Effects of habitat complexity and relative larval supply on the establishment of early benthic phase red king crab (*Paralithodes camtschaticus* Tilesius, 1815) populations in Auke Bay, Alaska

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Abstract

Between September 1996 and May 1998, the influence of habitat complexity and larval supply on the establishment of early post-settlement populations of red king crab (*Paralithodes camtschaticus*) was studied in situ in Auke Bay, southeast Alaska. Dive transects and suction dredge surveys conducted during fall 1996 and spring 1998 indicated that late age 0 to 1+ red king crabs were located only in the most complex habitat. This pattern was similar to patterns observed for early age 0 crabs, using settlement pails, during the summer of 1997. Early instars recruited into settlement pails containing ambient sediment at both the rocky cobble and shell-hash sites, but no settlement could be detected in muddy habitat. Population density of benthic age 0+ crab peaked in mid-July, then dropped throughout the summer, and greater densities were always observed in rocky cobble than in shell-hash. Simultaneous use of passive larval collectors ruled out the possibility that these patterns were simply a reflection of larval supply. Rather, the highest levels of larval supply were associated with the muddy site at which no settlement could be detected. The availability of complex habitat, defined simply as substrate rich in available crevice space that is scaled to the body size of the crab instars, appeared to be the primary determinant of the value of nursery habitat, and it is likely to be the critical factor determining early post-settlement survivorship within the population. Such considerations are vital to management of red king crab fisheries where complex nursery habitat is likely to be relatively rare and where conflicts with trawl fisheries and other anthropogenic disturbances to bottom habitat are a potential concern.

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1. Introduction

Commercial fishing for the red king crab (Paralithodes camtschaticus) in Alaskan waters has been an important industry for nearly 80 years. The American fleet began fishing in Cook Inlet in about 1920 and, by the end of the decade, Japan and Russia were operating factory processors in the Eastern Bering Sea (Miller, 1965). Recognizing the economic importance of the resource, the National Marine Fisheries Service (NMFS) has estimated red king crab abundance in annual Bering Sea trawl surveys since 1969 (Loher et al., 1998). Abundances have also been surveyed in the Kodiak region since 1971 (Blau, 1988; Orensanz et al., 1998). Depressed fisheries throughout coastal Alaska since the early 1980’s (Orensanz et al., 1998) have prompted research examining variability in recruitment of the species, much of which has focused on egg and larval biology, feeding and growth, reproductive biology and analysis of recruitment and stock-recruitment relationships (for reviews see Otto, 1986; Jewett and Onuf, 1988; Kruse, 1993; Zheng et al., 1996; Loher et al., 1998). Considerably less effort has been expended on quantitative ecological studies of age 0+ crab, at and shortly following settlement. Despite the lack of attention to early post-settlement red king crab, evidence from other crustaceans such as Dungeness crab (Cancer magister; Fernandez et al., 1993; Iribarne et al., 1994; Eggleston and Armstrong, 1995), homarid (Wahle, 1991; Wahle and Steneck, 1991) and palinurid lobsters (Booth, 1979; Howard, 1988; Parrish and Polovina, 1994; Polovina et al., 1995), Caribbean stomatopods (Steger, 1987) and freshwater crayfish (Quin and Janssen, 1989) indicates that recruitment to breeding stocks and fisheries may largely reflect mortality patterns of early juveniles.

As a single example, one of the most extensively studied commercial crustacean species in North America is the homarid lobster, Homarus americanus. Attempts to correlate trends in production of eggs or larval abundance with subsequent benthic populations have met with limited success (Scarratt, 1964; Harding et al., 1983; Fogarty and Idoine, 1986; Incze and Wahle, 1991). Meanwhile, life-history studies indicate that early post-settlement age classes exhibit cryptic behavior and have restrictive habitat requirements (Hudon, 1987; Wahle, 1991; Wahle and Steneck, 1991). Nursery habitat provides a refuge from predation by benthic fishes and invertebrates (Berrill and Stewart, 1973; Lavalli and Barshaw, 1986; Barshaw and Lavalli, 1988) and the extent and availability of such habitat can exert strong influence on patterns of settlement and early post-settlement survival (Incze and Wahle, 1991; Wahle and Steneck, 1991). Thus, in regions where suitable nursery habitat is limited, its availability may define the most restrictive population ‘bottleneck’ faced by H. americanus and have greater influence on recruitment patterns than absolute levels of larval supply (Wahle and Steneck, 1991; Cobb and Wahle, 1994).

Similar constraints likely affect red king crab. For approximately two years post-settlement, individual crab are characterized by a cryptic, solitary existence (Karinen, 1985; Stone et al., 1993). We adopt the terminology ‘early benthic phase’ after Wahle and Steneck (1991) to denote these cryptic individuals. The early benthic phase (EBP) is ecologically distinct from the social-aggregative (‘podding’) behavior displayed by older juveniles (Powell and Nickerson, 1965; Dew, 1990) and from the non-cryptic behavior of adults. Settlement seems to occur in relatively shallow water with areas of
heterogeneous rocky substrate such as cobble and boulder, especially when such substrate supports epiphytic or epifaunal communities (Sundberg and Clausen, 1977; McMurray et al., 1984; Karinen, 1985; Stevens and MacIntosh, 1991; Stevens and Kittaka, 1998). In many cases the availability of suitable substrate may be highly limited (Armstrong et al., 1993). Thus, if the production of juvenile crab from settlement areas is important in determining subsequent stock size, then processes that change the carrying capacity of nursery areas or their availability to settling larvae may have large impacts on the crab populations and their associated fisheries.

Nowhere is this more pertinent than in the southeastern Bering Sea. In the late 1970s the red king crab population of this region supported one of the most economically important single-species fisheries in the world with catches in 1980 of over 69 000 tons and a landed value estimated at over US $265 million (Otto, 1990) adjusted for inflation (BLS, 1999). Collapse of the stock in the early 1980s has not been followed by substantial stock recovery. The importance of early life-history stages in regulating recruitment has been acknowledged by regional fishery management agencies in recent models of red king crab population dynamics (Tyler and Kruse, 1996), and concern for protecting critical shallow water nursery habitat has prompted the establishment of highly restrictive no-trawl zones throughout Bristol Bay. Yet, research designed to ascertain settlement patterns in situ is clearly lacking, and sampling of post-settlement EBP populations has typically been conducted using gear such as towed nets and small towed dredges that are inefficient in complex habitats. In order to properly manage red king crab fisheries with regard to critical juvenile habitat, we need to understand the nature of nursery habitat and the processes generating settlement patterns.

