days, collectors recovered (C.n), pails recovered (P.n), and the total number of larvae (Lve) and juvenile instar crabs (Ins) collected at 6 m and 9 m depth.

Site	Sample Period	Deploy Date	Retrieve Date	Soak Days	Collectors					Pails				
					C.n	Lve	Ins	Lve	Ins	P.n	Lve	Ins	Lve	Ins
						6m Total		9m Total			6m Total		9m Total	
2008 High Intensity Sites														
IC	08-1	Apr-26	Jun-12	47	6	6	0	3	0	6	0	1	2	0
	08-2	Apr-26	Jun-27	62	6	1	4	6	10	6	3	0	0	0
	08-3	Apr-26	Jul-25	90	6	0	19	0	13	4	0	0	0	0
BC	08-1	May-22	Jun-20	29	6	0	0	0	0	6	0	0	0	0
	08-2	May-22	Jul-01	40	6	0	0	0	3	6	0	0	0	0
	08-3	May-22	Jul-31	70	6	0	0	0	0	6	0	0	0	0
SJ	08-1	May-11	Jun-14	34	6	0	0	8	0	6	0	0	1	4
	08-2	May-11	Jul-02	52	6	0	5	0	23	2	0	0	0	0
	08-3	May-11	Aug-08	89	6	0	14	0	20	3	0	0	0	0
2008 Low Intensity Sites														
CV	08-2	May-11	Jul-02	52	3	0	13	-	-	-	-	-	-	-
	08-3	May-11	Aug-08	89	3	0	13	-	-	-	-	-	-	-
HI	08-2	May-16	Jun-30	45	3	0	3	-	-	-	-	-	-	-
	08-3	May-16	Aug-01	77	3	0	3	-	-	-	-	-	-	-

Table 2.1. Continued.

					Collectors					Pails				
Site	Sample Period	Deploy Date	Retrieve Date	Soak Days	C.n	Lve	Ins	Lve	Ins	P.n	Lve	Ins	Lve	Ins
						6m Total		9m Total			6m Total		9m Total	
PI	08-2	Apr-26	Jun-30	65	3	0	6	-	-	-	-	-	-	-
	08-3	Apr-26	Aug-01	97	3	0	5	-	-	-	-	-	-	-
2009 Sites														
IC	09-1	May-11	Jun-13	33	9	1	0	3	0	-	-	-	-	-
	09-2	May-11	Jul-14	64	9	0	0	2	11	-	-	-	-	-
CV	09-1	May-03	Jun-11	39	9	9	8	-	-	-	-	-	-	-
	09-2	May-03	Jul-12	70	9	0	45	-	-	-	-	-	-	-

*Site: Indian Cove (IC), Barlow Cove (BC), St. James Bay (SJ), Couverden Islands (CV), Horse Island (HI), Portland Island (PI).

Table 2.2. Percent cover of habitat categories (bold text) and subcategories (plain text) classified from video frame analysis of habitat transects in 2008. Site abbreviations as in Table 2.1.

Habitat	Study Site.Depth (m)								
Categories Subcategories	IC.6	IC.9	BC.6	BC.9	SJ.6	SJ.9	CV.6	HI.6	PI.6
Substrate	**53.7**	**77.7**	**27.7**	**76.1**	**33.8**	**53.6**	**31.1**	**49.6**	**22.1**
Silty Mud	0.2	0	0.8	0	23.7	27.7	0	31.1	0
Silty Sand	29.1	55.6	26.9	75.5	1.8	0	3.7	0	6.4
Small Unconsolidated	4.7	2.4	0	0	0	0.4	2.0	5.4	1.2
Large Unconsolidated	2.1	1.2	0	0	0	0	19.6	0	10.4
Bivalve Shells	6.2	2.9	0	0.3	0.9	1.5	3.2	6.8	3.2
Crushed Shells	11.3	15.0	0	0.3	7.4	0	2.7	6.3	0.8
Diatom Mat	0	0	0	0	0	24.0	0	0	0
Terrestrial Debris	0.2	0.6	0	0	0	0	0	0	0
Macroalgae	**42.8**	**20.6**	**72.3**	**23.1**	**66.2**	**44.6**	**65.2**	**50.5**	**75.1**
Understory Kelp	16.4	8.2	0	5.1	0	0	21.8	47.8	43.4
Shotgun Kelp	19.1	7.4	0	0	0	0	41.4	0	30.5
Acid Kelp	2.3	1.8	0	0	0	0	0.7	2.7	1.2
Drift Algae	0.2	1.8	72.3	18.0	66.2	44.6	0	0	0
Algae Other	4.9	1.5	0	0	0	0	1.2	0	0
Macroinvertebrates	**3.5**	**1.8**	**0**	**0.9**	**0**	**1.9**	**3.7**	**0**	**2.8**
Parchment Tubeworm	0.2	1.8	0	0.9	0	0	0	0	0
Plumose Anemone	0	0	0	0	0	0	0.7	0	0.8
Orange Cucumber	0	0	0	0	0	0	0	0	0.4
Giant Cucumber	0	0	0	0	0	0	0.5	0	0
Mottled Seastar	0	0	0	0	0	0.4	0	0	0
Sunflower Star	3.3	0	0	0	0	1.1	2.5	0	1.6
Dungeness Crab	0	0	0	0	0	0.4	0	0	0

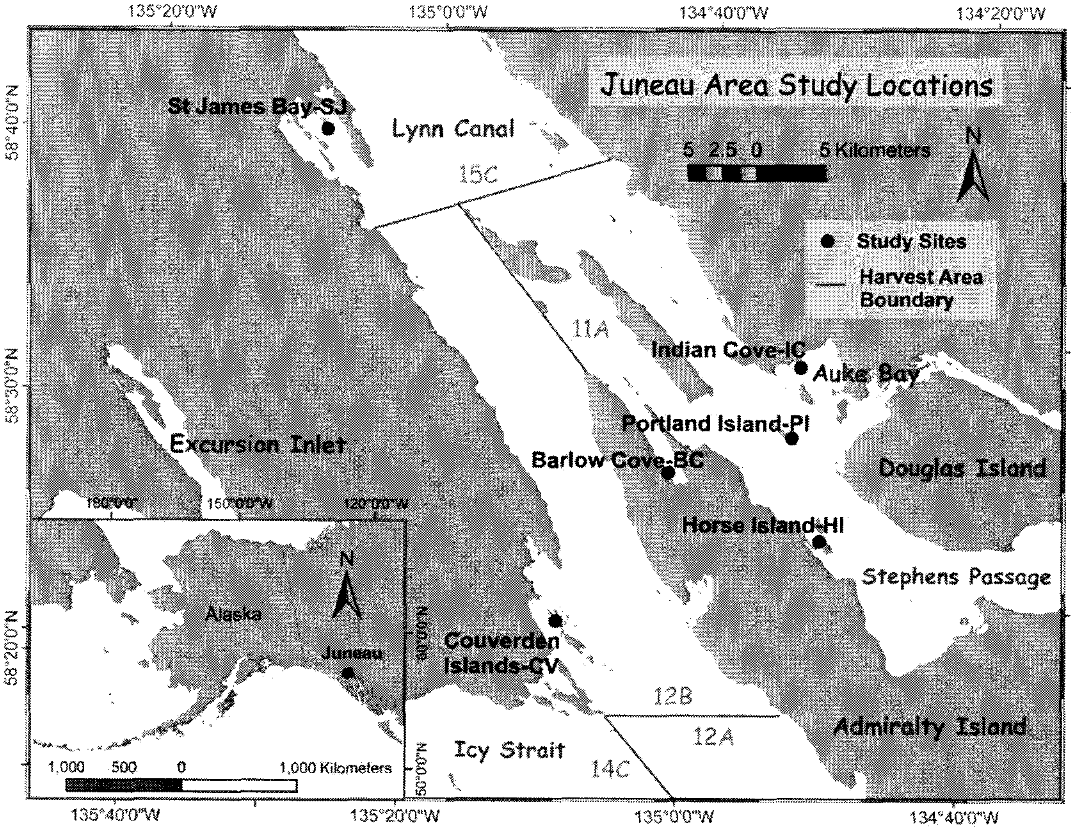

Figure 2.1. Study location with field sites near Juneau, and Alaska inset.

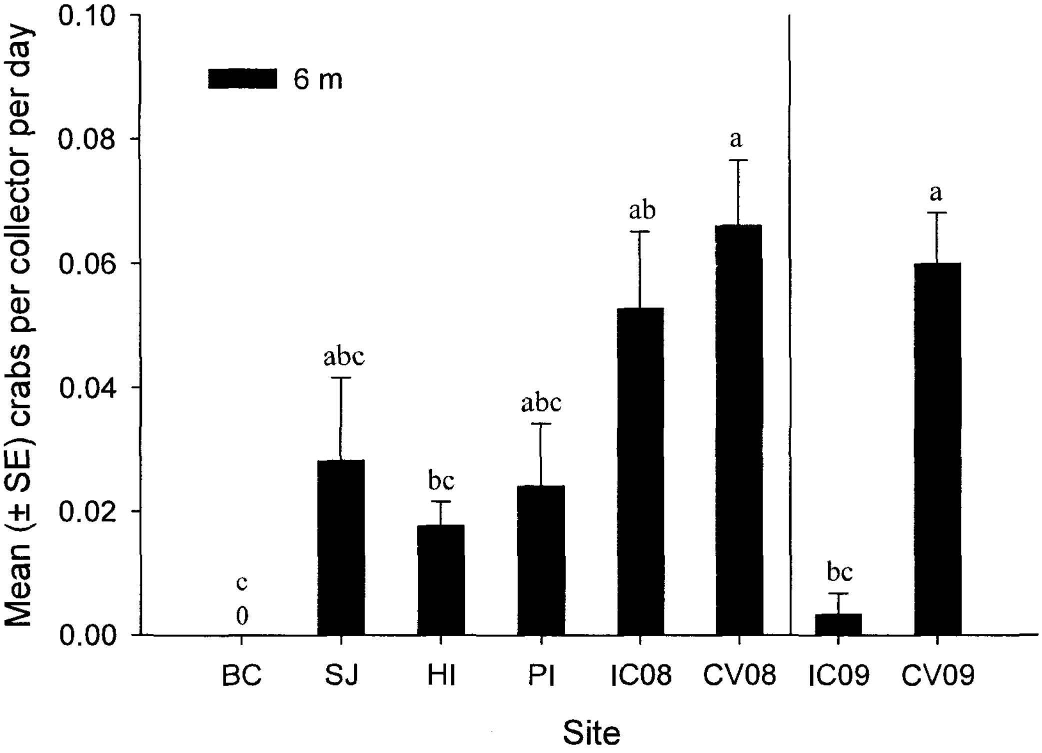

Figure 2.2. Total red king crab (larvae and instars) (mean crabs·collector^{-1}·day^{-1}) captured in larval settlement collectors at 6 m depth. All sites were sampled in 2008, and IC and CV were sampled in 2009. Letters above standard error bars indicate groups with similar means (Tukey's HSD, $p < 0.05$). Vertical line separates years 2008 and 2009; site abbreviations as in Table 2.1.

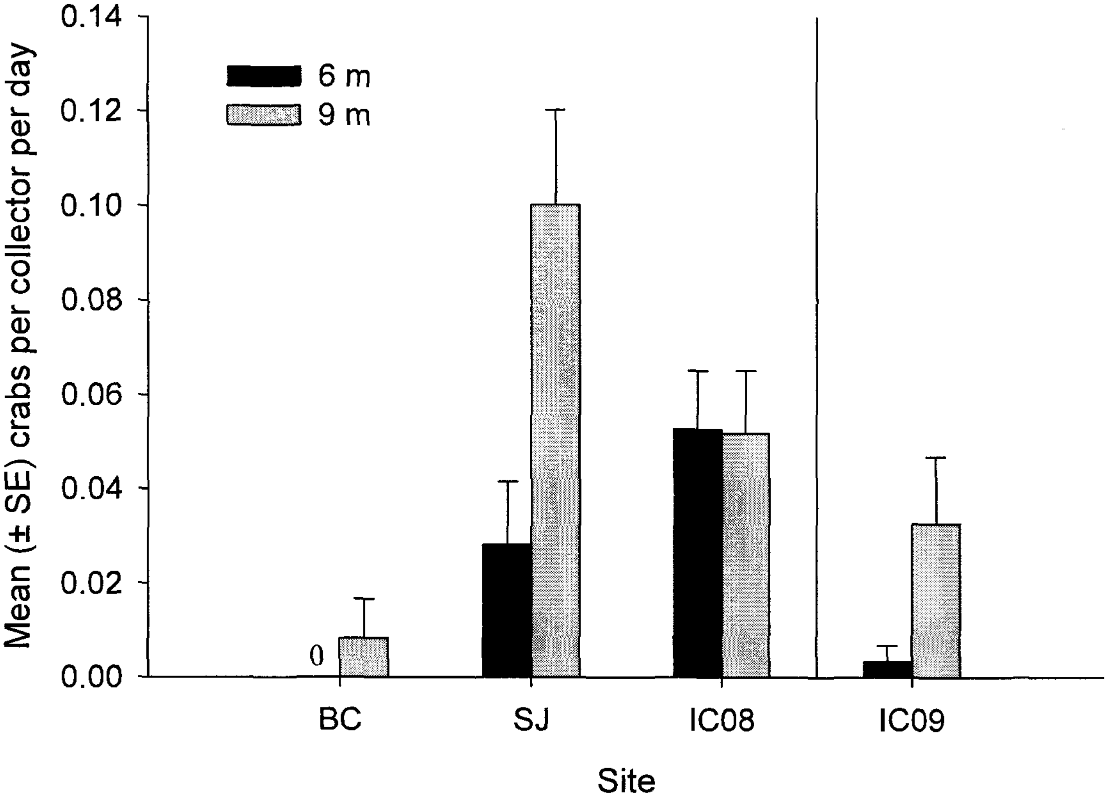

Figure 2.3. Total red king crab (larvae and instars) (mean crabs·collector^{-1}·day^{-1}) captured in larval settlement collectors at 6 m and 9 m depth with standard error bars. IC was sampled in 2008 and 2009. Vertical line separates years 2008 and 2009; site abbreviations as in Table 2.1.

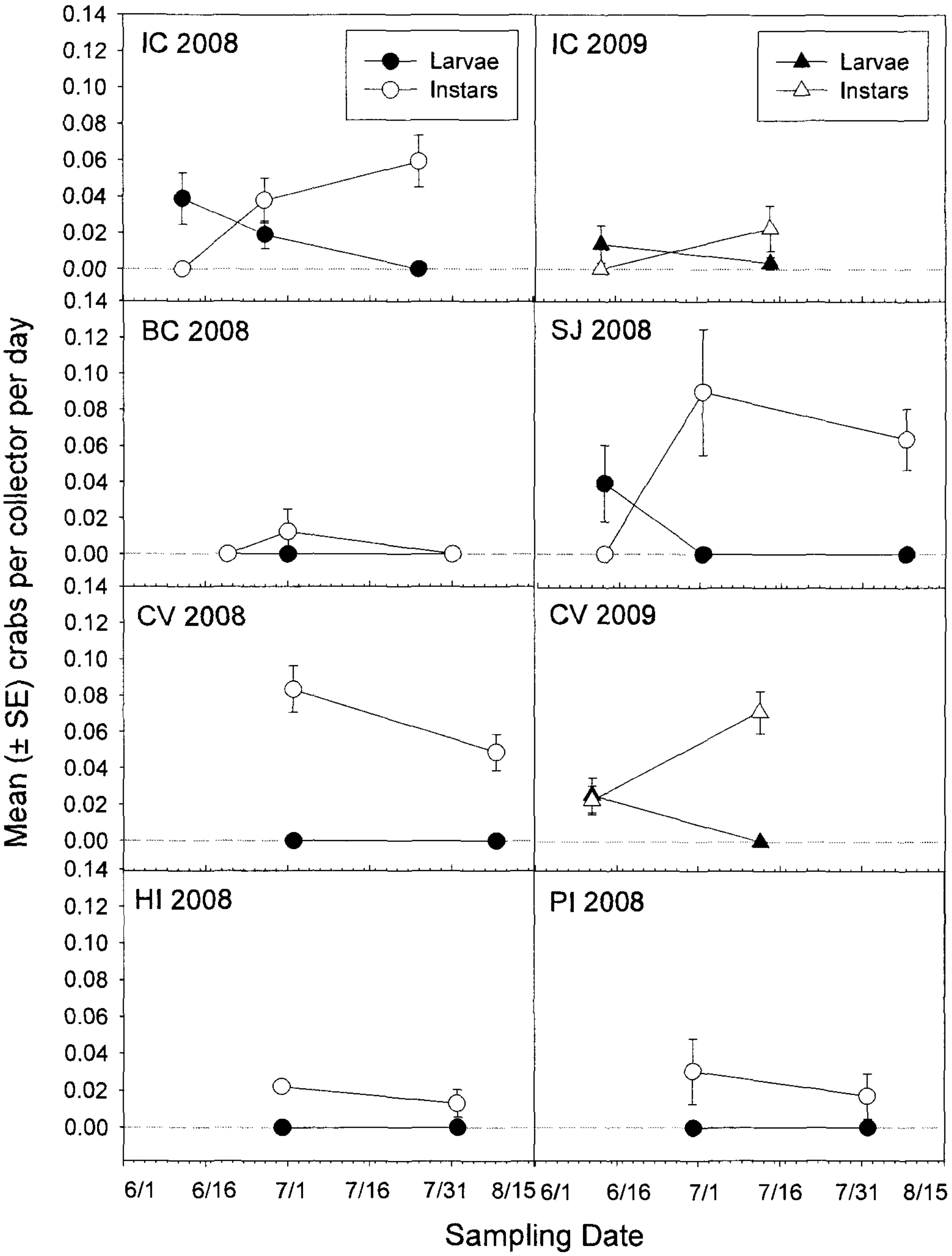

Figure 2.4. Settlement timing as measured by larval settlement collectors (mean crabs·collector^{-1}·day^{-1}) by site in 2008 (circles) and 2009 (triangles). Site abbreviations as in Table 2.1.

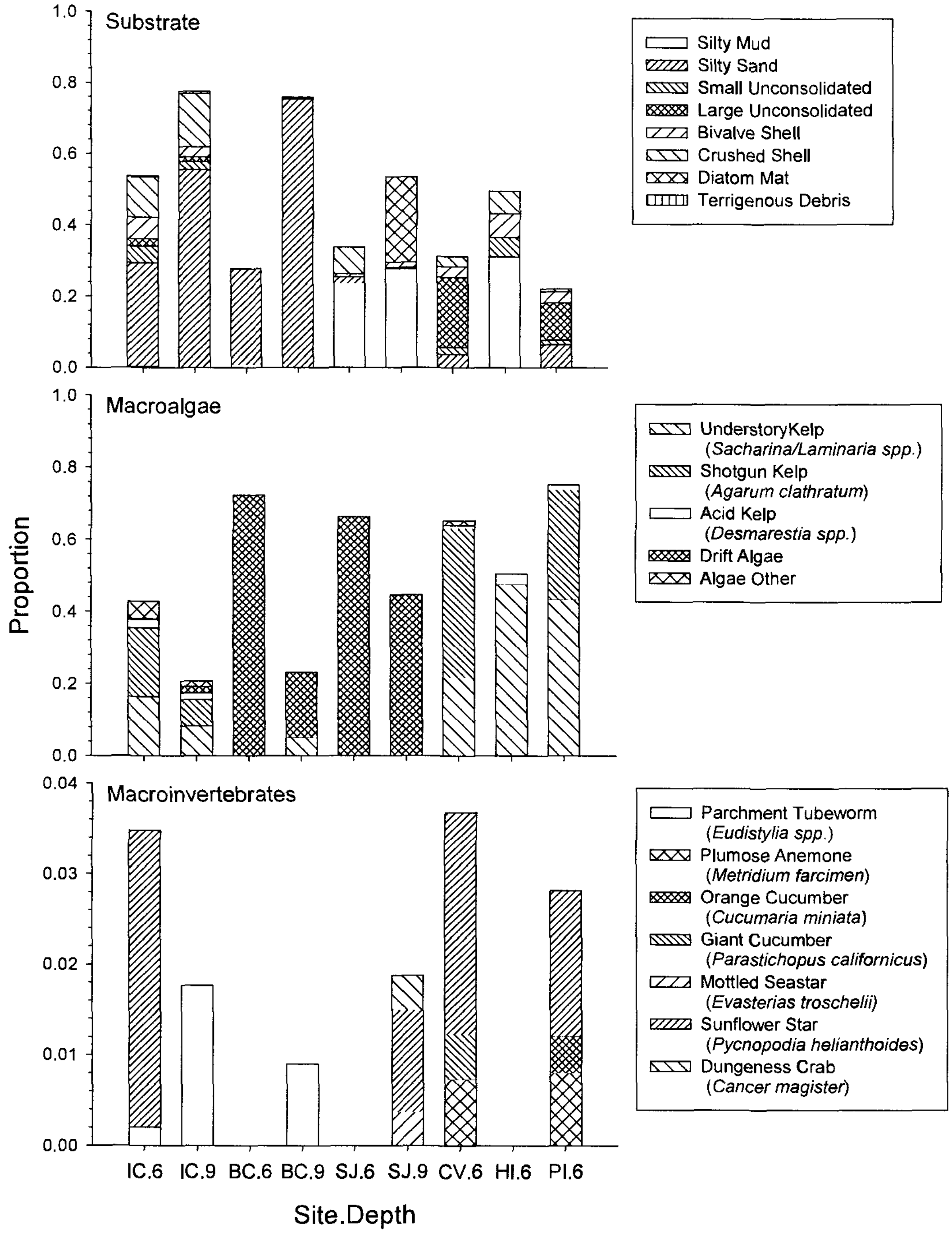

Figure 2.5. Benthic habitat composition at settlement sites and depths from dive video transects by proportion of habitat subcategories for substrate, macroalgae, and macroinvertebrates. The y-axis scale for macroinvertebrates is different from substrate and macroalgae. Site abbreviations as in Table 2.1.