The studies contained herein have been designed to address two research questions, in situ, through unbiased sampling of EBP red king crab in a variety of habitats by concurrent assessments of larval supply and resultant early post-settlement survivorship patterns (sensu Herrmkind et al., 1988; Eggleston and Armstrong, 1995). First, are EBP red king crab populations associated with specific substrates or biogenic assemblages? Second, are patterns of EBP abundance simply reflective of larval supply patterns, or are they structured by processes at or shortly after settlement? The answers to these questions will refine our ability to define critical nursery habitat for the species and to examine the influence of habitat constraints on year-to-year recruitment variability.

2. Methods

Systematic sampling was conducted in Auke Bay, Alaska between September, 1996 and May, 1998. Sampling included: 1) dive-transect and diver-operated suction-dredge surveys to quantify abundance of post-settlement red king crab in three different habitats, 2) larval collection to assess patterns of larval supply throughout the study area, 3) benthic habitat sampling to determine in situ post-settlement population densities of red king crab in three distinctly different habitats, and, 4) quadrate photography and sediment analysis to quantify important characteristics of the substrate and biogenic assemblages within each sampled habitat.
2.1. Study sites

Research was conducted in Auke Bay (58° 22’ N, 134° 40’ W), a small embayment in southeast Alaska located ~20 km north of Juneau (Fig. 1). Auke Bay is approximately 10 km² in area, opening to the southeast into Stephens Passage through a series of small islands. Primary short-term water circulation is driven by semidiurnal tides with average amplitudes of ~4 m and maximum spring tides of ~7 m. Most of the Bay is less than 60 m in depth and most of the substrate is comprised of sand, mud and silt. During September, 1996 preliminary SCUBA surveys were conducted throughout Auke Bay in order to assess shallow-water bottom characteristics and to survey juvenile red king crab.
populations at potential study sites. Based on these dives, the region surrounding Auke Cape (Figs. 1,2) was chosen as the study area. The Auke Cape area is characterized by a range of bottom-types in relatively close proximity to one another, at the same depth. Bottom composition in Auke Nu Cove and Indian Cove is dominated by fine, flocculant material, which we term ‘muddy silt’ habitat. Indian Point is typified by cobble, large angular stones, and boulders to 1 m in diameter, termed ‘rocky rubble’. The eastern and

Fig. 2. Location of study sites and associated activities around Auke Cape (refer to Table 1 for site characteristics). The sites labelled S1–S6 are shallow (12 m) sites, D1–D4 are deep (20 m) sites. Symbols indicate the location of each site as follows: (●) primary shallow sites; (○) additional shallow sites; (□) deep sites. Research conducted at each site is noted parenthetically following the site designator, as follows: dive transects t1–t4; dr = suction dredge sampling; lc larval collector deployment; p = settlement pail study.
western shorelines of the Cape are typified by a mix of sand and whole, crushed and pulverized bivalve shells, termed ‘sand/shell-hash’.

On September 28, 1996, following the qualitative observation dives, 4 line transects were conducted at four sites from Indian Point to Auke Nu Cove (Fig. 2) in order to better quantify EBP crab distribution and guide subsequent research efforts. At each site, two divers counted all red king crab found within 1 m of either side of a transect line that was set along the 14 m isobath. Choice of this depth contour was arbitrary. Divers examined beneath objects such as shells and rocks that were large enough to shelter individual crabs and small enough to physically overturn. Transect length at each site was preset at 50 m or until bottom characteristics began to change substantially. Final transect lengths were as follows: transects t1 and t2 were 50 m in length, t3 was 40 m in length, and t4 was 30 m in length.

Guided by the results of the dive surveys, a total of eight sites were selected, at which all of the following studies (suction dredge surveys, larval collection, settlement studies, and substrate characterization) were conducted: five of the sites were at a shallow depth of 12 m below mean low water, and three deeper at 20 m below mean low water (Fig. 2, Table 1). The 12 m depth was chosen in order to maximize allowable working time using SCUBA during high tide series. On the basis of the local bathymetry, the eastern shoreline of Auke Cape from Indian Point to Auke Nu Cove was chosen for the most comprehensive sampling (‘primary study sites’; S3, S4 and S5; Fig. 2, Table 1). A shoal area located just west of Auke Cape creates a basin (Indian Cove, see Fig. 2) that appears to have lower peak tidal flows than those along the eastern shore from Indian Point to Auke Nu Cove. This suggested to us that the eastern shore would likely be a more contiguous region in terms of physical parameters.

Table 1
Depth and substrate characteristics, amount of diver transect area, number of suction dredge quadrats sampled, number of larval collectors and settlement pails deployed at each site. Refer to Fig. 2 for site locations. The notation ‘n/a’ indicates that a particular activity was not conducted at the specific site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Bottom depth</th>
<th>Substrate type</th>
<th>Diver transect area (m²)</th>
<th>Number of suction dredge quadrats</th>
<th>Number of larval collectors</th>
<th>Number of settlement pails</th>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>S1</td>
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<td>muddy silt</td>
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<td>7</td>
<td>15</td>
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<td>12 m</td>
<td>sand/shell-hash</td>
<td>n/a</td>
<td>8</td>
<td>15</td>
<td>n/a</td>
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<tr>
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<td>8</td>
<td>15</td>
<td>32</td>
</tr>
<tr>
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<td>12 m</td>
<td>sand/shell-hash</td>
<td>100</td>
<td>7</td>
<td>15</td>
<td>32</td>
</tr>
<tr>
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<td>n/a</td>
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<tr>
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<td>n/a</td>
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<tr>
<td>S3</td>
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<tr>
<td>S4</td>
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<td>sand/shell-hash</td>
<td>n/a</td>
<td>8</td>
<td>n/a</td>
<td>n/a</td>
</tr>
</tbody>
</table>
2.2. Suction-dredge surveys

A suction-dredge was used to sample benthic habitat for EBP red king crab in a thorough and unbiased manner. The diver-operated underwater suction-dredge was constructed of a centrifugal water pump driven by a 5 hp gasoline engine, with a maximum delivery rate of 350 l min$^{-1}$ through 30 m of 37 mm diameter nylon hose. The pump remained on a support vessel as water was pumped from the surface to the site, where it was forced through a venturi nozzle that generated the negative pressure used to suction fauna and substrate from the benthos. Benthic material was suctioned through a 50 mm diameter intake. Effluent water and advected material exited the nozzle through a 50 mm diameter exhaust port, was decelerated through a series of increasingly larger pipes for a length of $\sim 5$ m, then filtered through a 40 l dual-sieve assembly, with a 1 cm square mesh initial filter, and a 2 mm square mesh terminal filter. Divers were able to change filter assemblies underwater as they became filled with effluent and/or quadrats were completed. The system allowed for efficient collection of mobile fauna such as EBP king crab that might otherwise have escaped detection under conditions of reduced visibility, and allowed removal of all material from the sampling quadrant, ensuring complete sampling of the area covered.

All five shallow sites and two of the deep sites were selected for suction-dredge sampling. Two of the sites were characterized by muddy silt substrate, four by sand/shell-hash, and one by rocky rubble (Fig. 2, Table 1). At each site a 16 m transect line was placed along the designated isobath beginning at a randomly assigned point. Every 2 m along the transect a 0.25 m$^2$ quadrat was dredged completely to a depth of 15 cm. At each site, either 7 or 8 quadrats were completed depending on time constraints (Table 1). All seven sites were sampled during early May 1997, and two sites (sites S3 and S4) were re-sampled on June 1, 1998 based on results from the settlement experiments described hereafter. Large material (> 1 cm) was sorted on the support vessel; finer material was preserved in buffered 10% formalin and sorted in the laboratory.

2.3. Larval collection

Larval collectors were deployed at seven of the sites (refer to Fig. 2, Table 1) around Auke Cape in order to assess relative larval supply throughout the study area. Larval collectors were patterned after those of Blau et al. (1990). They were constructed of a 75 cm length of 2.5 cm stretch-mesh polypropylene bait-bag material loosely stuffed with approximately 25 m of used, cleaned multistrand salmon gillnet as a settlement matrix. This resulted in a sausage-shaped collector averaging 25 cm in diameter and 60 cm in length. Each collector was buoyed at one end with two 9 cm $\times$ 14 cm foam gillnet floats, and weighted at the other with a pair of 2 kg housing bricks. A 25 cm tagline was used to tie the collector to the weights so that the collector was suspended in the water column, off the bottom. Each deployment of collectors consisted of a long-line (‘string’) of five collectors on a 40 m groundline, with an anchor and a surface buoy attached at each end. Individual collectors were spaced 5 m apart, with 10 m between the anchored end of the groundline and the first collector.
At each site collector-strings were oriented parallel to shore along either the 13 m or 21 m isobath at shallow and deep sites, respectively, so the individual collectors were suspended at the designated site depth. Collector-string placement and orientation was verified by divers at each shallow site. Fifteen collectors (three strings) were deployed at each shallow site, and ten collectors (two strings) at each deep site. At each shallow site a subset of the collectors was retrieved on each of three dates. Five of the collectors were retrieved in late-June, five more in mid-July, and the remaining five in late-July. At each deep site, where only ten collectors were deployed, only the first two periods were sampled. At all sites the retrieval order of specific collector-strings was randomly determined.

Upon removal from the water, individual collectors were placed in plastic bags, sealed and returned to shore for processing. On shore, collectors were slowly unraveled and all contents washed with cold fresh water to dislodge glaucothoe and benthic instar crab contained in the mesh. Crab larvae and instars were either immediately preserved in buffered 10% formalin for later analysis or enumerated and retained in sea water, alive, for other experimental purposes. Carapace length (CL) of all preserved specimens was measured to the nearest 0.03 mm using a dissecting microscope with an ocular micrometer.

The number of larvae and post-larvae captured in each collector were combined (a proxy for larval supply) and differences between sites and over time were compared using 2-factor ANOVA (type III mixed model, site = random factor, sampling date = fixed factor; dependent variable = larval/post-larval capture rate; independent variables = site, sampling date). Following ANOVA, differences between sites were compared using Fisher’s Protected Least-Squares Difference method. We omitted potentially biased data from one collection site (S1) since we received reports that some of the collectors at that site had been briefly removed from the water by curious passers-by, and one set of collectors was lost entirely.

2.4. Early post-settlement habitat use

In order to elucidate substrate-specific patterns of habitat use and survivorship in early post-settlement red king crab, three adjacent shallow sites, each with a different bottom-type, were chosen for additional study: S3 (rocky rubble site, hereafter referred to as ‘Indian Point’), S4 (sand/shell-hash site, ‘East Shore’), and S5 (muddy silt site, ‘Auke Nu Cove’). In early May 1997, 32 settlement pails were deployed at each site. Pails were chosen over other sampling methods since they allowed nearly simultaneous sampling of multiple plots, complete sampling of substrates with minimal disturbance to the sites, and very little chance for settled crab to escape sampling.

Settlement pails were round polyethylene containers 28 cm in diameter and 22 cm in depth (surface area = 0.062 m²; volume = 13 l). At each site, divers buried the pails to a depth of ~20 cm and filled them, in situ, with the substrate removed from the excavation pit. Care was taken to place excavation material back into each pail in the same stratification as it was removed from the excavation pit, i.e., deep anoxic materials were placed at the bottom of the pail and surface sediments returned to the surface of the pail. Pails were placed along the 12 m isobath at each site, in two lines of 16 pails each.
Pails were placed 2 m apart along each line, with the two lines spaced 3 m apart. Pails were retrieved from each site in sets of 8 randomly determined pails on four dates: in late-June, mid-July, late-July, and mid-September. Divers began the retrieval process by sealing each pail with a raised, threaded lid so that settled crab would be unable to escape when disturbed by the remainder of the process. Pails were then removed from the substrate and placed in a buoyed burlap sack for transfer to the surface, and were processed on shore. All substrate was sieved to separate particles into three size fractions: < 1 mm, 1–6 mm, and > 6 mm. Material > 6 mm was visually inspected for juvenile red king crab which were retained and preserved in buffered 10% formalin. Material 1–6 mm was preserved in formalin for later sorting with aid of a dissecting microscope. Since red king crab glaucothoe and first instars are typically > 1.5 mm CL (Nakanishi, 1987; see also Fig. 4) material < 1 mm was discarded.

Of primary interest was whether post-settlement crab densities, measured as the number of post-settlement crab per settlement pail, varied significantly between sites and over time. Initial analyses were conducted using \( t \)-tests to determine whether post-settlement densities at each site differed significantly from 0. Following these tests, further analysis of differences between sites and over time was compared using Poisson regression techniques since data from the experiment were Poisson-distributed, containing numerous zero values. Poisson regression was conducted using the computer software package SPlus (response variable = post-settlement counts; independent variables = site, sampling date). At one of the sites (Auke Nu Cove, see Section 3) no settlement was recorded. It was removed from the regression since its inclusion violated the underlying assumption of Poisson distributed data (model dispersion parameter with Auke Nu Cove data in the model = 0.6283; without Auke Nu Cove data = 0.9099; if dispersion parameter = 1, then sample mean = sample variance = true Poisson distribution).