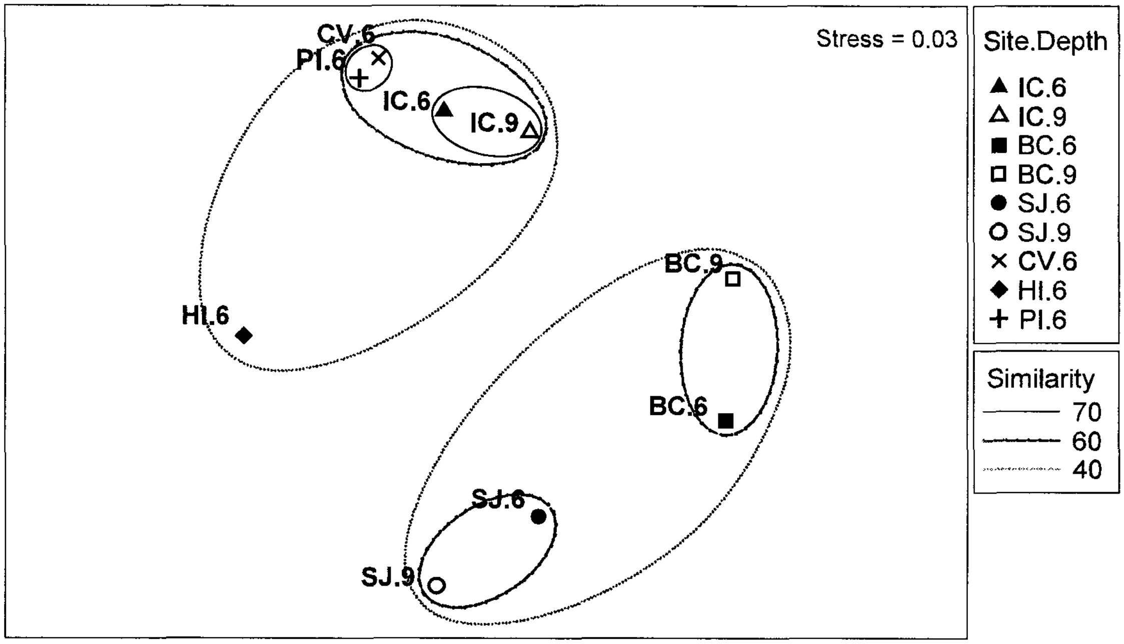

Figure 2.6. Multidimensional scaling (nMDS) ordination of settlement sites and depths based on Bray-Curtis similarities calculated from percent cover of benthic habitat types (two-dimensional stress = 0.03) (Table 2.2, Fig. 2.6). Contours indicate habitat similarity (minimum 70%, 60%, and 40%) among sites based on hierarchical clustering. Site abbreviations as in Table 2.1.

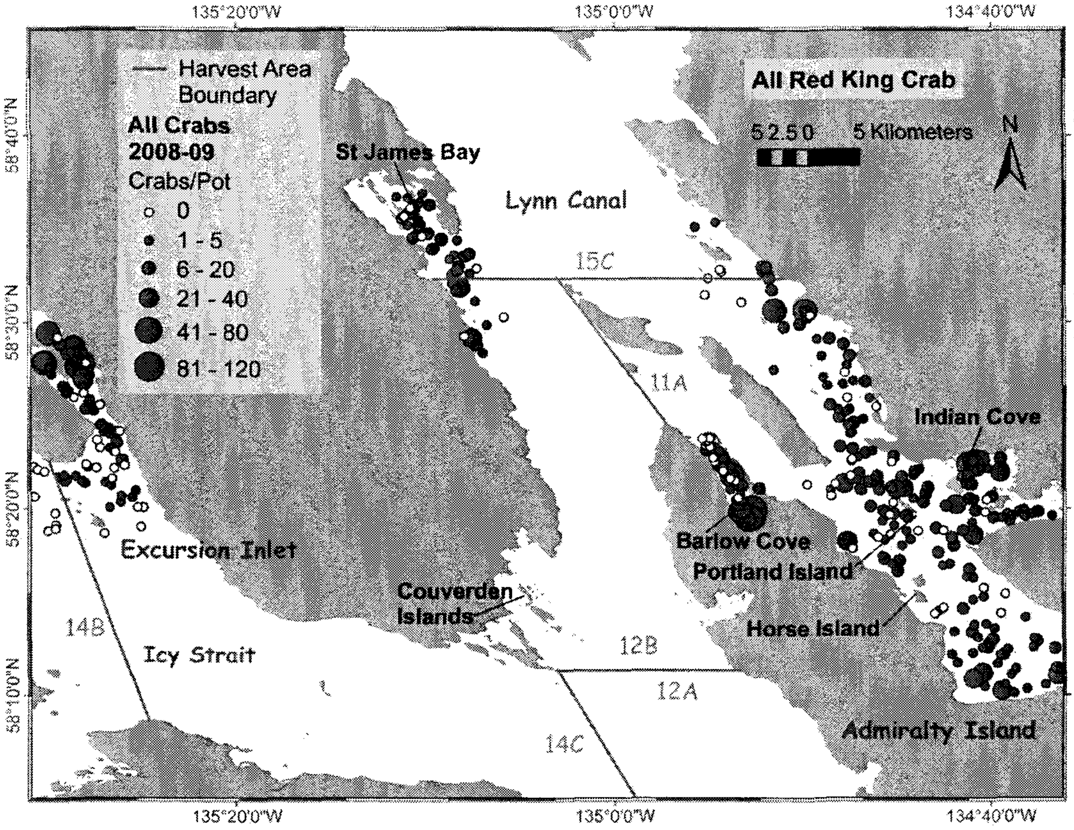

Figure 2.7. Spatial abundance (crabs·pot^{-1}) of all red king crabs from the Alaska Department of Fish and Game stock assessment pot survey in 2008-09 in the Juneau area, our study sites and harvest area boundaries are indicated for reference.

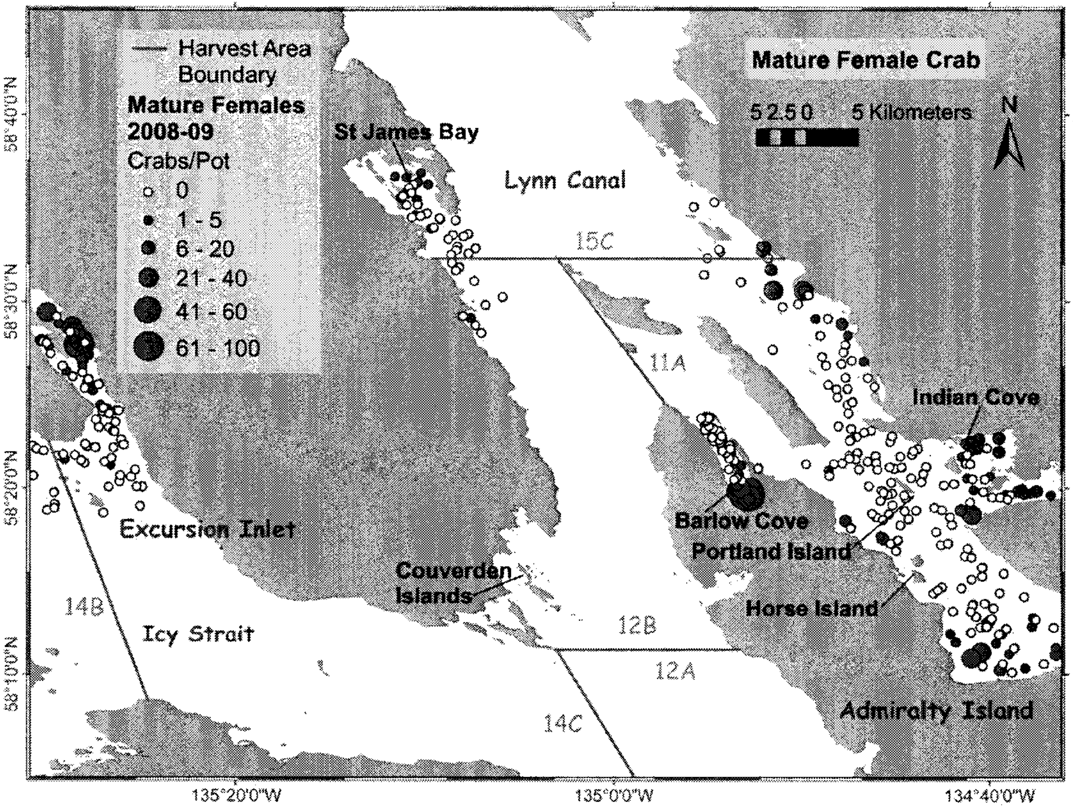

Figure 2.8. Spatial abundance (crabs·pot^{-1}) of mature female red king crab (84-169 mm CL) from the Alaska Department of Fish and Game stock assessment pot survey in 2008-09 in the Juneau area, our study sites and harvest area boundaries are indicated for reference.

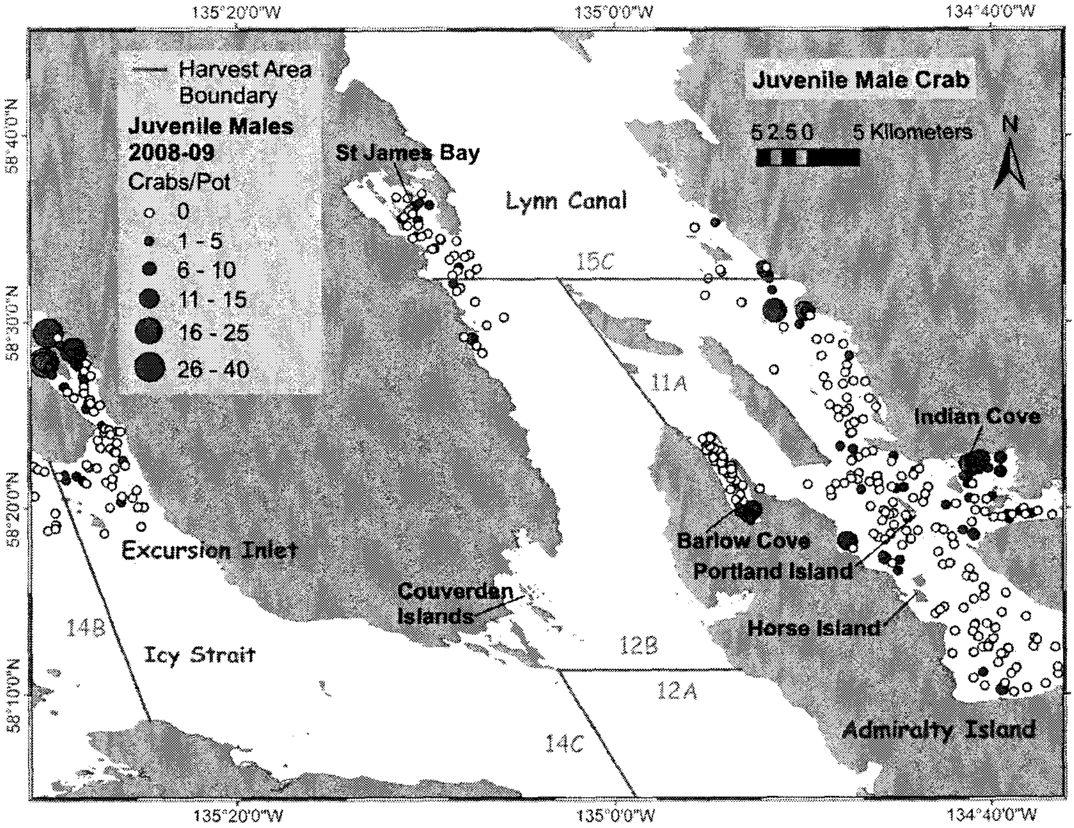

Figure 2.9. Spatial abundance (crabs·pot^{-1}) of juvenile male red king crab (< 129 mm CL) from the Alaska Department of Fish and Game stock assessment pot survey in 2008-09 in the Juneau area, our study sites and harvest area boundaries are indicated for reference.

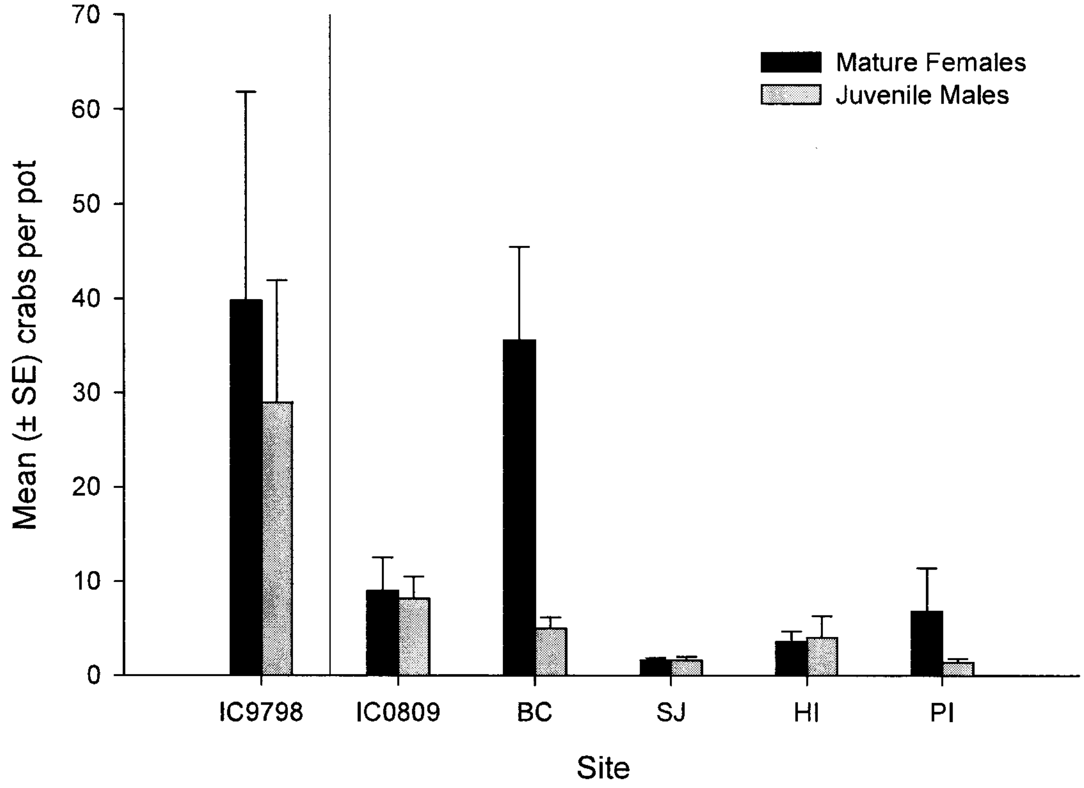

Figure 2.10. Mean abundance estimates (crabs·pot^{-1}) of mature female (84-169 mm CL) and juvenile male (< 129 mm CL) red king crab with standard error bars, including the nearest five stock assessment survey pots from our larval collection sites Indian Cove in 1997-98 and 2008-09, and Barlow Cove, St. James Bay, Horse Island, and Portland Island in 2008-09. Estimates for the Couverden Islands are not included because the nearest station pot in 2008-09 was 24 km away. Vertical line separates years 1997-98 and 2008-09. Data provided by ADF&G.

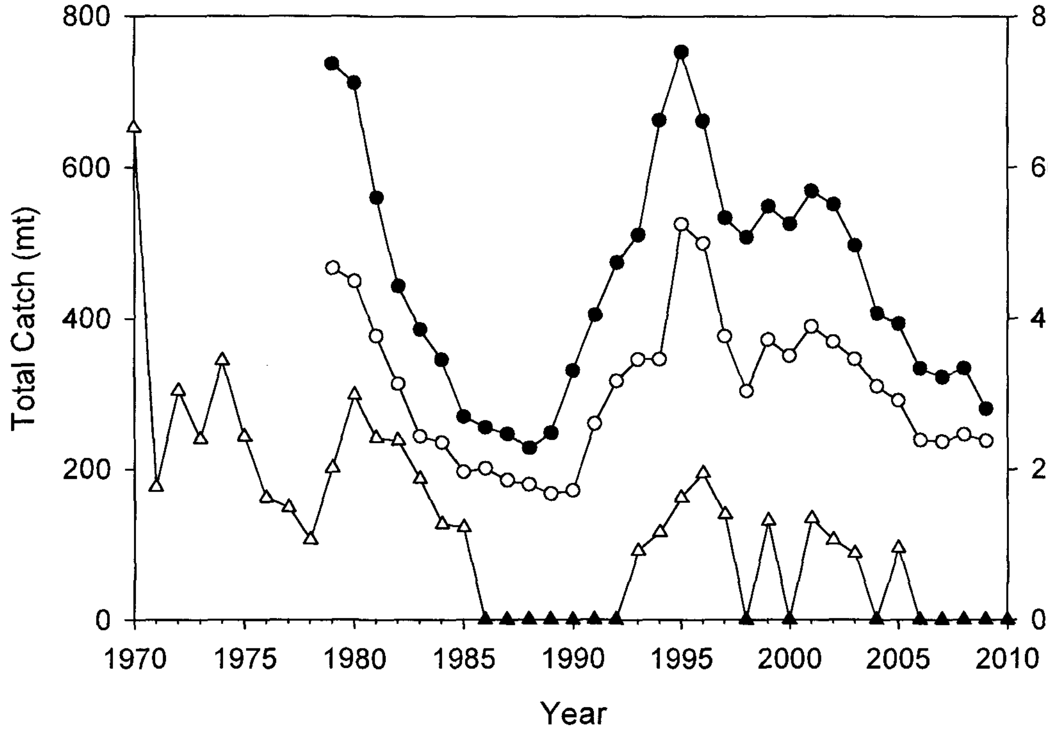

Figure 2.11. Historical trends of red king crab in metric tons (mt) for southeast Alaska, including catch from the 1970 season through 2009 (open triangles) and biomass (mt) of legal (open circles) and mature (closed circles) male red king crab from southeast Alaska survey areas from 1979 through 2008. The fishery was closed in 1986-1992, 1998, 2000, 2004, and 2006-2009 (closed triangles). Data provided by ADF&G.

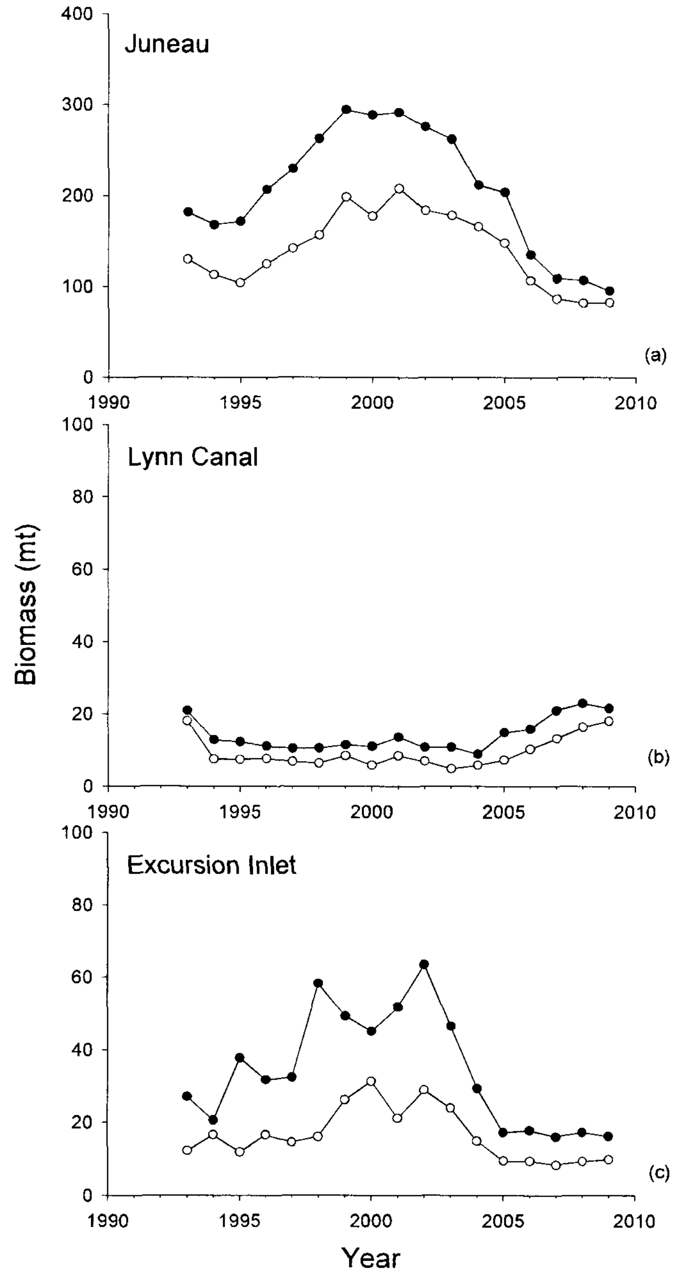

Figure 2.12. Biomass estimates (mt) of legal (open circles) and mature (closed circles) male red king crab from 1993-2009 in northern southeast Alaska stock assessment survey areas, including (a) Juneau, which includes our Indian Cove, Horse Island, and Portland Island study sites, (b) Lynn Canal, which includes our St. James Bay site, and (c) Excursion Inlet. The y-axis scale for Juneau is different from Lynn Canal and Excursion Inlet. Data provided by ADF&G.

Chapter 3

Red king crab (*Paralithodes camtschaticus*) early post-settlement habitat choice: structure, food, and ontogeny[1]

Abstract

Little is known about nursery habitat function for red king crab (*Paralithodes camtschaticus*), a commercially important species that associates with complex benthic habitats from settlement through the first two years of life. During settlement, red king crab actively seek complex benthic habitats, with high availability of vertical structure and crevice space. Habitat choice for early juvenile red king crab may be driven by habitat complexity, or a function of several potential mechanisms, including foraging requirements and shifting ontogeny. We established habitat preference and foraging behavior for two size classes of age 0 red king crab (small 2-4 mm, and large 7.5-9 mm carapace length) with laboratory experiments using habitat treatments composed of individual complex substrates that were living, biogenic substrates, including structural invertebrates, bryozoans and hydroids, and macroalgae in branched and blade forms. Non-living structural mimics of the biogenic substrates were presented to crabs as clean and fouled mimic treatments. We quantified the proportion of crab associations and foraging activity with single habitat treatments within a 24-h period. Substrates that were statistically attractive to small crabs were paired to test small crab foraging behavior. A variety of substrates were statistically attractive to red king crab. Small crabs associated with complex biogenic habitats and fouled mimics (group mean ± SE, 64% ± 4%) more often than clean mimics (29% ± 4%), and preferred to forage on the structural invertebrates (foraging frequency 81%) when presented with paired biogenic and fouled mimic substrates. Large crabs associated with habitats composed of structural invertebrates (group mean ± SE, 78% ± 2%) statistically more often than macroalgae and

[1] Pirtle, J. L., Stoner, A. W., 2010. Red king crab (*Paralithodes camtschaticus*) early post-settlement habitat choice: structure, food, and ontogeny. In: Journal of Experimental Marine Biology and Ecology, 393, 130-137.

fouled and clean mimics (32% ± 5%). Strong attraction to structural invertebrates by early juvenile red king crab is likely driven by foraging opportunities. Our experiments demonstrate that biological habitat features may be functionally more important to early juvenile red king crab than complex physical structure alone. Habitats formed by structural invertebrates, in particular, may enhance growth and survival of early post-settlement stage red king crab in excess of other highly structured habitats, including macroalgae and complex physical substrates.

3.1 Introduction

Red king crab (*Paralithodes camtschaticus*) was historically the most economically important crustacean fishery in Alaska from the late 1960s until its collapse in the early 1980s (Orensanz et al., 1998; Zheng and Kruse, 2000). Overharvest and unfavorable environmental conditions contributed to low fishery recruitment, and stocks have not recovered to pre-collapse levels (Orensanz et al., 1998; Woodby et al., 2005). Successful recruitment for marine fish and crustaceans depends upon early life stage survival (Jones et al., 1982; Wahle and Steneck, 1991; Eggleston and Armstrong, 1995; Loher and Armstrong, 2000). In the case of red king crab, we know little about factors contributing to early life stage success, including which habitats serve as functional nurseries and why. If we can gain an understanding of the processes that affect red king crab early life stages, such as nursery habitat function, then we may better understand conditions that contribute to population fluctuation and recovery.

Survival from settlement through early post-settlement stages for many crustaceans is strongly affected by habitat choice. During settlement, several species including Dungeness crab (*Cancer magister*) (Eggleston and Armstrong, 1995), blue crab (*Callinectes sapidus*) (Pardieck et al., 1999), American lobster (*Homarus americanus*) (Wahle and Steneck, 1991) and red king crab (Loher and Armstrong, 2000) actively seek complex benthic habitats. Complex habitats have high availability of vertical structure and crevice space, proportional to the body size of the occupant (Caddy, 1986; Eggleston et al., 1990) and provide shelter for cryptic, early post-settlement stages. For American lobster, survival of the early post-settlement stage is higher than for older juveniles that outgrow complex habitats and encounter greater risk to mortality (Wahle, 2003). It is likely that similar habitat-survival relationships function for red king crab populations (Stoner, 2009).

Red king crab in the early post-settlement stage (to 1 year, 2-12 mm carapace length (CL)), (Donaldson et al., 1992) are cryptic and remain separate from older juveniles and adults in nearshore habitats (Karinen, 1985) (Fig. 3.1). These early juvenile red king crab are most abundant in complex habitats, including physical substrates such as fractured rock rubble, cobbles, pebbles, and broken shells, and avoid low complexity mud and sand (Sundberg and Clausen, 1977; Loher and Armstrong, 2000). Early juvenile red king crab also associate with complex, biogenic habitats such as macroalgae and structural invertebrates, including hydroids, bryozoans, sponges, anemones, and polychaete tube worms, which often cover hard substrates (Powell and Nickerson, 1965; Sundberg and Clausen, 1977; McMurray et al., 1984; Rodin, 1985; Dew, 1991). Complex biogenic habitat created by structural invertebrates and macroalgae may provide important food sources for red king crab during early post-settlement stages. Complex habitats, in general, provide shelter and refuge from predators until individuals outgrow available crevice space (Crowder and Cooper, 1982). Around age 2 (approximate size 25 mm CL), red king crab emerge from complex habitats to form mobile aggregations of many individuals (Powell and Nickerson, 1965; Dew, 1990; Zhou and Shirley, 1998), potentially due to food or space limitations. Whether or not certain habitats are preferred by early juvenile red king crab over others, and why, and whether or not ontogenetic shifts drive patterns of habitat preference are critical and unknown aspects of nursery habitat function for red king crab.

The goal of this chapter is to understand mechanisms of red king crab habitat associations during the first year post-settlement. In particular, does structural complexity of the habitat, the presence of foraging opportunities, or both, drive habitat associations? We establish post-settlement habitat preference and foraging behavior for two size classes of age 0 red king crab (2-4 mm and 7.5-9 mm CL) with manipulative laboratory experiments using a variety of complex habitats, including biogenic and non-living habitats. Our hypotheses are as follows: 1) red king crab associate with complex biogenic habitats more often than non-living, physical habitats of similar structure; 2) red king crab forage on biogenic habitat more often than biologically fouled physical habitats of similar structure; and 3) habitat choice differs between the two size classes of post-settlement red king crab.

3.2. Methods

3.2.1 Animals

Age 0 red king crab in the present study were hatched from wild female red king crab collected from the Bering Sea, Alaska, and cultured by the cooperative Alaska King Crab Research, Rehabilitation, and Biology Program (AKCRRAB) (Alaska Sea Grant, 2008). Ovigerous female crabs were transported to the Alutiiq Pride Shellfish Hatchery in Seward, Alaska, and maintained in the ambient seawater facility until larval release in early spring 2008. Larvae were raised in 1,200-L tanks on a diet of enriched *Artemia* nauplii daily until settlement in late May 2008 (Daly et al., 2009). Young crabs were shipped to the Alaska Fisheries Science Center's Behavioral Fisheries Ecology Laboratory, in Newport, Oregon, and to the University of Alaska Fairbanks, School of Fisheries and Ocean Sciences in Juneau, Alaska, in June 2008. Juvenile crabs were maintained at each facility in flow through natural seawater (mean ± SE, 8.3 ± 0.1 °C) in mass rearing tanks with a complex substrate of artificial seaweed composed of polypropylene cord or plastic fiber. Crabs were fed to excess on a daily diet of raw, blended shrimp, Otohime™ pellets, and calcium supplement in a gelatin matrix. Crabs were reared through several molts for use in experiments.

3.2.2 Treatments

Habitat preference and foraging behavior were tested for two size classes of age 0 red king crab, including small crabs of 2-4 mm carapace length (CL) and large crabs 7.5-9.0 mm CL, with approximate ages of 3-4 months and 6-7 months post-settlement in the lab, respectively. We tested whether red king crab prefer complex biogenic and complex physical substrates as shelter, as food, or both. Experimental, living biogenic habitats were composed of bryozoan (*Microporinia borealis*) (B), hydroid (*Obelia spp.*) (H), and macroalgae of two morphologies, including branched red (*Neorhodomela larix*) (N), and brown blade (*Agarum clathratum*) (A) forms. All four substrates naturally occur in habitats used by red king crab in Alaska (Orlov, 1964; Powell and Nickerson, 1965; Vinogradov, 1968; Sundberg and Clausen, 1977), and were collected in southeast

Alaskan waters, with the exception of *N. larix* that was collected in Newport, Oregon. In a prior laboratory study, *Neorhodomela larix* and *Obelia spp.* were among preferred settlement substrates for red king crab (Stevens, 2003). Live substrata were collected from docks, the low intertidal zone, and by divers using SCUBA. Live substrate treatments were rinsed in seawater and cleaned by hand to remove epifauna and epiphytes prior to experimental trials. Fresh substrate was used in each trial.

Structural mimics of the biogenic habitats were constructed from various synthetic and natural fiber materials to represent complex physical structure without food (i.e., bryozoan mimic (BM), hydroid mimic (HM), branched macroalgae mimic (NM), and blade macroalgae mimic (AM)). Fouled mimics were structural mimics that were biologically fouled in seawater to represent complex physical structure with at least a trace of food or chemical attractant (i.e., BMF, HMF, NMF, and AMF). Fouling was accomplished by suspending clean mimics in ambient, unfiltered seawater in the lab or from a dock for a period of at least 3 wk to generate a thin biological film on all surfaces. Fresh, fouled mimics were used in each experimental trial. Clean, white sand (either quartz (#30 0.5 mm) or coral sand) was used as the base substrate in all experiments. At the end of each trial, sand was rinsed with fresh seawater to remove all debris and then reused.

In summary, biogenic treatments were bryozoan (B), hydroid (H), branched macroalgae (N), and blade macroalgae (A). Structural mimics of the biogenic habitats were BM, HM, NM, and AM. Biologically fouled mimics were BMF, HMF, NMF, and AMF.

3.2.3 Habitat experiments

Experiments were conducted in 8 cm deep rounded square (21 cm L, 21 cm W) or round (25 cm D) containers of clear plastic lined with 2 cm of sand and a substrate treatment (Fig. 3.2 a). Containers were filled with seawater and maintained in a circulating water bath (mean ± SE 8.7 ± 0.1 °C) with opaque covers to limit overhead light (Fig. 3.2 b), or in a cold room with a light cycle of 12 h light: 12 h dark at 8 °C.

3.2.3.1 Habitat choice

The frequency of association of small and large age 0 crabs were tested separately with individual complex biogenic (B, H, N, A), clean mimic (BM, HM, NM, AM) and fouled mimic (BMF, HMF, NMF, AMF) substrates. Trials were conducted in Newport (N, NM, NMF) and Juneau (B, H, A, BM, HM, AM, BMF, HMF) with small crabs in September-October 2008. The AMF treatment was not used in Juneau due to low availability of small crabs when the trial would have been conducted. Crabs were treated similarly at both locations.

Trials with small crabs (2-4 mm CL) were replicated a total of six times for each substrate treatment. A total of ten small crabs were gathered haphazardly from mass rearing tanks ($n > 300$ individuals) and placed in an experimental container at the beginning of a daily light cycle, together with three pieces of a single substrate treatment that were approximately equal in size, and mutually occupying approximately one third of the available open space without contact (Fig. 3.2 a). After a period of 3 h, counts of all positive and negative crab associations with the substrate were recorded within each container. Positive associations were defined as a crab being on or under the substrate, and negative associations were crabs located at the edge of the container or on open sand. Association counts were repeated at 6 and 24 h from the start of the experiment to obtain a general association pattern within a 24-h period. Crabs were returned to the mass rearing tanks at the completion of a trial, following haphazard sampling of the population for the next replicate trial.

Single substrate, habitat choice trials were conducted with large crabs in Newport from December 2008 to January 2009 when crabs were 7.5-9 mm CL. Crabs of this size range were estimated to represent late stage age 0 crabs (mean 9.33 mm CL) (Donaldson et al., 1992). Trials with large crabs used similar methods as with small crabs, with six replicate trials conducted in a cold room with a light cycle of 12 h light: 12 h dark at 8 °C; however, a total of six large crabs, rather than ten large crabs, were placed in the larger containers (25 cm D) to maintain comparable densities. Preliminary experiments with large and small crabs showed that all crabs could be positively associated with the amounts of substrate used in the experiments.

3.2.3.2 Foraging behavior

The second experiment quantified foraging activity of small and large crabs associating with experimental substrates. Foraging was defined as repeated chelae movement from the substrate to the mouth parts of an individual crab. Foraging was recorded as positive for an individual crab when at least three chelae to substrate to mouth movements were observed during association counts.

Small crab foraging trials were conducted in Juneau during October 2008, following the habitat choice experiment. Foraging was quantified for small crabs with paired treatments of a subset of substrates that were statistically attractive during the single substrate, habitat choice experiment. Substrate treatments included paired combinations of B, H, A, BMF, and HMF. Treatments of N and NMF were not included because they were not available in Juneau, and AMF was not used with small crabs during the habitat choice experiment. The paired foraging experiment followed similar methods as the habitat choice experiment, using a total of ten small crabs for each of six replicate containers for each treatment. Except that the substrates were applied as orthogonally paired treatments arranged uniformly within experimental containers using three interspersed pieces of each substrate of approximately the same total area, evenly spaced without contact. Foraging activity was recorded for individual paired substrates within each container at 3, 6, and 24 h to obtain a general pattern within a 24-h period.

Foraging was quantified for large crabs during the single substrate, habitat choice experiment in Newport from December 2008 to January 2009, using complex biogenic (B, H, A, N), clean mimic (BM, HM, AM, NM) and fouled mimic (BMF, HMF, AMF, NMF) substrates.

3.2.3.3 Grain size

Grain-size experiments were conducted with different complex rock substrates and sand to explore the potential influence of interstitial crevice space provided by non-living habitats. These experiments were conducted in Newport during November 2008.

The association of small and large age 0 crabs was quantified and compared among substrates with varied grain size including small cobble (15-50 mm), pebble (7-15 mm), granule (2-4 mm), and sand (0.5 mm). The experiment followed the same general methods as the habitat choice experiments, except that the containers were sectioned into four quadrants and each quadrant was lined with a different grain size treatment. Thus, each of the four substrate treatments was presented in an individual container as a choice. Counts of positive associations among substrate treatments were recorded at 3, 6, and 24 h to obtain a general pattern of habitat associations in a 24-h period.

3.2.4 Analysis

Analysis of variance (ANOVA) ($\alpha = 0.05$) was applied to the habitat choice experiments, the foraging experiment with large crabs, and the grain-size experiments to determine the effect of substrate type on crab habitat choice. The ANOVAs were based on the proportion ($p = 1/n$) of positive crab associations with individual substrate treatments. Preliminary analysis by repeated measures ANOVA did not detect consistent, biologically meaningful patterns of habitat shifts with time. Consequently, data were pooled across time periods (3, 6, and 24 h) for a more robust evaluation of habitat choice within 24 h, using one-way ANOVAs. Data were the arcsine square root transformed mean of the proportion of positive associations (p) for each time period. Data were tested for equality of variances by Bartlett's and Levine's tests ($\alpha = 0.05$) and ANOVAs were conducted when test results were not significant ($p > 0.05$). Significant differences ($p < 0.05$) from one-way ANOVAs were compared among treatment means using Tukey's Honest Significant Difference (HSD) test.

Foraging experiments for small crabs were analyzed using a Chi-square test of equal proportions ($\alpha = 0.05$). There was no evidence of consistent foraging shifts with time. Consequently, data were pooled across time periods (3, 6, and 24 h) for a more robust evaluation of habitat choice in a 24 h period. Data were the mean of the sum of positive associations within each time period. The null hypothesis was an equal proportion ($p = 1/n$) of crab foraging activity among (n) substrate choices (i.e., $n = 5$, $p = 1/5$, $H_o = 20\%$).

3.3 Results

3.3.1 Habitat choice

Small crabs did not equally prefer substrate treatments in the habitat choice experiment ($p < 0.001$) (Table 3.1, Fig. 3.3). The proportion of small crabs associating with biogenic substrates and fouled mimics was significantly greater than the proportion associated with clean mimics (Table 3.2). Bryozoan (B) had the greatest proportion of small crab associations (mean ± SE, 0.74 ± 0.05), followed by hydroid (H) (0.71 ± 0.02), branched algae (N) (0.64 ± 0.05), blade algae (A) (0.62 ± 0.04) and fouled mimics of hydroid (HMF) (0.62 ± 0.01), branched algae (NMF) (0.59 ± 0.04), and bryozoan (BMF) (0.58 ± 0.03) (Table 3.2, group a).

Large crabs did not equally associate with substrate treatments in the habitat choice experiment (p <0.001) (Table 3.1, Fig. 3.4). However, large crab associations did not follow the same pattern demonstrated with small crabs (Table 3.2). The proportion of large crabs associating with bryozoan (B) (mean ± SE, 0.83 ± 0.01) and hydroid (H) (0.73 ± 0.03) was significantly greater than the proportion associated with all other substrates (Table 3.2, group c). However, dissimilar to small crabs, large crabs did not choose all biogenic and fouled mimic substrates more often than clean mimics (Table 3.2). Proportional associations of large crabs with branched algae (N) (0.57 ± 0.06), blade algae (A) (0.31 ± 0.03), and fouled mimics of bryozoan (BMF) (0.40 ± 0.07) and blade algae (AMF) (0.35 ± 0.06), were not significantly different from clean mimics of bryozoan (BM) (0.59 ± 0.08) and blade algae (AM) (0.35 ± 0.05) (Table 3.2, group d). Although, these substrates (N, A, BMF, AMF, BM, AM) (Table 3.2, group d) were chosen significantly more often by large crabs (group mean ± SE 0.43 ± 0.06) than fouled and clean mimics of hydroid (HMF, HM) (0.16 ± 0.02, 0.21 ± 0.06) and branched algae (NMF, NM) (0.15 ± 0.03, 0.11 ± 0.04) (Table 3.2, group e).

3.3.2 Foraging behavior

Large crabs did not forage among substrate treatments equally in the habitat choice experiment (p <0.001) (Table 3.3, Fig. 3.5). Large crabs foraged on bryozoan (B) (mean ± SE, 0.42 ± 0.06) and hydroid (H) (0.36 ± 0.02) (Table 3.3, group a) significantly more often than blade algae (A) (0.09 ± 0.03) and fouled mimics of bryozoan (BMF) (0.04 ± 0.02), hydroid (HMF) (0.02 ± 0.01), and blade algae (AMF) (0.01 ± 0.01) (Table 3.3, group b).

Small crabs did not forage equally among paired substrates (B, H, A, BMF, HMF) ($\chi^2 = 65.39, p < 0.001$) (Table 3.4, Fig. 3.5). Small crabs foraged on bryozoan (B) (70.0% of crabs exposed to bryozoans) and hydroid (H) (47.8%) more frequently, than blade algae (A) (10.6%) and fouled mimics of bryozoan (BMF) (10.0%) and hydroid (HMF) (7.8%) (Table 3.4). The design to test small crab foraging behavior was different than the design for large crabs. However, the results of both experiments demonstrate that small and large crabs both foraged more often on habitats composed of structural invertebrates, than habitats of macroalgae and fouled structural mimics (Fig. 3.5).

3.3.3 Grain size

Small and large crabs did not equally associate with treatments of different grain sizes ($p < 0.001$) (Table 3.5, Fig. 3.6). Substrates in order of decreasing grain-size were cobble, granule, pebble, and sand. Small crabs chose cobble (mean ± SE, 0.35 ± 0.04) and granule (0.34 ± 0.03) (Table 3.6, group a) significantly more often than pebble (0.21 ± 0.04) and sand (0.11 ± 0.02) (Table 6, group b). Large crabs chose cobble (mean ± SE, 0.42 ± 0.03) and pebble (0.32 ± 0.03) (Table 3.6, group c) significantly more often than granule (0.16 ± 0.02) and sand (0.10 ± 0.02) (Table 3.6, group d).

3.4 Discussion

The experiments reported in this study show that early post-settlement stages of red king crab have strong habitat preferences. An important feature of natural habitats selected by early juvenile red king crab is structural complexity. Structural complexity, however, does not fully explain red king crab habitat choice. Biogenic habitats provide crabs with complex structure in addition to foraging opportunities that physical structure alone does not. Living, biogenic habitats formed by structural invertebrates in particular should represent high quality nursery habitat for red king crab, promoting early life stage success and overall population strength.

3.4.1 Habitat structural complexity

Early post-settlement stage red king crab preferred substrates with high availability of crevice space and structure proportional to their body size, when given a choice between complex substrates in laboratory experiments. This response establishes that red king crab continue active selection for complex substrates through early post-settlement stages, as previously demonstrated for settling red king crab larvae (Stevens and Kittaka, 1998; Loher and Armstrong, 2000; Stevens, 2003).

Active selection for complex substrates by red king crab early juveniles underscores the importance of habitat complexity from settlement through early post-settlement stages for red king crab and other crabs and lobsters with similar early life history habitat ecology. Early post-settlement stage red king crab have been observed to be most abundant in complex, unconsolidated hard substrates such as cobble, rock rubble, and shell hash (Karinen, 1985; Freese and Babcock, 1989; Loher and Armstrong, 2000), and among structural invertebrates and macroalgae, living, biogenic structures that grow on hard substrates (Powell and Nickerson, 1965; Sundberg and Clausen, 1977; McMurray et al., 1984; Rodin, 1985; Dew, 1991). Similarly, American lobsters depend on cobble habitats during early post-settlement stages (Wahle and Steneck, 1991; Wahle and Steneck, 1992), and other crab species are known to shelter in bivalve shells, algae and eelgrasses (Fernandez et al. 1993; Eggleston and Armstrong, 1995; McMillan et al., 1995). Blue king crab (*Paralithodes platypus*), a sister species to red king crab, appear to mimic fragmented bivalve shells as early juveniles in nearshore nurseries where shell hash is a common feature (Armstrong et al., 1985; Tapella et al., 2009). Complex habitats provide shelter and refuge from predators for early life stages (Crowder and Cooper, 1982). Loss or fragmentation of complex habitats, for example, has lead to increased mortality, reduced foraging abilities, and affected early life stage success for many marine species (Caddy, 2008). Loss of complex habitats important to juvenile red king crab, and other crustaceans, is likely to be detrimental to early life stage success.