2.5. Substrate characterization

In May 1998, following the final suction-dredge sampling, each site was photographed for analysis of percent cover of substrate and epibiota, and sediment samples were collected for grain size analysis. At each site, two divers worked along a transect placed along the 12 m isobath. Starting at one end of the transect, a total of six 50 cm \( \times \) 50 cm quadrat photographs was taken, spaced 2 m apart. Photographs were projected onto paper sheets and all large discernible objects outlined and identified. Tracings were scanned into a computer graphics program (Deneba Canvas, version 3.5) and the scaled horizontal areas measured using the digitizing function. Film resolution allowed identification of objects larger than \( \sim 0.75 \text{ cm}^2 \) in horizontal surface area. Discernible objects fell into 5 major categories: rock, shell, sediment, epifauna, and epiphytes. These categories were used in analyses of percent cover between quadrats and sites.

Sediment samples were taken beginning at the point along the transect line where quadrat photography was completed. Since sediment samples were intended to characterize surface sediments likely to be explored by settling larvae, sediment was sampled only to a depth of approximately 5 cm. Plots measuring 13 cm \( \times \) 15 cm were sampled by gently ‘slicing’ sediments off the surface using a rectangular plastic container which was
then sealed underwater. Three samples from each site were used for analysis. At Auke Nu Cove and East Shore, sediment samples were taken at 2 m spacing. At Indian Point, rock larger than 13 cm × 15 cm was common on the substrate surface. Thus, samples were taken in patches of exposed sediment that were nearest to the designated 2 m spacing. Samples were separated into nine size fractions from cobble (32–256 mm particle diameter, Phi scale range = −5 to −8) to fines (<0.0625 mm, Phi < 4) (refer to Wentworth (1922) and Krumbein (1936) for standard sediment particle size categories). Separation was accomplished using a combination of wet and dry sieving techniques, after Mudroch et al. (1997). Wet sieving was found to be effective for particles larger than 0.25 mm in average diameter and was used to separate all larger size fractions. Separation of finer particles was not satisfactory using wet sieve techniques, as cohesive mud particles had a tendency to repeatedly clog the screens. Particles <0.25 mm were dried at 40°C, followed by manual treatment to disperse aggregates, then dry-sieved. All sediment fractions were thoroughly dried at 40°C prior to final weighing.

Substrate characteristics will be described using two metrics: ‘sediment composition’, and ‘surface cover’. Sediment composition refers to the full range, or distribution, of particle sizes that comprise the sediment from the substrate surface to a depth of approximately 5 cm; i.e., all material found within sediment samples. Surface cover simply refers to items exposed at the surface of the substrate, visible in quadrat photographs. Cover items are those materials that a newly settled crab would contact by exploring the surface without digging or burrowing.

2.6. Retrospective data analysis

In order to more fully interpret our results with respect to research from other geographical regions, reanalyses of two existing data sets were conducted. We compared densities of EBP crab sampled via suction-dredge in this study, with other surveys of EBP red king crab that employed a variety of methods. Three previous studies are complementary to our results: Sundberg and Clausen (1977), McMurray et al. (1984), and Stevens and MacIntosh (1991). Sundberg and Clausen (1977) also used suction dredge and reported results in units equivalent to ours, that is, as number of EBP crab m−2. The other two studies employed towed apparatus and reported data in different units than us, thus we returned to their original tow-by-tow records to estimate the crab densities they captured (Stevens and MacIntosh, 1991; D. Armstrong, unpublished data).

Density estimates were calculated in the following manner. In each data set, the number and size of crab captured were available for individual tows, as well as tow-length and gear descriptions. Sampling gear included beam trawl (Stevens and MacIntosh, 1991), rock dredge (McMurray et al., 1984) and try net (McMurray et al., 1984). Area swept was calculated for each tow as: Area Swept = (Gear Width) × (Tow Length). This assumed a tow-width equal to the width of the gear for rigid-frame sampling gear (beam trawl and rock dredge), and a tow-width of 4.4 m for the try net (otter trawl with head-rope length = 5.4 m). Density of age 0+ crab was then calculated as: Crab Density = (catch)/(area swept), resulting in numbers per square meter in each tow. Age of crab was determined from inspection of length-frequency distributions of
the captured crab (in McMurray et al. (1984), \( n = 138 \) crab, all < 10 mm CL; in Stevens and MacIntosh (1991), \( n = 36 \) crab, < 16 mm CL). Calculations only included tows in which age 0 + red king crab were caught (‘successful’ tows), assuming that all unsuccessful tows were conducted in non-nursery habitat. As such, the resultant estimates should: a) overestimate catch rates if unsuccessful tows were conducted within nursery habitat, or b) underestimate catch rates if successful tows were not completely contained within appropriate habitat.

3. Results

3.1. Dive transects and suction dredge surveys

Early benthic phase (EBP; cryptic individuals generally < 1.5 years post-settlement) red king crabs were found only in the most physically complex substrates during both transect surveys and suction dredge sampling. A total of eight EBP crabs, estimated to be approximately 15 months post-settlement, were found during dive transects: five crabs in the rocky rubble at Indian Point, three beneath a piece of corrugated fiberglass roofing material in the sand/shell-hash along the east shore of Auke Cape, and none in the muddy silt bottom in Auke Nu Cove. In both 1997 and 1998, the only crabs located via suction dredge were found at Indian Point (1997: \( n = 4 \), average density = 2.0 ± 1.1 individuals m\(^{-2}\), estimated age = 10 months post-settlement, average size = 6.9 ± 0.1 mm CL; 1998: \( n = 4 \), average density = 2.0 ± 1.3 individuals m\(^{-2}\), estimated age = 11 months post-settlement, average size = 10.1 ± 0.5 mm CL). These results are comparable to those reported by Sundberg and Clausen (1977) in Cook Inlet (Tables 2 and 3). Densities were much higher than reported for the southeast Bering Sea, presumably due to more efficient sampling methods used in this study.

3.2. Larval collection

Results of ANOVA indicate that differences in larval supply, expressed as the average number of larvae and postlarvae per collector, were apparent between sites (Table 4). Pair-wise comparisons of larval supply at each site, at the 5% level of significance, yield the following groupings: \((S5) > (S3 = S4) > (S2 = D1 = D3)\). In general, the greatest abundance of glaucothoe occurred in shallow water along the east side of the Cape. Larval supply was highest over muddy silt bottom in Auke Nu Cove (S5) and was at intermediate levels at East Shore (S4) and Indian Point (S3). Larval supply was lowest on the western shore of Auke Cape (S2) and at 20 m depth (D1, D3).