3.4.2 Biogenic habitat value

Our results are the first to separate the role of living, complex biogenic habitats from complex physical structure in red king crab early post-settlement habitat choice. A strong preference by red king crab for living, biogenic substrates, most notably when foraging, supports the hypothesis that early juvenile red king crab are more attracted to complex biogenic habitats than other complex structures. Red king crab of two size classes associated with living, biogenic habitats and fouled structural mimics of biogenic habitats more often than physical structure during trials with a single substrate choice, demonstrating that the biological qualities of the substrates were more important than physical structure to red king crab. In particular, strong preference for structural invertebrates by small and large red king crab, implies that habitats formed by structural invertebrates have valuable qualities for crab that exceed the attractive qualities of other highly structured biogenic substrates, including macroalgae, and fouled physical structures. Complex biogenic habitats, especially structural invertebrates, should represent high quality nursery habitat for structure-seeking early juvenile red king crab.

Although early juvenile red king crab preferred structural invertebrates over other complex biogenic substrates, the mechanisms of these associations are not fully understood. For example, in nearshore nursery habitats, red king crab may actively form associations with structural invertebrates because invertebrates are a preferred habitat choice, as demonstrated by this study. Indeed, early post-settlement stage red king crab have been found exclusively in habitats with invertebrate cover, including hydroids, bryozoans, polychaetes, and mussels (McMurray et al., 1984; Stevens and MacIntosh, 1991). However, red king crab may simply respond to strong shelter-seeking tendencies and form opportunistic associations with the first highly complex substrate encountered, gaining advantages like foraging opportunities when structural invertebrates are present.

Opportunistic habitat associations are one possible explanation for why early juvenile red king crab have been observed in habitats that were not most preferred in laboratory experiments. Macroalgae, for example, provide highly complex biogenic habitat during spring and summer months when algae biomass is greatest, often dominating shallow, hard substrate communities (Calvin and Ellis, 1981; Kain, 1989). While macroalgae were not the most preferred biogenic substrates in our experiments, red king crab were attracted to macroalgae, and have been observed in association with macroalgae in nearshore habitats (Orlov, 1964; Vinogradov, 1968; Loher and Armstrong, 2000). Red king crab early juveniles have also been found in complex habitats with low or absent biogenic cover including rock rubble, cobble, gravel and shell hash (Karinen, 1985; Freese and Babcock, 1989; Loher and Armstrong, 2000).

It is further possible that red king crab and other crustaceans with strong early life stage structure-seeking tendencies are more likely to associate with less preferred habitats, like physical substrates, when more attractive biogenic habitats are sparse or unavailable. Nearshore locations with complex benthic habitats where juvenile red king crab have been observed are not likely composed of one substrate type, but a combination of several substrates, including structural invertebrates, macroalgae, and physical substrates with variable cover by each, ranging from abundant to rare. It is unclear whether or not red king crab early life stage success is affected by the relative availability of complex biogenic habitat at nursery locations, compared to the availability of other complex habitat types. The role of habitat availability should be tested with field experiments at nursery locations.

3.4.3 Habitat shifts with crab size or age

The experiments reported in this study suggest that habitat selectivity by red king crab continues after settlement and shifts with crab size or age. Small crabs (2-4 mm CL) clearly associated with biogenic habitats and fouled mimics over all others, and large crabs (7.5-9 mm CL) preferred structural invertebrates, and a mix of other complex structures. Behavioral habitat shifts for red king crab may be similar to those well known among lobsters. Spiny lobster (*Panulirus argus*) demonstrate habitat shifts in distinct stages with growth, where pueruli settle in macroalgae and shift to crevices, eventually venturing into open spaces when they are large enough to avoid predation (Childress & Herrnkind, 1994).

It is not yet clear whether variation in habitat use among early juvenile stages of red king crab is due to shifting foraging demands, shelter requirements, anti-predation behavior, or a complex function of several potential mechanisms. American lobster may change habitat use due to their shifting response to predators with growth, increased energetic demands due to growth, or by both mechanisms (Wahle, 1992). Similarly, red king crab may outgrow shelter-providing settlement habitats in stages and require more substantial food sources for sustained growth. In our experiments, both small and large red king crab preferred to forage on structural invertebrates. However, small crabs foraged on fouled mimics more than twice as often as large crabs, suggesting that larger crabs require more substantial food sources. This result implies that food requirements likely shift with size or age and possibly influence habitat associations during early post-settlement stages for red king crab, and other crustaceans with similar early juvenile habitat requirements, including blue king crab and the poorly understood golden king crab (*Lithodes aequispinus*), known to associate with structural invertebrates as early juveniles in deep habitats (Krieger and Wing, 2002). Much remains to be examined regarding the influence of ontogeny in red king crab early life history habitat ecology.

3.4.4 Foraging behavior

We quantified foraging through behavioral experiments that demonstrated strong attraction of early post-settlement stage red king crab to structural invertebrates. Crabs also foraged on macroalgae and biologically fouled non-living structural mimics, but bryozoans and hydroids were the preferred foraging substrates of both small and large crabs. Structural invertebrates likely provide food for early juvenile red king crab through direct consumption. Unidentifiable soft tissues found in early juvenile red king crab gut contents (Pearson et al., 1984) may actually be the soft tissues of habitat-forming invertebrates. Crabs in our experiments did not destroy invertebrate structures (i.e., hydroid casing and bryozoan skeleton) while foraging, but they appeared to remove bits of soft tissue with their claws. Feeding in this way is likely to lead to fragments of unidentifiable soft tissues in the gut that may be difficult to identify by gut analysis alone. For this reason, we recommend that gut content analysis be paired with foraging observations if applied in future studies with king crabs. It is also possible that early juvenile red king crab consume epifauna and epiphytes on invertebrates or macroalgae without actually consuming the biogenic habitat. Associated organisms may include those reported in the gut contents of young crabs, including small crustaceans, gastropods, benthic diatoms, and foraminifera (Feder et al., 1980; Pearson et al., 1984). Our biogenic habitat treatments were rinsed and cleaned prior to experiments, so the opportunity to graze on associated items may have been reduced from natural habitats. Fouled mimics were not cleaned, however, and presented non-living structure with a thin layer of biological film that may have contained small, consumable items such as benthic diatoms. Foraging behavior of early post-settlement stages of red king crab further implies that food availability, and not just physical structure, is important. Structural invertebrates, in particular, that provide foraging opportunities and complex habitat, may enhance juvenile red king crab growth and survival over habitats formed by macroalgae or complex physical structure alone. Studies are needed to compare growth rates and survival of red king crab post-settlement stages in habitats with a variety of naturally occurring potential prey items, including structural invertebrates.

3.4.5 Role of predation in habitat choice

Foraging opportunities likely attract early juvenile red king crab to structural invertebrates over other highly structured habitats. However, attraction of red king crab to complex habitats in general is probably an adaptation to high predation pressure during early benthic life. It is well established that complex habitats provide refuge for shelter-seeking early life stages (Crowder and Cooper, 1982). It follows that if complex habitats with shelter-providing structure and crevice space are unavailable, then red king crab would be more vulnerable to predators.

Red king crab may become less naïve and more adept at predator avoidance with growth, even among the earliest juvenile stages. Laboratory studies have observed this type of behavior. Newly settled red king crab larvae did not seek shelter in the presence of larger conspecific predators in the laboratory, whereas crabs with at least one molt post-settlement sheltered in complex habitats, where survival was greater than in habitats without shelter (Stevens and Swiney, 2005). Predator-associated sheltering has been observed using video for red king crab juveniles (5 mm CL) exposed to Pacific halibut (*Hippoglossus stenolepis*) as a predator, where complex substrates significantly reduced both encounter rates and capture success of red king crab prey (Stoner, 2009). It is thought that American lobster undergo a population bottleneck post-settlement, due to high mortality from predation in areas of limited shelter-providing habitat throughout their range (Wahle and Steneck, 1991). Habitat availability and predation may limit red king crab populations during the first year post-settlement. Our laboratory experiments tested habitat associations and foraging behavior for early juvenile red king crab without the influence of predators. When young crabs are mortally threatened, their refuge response may be stronger than the need to forage, and crabs likely seek shelter with any available structure whether or not biogenic habitats are present.

The strong affinity of early juvenile red king crab for highly complex habitats appears to be an important adaptation. Early post-settlement stages of red king crab likely gain shelter and refuge from predators within complex habitats, and foraging and growth opportunities when biogenic substrates are present. We suggest that optimal nursery habitats for red king crab are those that accommodate a range of body sizes while providing adequate foraging opportunities from biogenic habitats, in particular structural invertebrates, and where the tradeoff between foraging and predation risk is reduced. As the relative role of predation in habitat choice is unclear, we recommend habitat associations be examined in the presence of predators for early post-settlement stage red king crab. Our present understanding of early life stage success for red king crab and other species with similar post-settlement habitat ecology will be improved as mechanisms of nursery habitat function continue to be uncovered.

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Table 3.1. Results of one-way analysis of variance (ANOVAs) to test the effect of substrate type on habitat choice of small (2-4 mm CL) and large (7.5-9 mm CL) age 0 red king crab. The null hypothesis of no difference in proportion of associations is rejected (*p* <0.001).

Stage	Source	*df*	SS	MS	F	*p*
Small	Substrate	10	2.52	0.25	24.38	<0.001
	Error	55	0.57	0.01		
	Total	65	3.09			
Large	Substrate	11	4.65	0.42	22.49	<0.001
	Error	60	1.13	0.02		
	Total	71	5.78			

Table 3.2. Mean proportion (± SE) of positive associations of small (2-4 mm CL) and large (7.5-9 mm CL) age 0 red king crab with substrate treatments, including live substrates (bryozoan, hydroid, branched algae, and blade algae), fouled structural mimics, and clean mimics. Trials with fouled blade algae mimics were not conducted with small crabs.

Type	Substrate	Small	Large
Live	B	0.74 (0.05) a	0.83 (0.01) c
	H	0.71 (0.02) a	0.73 (0.03) c
	N	0.64 (0.05) a	0.57 (0.06) d
	A	0.62 (0.04) a	0.31 (0.03) d
Fouled	BMF	0.58 (0.03) a	0.40 (0.07) d
	HMF	0.62 (0.01) a	0.16 (0.02) e
	NMF	0.59 (0.04) a	0.15 (0.03) e
	AMF	nd	0.35 (0.06) d
Mimic	BM	0.31 (0.05) b	0.59 (0.08) d
	HM	0.27 (0.05) b	0.21 (0.06) e
	NM	0.18 (0.03) b	0.11 (0.04) e
	AM	0.39 (0.03) b	0.35 (0.05) d

Tukey's HSD was calculated with arcsine square root transformed proportions. Letters indicate groups with similar means. nd, no data.

Table 3.3. Results of one-way analysis of variance (ANOVA) to test the effect of substrate type on foraging activity of large (7.5-9 mm CL) age 0 red king crab. Mean proportion (± SE) of crab foraging counts with substrate treatments, including live substrates (bryozoan, hydroid, and blade algae) and fouled structural mimics. Foraging by large crabs on clean structural mimics was not observed. The null hypothesis of no difference in proportion of foraging activity is rejected (*p* <0.001).

Source	*df*	SS	MS	F	*p*
Substrate	5	2.53	0.51	30.79	<0.001
Error	30	0.49	0.02		
Total	35	3.02			

Group	Substrate	Mean (± SE)
Live	B	0.42 (0.06) a
	H	0.36 (0.02) a
	A	0.09 (0.03) b
Fouled	BMF	0.04 (0.02) b
	HMF	0.02 (0.01) b
	AMF	0.01 (0.01) b

Tukey's HSD was calculated with arcsine square root transformed proportions. Letters indicate groups with similar means.

Table 3.4. Chi-square analysis of equal proportions for small (2-4 mm) age 0 red king crab foraging among paired substrates, including bryozoan (B), hydroid (H), blade algae (A), and fouled hydroid and bryozoan mimics (HMF, BMF). The null hypothesis of equal proportions (20.0%) is rejected ($p < 0.001$).

Substrate	Frequency	Frequency %	Association %
B*	42.00	47.91	70.00
H*	28.76	32.70	47.78
A	6.33	7.22	10.56
FHM	6.00	6.84	10.00
FBM	4.67	5.32	7.78
$\chi^2 = 65.39$ $p < 0.001$ $df = 4$ $n = 88$			

* Significant

Table 3.5. Results of one-way analysis of variance (ANOVAs) to test the effect of substrate grain-size on habitat choice of small (2-4 mm CL) and large (7.5-9 mm CL) age 0 red king crab. The null hypothesis of no difference in proportion of associations is rejected (*p* <0.001).

Stage	Source	*df*	SS	MS	F	*p*
Small	Substrate	3	0.37	0.12	16.03	<0.001
	Error	20	0.16	0.01		
	Total	23	0.53			
Large	Substrate	3	0.57	0.19	31.37	<0.001
	Error	20	0.12	0.01		
	Total	23	0.69			

Table 3.6. Mean proportion (± SE) of crab associations with substrate treatments of varied grain-size (cobble>pebble>granule>sand).

Substrate	Small	Large
Cobble	0.35 (0.04) a	0.42 (0.03) c
Pebble	0.21 (0.04) b	0.32 (0.03) c
Granule	0.34 (0.03) a	0.16 (0.02) d
Sand	0.11 (0.02) b	0.10 (0.02) d

Tukey's HSD was calculated with arcsine square root transformed proportions. Letters indicate groups with similar means.

Figure 3.1. Red king crab (age 0, 2 mm CL) on monofilament gill net mesh in the lab.

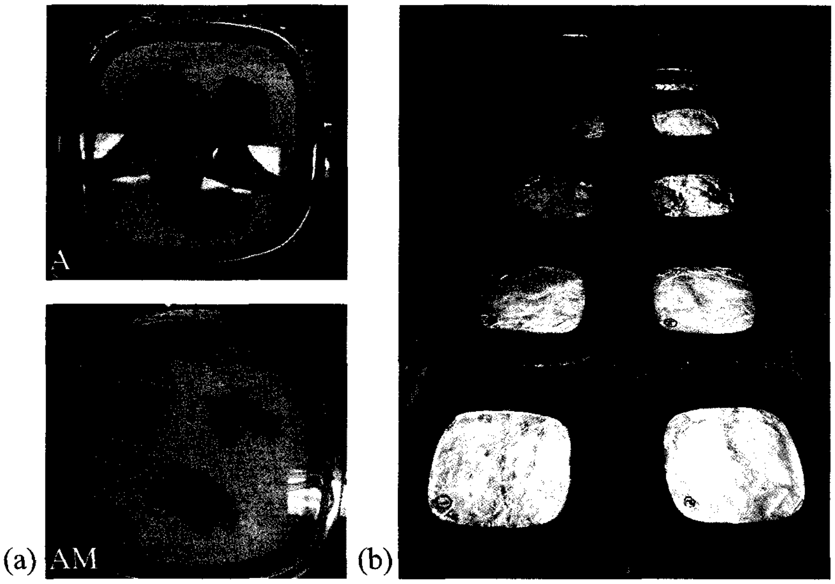

Figure 3.2. (a) Containers with treatments of blade algae (A) and blade algae mimic (AM); (b) experimental set-up with replicate containers.

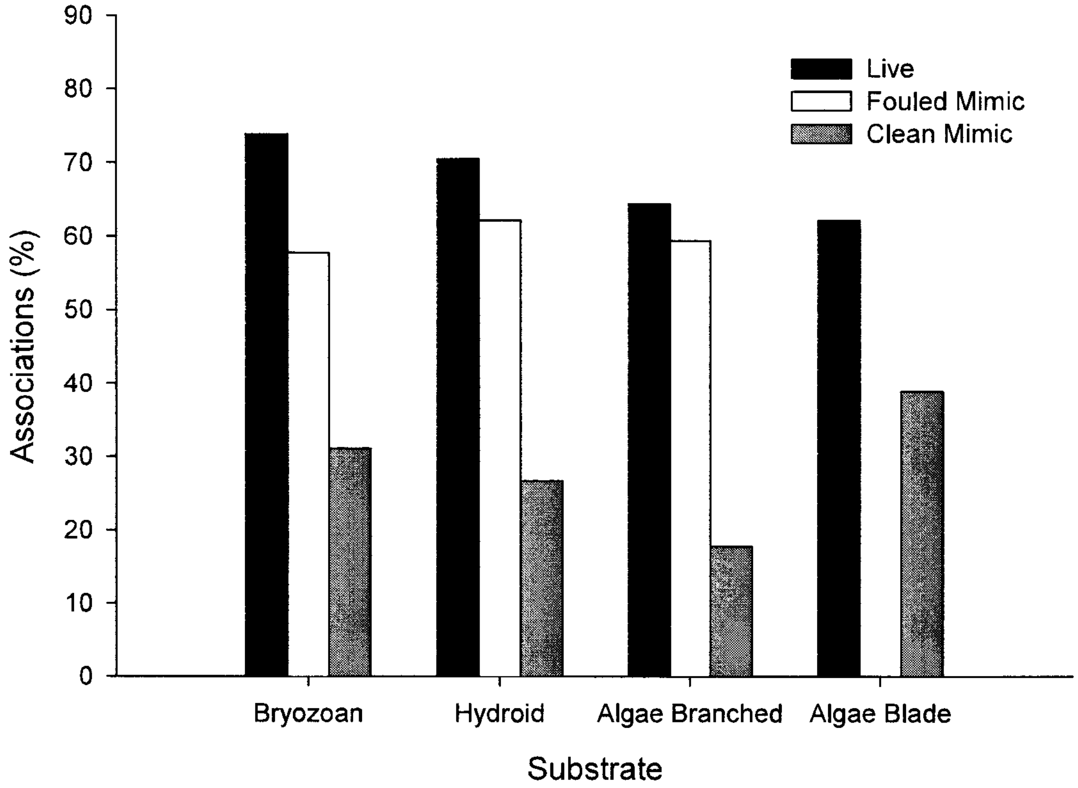

Figure 3.3. Percentage of small, age 0 red king crab (2-4 mm CL) that associated with single substrate treatments, including live substrates (bryozoan, hydroid, branched algae, and blade algae), fouled structural mimics, and clean mimics (e.g., given the opportunity, 74% of small crabs associated with bryozoans).

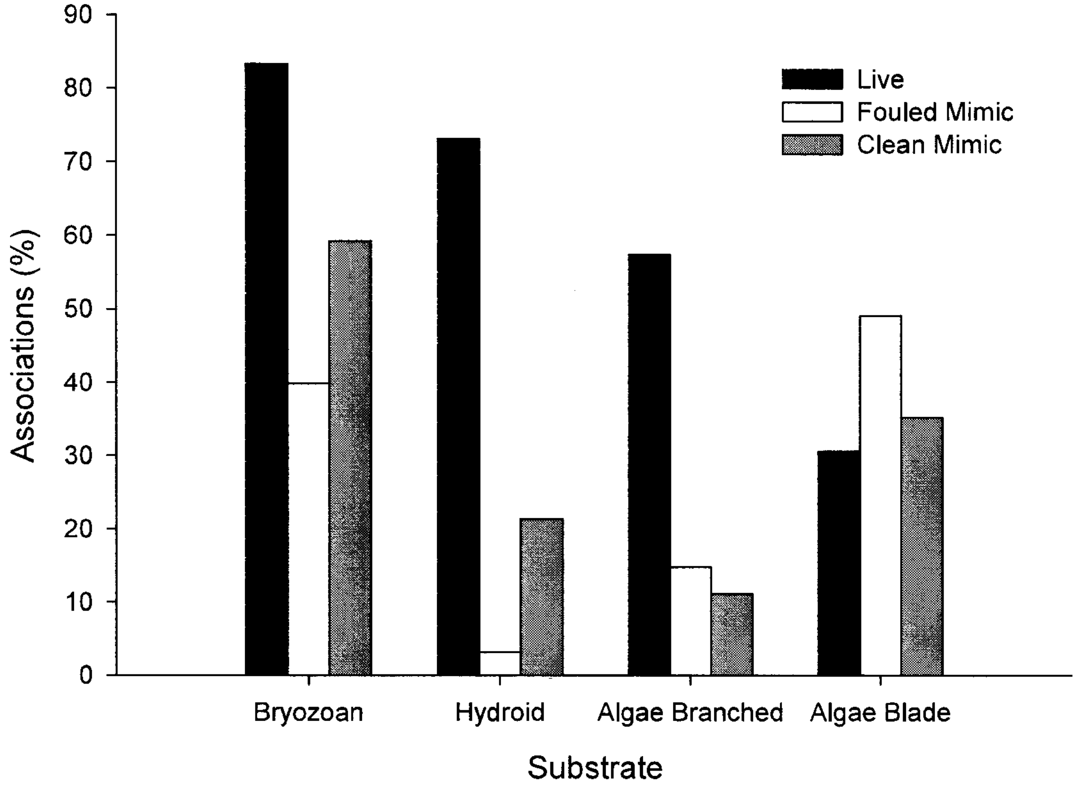

Figure 3.4. Percentage of large, age 0 red king crab (7.5-9 mm CL) that associated with single substrate treatments, including live substrates (bryozoan, hydroid, branched algae, and blade algae), fouled structural mimics, and clean mimics (e.g., given the opportunity, 83% of large crabs associated with bryozoans).

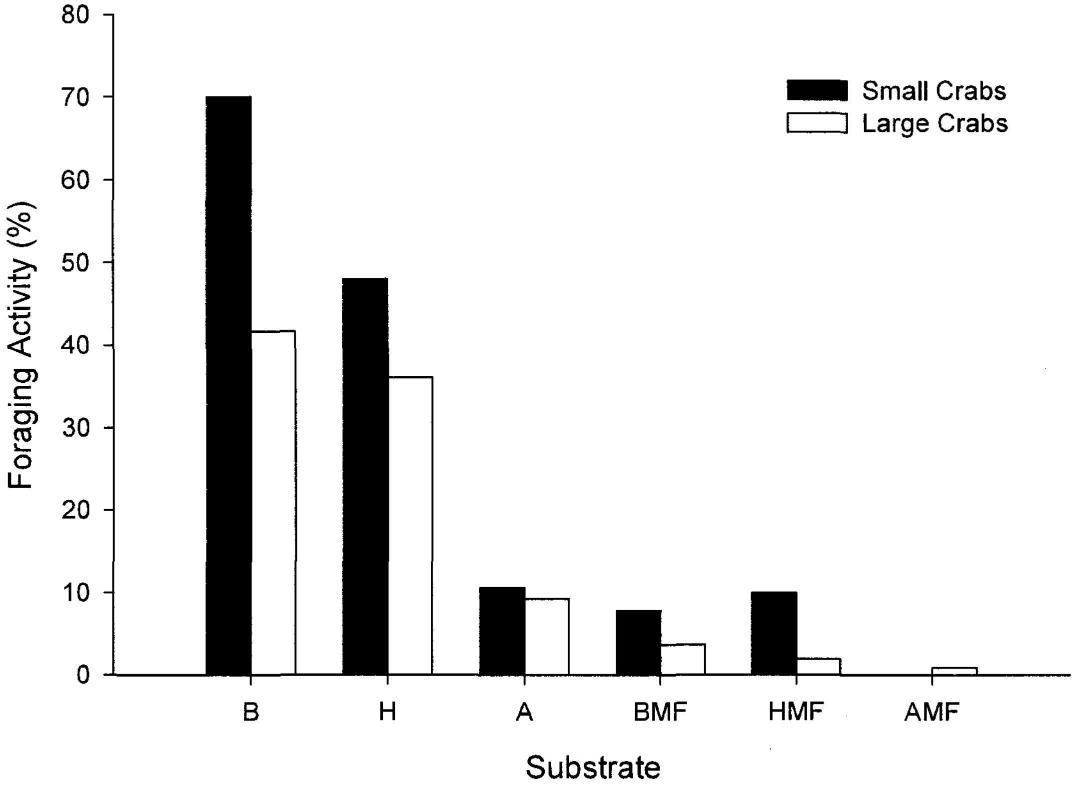

Figure 3.5. Percentage of small (2-4 mm CL) and large (7.5-9 mm CL) age 0 red king crab that foraged on experimental substrates, including bryozoans (B), hydroids (H), blade algae (A), and fouled mimics of bryozoans (BMF), hydroids (HMF), and blade algae (AMF) (e.g., given the opportunity, 70% of small crabs foraged on bryozoans).

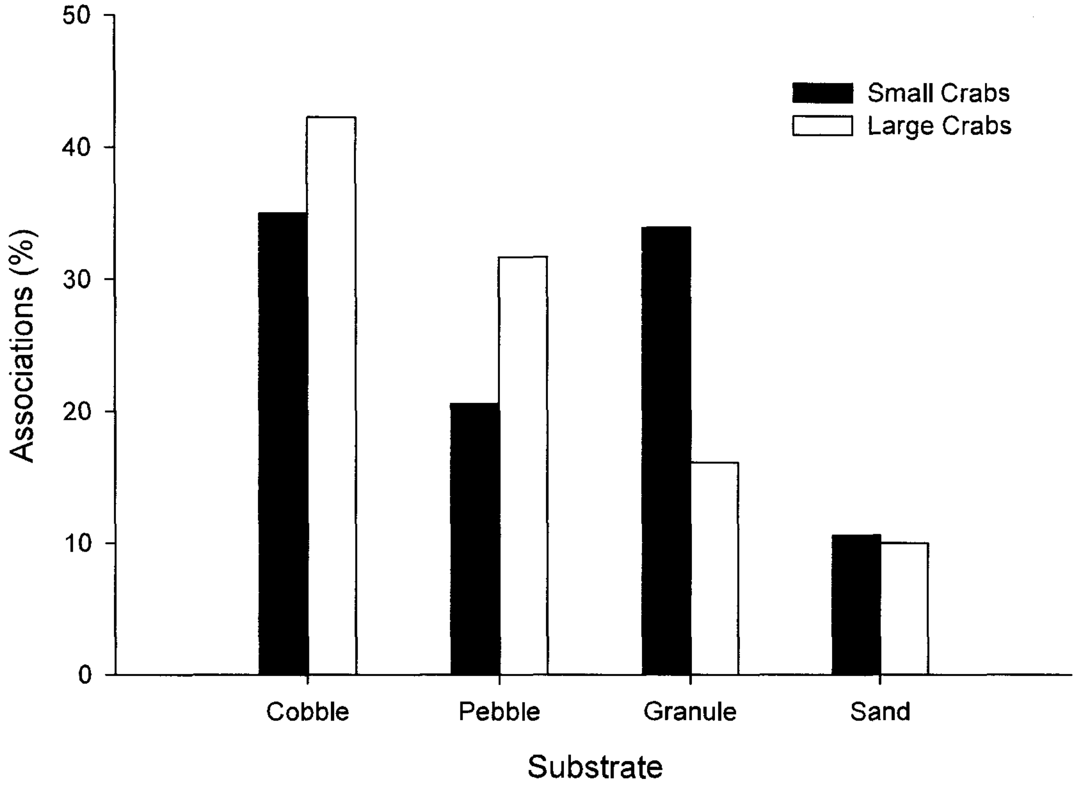

Figure 3.6. Percentage of small (2-4 mm CL) and large (7.5-9 mm CL) age 0 red king crab that associated with substrate treatments of varied grain-size (cobble>pebble>granule>sand) (e.g., given the opportunity, 35% of small crabs associated with cobble).

Chapter 4

Habitat structure influences survival and predator-prey interactions of early juvenile red king crab (*Paralithodes camtschaticus*)[1]

Abstract

Highly structured nursery habitats promote survival for juvenile stages of many species by providing refuge from predators and foraging opportunities. 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 (age 0) 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. Habitat structural complexity may have greater influence on survival of early juvenile stage red king crab than predator behavior. Survival was higher in the presence of complex habitat for age 0 crabs with Pacific cod (*Gadus macrocephalus*) predators in the laboratory and for age 0 and age 1 crabs with fish and invertebrate predators in the field because predator foraging efficiency was decreased by increased habitat complexity. Crab activity and refuge response behavior varied with crab stage and habitat. Age 0 crabs were cryptic and avoided 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 likely to flee or fight an attacking predator and were less likely to remain motionless in the absence of structural refuge. Complex habitats, cryptic behavior, and direct defense improve juvenile red king crab survival against certain predators, including demersal fishes. Understanding conditions that contribute to early life stage success will advance understanding of population fluctuation for this depressed fishery resource species.

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[1] Pirtle J. L., Eckert G. L., and A. W. Stoner. Habitat structure influences survival and predator-prey interactions of early juvenile red king crab (*Paralithodes camtschaticus*). Prepared for submission to Marine Ecology Progress Series.

4.1 Introduction

Habitat structural complexity has a profound effect on the ecology of associated organisms (Crowder and Cooper 1982, Stoner and Lewis 1985, Holbrook and Schmidt 1988, Wahle and Steneck 1991, Carr 1994, Hovel and Fonseca 2005). Structurally complex habitats have high surface area relative to their size and high availability of crevice space to provide shelter for smaller organisms (Caddy 1986, Eggleston et al. 1990). Complex habitats in aquatic environments may include aggregated boulders, rock wall crevices, and biogenic habitats formed by seagrasses, macroalgae, and invertebrates such as hydroids, corals, and sponges. These habitats are threatened by human activities including pollution (Fabricius 2005), coastal development (Short and Wyllie-Echeverria 1996), destructive fishing practices (Watling and Norse 1998), or a cascade of disturbances (Butler et al. 1995). Loss of habitat affects the ecology of associated organisms, including survival, reproductive potential and early life stage success.

Because predation is a highly influential mechanism affecting survival of early life stages, nursery habitats with structurally complex features are critical for many aquatic organisms, such as marine gastropods (Ray and Stoner 1995), dragonfly larvae (Pierce 1988), crayfish (Stein and Magnuson 1976), lobsters (Herrnkind and Butler 1986), salmonids (Magnhagen 1988), sunfish (Werner et al. 1983), and salamanders (Holomuzki 1986). For example, 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 and Fonseca 2005). Predator foraging efficiency is often decreased in complex habitats, which increases early life stage survival (Crowder and Cooper 1982, Lima and Dill 1990, Wahle and Steneck 1992, Laurel and Brown 2006), as demonstrated for young bluegill sunfish (*Lepomis macrochirus*) that shelter in vegetated freshwater habitats where foraging efficiency of largemouth bass is greatly reduced (Werner et al. 1983, Gotceitas and Colgan 1987). Complex habitat associations are important for American lobsters (*Homarus americanus*) from settlement until individuals outgrow the most vulnerable early juvenile stages (Wahle and Steneck 1992).

Predator-prey interactions have substantial effects beyond removal of individuals for early life stages, including trade-offs between foraging and predation risk (reviewed by Werner 1992). Highly structured nursery habitats support growth of early life stages by providing foraging opportunities (Mittelbach 1984, Marx and 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 and Magnuson 1976), including retreat to refuge structure, reduced activity, reduced foraging, and direct defense (Stein and Magnuson 1976, Gilliam and Fraser 1987, Gotceitas and Colgan 1987, Laurel and Brown 2006). This trade-off results in reduced growth rates (Werner et al. 1983, Werner 1991, Werner 1992, Tupper and Boutilier 1995), with population-level consequences like reduced reproductive potential. Furthermore, prey response behaviors often change with ontogeny, as foraging-risk implications are altered and individuals outgrow refuge habitat (Stein and Magnuson 1976, Werner and Hall 1988, Wahle and Steneck 1991, Sandt and Stoner 1993, Spanier et al. 1998). Investigating predator-prey interactions, including refuge response behavior and survival relative to habitat 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 complex life cycle with dispersive larval stages (2-4 month planktonic period) and benthic juveniles and adults (Marukawa 1933, Shirley and Shirley 1989). In Alaska during June-July, larval red king crab settle to nearshore nursery habitats where crabs in the early juvenile stage (0-2 years; 2-25 mm carapace length (CL)) (Donaldson et al. 1992, Loher and Armstrong 2000) are solitary and cryptic, and live in a habitat different from older juveniles and adults (Karinen 1985). This life stage is most abundant in complex habitats including fractured rock, cobbles, and bivalve shells (Sundberg and Clausen 1977, Loher and Armstrong 2000) and complex biogenic habitats formed by macroalgae and structural invertebrates, including hydroids and bryozoans (Sundberg and Clausen 1977, McMurray et al. 1984, Rodin 1985). Associating with complex habitats should reduce predation of the early juvenile stage, including predation by conspecifics because red king crab are highly cannibalistic (Stevens and Swiney 2005). Habitat choice is also driven by foraging opportunities, in particular when biogenic habitats are present (Pirtle and Stoner 2010). Around age 2 (approximate size 25 mm CL), juvenile crabs emerge from complex habitats to form "pods," mobile aggregations of hundreds to thousands of individuals (Powell and Nickerson 1965, Dew 1990). Crabs are reproductively mature around age 7 and males reach legal catch size for the Alaska fishery at ages 8 and 9 (McCaughran and Powell 1977).

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 and Kruse 2000). At present, many red king crab populations throughout Alaska remain depressed, 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, female bycatch in trawl fisheries, North Pacific ocean-atmospheric conditions, loss of settlement habitat, and predation by groundfish such as cod and flatfishes (Armstrong et al. 1993, Tyler and Kruse 1996, Orensanz et al. 1998, Zheng and Kruse 2000, Dew and McConnaughey 2005, Zheng and Kruse 2006, Bechtol and Kruse 2009, Kruse et al. 2009).

Increased groundfish abundance in the North Pacific coincided with the collapse of red king crab (Bakkala 1993, Bailey 2000, Bechtol 2009), implicating groundfish as potential predators of vulnerable juvenile stages with population-level consequences (Tyler and Kruse 1996, Zheng and Kruse 2006, Kruse et al. 2009). Population modeling has demonstrated a strong negative association between Pacific cod (*Gadus macrocephalus*) biomass and red king crab recruitment (Zheng and Kruse 2006, Bechtol 2009). However, lack of recovery for red king crab has not been directly linked to groundfish predation. Recruitment success for marine fish and crustaceans depends upon early life stage survival (Jones et al. 1982, Wahle and Steneck 1991, Eggleston and Armstrong 1995, Loher and Armstrong 2000). If we can gain understanding of factors that support red king crab early life stage success, then we may better understand conditions that contribute to population fluctuation for this depressed fishery resource species.

Habitat-mediated survival of early juvenile red king crab was examined in the laboratory with Pacific halibut (*Hippoglossus stenolepis*) as a fish predator by Stoner (2009). This study demonstrated that 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. Crab survival was substantially increased by the addition of complex habitat structure in the presence of this predator because crabs had a structure-seeking refuge response and halibut did not attack crabs associated with structural habitat (Stoner 2009). Whether or not complex habitat structure mediates crab survival with 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 field nursery locations.

In this study, we examined the effects of habitat structure on survival and refuge response behavior of early juvenile red king crab (age 0 and 1 yr) with laboratory and field experiments. We tested habitat choice in the laboratory without predators, in habitats with and without structure, and survival in those habitats with Pacific cod as a fish predator with age 0 crabs. We then assessed crab survival in nearshore nursery habitats with and without structure and identified predators and crab refuge response behavior with age 0 and age 1 crabs. We investigated the following three hypotheses: 1) habitat choice is influenced by perceived predator threat; 2) survival is greatest within habitats of complex structure; and 3) refuge response behavior is different between habitats with and without structure and with crab size or age.

4.2 Materials and Methods

4.2.1 Habitat Choice Experiment Predators Absent

We tested habitat preference of age 0 red king crab in the absence of predators to determine whether crabs associate with complex biogenic habitats more often than habitats of complex physical structure and sand. Biogenic habitat treatments were hydroids (*Obelia spp.*) and a composite of hydroids and branched macroalgae (*Neorhodomela larix*). Structural mimics of these two biogenic habitats were used to compare the response of the crabs to nonliving complex physical structure. Sand (0.5 mm diameter grain quartz) was used as the treatment without structure and as the base substrate in all other treatments. We used hatchery-reared red king crab from wild-captured female crab from Bristol Bay, Alaska, that were supplied by the Alaska King Crab Research Rehabilitation and Biology Program. All of the laboratory trials were conducted in the seawater facilities of the Alaska Fisheries Science Center (AFSC) in Newport, Oregon.

A total of 20 age 0 crabs (8-10 mm CL) were introduced to tanks (1.1 m diameter x 0.35 m depth). Substrate in each tank was composed of 1 cm of sand and 22 pieces of one habitat treatment placed on top of the sand and interspersed throughout the tank (Fig. 4.1). The habitat treatments were hydroids, complex biogenic habitat of hydroids and macroalgae, hydroid mimics, complex biogenic mimics, and sand. The total count of positive associations of crabs with the habitat (i.e., on or under) was recorded at 3 h. Each habitat treatment was replicated three times for a total of 15 trials. The arcsine-transformed ($\arcsin\sqrt{p_i}$) proportion of crab associations with each habitat treatment was compared with single-factor ANOVA ($\alpha = 0.05$) and Tukey's HSD post-comparison tests. All analyses were performed using SAS (version 9.2).

4.2.2 Laboratory Predation Experiment

We tested survival of crabs in the presence of fish predators when crabs were presented with the same habitats from the habitat choice experiment. Fish predators were age 1 Pacific cod (175-220 mm fork length (FL)) that were collected as age 0 fish from the waters off Kodiak Island, Alaska, and grown to this size in the seawater facilities of the AFSC in Newport, Oregon.

Predation trials were conducted in three circular, flat bottomed tanks (1.4 m diameter x 0.75 m depth) supplied with continuous flows of filtered seawater at 7 °C (± 0.5 °C). The tanks were located in a light-controlled room with a daily light cycle of 12 h light:12 h dark, with a manual rheostat. The tanks were lined with 1 cm of sand. Pairs of cod were used in the experiment because fish predators are known to perform more consistently with social facilitation (Stoner and Ottmar 2004, Ryer et al. 2004). Pairs of cod were transferred to the tanks two weeks prior to the first trials so that they could acclimate to their new surroundings in the tanks. At the end of week two, the pairs were presented with 10 age 0 red king crab (5-7.5 mm CL) as prey on sand habitat in one preliminary trial for 24 h to ensure that the fish were motivated to forage on red king crab as prey 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 ready for experimental trials after two 3-h preliminaries were completed when 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 and then deprived of food prior to the first experimental trial for 48 h to ensure that they were active and uniformly motivated to forage during the experiment.

Experimental trials were conducted using similar methods to Stoner (2009) with some modification. Six fish pairs received each of the five habitat treatments (28 pieces per treatment) once. A total of 20 age 0 crabs were introduced to each tank with a habitat treatment and fish pair in the dark and allowed to establish in microhabitats for 30 min when the lights were slowly raised. Fish pairs were then allowed to consume crabs for 3 h. The tanks were monitored with overhead video cameras to record cod behavior during the trials. Surviving crabs and their habitat association were counted at the end of a trial. Habitat structure was examined by hand to detect crabs that had attached themselves out of sight. Following an experimental trial, fish pairs were fed to satiation on krill and then deprived of food for 48 h before the start of the next trial. Tanks were cleaned and subsequent habitat treatments were arranged in the tanks 15-20 h prior to the start of the next trial. The sequence of habitat treatments was randomized among three fish pairs in three tanks. When a pair had completed all habitat treatments once, the pair was removed and replaced by a new pair that began the process with the preliminary trials. The number of crabs consumed by cod was compared among habitat treatments using a randomized block ANOVA ($\alpha = 0.05$) where habitat treatment ($n = 5$) was a fixed factor and fish pair ($n = 6$) was a random blocking factor. Tukey's post-comparison tests were applied to test for differences among habitat treatments.

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 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 would search through the habitat structure, we referred to this behavior as browsing, defined as committed investigating 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 for a selection of 15 trials that included three randomly selected trials from each habitat treatment. Fish attack to consumption rate ($\text{consumed}\cdot\text{attack}^{-1}$) was calculated for a trial as the proportion of known crabs consumed, based on the count of crabs at the beginning minus the count at the end of each trial, divided by the total attacks observed from video. Fish activity index was scored by breaking the selected trials into 15 minute segments and reviewing the first 5 min of each segment for the count of instances when an individual fish would cross from one quadrant of the circular tank to another. Fish attack to consumption rate, total attacks, total browsing events, and activity index were tested for the effect of habitat type on cod foraging behavior with single-factor ANOVA.

4.2.3 Field Predation Experiment

Field tethering studies are useful to improve understanding of relative predation rates in benthic communities and are complementary when combined with laboratory studies (Aronson and Heck 1995). We tested the effect of habitat structure on survival of early juvenile red king crab in the field in nearshore nursery habitats near Juneau, Alaska, during September-November 2009. Preliminary SCUBA surveys at our field site, Yankee Cove (58° 35.4' N, 134° 54.4' W, North American Datum of 1983), in July-August 2008 and August-October 2009 identified diverse macrofauna communities including juvenile red king crab and potential fish and invertebrate predators such as Pacific cod. In our experimental trials, we used two 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 had been captured from the Juneau area during June-July 2009 using larval settlement collectors (Blau and Byersdorfer 1994, Pirtle 2010) and reared in the laboratory through at least two molt cycles until crabs were 4-8 mm CL. Wild age 1 red king crab were captured the previous year using the same collectors in 2008 (Pirtle 2010) and reared for over a year until the time of the experiment, when crabs were 16-28 mm CL.

We tethered individual crabs by gluing a length of monofilament line (0.45 kg breaking strength) to the carapace of a crab using cyanoacrylate glue (e.g., Heck and Thoman 1981) and then attaching the monofilament to an eyebolt anchored in a concrete slab (30.5 cm diameter x 5 cm). The monofilament line length was equal to the radius of the slab and allowed the crab to move freely on the slab. 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. We tested potential artifacts due to tethering in the laboratory prior to field experiments using age 0 crabs, including the ability of age 1 cod and halibut predators to consume tethered crabs and the ability of tethered crabs to avoid entanglement in experimental habitats. Fish predators quickly consumed tethered and un-tethered crabs in laboratory tanks on sand and did not show negative effects due to consuming tethered prey, such as disinterest, choking, or entanglement. The crab entanglement test demonstrated that tethered age 0 crabs moved freely through dense hydroid structure, occupying a variety of locations during 24-h trials.

Field predation habitat treatments included hydroids with crushed shells and gravel (structure), crushed shells and gravel (without structure), and a procedural control composed of crushed shells and gravel covered by mesh to control for predation during the experiment while still subjecting crabs to handling methods. Divers using SCUBA deployed three experimental stations where the three habitat treatments were located, spaced 5-7 m apart at ca. 8-12 m depth and arranged adjacent to a rocky reef with boulders and understory macroalgae (Fig. 4.1). We used high resolution digital time-lapse video (704 x 480 resolution at 7 images·sec^{-1}) with a ring of 15 LED lights (Well-Vu Nature Vision Inc., 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. Lights were adjusted to the minimum illumination required to view the apparatus clearly during hours of darkness (Fig. 4.1). Divers established the habitat treatments and crabs at the underwater camera stations during daylight hours, between 10:00 am and 1:30 pm Alaska Standard Time. The three habitat treatments were replicated five times for both age 0 and age 1 crabs, which was the sample size that could be accomplished before the weather in late-fall became too inclement to continue the experiment. The location of each treatment was chosen randomly among the three stations for the 30 trials, with age 0 and age 1 crabs alternating every other day. 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 arcsine-transformed proportion of surviving crabs was compared among habitat type and stage using a two-factor general linear model (GLM) ($\alpha = 0.05$) and Tukey's multiple comparison tests.