Larval abundance within collectors did not vary significantly over time during the study (df = 2, \( P = 0.1807 \); Fig. 3). The lack of temporal variation suggests that the majority of settlement had already occurred by late-June and that collectors were effective in retaining settled individuals over the study period. This is further supported by examining the size composition of larval/post-larval king crab populations within the collectors during each sampling period (Fig. 4). While the collectors sampled earliest were populated primarily by glaucothoe, only 7.2% of the crab collected in mid-July
Table 2
Density of EBP red king crab located at the Indian Point nursery habitat in this study compared to data from other researchers in Cook Inlet and the southeast Bering Sea. Levels observed in this study are similar to those observed by Sundberg and Clausen (1977). Much lower densities observed in the southeast Bering Sea are probably due to much less effective sampling methods.

| Author(s) Crab age, in years Gear used Estimated population density ( # crab m⁻²) |
|---|---|---|---|
| This study late 0+ (Southeast Alaska) diver-operated suction dredge 1997: 2.0±1.1 1998: 2.0±1.3 |
| Sundberg and Clausen (1977) 0+ (Cook inlet) (August–Sept) A) diver-operated suction dredge A)1.33±1.47 B) hand collection of erect Bryozoa B) 1.95 (error unreported); 3.85 crabs kg⁻¹ of Flustrillidra, wet weight |
| McMurray et al. (1984) 0+ to 2+ (Southeast Bering Sea) (April–Sept) A) rock dredge (0.9m × 0.4m rigid frame, net mesh-size not reported) A) 0.037±0.057 B) try net (5.4 m head-rope length, net mesh-size not reported) B) 0.0021±0.0032 |
| Stevens and McIntosh (1991) 0+ to 2+ (Southeast Bering Sea) (May–June) beam trawl (3.0 m × 0.6m rigid frame, 12 mm stretch-mesh cod end) 0.00066±0.00059 |

were at this stage of development, and by late-July no glaucothoe were present. Inspection of the larval/post-larval size-distributions (Fig. 4) suggests that over half of the post-larvae sampled in late-July had reached the second instar, indicating little new settlement, but retention and growth of individuals that had settled earlier. The interaction of (sampling period × site) on larval abundance showed no statistically significant trend (df = 8, P = 0.0535).

3.3. Early post-settlement habitat use

In order to facilitate comparison of results on use of early post-settlement habitat with the suction-dredge sampling, we report postlarval population densities normalized as the number of settlers per square meter of pail area. Postlarval density patterns were site-specific, as well as temporally structured (Fig. 5). Significantly detectable abundances of settled crabs were found in both the rocky rubble at Indian Point and the shell-hash at East Shore during all sampling periods (East Shore, t = 36.9898, P < 0.001; Indian Point, t = 25.7380, P < 0.001) while no glaucothoe or postlarvae were detected at any time in muddy silt at Auke Nu Cove. With respect to East Shore and Indian Point, differences in postlarval density varied significantly between the two sites and between sampling periods (Table 5). Throughout time, postlarval crab density in rocky rubble habitat was approximately three times greater than in sand/shell-hash substrate (rocky rubble > sand/shell-hash > muddy silt; see Fig. 5). Densities were significantly higher during mid-July than at any other time, after which they fell to levels similar to initial, late-June densities and remained at those levels into mid-September.

In addition to age 0+ crab, a total of four age 1+ individuals were found in
Table 3
Substrate characteristics and biogenic associations reported for early benthic phase red king crab (age 0 to 2+) in this study, and by other researchers throughout the Gulf of Alaska and Bering Sea

<table>
<thead>
<tr>
<th>Author(s)</th>
<th>Sampling method</th>
<th>Biogenic correlate(s)</th>
<th>Substrate correlate(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southeast Alaska:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>This study</td>
<td>suction dredge,</td>
<td>none apparent</td>
<td>rocky rubble, cobble</td>
</tr>
<tr>
<td></td>
<td>diver transects,</td>
<td></td>
<td>shell-lush</td>
</tr>
<tr>
<td></td>
<td>settlement pails</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Karinen (1985)</td>
<td>diver observation</td>
<td>none reported</td>
<td>shale, slate,</td>
</tr>
<tr>
<td></td>
<td>overlapping debris</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freese and Babcock (1989)</td>
<td>diver observation</td>
<td>none reported</td>
<td>shale, cobble, gravel,</td>
</tr>
<tr>
<td></td>
<td>pebble</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cook inlet &amp; Kodiak:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sundberg and Clausen (1977)</td>
<td>suction dredge,</td>
<td>Spn, Bryo (= Flsp &amp; Dnsp),</td>
<td>“coarse substrate” (shell,</td>
</tr>
<tr>
<td></td>
<td>bottom skimmer</td>
<td></td>
<td>cobble, boulder)</td>
</tr>
<tr>
<td>Powell and Nickerson (1965)</td>
<td>diver observation</td>
<td>Kelp, SSt, possibly Barn</td>
<td>rock crevices, pilings</td>
</tr>
<tr>
<td>Dew (1990, 1991),</td>
<td>diver observation</td>
<td>SSt (= Et &amp; Aa), Anem (= Mr)</td>
<td>pilings</td>
</tr>
<tr>
<td>Dew et al. (1992)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Southeast Bering Sea:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anonymous (1959)</td>
<td>commercial tangle net</td>
<td>Hydra; fouling organisms</td>
<td>not reported</td>
</tr>
<tr>
<td>McMurray et al. (1984)</td>
<td>try net, rock dredge</td>
<td>Bryo, TPly, SSt (= Aa), Urch (= Sd)</td>
<td>gravel</td>
</tr>
<tr>
<td>Stevens and MacIntosh (1991)</td>
<td>beam trawl</td>
<td>beam trawl</td>
<td>not reported</td>
</tr>
<tr>
<td>Kamchatka:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orlov (1964)</td>
<td>net (not described)</td>
<td>Algae (= Ansp, Srp)</td>
<td>not reported</td>
</tr>
<tr>
<td>Vinogradov (1968)</td>
<td>Sigoby trawl,</td>
<td>Hydra, RdAl, SSt (= Lpsp)</td>
<td>not reported</td>
</tr>
<tr>
<td>Rodin (1985)</td>
<td>not reported</td>
<td>Spn, Hydr, Echn</td>
<td>not reported</td>
</tr>
</tbody>
</table>

* Biota abbreviated as follows: Spn = sponge; Bryo = bryozoan; Hydra = hydroid; RdAl = red algae; SSt = sea star; Barn = barnacle; Anem = anemone; TPly = tubicolous polychaete; Urch = sea urchin; Echn = echinoderm; Flsp. = Fustrellidra sp.; Dnsp = Dendrobranchia sp.; Et = Evasterias troschelli; Aa = Asterias amurensis; Lpsp = Leptasterias sp.; Ms = Metridium senile; Sd = Strongylocentrotus droebachiensis; Ansp = Ahnfeltia sp.; Srp = Sargassum sp.

settlement pails at Indian Point over the course of the experiment. These individuals had apparently moved into the pails from the surrounding substrate, indicating a temporal overlap in nursery usage by the 1996 and 1997 cohorts. Age 1+ crab ranged in size from 8.35 to 15.50 mm CL, with larger individuals found later in the summer (Fig. 6).