Field videos were reviewed to assess crab behavior and predator-prey interactions. The time from crab deployment to mortal attack was totaled (00h:00min) for each crab mortality and the predator was 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 also identified. Crab behavior was quantified as the proportion of time spent engaged in the following activities during the experiment, from the time of deployment until mortal attack or recovery: 1) motionless; 2) sorting through the substrate with chelae (sorting); 3) moving laterally through the habitat (moving); and 4) climbing the habitat structure (climbing). Crab response behavior was quantified separately for predator attacks and direct interactions by potential predators (i.e., approach). 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 by attacking with chelae (fight); 3) stopping activity upon interacting with a predator (stop); and 4) no observed response (none). For the activity analysis, the arcsine-transformed proportion of the total time a crab was engaged in a trial was compared among activity type, habitat type and crab stage with multifactorial ANOVA ($\alpha = 0.05$). For the response analysis, the arcsine-transformed proportion of the response events for each trial was compared among response type, habitat type, and crab stage with multifactorial GLM ($\alpha = 0.05$) due to unbalanced sample size. Tukey's multiple comparison tests were applied to test for differences among levels of significant factors.

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 two untethered age 1 crabs in a laboratory tank with two seastars monitored by overhead video for 24 h and replicated this experiment three times with different crabs each trial.

4.3 Results

4.3.1 Habitat Choice Predators Absent

Early juvenile red king crab preferred biogenic habitats of hydroids and macroalgae significantly more than structural mimics, and crab preferred all structural habitats more than sand when fish predators were absent (*df* effect/total = 4/29, $F = 84.58$, $p < 0.0001$, Fig. 4.3). Crabs in the experiment associated with structure over open sand spaces in the biogenic habitat treatments, including (mean ± SE) 93% ± 3% of the time with hydroids and 83% ± 3% with hydroids and macroalgae. Crabs associated less often with structural mimics of these habitats, including 45% ± 7% of the time with hydroid mimics and 34% ± 6% with hydroid and macroalgae mimics. Structural habitat may facilitate survival of vulnerable, newly molted crabs, as demonstrated in this experiment by a crab that safely molted and was found at the top of a hydroid with its exuvium, presumably successfully avoiding cannibalism by conspecifics. Conversely, conspecifics consumed another crab that molted on sand habitat within the first hour of the experiment.

4.3.2 Laboratory Predation

Survival of age 0 red king crab, when exposed to age 1 cod as fish predators, was greatest in structural habitats. Cod consumed significantly more crabs on open sand habitat (mean ± SE, 10.5 ± 1.3 out of 20) than all habitats with complex structure (5.8 ± 0.5 crabs out of 20) (*df* effect/total = 4/29, $F = 13.82$, $p < 0.0001$, Table 4.1 and Fig. 4.4). A significant effect of fish pair resulted from two trials, where one pair consumed fewer crabs than others in hydroids and one pair consumed fewer crabs than others in complex biogenic habitat ($df = 5/29$, $F = 11.28$, $p < 0.0001$). Habitat alone was significant when fish pairs were not included as a factor in the analysis ($df = 4/29$, $F = 4.52$, $p < 0.01$). These two trials were excluded from video analysis for fish predator behavior. Upon recovery at the end of a trial, all surviving crabs were found associated with structural habitat or habitat mimics. These survivors were recovered under the habitat structure or clinging to the structure with flattened bodies and limbs drawn inwards, a behavior quite different from an aggressive or defensive posture when crabs extend their spiny walking legs with 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.

Cod as fish predators would often make several attacks on juvenile red king crab prey before successful consumption and consumed significantly more crabs per attack on sand habitat (mean ± SE, 0.66 ± 0.1) than all structural habitat treatments (0.30 ± < 0.1) (*df* effect/total = 4/14, $F = 3.94$, $p = 0.04$, Fig. 4.5), observed from video of the laboratory predation experiment. Total attacks (22.9 ± 2.2) ($df = 4/14$, $F = 1.31$, $p = 0.30$) and browsing events (43.8 ± 6.6) ($df = 3/11$, $F = 0.99$, $p = 0.45$) were not significantly different among habitat treatments (Fig. 4.6). Cod pairs made from 8-35 attacks and 17-91 browses in structural habitats (Fig. 4.6). The first attack occurred within the first 5 min after raising the lights for a variety of habitat types in 10 out of 15 trials reviewed. Attacks in four out of 15 trials occurred within the first 30 min, and the first attack in one trial with hydroid and algae mimics did not occur until 78 minutes. Cod activity was not significantly different among habitat treatments ($df = 4/14$, $F = 1.71$, $p = 0.22$, Fig. 4.7). Cod were motivated to locate and capture red king crab prey and spent most of the trial duration actively browsing through the habitat structure or investigating crab targets on sand.

4.3.3 Field Predation

All crabs were recovered from the mesh-covered procedural control. Survival of tethered early juvenile red king crab exposed to predators in the field was greater in the presence of structural habitat than in the absence of structural habitat (*df* effect/total = 2/29, $F = 26.80$, $p < 0.0001$, Fig. 4.8). Survival between the structural treatment and the procedural control was not significantly different (Tukey's HSD). Survival was not significantly different between crab stages (*df* = 1/29, $F = 3.60$, $p = 0.07$). However, all age 0 crabs ($n = 5$) survived the structural habitat treatment and 20% (one crab) survived the habitat without structure. A total of 60% of age 1 crabs (three of five crabs) survived the structural habitat treatment, and none survived the habitat without structure.

Predators that consumed three age 0 crabs were small sculpin (Cottidae) (Genus *Artedius*, *Clinocottus*, or *Oligocottus*), Alaska ronquil (*Bathymaster caeruleofasciatus*), and sunflower star (Table 4.2). The ronquil and sunflower star attacked during evening hours. The predator that consumed the fourth crab could not be determined because the video was corrupt; however, a fish predator is likely because the crab carapace and eyes remained attached to the tether, as observed in some of the laboratory tethering artifact trials with fish. Time from crab deployment to consumption varied among crabs in the no structure treatment from 2 min to 10 h 49 min (Table 4.2). The attack leading to consumption by the small sculpin (approximate 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*) (approximate length 30 cm) after 2 h 36 min (Table 4.2). Only one age 0 crab survived in the no structure treatment; it had burrowed under the crushed shell and gravel where it intermittently remained for 19 h 2 min of the 24 h trial.

All predation observed on age 1 crab was by the sunflower star with four out of six mortal seastar attacks occurring during the evening or early morning hours of darkness (Table 4.2). Seastars consumed four crabs in the habitat without structure and two crabs in the habitat with structure. The predator of the other crab consumed in habitat without structure may have also been a seastar, but 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 turned to face the approaching seastar to fight but were restrained by the tether. In laboratory tethering artifact trials that followed the field predation experiment, crabs fled from approaching seastars, easily escaped physical contact, and none of the crabs were consumed.

A variety of taxa passed through the camera field of view, approached the experimental apparatus to interact with the habitat treatment or the crab, and attacked crabs in the field predation experiment. Crabs were attacked unsuccessfully on 33 occasions by a variety of taxa, including sunflower stars, a variety of small sculpins, northern ronquil (*Ronquilus jordani*), whitespotted greenling (*Hexagrammos stelleri*), and Pacific lyre crab (*Hyas lyratus*) (Table 4.2). Taxa that directly interacted with the crabs on 58 additional occasions included sunflower stars, small sculpins, northern ronquil, whitespotted greenling, Arctic shanny (*Sticheus punctatus*), crescent gunnel (*Pholis leata*), Pacific lyre crab, and several hermit crabs and shrimps (Table 4.2). 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 4:00 pm to 8:00 am, with peak cod activity from midnight until 2:00 am. These cod overall were not interested in the tethered crabs and interacted with crabs on only seven occasions and browsed the habitat structure on 91 total occasions during the evening (mean browses each trial ± SE, 11.3 ± 4.4) out of hundreds of sightings near the camera lights. Cod attraction to the camera lights and relative disinterest in the tethered red king crab may have been an experimental artifact, due to the presence of light attracting pelagic zooplankton as another food source for cod. A variety of other taxa were recorded on video in the camera field of view (Table 4.2). Steller sea lions (*Eumetopias jubatus*), harbor seals (*Phoca vitulina*), and a cormorant (*Phalacrocorax pelagicus*) were recorded on video and may have been investigating the cameras or hunting animals attracted to the experimental apparatus.

Crab behavior in field predation trials varied by activity type, habitat type, and stage, demonstrated by significant interaction among these three factors (*df* effect/total = 3/31, $F = 4.88, p = 0.01$, Table 4.3). Age 0 crabs were most often climbing (mean percent time ± SE, 66% ± 15%) in habitats with structure and were observed foraging on hydroids (Fig. 4.9). However, in habitats without structure, age 0 crabs were most often motionless (85% ± < 0.1%) with bursts of movement for short duration (Fig. 4.10). Age

1 crabs spent most of the time moving (69% ± 13%) in habitats without structure, and were most often motionless (62% ± 29%) in structural habitat, resting under the hydroids.

Crabs demonstrated a variety of response behaviors when attacked or approached by a potential predator. Crab response to a predator attack among 45 events varied by response type and stage, as a significant interaction between these factors (*df* effect/total = 3/55, $F = 5.76$, $p < 0.01$, Table 4.4). The presence of structure was not a significant factor in crab response to an attack ($df = 1/55$, $F < 0.01$, $p = 0.91$, Table 4.4). Age 0 crabs most often had no observed response when attacked in habitats with structure (mean percent response ± SE, 50% ± 50%) or habitats without structure (SE, 56% ± 26%). Age 0 crabs would also stop activity and remain motionless in structural habitats (50% ± 50%) and in habitats without structure (19% ± 19%) (Fig. 4.11). Age 0 crabs only occasionally attempted to flee or fight when attacked. However, when age 1 crabs were attacked, this stage most often responded by fighting a predator directly in habitats with structure (55% ± 6%) and without structure (33% ± 33%) or by attempting to flee in structural habitats (36% ± 6%) and in habitats without structure (40% ± 21%).

Crabs of both stages most often did not respond when approached by a predator ($df = 3/43$, $F = 40.04$, $p < 0.0001$, Table 4.5 and Fig. 4.11). The presence of structure ($df = 1/43$, $F = 0.04$, $p = 0.85$) and stage ($df = 1/43$, $F = 0.04$, $p = 0.85$) were not significant factors in crab response to an approach (Table 4.5). 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% ± 13%) and would flee from a predator in habitats with structure (8% ± 8%) and without structure (13% ± 13%), but did not respond by fighting (Fig. 4.11). Age 1 crabs would flee from an interaction in habitats with structure (16% ± 10%), in habitats without structure (11% ± 11%), and would fight in habitats without structure (3 % ± 3%), but were not observed to stop their current activity like age 0 crabs.

4.4 Discussion

4.4.1 Habitat structural complexity and crab survival

The presence of highly structured complex habitat increased red king crab survival when they were exposed to a variety of predators in laboratory and field experiments, which demonstrates that habitat complexity is an integral part of early juvenile red king crab survival. Habitats with complex vertical structure and crevice space provided young red king crab adequate cover to facilitate crypsis as a survival strategy. Cryptic behavior likely increases crab survival in complex habitat because predator detection is reduced by the habitat structure (Lima and Dill 1990), compared to exposed habitats where small crabs are quite vulnerable. Active selection of complex habitat was demonstrated here and in previous laboratory studies (Stevens and Swiney 2005, Stoner 2009, Pirtle and Stoner 2010), and is a behavior that should contribute to greater survival and foraging opportunities for early juvenile red king crab.

Habitat structural complexity increased crab survival by modifying interactions between fish predators and red king crab as prey. In laboratory experiments, 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. This result was similar to age 1 Pacific halibut where prey encounter rate and capture success diminished when foraging on age 0 red king crab 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 dolomieui*) was greatly reduced when juvenile crayfish associated with macrophyte habitats (Stein and Magnuson 1976), and for bluegill sunfish (*Lepomis macrochirus*) consuming various prey items in habitats of high macrophyte densities (Crowder and Cooper 1982).

Cod and halibut have different foraging strategies as predators of early juvenile red king crab. Cod in our laboratory experiment would actively search the tank for crabs in open spaces and browse through structural habitat to locate and attack crabs. In contrast, halibut did not search for crabs associated with structure and would ambush crabs in open spaces and at the edge of structure (Stoner 2009). Activity levels were also different between these two predators. Cod in our experiment did not alter activity levels between habitats with and without complex structure. However, halibut were less active with the addition of complex structure. Because crab survival was high in structural habitats in the presence of both fish predators with different foraging behaviors, habitat structural complexity may have greater influence on red king crab survival than predator behavior.

4.4.2 Crab habitat choice and predation threat

Our experiments demonstrated that red king crab early juvenile habitat choice was influenced by predator threat perceived by the crabs. 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 prefer biogenic habitats due to foraging opportunities provided by those habitats, over habitats of complex physical structure alone (Pirtle and 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 and Magnuson 1976). Red king crab responded to age 1 cod as 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 and Swiney 2005, Stoner et al. in press). 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 and Steneck 1992), spiny lobster (Herrnkind and Butler 1986), and Atlantic cod (*Gadus morhua*) (Tupper and Boutilier 1995). This behavioral response has implications for the distribution of early juvenile red king crab among available habitats at nursery locations.

Refuge-seeking behaviors that promote early life stage survival have been associated with tradeoffs between predation risk and energetic return or growth. The tendency of early juvenile red king crab in laboratory and field experiments to shelter with the closest structural habitat and alter or reduce activity levels may lead to depressed energy intake when associating with suboptimal food sources under high predation pressure or for long duration. Several studies have established that aquatic prey will reduce foraging and other activity levels in the presence of predators at the expense of energetic return, including juvenile crayfish (Stein and Magnuson 1976), anuran tadpoles (Werner 1991), salmonids (Dill and Fraser 1984, Magnhagen 1988), and sunfish (Werner et al. 1983). Small 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, Gotceitas and Colgan 1987, Werner and Hall 1988). Red king crab may have a similar response if predators confine early juvenile stages to refuge habitats where prey items may be optimal for newly settled crabs but less optimal for growth to larger juvenile stages. Delayed growth may affect time to maturity with population-level consequences such as reduced reproductive potential.

4.4.3 Crab activity and refuge response with ontogeny

Crab activity was dependent on crab size or age and habitat complexity. Our field experiments demonstrated that age 0 crabs were consistently cryptic, associating with hydroid structure at any opportunity, and remaining motionless in exposed habitat. By comparison, age 1 crabs were very active in exposed habitat and less active in the hydroid structure, until provoked. Lima and Dill (1990) proposed that prey activity should depend on the perceived security of an animal against its background when predators are nearby. 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.

Crab response behavior to a perceived predator threat was also dependent on crab size or age, but not habitat complexity. Tethered age 1 crabs in the field experiment demonstrated a defensive response when attacked, and would most often fight a predator or attempt to flee. In contrast, tethered age 0 crabs would halt their activity or did not respond at all when attacked, continuing to climb when associated with habitat structure. The response of age 0 crabs is characteristic of cryptic behavior, seeming almost oblivious to the danger of predation. This response was similar to surviving age 0 crabs in the laboratory experiment that were most often recovered clinging to the habitat structure.

An unsuccessful flight response by red king crab to an attack during the field predation experiment was likely an artifact of tethering. We expect that crabs would successfully flee when threatened if the flight response was attempted with time to escape, as evidenced by the ability of untethered age 1 crabs to avoid seastar predators in the lab. In the field, age 1 crabs survived attacks by seastars in structural habitat by maneuvering through the structure and nipping an attacking seastar with raised chelae until the seastar retreated, while others were able to escape until the next attack. Direct defense behavior that was most often observed with age 1 crabs only functioned to delay mortality of tethered individuals in the field.

Behavioral differences in activity and refuge response suggest that size drives ontogenetic shifts for juvenile red king crab. We identified two 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 and Stoner 2010). Our age 1 crabs were 16-28 mm CL, within range of the approximate size when crypsis may end and social behavior begins, around 25 mm CL or age 2 (Powell and Nickerson 1965, Dew 1990). If the adaptive significance of aggregation for red king crab is increased vigilance or safety in numbers (reviewed by Lima and 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, similar to lobsters (Wahle and Steneck 1992) and crayfish (Stein and Magnuson 1976). However, aggregation 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 (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 and Stoner 2010). We suggest this advantage may be lost on larger individuals as early as age 1, when certain habitats no longer provide appropriate refuge or foraging opportunities.

4.4.4 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. When given the opportunity to forage on unsheltered crabs in sand habitat in the laboratory experiment, cod consumed on average only half of the available crabs. Cod may be deterred from consuming red king crab due to the spiny body armor covering their carapace and limbs. This additional defense may have contributed to the tentative predation behavior by cod observed during the laboratory experiment. For example, a cod predator would bite a crab and quickly drop it, or the same predator would 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 and Armstrong 2000, Pirtle 2010), including our field experiment site, we observed no cod predation on tethered crabs during the field experiment. It is interesting that cod (approximate length 200 mm) observed during the field experiment were not interested in consuming red king crab, and instead foraged on pelagic zooplankton attracted to the camera lights.

Potential fish predators of early juvenile stage red king crab may include sculpins, certain flatfishes, and other demersal fishes. Sculpins and Alaskan ronquil consumed age 0 crabs in our field experiment, apparently not deterred by spiny body armor. These fishes inhabit inshore locations where they co-occur with early juvenile red king crab

(Dean et al. 2000, Loher and Armstrong 2000, Pirtle 2010). Previous laboratory studies demonstrated that halibut were efficient predators of red king crab early juvenile stages (Stoner 2009). Halibut were not observed at our field predation site, but halibut nursery grounds (Norcross and Mueter 1999, Stoner and Titgen 2003) have potential spatial overlap with red king crab nursery locations (Pirtle 2010).

It is interesting to examine groundfish diet analysis from fishery resource surveys when considering predators of early juvenile red king crab. Red king crab were not a major diet component for any species examined by the surveys. Softshell adult red king crab were found sporadically in the stomach contents of Pacific cod (Jewett 1978, Livingston 1989, Livingston et al. 1993, Livingston and deReynier 1996, Lang et al. 2005) and Pacific halibut (Gray 1964, Livingston and deReynier 1996, Lang et al. 2005), but not juvenile stage crabs. However, yellowfin sole (*Pleuronectes asper*) (Haflinger and McRoy 1983, Livingston et al. 1993) and walleye pollock (*Theragra chalcogramma*) (Livingston et al. 1993, Livingston and deReynier 1996, Lang et al. 2005) consumed settlement stage larvae and early juvenile stage crabs. Non-harvested sculpins (Cottidae) also consumed early juvenile crabs (Jewett and Powell 1979).

We do not fully understand the impact of predation on red king crab early juvenile stages and the recovery of depressed 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. Further studies may include diet analysis of potential predators that correspond with periods when these predators and early juvenile stage red king crab co-occur in nursery locations. Although we did not observe cannibalism on early juvenile stage crabs by larger red king crab, the extent that cannibalism occurs should be investigated with integrated laboratory and field studies.

4.5 Acknowledgements

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Table 4.1. Results of ANOVA with randomized block design for the cod laboratory predation experiment. Habitat is a fixed effect and fish pair is 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			

Table 4.2. Taxa present at the field experiment site that were considered potential predators of small red king crab. Behavioral interactions are listed that include taxa that 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 stage (age 0 or age 1) is indicated for attacks and consumption with time from crab deployment in the habitat treatment until successful consumption (00h:00min).

	Behavioral Interactions			
Taxa Common and Scientific Names	Appear	Approach (a, b)	Attack (stage)	Consume (stage, time)
Pacific cod *Gadus macrocephalus*	X	X (a, b)	-	-
Walleye pollock *Theragra chalcogramma*	-	-	-	-
Kelp greenling *Hexagrammos decagrammus*	X	-	-	-
Whitespotted greenling *Hexagrammos stelleri*	X	X (a, b)	X (0, 1)	-
Copper rockfish *Sebastes caurinus*	-	-	-	-
Dark dusky rockfish *Sebastes ciliatus*	X	-	-	-
Quillback rockfish *Sebastes maliger*	-	-	-	-
Buffalo sculpin *Enophrys bison*	X	-	-	X (0, 02:36)
Great sculpin *Myoxocephalus polyacanthocephalus*	-	-	-	-
Crested sculpin *Blepsias bilobus*	X	X (b)	-	-

Table 4.2. Continued.

Taxa Common and Scientific Names	Behavioral Interactions Appear	 Approach (a, b)	 Attack (stage)	 Consume (stage, time)
Silverspotted sculpin	-	-	-	-
Blepsias cirrhosus				
Red Irish lord	-	-	-	-
Hemilepidotus hemilepidotus				
Undefined sculpins	X	X (a, b)	X (0, 1)	X (0, 00:02)
Artedius, *Clinocottus*, or *Oligocottus spp.*				
Sturgeon poacher	-	-	-	-
Agonus acipenserinus				
Arctic shanny	X	X (a, b)	-	-
Sticheus punctatus				
Northern ronquils	X	X (a, b)	X (0, 1)	-
Ronquilus jordani				
Alaskan ronquil	X	X (a, b)	X (0)	X (0, 07:21)
Bathymaster caeruleofasciatus				
Starry flounder	X	X (b)	-	-
Platichthys stellatus				
English sole	-	-	-	-
Pleuronectes vitulus				
Yellowfin sole	-	-	-	-
Limada aspera				
Crescent gunnel	X	X (b)	-	-
Pholis leata				
Undefined Moonsnails	X	X (b)	-	-
Euspira spp.				

Table 4.2. Continued.

	Behavioral Interactions			
Taxa Common and Scientific Names	Appear	Approach (a, b)	Attack (stage)	Consume (stage, time)
Giant Pacific octopus *Enteroctopus dofleini*	-	-	-	-
Red king crab *Paralithodes camtschaticus*	-	-	-	-
Dungeness crab *Cancer magister*	X	X (b)	-	-
Helmet crab *Telmessus cheiragonus*	-	-	-	-
Pacific lyre crab *Hyas lyratus*	X	X (a, b)	-	-
Undefined Hermit Crabs *Pagurus* and *Elassochirus spp.*	X	X (b)	-	-
Undefined Shrimps Pandalidae	X	X (b)	-	-
Sunflower star *Pycnopodia helianthoides*	X	X (a, b)	X (0, 1)	X (0, 10:49) (1, *)
Steller sealion *Eumetopias jubatus*	X	-	-	-
Harbor seal *Phoca vitulina*	X	-	-	-
Pelagic cormorant *Phalacrocorax pelagicus*	X	-	-	-

*Time until *P. helianthoides* strike on age 1 crabs (14:08; 01:03; 12:12; 20:31; 00:16; 18:31)

Table 4.3. Results of multifactorial ANOVA for the total time a crab was engaged in the experiment with crab activity type, habitat (structure, no structure), and crab stage (age 0, age 1).

Source	*df*	SS	MS	*F*	*p*
Activity (A)	3	2.22	0.74	16.95	<0.0001
Habitat (H)	1	<0.01	<0.01	0.06	0.81
Stage (S)	1	<0.01	<0.01	0.00	0.94
A•H	3	1.53	0.51	11.68	<0.0001
A•S	3	0.66	0.22	5.06	<0.01
H•S	1	<0.01	<0.01	0.08	0.79
A•H•S	3	0.63	0.21	4.88	0.01
Error	16	0.70	0.04		
Total	31	5.76			

Table 4.4. Results of multifactorial GLM for crab response to a predator attack with response type, habitat (structure, no structure), and crab stage (age 0, age 1) using the adjusted sum of squares and mean squared error.

Source	*df*	SS	MS	*F*	*p*
Response (R)	3	0.52	0.17	0.68	0.57
Habitat (H)	1	<0.01	<0.01	<0.01	0.91
Stage (S)	1	<0.01	<0.01	0.01	0.91
R•H	3	0.27	0.09	0.35	0.79
R•S	3	4.41	1.47	5.76	<0.01
H•S	1	<0.01	<0.01	0.01	0.91
R•H•S	3	0.36	0.12	0.48	0.70
Error	40	10.20	0.26		
Total	55	15.78			

Table 4.5. Results of multifactorial GLM for crab response to an interactive predator approach with response type, habitat (structure, no structure), and crab stage (age 0, age 1) using the adjusted sum of squares and mean squared error.

Source	*df*	SS	MS	*F*	*p*
Response (R)	3	8.90	2.97	40.04	<0.0001
Habitat (H)	1	<0.01	<0.01	0.04	0.85
Stage (S)	1	<0.01	<0.01	0.04	0.85
R·H	3	0.01	<0.01	0.04	0.99
R·S	3	0.22	0.07	0.99	0.41
H·S	1	<0.01	<0.01	0.04	0.85
R·H·S	3	0.02	0.01	0.10	0.96
Error	28	2.07	0.07		
Total	43	12.51			

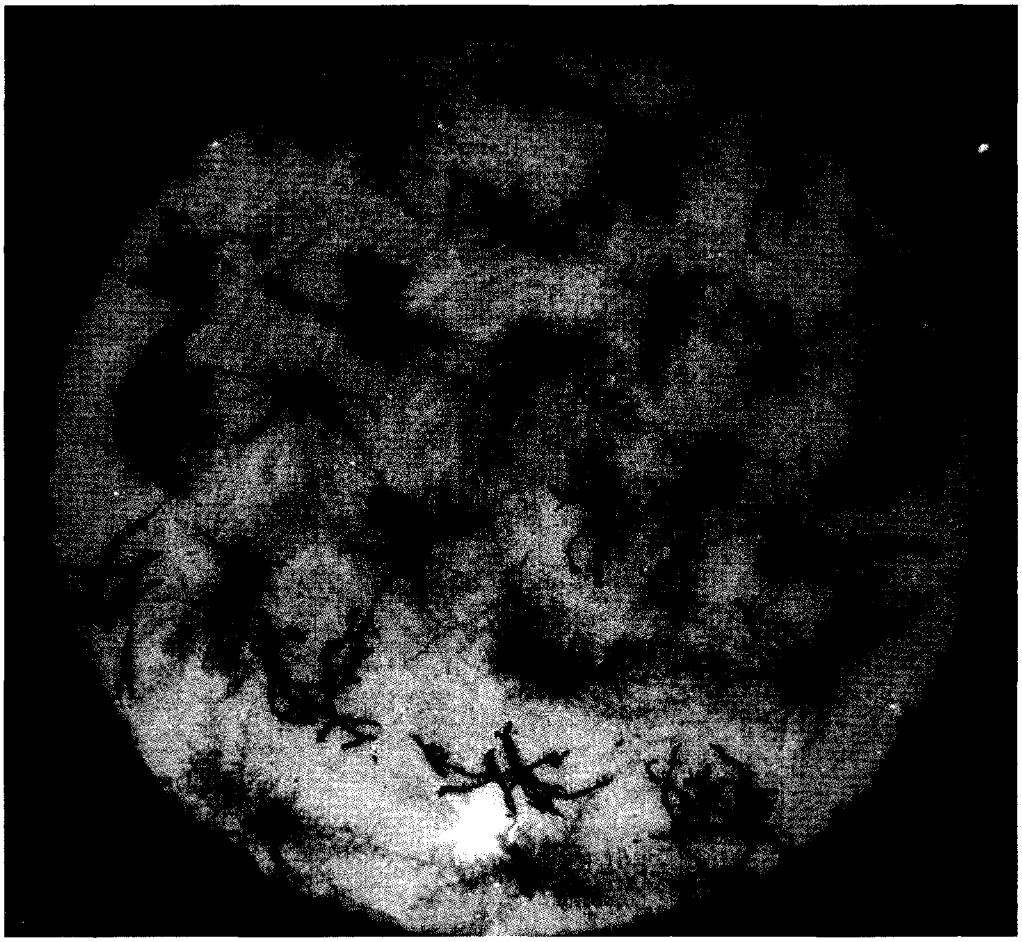

Figure 4.1. Laboratory predation trial with a pair of age 1 Pacific cod and the complex biogenic habitat treatment of branched macroalgae and hydroids on sand.

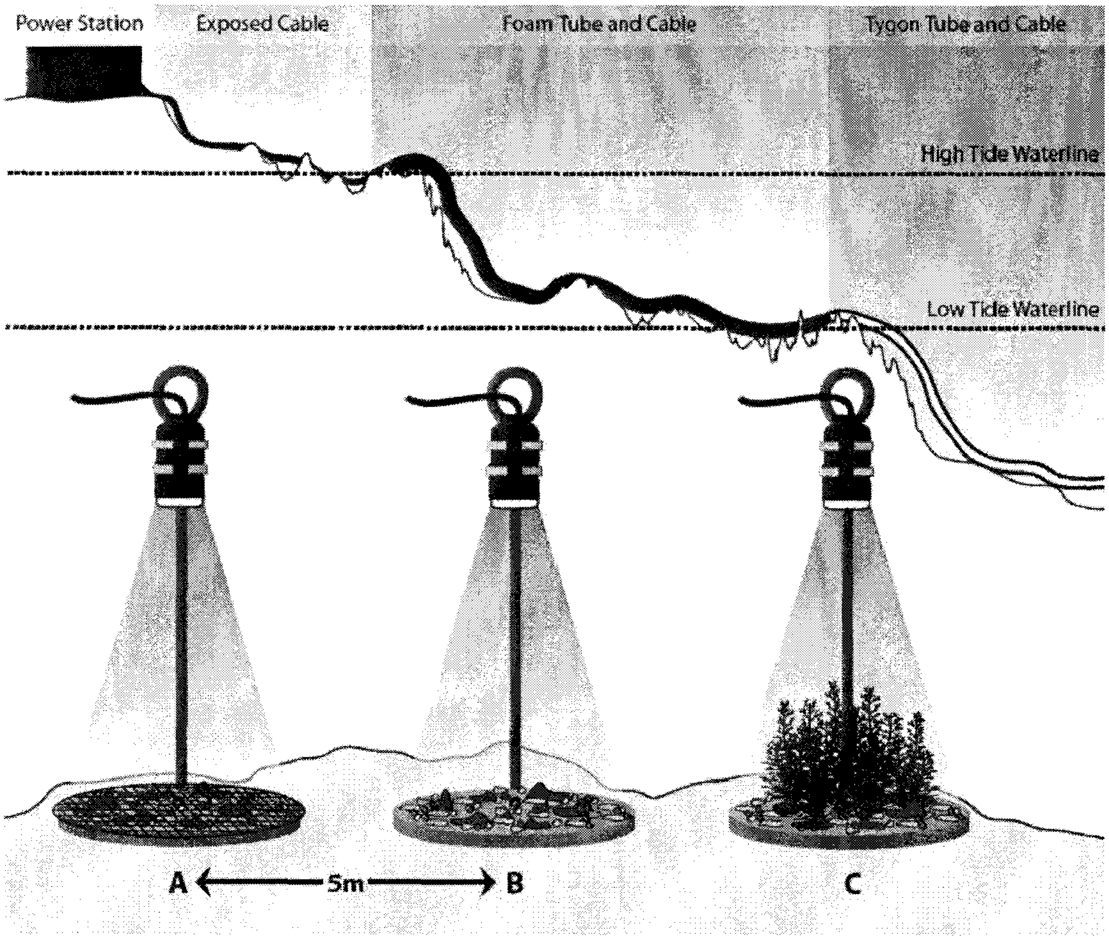

Figure 4.2. Field experiment setup, illustrating the camera cable path from the shore-based power station, through the intertidal zone, to three subtidal camera stations, spaced 5-7 m apart at ca. 8-12 m depth and located at the base of a rock reef with boulders and macroalgae. Cameras are mounted on sand anchors above concrete slabs with the location of the following habitat treatments presented at random each trial: a) no structure, mesh-covered procedural control; b) no structure habitat with crushed shells and gravel; and c) structural habitat with hydroids.

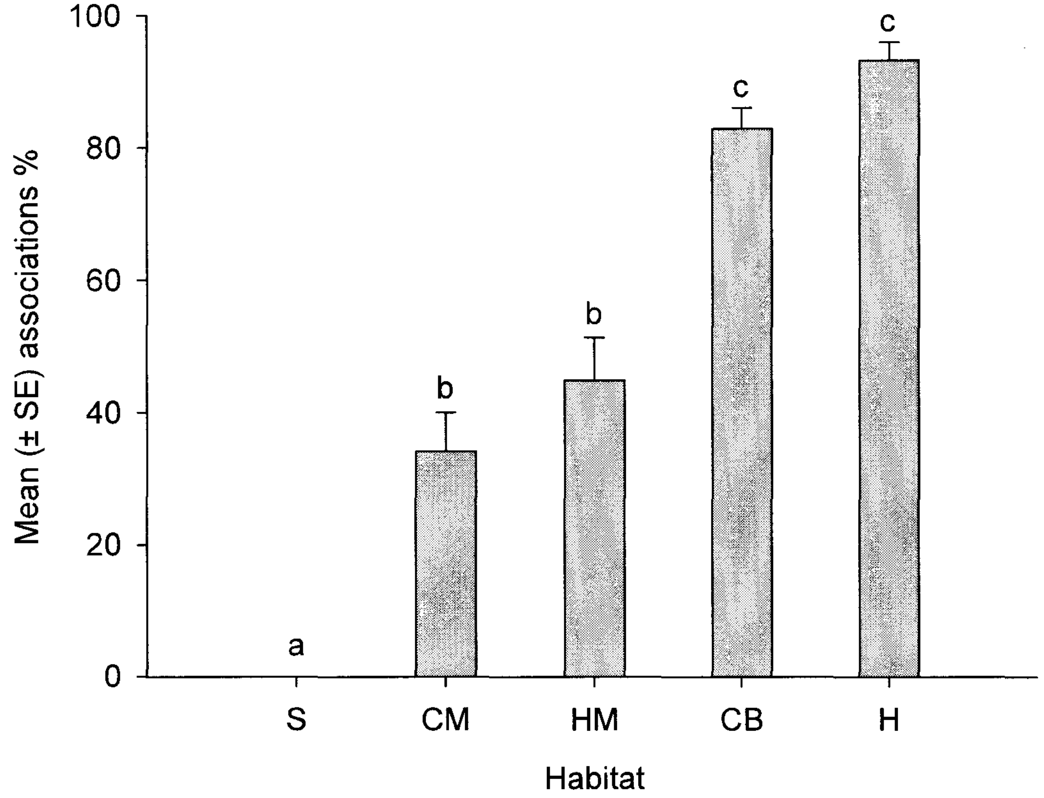

Figure 4.3. Mean (± SE) percentage of age 0 red king crab that associated with habitat treatments when no fish predator was present in laboratory trials, including sand (S), complex biogenic mimics (CM), hydroid mimics (HM), and live complex biogenic habitat of algae and hydroids (CB), and hydroids (H). Crabs associated with living complex habitat more often than structural mimics and with structural habitat more than sand habitat alone (p <0.0001, single-factor ANOVA). Letters indicate successive groups with similar means (Tukey's HSD).

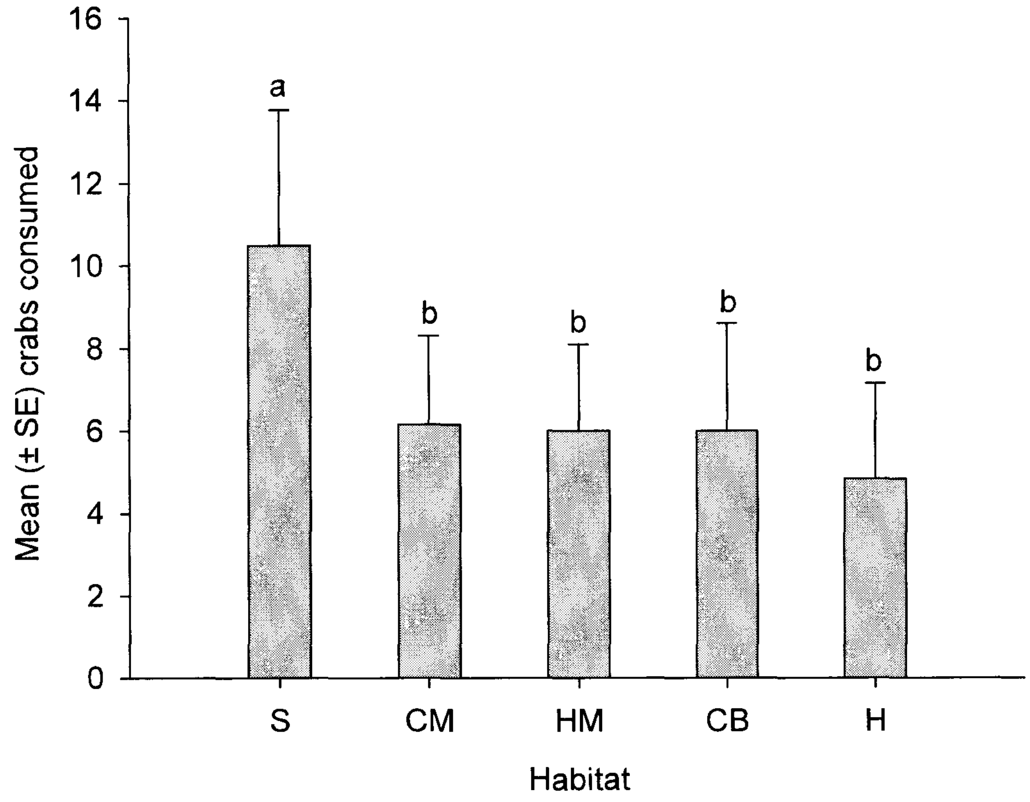

Figure 4.4. Mean (± SE) age 0 red king crab (*n* = 20) consumed by cod in laboratory predation trials. Cod consumed significantly more crabs on sand habitat than all structural habitat treatments ($p < 0.0001$, ANOVA with randomized block design). Letters indicate successive groups with similar means (Tukey's HSD); habitat abbreviations as in Fig. 4.3.

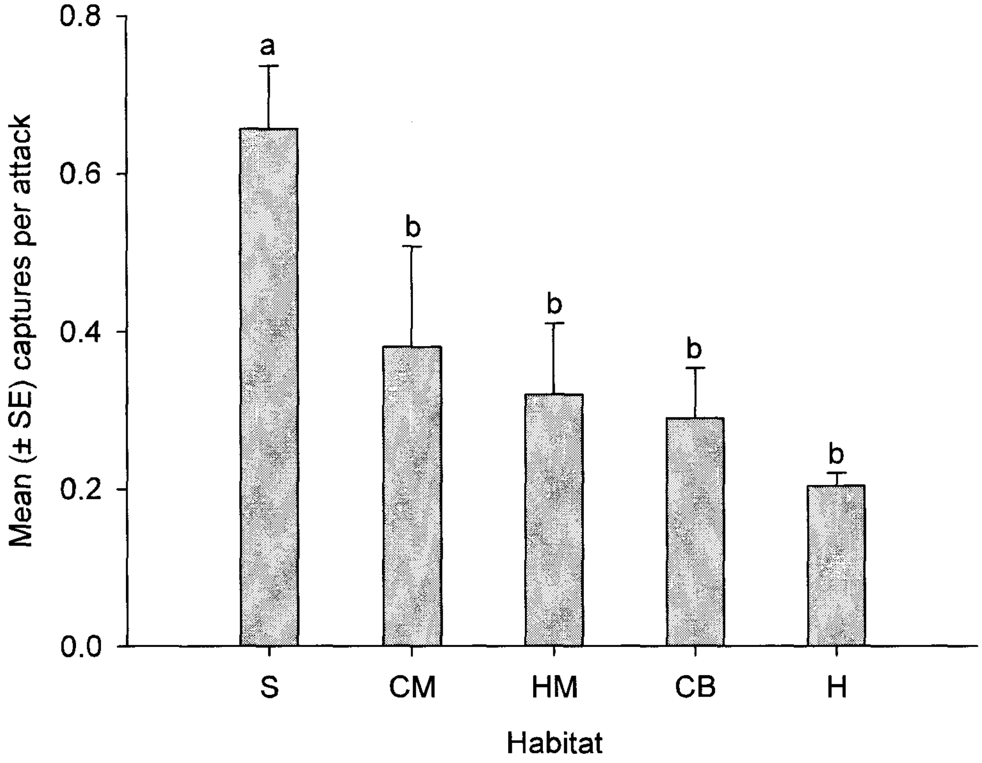

Figure 4.5. Mean (± SE) proportion of age 0 red king crab consumed for each attack by cod in laboratory predation trials. Cod consumed significantly more crabs with each attack on sand habitat than all structural habitat treatments ($p = 0.04$, single-factor ANOVA). Letters indicate successive groups with similar means (Tukey's HSD); habitat abbreviations as in Fig. 4.3.

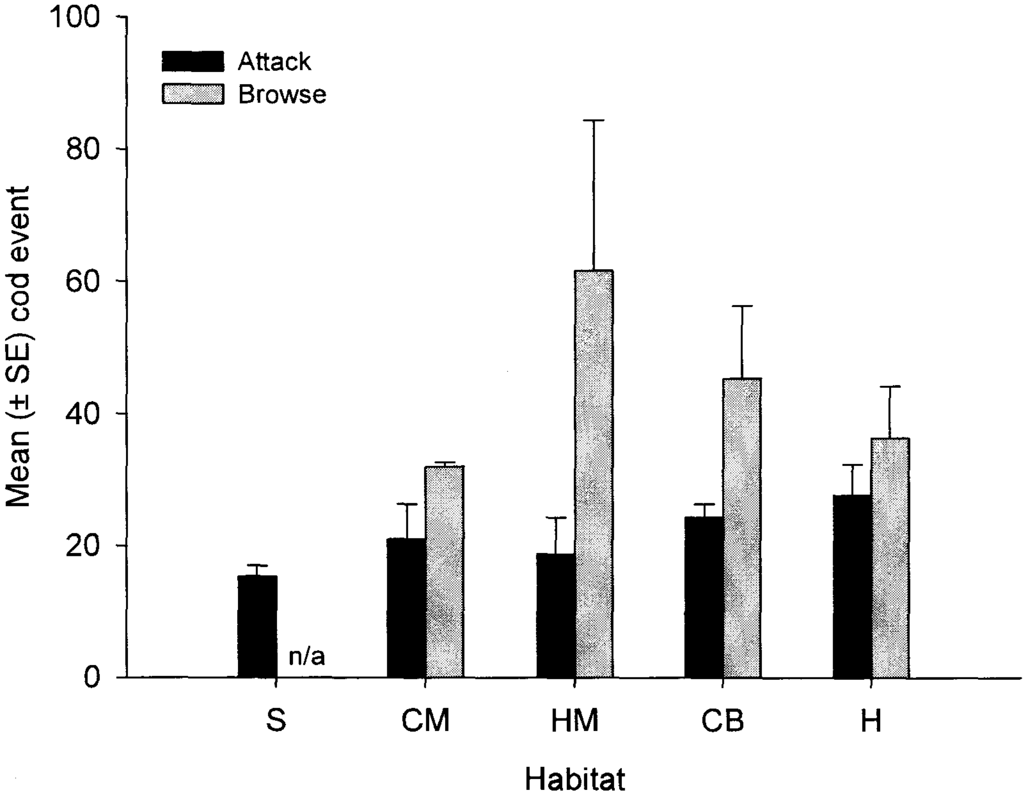

Figure 4.6. Mean (± SE) count of attacks and browsing events by cod in laboratory predation trials with age 0 red king crab. Cod attacks and browsing events were not significantly different among habitat treatments (single-factor ANOVA). Habitat abbreviations as in Fig. 4.3.