Table 4
Summary results of 2-factor ANOVA testing the effects of date and site on combined larval plus postlarval red king crab densities observed in larval collectors

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F-value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td>2</td>
<td>24.7167</td>
<td>12.3583</td>
<td>1.7576</td>
<td>0.1807</td>
</tr>
<tr>
<td>Site</td>
<td>5</td>
<td>1478.7167</td>
<td>295.7433</td>
<td>0.4206</td>
<td>0.0001</td>
</tr>
<tr>
<td>Interaction</td>
<td>8</td>
<td>115.6500</td>
<td>14.4563</td>
<td>2.0560</td>
<td>0.0535</td>
</tr>
<tr>
<td>Residual</td>
<td>64</td>
<td>450.0000</td>
<td>7.0312</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Fig. 3. Abundance of red king crab in larval collectors deployed at 7 sites around Auke Cape. No data were available for site S1 in late June and mid-July due to loss of collectors. Abundance was not determined at deep sites in late July; collectors at deep sites were devoid of crabs in mid-July. Error bars represent one standard error about the mean. Statistical tests indicate three groupings with regard to post-larval abundance: (S5) > (S3 & S4) > (S2 & D1 & D3).

3.4. Substrate characteristics

Indian Point is characterized primarily by rocky cover, a feature which is much reduced at East Shore and essentially absent from Auke Nu Cove (Fig. 7). Approximately 80% of the bottom at Indian Point is large, loose cobble, rocky rubble and boulder. These are angular rock fragments measuring approximately ten centimeters to a meter in maximum diameter and even the sediments underlying this surface layer are laden with larger particles such as cobble and pebble, which comprise more than half of the overall sediment composition (Fig. 8). In contrast, the only large surface cover items at Auke Nu Cove are shells and shell fragments that represent less than 2% of the total cover (Fig. 7). While grain-size analyses indicate that nearly 10% of the sediment at Auke Nu Cove is comprised of cobble-sized particles and nearly 20% is pebble-sized, these particles are almost completely submerged in fine sediment (Fig. 8) making them unavailable as cover for settling glaucothoe. The East Shore site represents a transition between the former two habitats (Figs. 7, 8). A small amount of rock and shell is found at the surface, and sediments are coarser in texture than at Auke Nu Cove. East Shore is
Fig. 4. Size and instar composition of red king crab glaucothoe and early benthic instars from larval collectors, late June through late July. Data from all sites are pooled for late June and mid-July. Late July depicts only crab from the Auke Nu Cove site, since post-larvae from the other sites were not measured, being retained for use in separate behavioral experiments.
Fig. 5. Age 0+ red king crab densities (normalized as number m$^{-2}$) at the three primary study sites as observed in settlement pails (open symbols) during the summer of 1997, and in situ by suction dredge (closed symbols) the following spring, bars represent one standard error about the mean. Population densities were significantly higher in mid-July than on all other dates; differences between sites are also significant at the 0.05 level (see Table 4).

typified by a more even mix of particle sizes with substantial amounts of coarse sand and ‘pebble’, much of which is actually crushed shell of various sizes.

It is important to note that none of the sites were substantially colonized by vertically protruding (‘erect’) epibiota. Percent-cover estimates for epifauna at each site were as follows: Indian Point = 0.2±0.2%, East Shore = 0.2±0.1%, Auke Nu Cove = 0.02±0.03%. Epifaunal cover at Indian Point was comprised primarily of anemones. Protruding bivalve siphons and a single bryozoan colony occurred at East Shore. At Auke Nu Cove a single ascidian was the only erect epibiont noted. At Indian Point, three species of brachiopod (*Laqueus californianus*, *Terabratula transversa*, and *Hemithiris psittacea*) were also observed, but since they were found exclusively on the underside of rocks they do not appear in these percent cover estimates. However, their overall cover seemed similarly low.

Epiphytic cover was more site-dependent. None appeared in the quadrat photos from East Shore and Auke Nu Cove. At Indian Point, kelps (*Laminaria* spp. and *Agarum*
Table 5
Summary results of Poisson regression analyses testing the effects of site and sampling date on densities of post-settlement red king crab in settlement pails. The t-statistics associated with the site variable compare early-post settlement survival rates at East Shore to that at Indian Point. In an attempt to resolve all significant differences between between sites, the model was run multiple times with respect to date. Reported here are the results comparing each date to mid-July (configuration A) and to mid-September (configuration B). These indicate that post-settlement densities during mid-July were different from all other dates, and that late June, late July, and mid-September were not significantly different from one another.

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Estimated coefficient</th>
<th>Standard error</th>
<th>t-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>East Shore</td>
<td>−1.06947</td>
<td>0.35226</td>
<td>−3.0598*</td>
</tr>
<tr>
<td>Sampling date (model configuration A):</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>late June</td>
<td>−1.48396</td>
<td>0.49902</td>
<td>−2.97377*</td>
</tr>
<tr>
<td>late July</td>
<td>−1.01397</td>
<td>0.41822</td>
<td>−2.42451*</td>
</tr>
<tr>
<td>mid-September</td>
<td>−0.03698</td>
<td>0.35642</td>
<td>0.07144</td>
</tr>
<tr>
<td>Sampling date (model configuration B):</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>late June</td>
<td>0.95327</td>
<td>0.43925</td>
<td>2.17020*</td>
</tr>
<tr>
<td>mid-September</td>
<td>0.25071</td>
<td>0.55642</td>
<td>−0.45057</td>
</tr>
</tbody>
</table>

* Significant at the 0.05 level.

clathrum) were a common member of the community. They appeared in quadrat photos at a density of 4.7 ± 3.2 holdfasts m⁻². Their total percent cover was not calculated for the following reasons: 1) kelp cover is seasonally variable and relatively low at 12 m

Fig. 6. Size of age 0+ red king crab collected from settlement pails (closed symbols) and suction dredge quadrats (open symbols) in 1997 (circles) and 1998 (triangles). Estimated ages are based on a settlement date of June 30th, consistent with the larval settlement patterns observed during 1997. The dashed line is a linear regression through the points (line equation: \( y = 0.070x - 16.87; r^2 = 0.94 \)) and has been included only to highlight that larger individuals were collected later in the summer.
Fig. 7. Percent cover of the three major substrate types (rock, shell, and sediment) at each of the three primary study sites. Error bars represent one standard error about the mean.

depth during the spring and early summer when red king crab glaucothoe are settling, and, 2) in order to maintain consistancy between the settlement pails, kelp was avoided when filling them with substrate. Thus, densities at the site did not reflect experimental conditions within the pails. Of the 31 settlement pails retrieved, only 4 contained kelp while 17 contained early post-settlement red king crab.