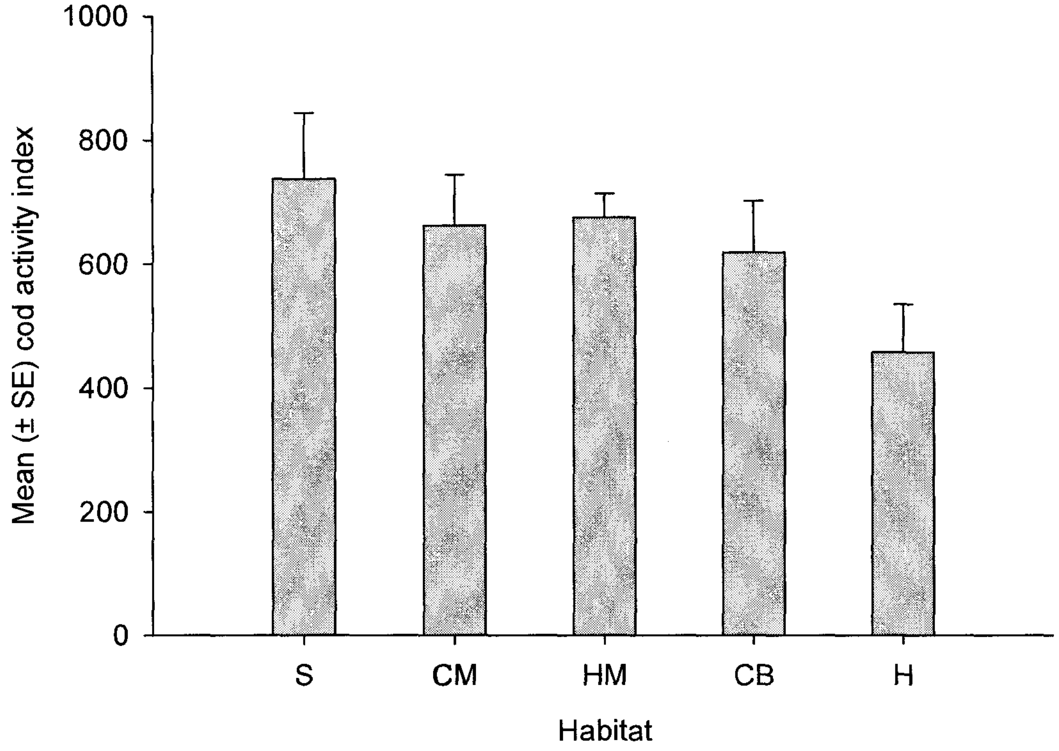

Figure 4.7. Mean (± SE) cod activity index in laboratory predation trials with age 0 red king crab. Cod activity was not significantly different among habitat treatments (one-factor ANOVA). Habitat abbreviations as in Fig. 4.3.

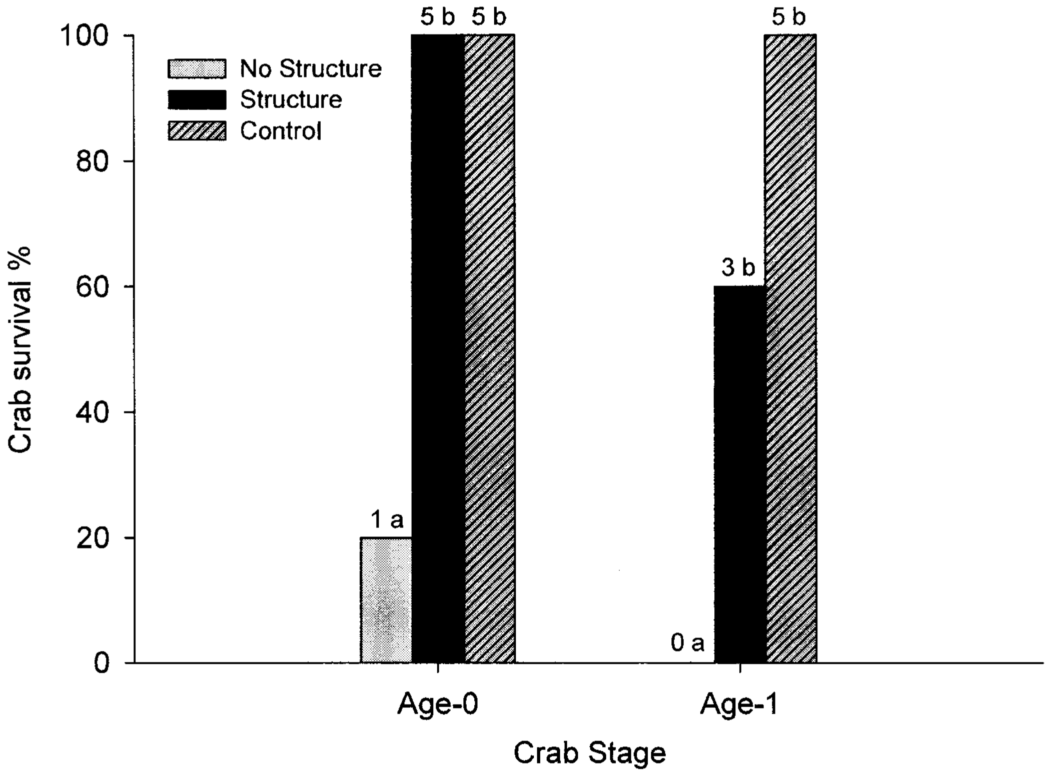

Figure 4.8. Percent survival of tethered red king crab stages (age 0 and age 1) in the field predation study. Habitat treatments included no structure, structure, and a control. Crab survival was significantly greater in structure and the control than in no structure ($p <$ 0.0001, two-factor GLM). Survival in structure was not significantly different from the control and survival was not significantly different between crab stages. Numbers above bars indicate the number of crabs surviving in that habitat; letters indicate successive groups with similar means (Tukey's HSD).

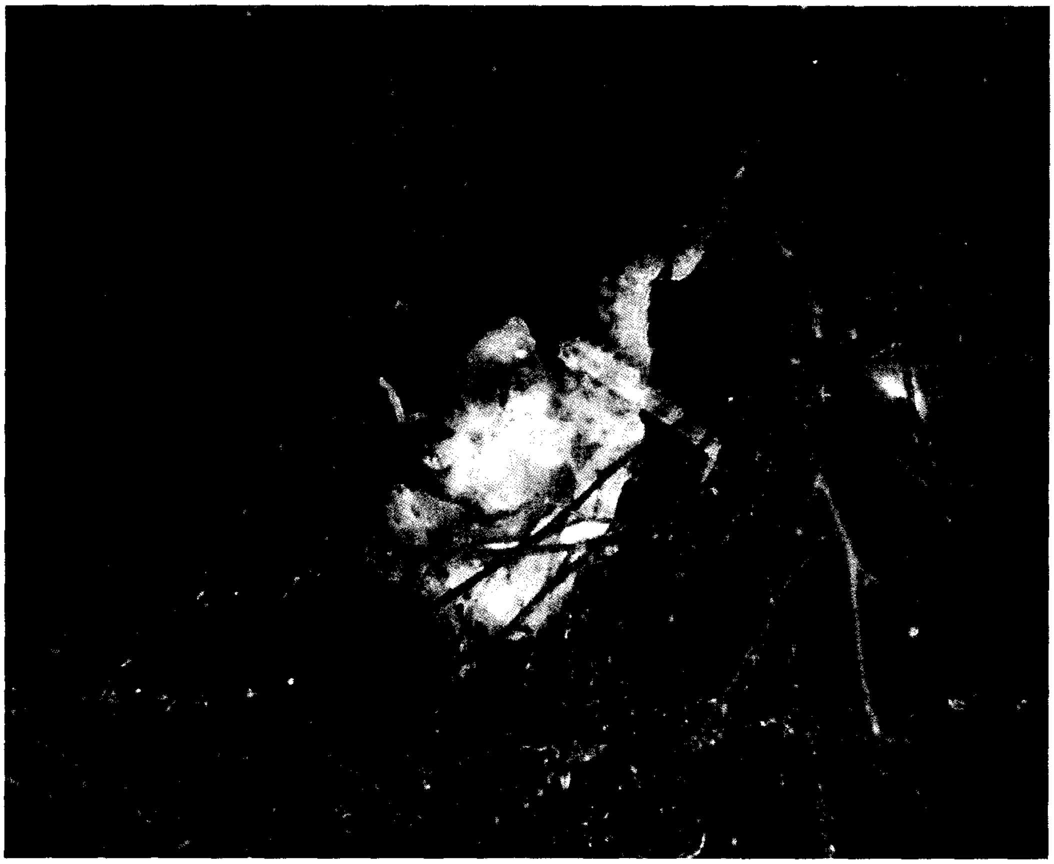

Figure 4.9. Tethered age 0 red king crab (7 mm carapace length) that survived the field predation experiment in structural habitat with dense hydroid cover exposed to a variety of predators.

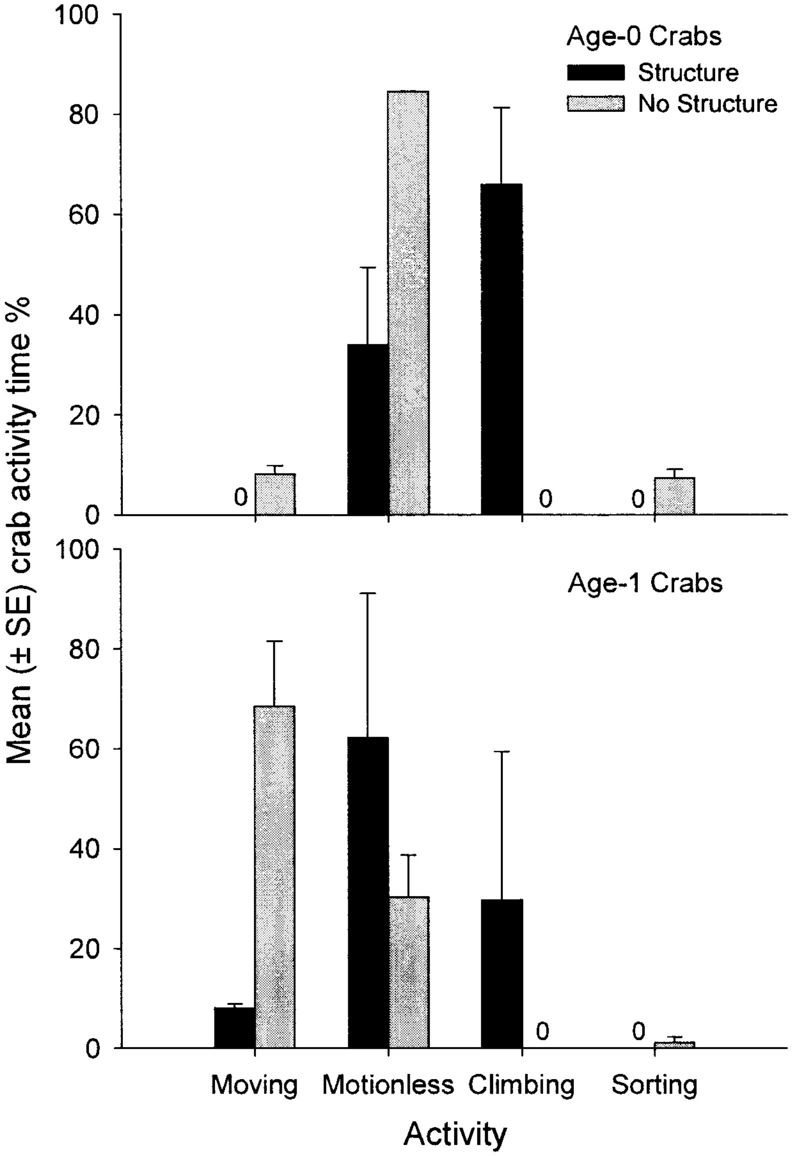

Figure 4.10. Mean (± SE) crab activity patterns for age 0 and age 1 crabs in the field predation study by habitat type (structure, no structure), expressed as percent time spent in each activity over the duration of a trial (maximum 24 h), including moving, motionless, climbing, and sorting through the gravel and shell substrate. Crab activity varied by activity type, habitat, and stage, as a significant interaction among these factors ($p < 0.01$, multifactorial ANOVA).

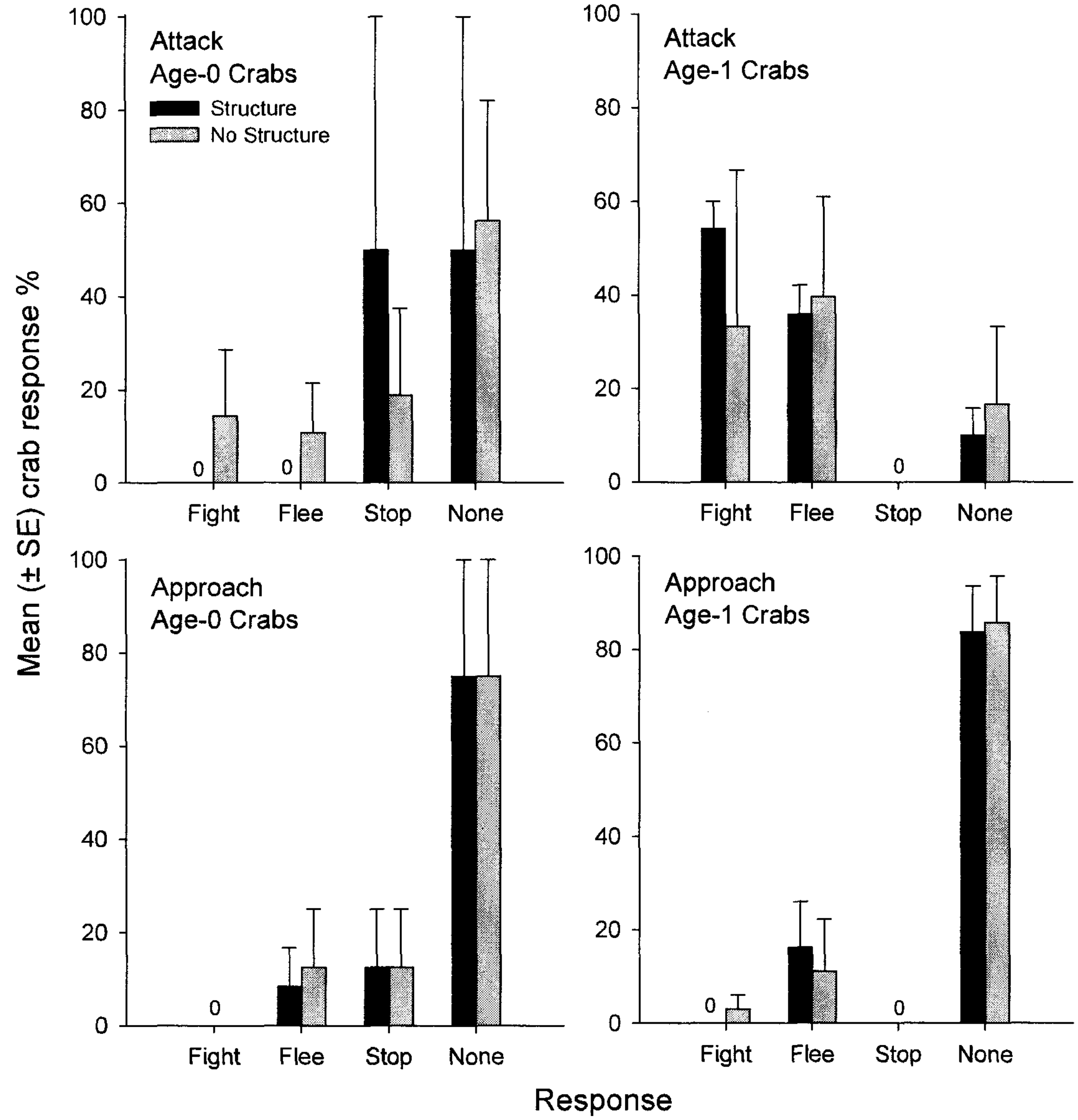

Figure 4.11. Mean (± SE) crab response behavior to a predator attack or an approach with a direct interaction for age 0 and age 1 crabs in the field predation study by habitat type (structure, no structure), expressed as percent of each response type observed, including fighting, fleeing, stopping activity, and no response. Crab response to an attack varied by response type and stage, as a significant interaction between these factors ($p <$ 0.01, multifactorial GLM). Crabs most often did not respond when approached by a predator ($p < 0.0001$, multifactorial GLM, Tukey HSD). The presence of structure was not a significant factor in crab response to either an attack or an approach, and crab stage was not a significant factor in response to an approach.

General Conclusions

The first chapter of this research examined relationships between marine habitat and the composition and spatial distribution of shallow subtidal communities in southeast Alaska (Chapter 1). This study identified patterns of subtidal community structure at regional and local spatial scales for macroalgae, fishes, and benthic invertebrates, and quantitatively linked those patterns to environmental variability and benthic habitat. Regional community structure was associated with a major hydrographic gradient of decreasing salinity and increasing temperature from the outer coast to the inner coast. Species distribution at local spatial scales among sites within regions was related to benthic habitat composition.

Southeast Alaska was an interesting location for this type of study due to the complex nature of the coastline that creates spatial separation and environmental variability between the inner coast and outer coast regions. Patterns of marine community structure had not been previously studied in southeast Alaska in a way that relates observations of species distribution to the marine environment. This basic understanding can now be used to develop testable hypotheses about ecological processes in this fjord-estuary system and ecological mechanisms of habitat associations for individual species.

Red king crab was an ideal subject to investigate the role of habitat to support early life stages of a fishery resource species in Alaska nearshore marine ecosystems. Marine habitat is important to red king crab early life stages for several reasons. For example, annual variability in spring water temperature affects red king crab larval development in the plankton and settlement timing, and availability of complex benthic habitat structure is important during settlement and for early benthic stages. Population strength for red king crab may be most limited by early life stage success. The next three chapters of this dissertation focused on red king crab early life stage ecology and nursery habitat function.

Red king crab larval supply, settlement timing, and benthic habitat were studied at six sites in the Juneau area of southeast Alaska during 2008 and 2009 (Chapter 2). Red king crab larval supply varied spatially among sites in 2008 and 2009. Sites with high larval supply in the Juneau area were Indian Cove in Auke Bay, the Couverden Islands, and St. James Bay. Sites with low larval supply were Barlow Cove, Portland Island, and Horse Island. Local oceanographic processes that influence red king crab larval transport from hatching to settlement locations, including water circulation, are poorly understood and may be responsible for spatial variation in larval supply. Settlement timing for red king crab was consistent between 2008 and 2009 and with historical data from the 1980s and 1990s with variation on the order of one month. Benthic habitat availability for settling larvae and early juvenile stages varies spatially among locations in this area. Sites with both high larval supply and complex habitat have potential to serve as red king crab nurseries.

The mechanisms of red king crab habitat associations during the first-year post-settlement were examined with laboratory experiments to determine if habitat choice in the absence of predators is driven by structural habitat complexity, or the presence of other habitat attributes that are attractive to young crabs (Chapter 3). These experiments demonstrated that habitat choice for red king crab is strongly influenced by foraging opportunities, in particular when biogenic habitats are present. Biogenic habitats formed by structural invertebrates in particular were more attractive to early juvenile red king crab than complex physical structure alone. Biogenic habitats may enhance growth and survival of early post-settlement stage red king crab in excess of other highly structured habitats.

The final chapter of this research investigated the role of complex habitat structure in survival and predator-prey interactions of early juvenile red king crab with experiments in the laboratory and field experiments at a nursery location (Chapter 4). Early juvenile red king crab had a structure-seeking refuge response when predators were present. Although crabs preferred complex biogenic habitats over complex physical structure when predators were absent, crabs associated with any available structural habitat when a fish predator was present. Habitat structural complexity may have greater influence on survival of early juvenile stage red king crab than predator behavior. Survival of early juvenile crab (age 0 and 1 yr) was higher in the presence of complex habitat with Pacific cod predators in the laboratory and with predators in the field. Complex habitats increased crab survival with predators because predator foraging efficiency was decreased by increased structural habitat complexity. Crab refuge response behavior was different between age 0 and age 1 crabs, suggesting that size drives ontogenetic shifts in habitat use for juvenile red king crab. Complex habitats, cryptic behavior, and direct defense improved juvenile red king crab survival against certain predators, including sculpins and other demersal fishes.

Early life stage survival for many commercially important crustaceans is strongly influenced by availability of high quality nursery habitat. This body of work demonstrates that complex benthic habitats are clearly important for red king crab during settlement and for early post-settlement stages because they provide settlement substrate, foraging opportunities, and structural refuge from predators. This body of research forms a significant contribution to knowledge of how nursery habitats support red king crab and improves understanding of nursery habitat function for fishery resource species in Alaska nearshore marine ecosystems. Further studies of this nature will advance understanding of the importance of habitat for marine species.