4. Discussion

Our results expand the understanding of appropriate early post-settlement substrate and nursery habitat for red king crab. They demonstrate that in situ populations of late age 0+ to age 1+ red king crab are strongly associated with complex habitat and are not found on homogeneous muddy bottom. Early postlarvae and age 1+ crabs were found in rocky rubble habitat while no settlement or postlarvae was detected on muddy silt substrate. The data also indicate the potential for settlement and post-settlement
Fig. 8. Composition of sediments at the three primary study sites. Particle sizes have been divided into 5 categories as follows: cobble (particle diameter > 32 mm; Phi < −5), pebble and granule (2 to 32 mm diameter; Phi −1 to −5), coarse to medium sand (0.25 to 2 mm diameter; Phi −1 to 2), fine to very fine sand (0.063 to 0.25 mm diameter; Phi 2 to 4), and mud/fines (< 0.063 mm diameter; Phi > 4). Error bars represent one standard error about the mean.

survival in shell-hash habitat of relatively intermediate complexity, though early post-settlement crab abundance was significantly lower than in rocky habitat.

Early benthic phase abundances were not a reflection of relative larval supply. Larval delivery, measured as abundance of crabs in larval collectors, was approximately twice as high over muddy substrate than over rocky rubble or shell-hash. These results are similar to patterns of settlement and recruitment observed in two other commercially important decapods, the Caribbean spiny lobster (*Panulirus argus*) and Dungeness crab (*Cancer magister*). In the former, Herrnkind et al. (1988) found significantly higher postlarval spiny lobster abundances within stands of unsilted benthic algae than in silted stands, despite greater influx of puerulus larvae to silted sites. For Dungeness crab,
Eggleston and Armstrong (1995) observed approximately four times as many post-settlement crabs in shell debris than in mud, despite no difference in the supply of postlarvae to those habitats.

In contrast to larval supply constraints, these postlarval abundance patterns appear to be established via direct interactions between the larvae and settlement habitat, either through active habitat choice by settling individuals or through the removal of settlers from poor habitat shortly thereafter. In our study, it is unclear whether the absence of postlarval red king crab from muddy habitat was due to larval choice at settlement, or predation or emigration following settlement. However, if due to post-settlement processes, these must have occurred rapidly since the first three sampling periods were spaced at 2-week intervals. If glaucothoe had settled into muddy silt and were subsequently removed, then total mortality or emigration of the population must have occurred over these brief periods. This is a reasonable possibility. Rapid post-settlement mortality has been observed in Dungeness crab even within preferred habitat (Eggleston and Armstrong, 1995) and the muddy benthos at Auke Nu Cove would afford very little protection from predators, especially since early instar red king crab seem unable to burrow (T. Loher, unpublished data).

Alternatively, red king crab glaucothoe may be able to assess habitat quality prior to final settlement and actively avoid homogeneous, flat substrates when others are available. Active choice of settlement microhabitat by larvae is a common feature across taxa, and has been noted for various species of teleost fish (Burke et al., 1991; Breitburg et al., 1995; see review in Victor, 1991) and marine invertebrates (Keough and Downes, 1982; Butman, 1987; Caceres-Martinez et al., 1994; see review in Crisp, 1974), including decapod Crustacea (Herrnkind et al., 1988; Jensen, 1991; Harvey, 1993), and microhabitat choice has also been demonstrated for red king crab under laboratory conditions (Stevens and Kittaka, 1998). Given a choice between filamentous mesh substrate, gravel, or bare sand, red king crab glaucothoe preferred the most physically complex substrate (filamentous plastic mesh) and were rarely observed on open sand. Individual larvae ‘were observed to descend into the sand tray, touch the sand, and then swim up and away within a few seconds’ (Stevens and Kittaka, 1998). Taken together, our field results and the laboratory data of Stevens and Kittaka (1998) demonstrate that red king crab larvae, in situ, should be expected to actively select complex habitat at settlement. Productive nursery areas will be comprised of such substrate, and mortality will be rapid among glaucothoe unable to locate such habitat before settlement.

An important aspect of our results is to expand understanding of which physical/biological attributes constitute good nursery habitat. A review of the existing literature on red king crab (Table 3) suggests that nursery habitat is largely defined by biotic parameters. In particular, many authors report associations between EBP red king crab and a variety of biogenic materials including mussel byssus, filamentous algae, hydroids, bryozoans, and even sea stars. In short, vertically protruding epibiota has repeatedly been shown to support populations of early post-larval crab (refer to Table 3) and such associations led Jewett and Onuf (1988) to conclude in their review of red king crab habitat preference that ‘juvenile crab distributions correlate better with biological parameters than physical parameters’. However, in our study substantial in situ postlarval populations occurred under conditions characterized by a paucity of erect
biogenic material and resulted in apparently high long-term survival rates. Estimates of late age 0+ population densities in the Indian Point nursery habitat are as high as has been observed within complex biogenic substrates (Sundberg and Clausen, 1977; see Table 2) yet the only notable erect epibionts at the site were kelps, and occasionally brachiopods on the underside of rocks. Settlement pails were devoid of erect bryozoans, hydroids, mussels and colonial ascidians, as was the site in general. It is possible that the higher abundance of epiphytes at Indian Point enhanced post-settlement survival or immigration rates. However, kelp die-back during the winter largely eliminates it from the site, making it difficult to invoke as a factor effecting the spring suction-dredge survey results, and kelps were intentionally excluded from the settlement pails and therefore were not responsible for the early postlarval abundance patterns that we observed in the pails at Indian Point and East Shore.

As a settlement surface, biogenic material has generally been ascribed two functions: a food resource for early instars (Marukawa, 1933; Sundberg and Clausen, 1977; McMurray et al., 1984; Jewett and Onuf, 1988; Blau et al., 1992) and physical refuge from disturbance, cannibalism and predation (Sundberg and Clausen, 1977; McMurray et al., 1984; Jewett and Onuf, 1988; Blau et al., 1992; Armstrong et al., 1993; Stevens and Kittaka, 1998). Clearly, rock or shell would not serve the former function, yet our results are not consistent with the notion of food-limitation leading to reduced survivorship or growth in the rocky habitat. Survivorship must be considered good in the Indian Point nursery and the observed size of crab at Indian Point approximately one year post-settlement (see Fig. 3) is consistent with the range of age 1 sizes reported for red king crab throughout the species' geographic range, suggesting normal growth rates. Age 1 CL has been reported at ~8.2 mm in the Sea of Japan (Kurata, 1961), 9.0–10.2 mm off Kamchatka (Orlov, 1964), 6.5–11.0 mm in the southeast Bering Sea (Kurata, 1961; Weber, 1967), and 11.2 mm around Kodiak (Donaldson et al., 1992). Crab in this study, estimated to be between 11 and 13 months post-settlement, ranged from 8.3 to 11.1 mm CL.

Furthermore, dietary studies of EBP red king crab do not strongly support the contention that erect biogenic material serves as a primary food source for EBP red king crab. Pearson et al. (1984) report that the diet of juveniles 9–25 mm CL in Bristol Bay is comprised primarily of 'floc' (unidentifiable soft tissues) and sand, in addition to the sand dollar *Echinarchnus parma* and various Crustacea, gastropods, and forams. Similarly, Feder et al. (1980) report sediment, sponge spicules and unidentified materials, along with crustaceans, polychaete setae, forams and diatoms as the most common items found in 3–5 mm CL red king crab in Kachemak Bay. Despite the fact that crab were actively collected from the filamentous bryozoan *Flustrellidra* (= *Flustrella*) sp., only 11% of the sampled instars appeared to have consumed it, leading them to conclude that the *Flustrellidra* sp. was unlikely to be a primary food source.

A more reasonable explanation of observed postlarval abundance patterns in red king crab is simply that increased physical complexity of the substrate results in enhanced settlement and post-settlement survival rates, regardless of whether or not that substrate is of biogenic origin. Physical structure commonly appears to shape benthic invertebrate communities, and suites of suitable benthic habitat have been identified for a number of
crustacean species. For example, research on the puerulus larvae of spiny lobsters (*Panulirus argus*) has revealed that food availability may have little influence on settlement patterns when compared to the influence of physical structure (Herrnkind and Butler, 1986). Settling pueruli always selected complex habitats over simple ones, even when settlement surfaces were rinsed to render them depauperate in food resources. For the blue crab, *Callinectes sapidus*, eelgrass and vegetated habitats have long been recognized as critical post-settlement habitat (Orth and van Montfrans, 1987, 1990; Wilson et al. 1987, 1990) but only more recently has it been realized that substrates such as oyster shell (Dumbauld et al., 1993; Eggleston and Armstrong, 1995; Reaugh et al., 1996; Eggleston et al., 1998) and coarse woody debris (Everett and Ruiz, 1993) can serve the same function.

These coarse substrates appear to offer refuges from predators. As such, their most relevant parameter appears to be more precisely defined by the physical scaling of crevice space to the body dimensions of the refuge-seeking organism than by other considerations (Caddy and Stamatopoulous, 1990; Eggleston et al., 1990; Hacker and Steneck, 1990; Gee and Warwick, 1994). In the blue king crab, *Paralithodes platypus*, shell debris has been identified as important nursery habitat (Armstrong et al., 1985). The dorso-ventral flattening of the carapace in EBP individuals conforms well to the physical architecture of the shell debris, which is comprised of overlapping layers of relatively flat shell fragments (Armstrong et al., 1985). Especially important in determining a nursery habitat’s overall production of a species may be its ability to provide suitable refuges for the largest cryptic size-classes of the population (Caddy and Stamatopoulous, 1990; Eggleston et al., 1992; Butler and Herrnkind, 1997). For red king crab, this would represent individuals approximately 1.5 years of age, immediately prior to initiation of social-aggregative podding behavior. From our results it appears that the survivorship of these individuals is determined less by epifaunal cover, per se, than it is by the habitat complexity, especially with regard to availability of physical refugia.

5. Conclusion

In summary, our results indicate that in situ post-settlement survival patterns of red king crab are habitat-specific, established very shortly after settlement, and not necessarily reflective of larval supply. Post-settlement survivorship was associated with habitat complexity and the most important habitat characteristic appeared to be the relative availability of refuge space for benthic instars. Larval delivery to homogeneous muddy habitat did not result in any detectable postlarval abundances. Physically complex habitats produced crabs of pre-podding sizes while less physically complex substrate did not. Erect biogenic material did not appear to be necessary for the establishment of relatively high-density EBP crab populations. It is not to suggest that epibiota does not serve as an important source of nursery habitat, but rather, that its value should be weighed in terms of its physical structure rather than its biotic nature, per se.

Overall, our results have important implications for a commercial fishery presently attempting to resolve management issues in the southeast Bering Sea and elsewhere. One
major concern to the fishery has been the desire to ameliorate the potential impacts of bottom-trawling within critical habitats (BSOC, 1998). Quantifying the location, composition and relative vulnerability of potential nursery habitats will be needed in order to achieve this goal and to evaluate the most effective spatial arrangement of trawl exclusion zones. The present southeast Bering Sea nearshore trawl exclusion area, meant to protect juvenile nursery habitat (see Loher et al., 1998), was established largely without such information. As such, it has been difficult for management to justify the extent of the restrictions in a multi-species and multi-user resource, prompting regional management agencies to call for expanded research on trawl impacts and habitat assessments (BSOC, 1998). The existing literature on red king crab early habitat use is somewhat biased toward the notion that biogenic material is critical in defining high quality nursery areas (Jewett and Onuf, 1988; see Table 3), but our data indicate that this is not necessarily true. We suggest that habitat assessments and nursery designations consider the 3-dimensional structure of the benthos, recognizing that complex non-biogenic substrates may be of large value to recruitment within the population. Characterization of biogenic communities may be most important when attempting to determine a given nursery’s relative resistance to natural and anthropogenic disturbance and degradation. It is possible that disturbance does not effect biogenic habitats in the same way that it does nurseries comprised of large cobble, rocky rubble, and boulder. If so, the relative importance of different habitat types in generating recruitment could be altered in the face of trawl-induced impacts. This hypothesis warrants additional examination.

Finally, our results indicate that EBP red king crab abundance and the number of pre-podding crab produced within a given area cannot simply be predicted from larval abundance without an understanding of the spatial relationships between the larval pool and nursery habitat. While larval supply is clearly critical in order to establish EBP crab populations, it must be delivered to appropriate habitat to result in viable EBP populations. High reproductive output will be of little or no value if the larvae are delivered to inappropriate habitat. A population’s reproductive success, measured in terms of average fecundity and total larval production, may be of less importance in determining recruitment and population abundance than the spatial arrangement of breeding stock relative to local oceanographic features that link larval supply to specific nurseries. While intuitive from an ecological perspective, this fact is largely ignored in present management schemes and deserves further attention.

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References


