RESEARCH ARTICLE

Effects of macroalgal structural complexity on nearshore larval and post-larval crab composition

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Abstract Larval and post-larval crab distribution was surveyed in three different habitats in Kachemak Bay, Alaska to determine temporal and spatial variability. Distribution varied temporally and spatially from June 2005 to September 2006. Nine sites of varying habitat complexity were surveyed monthly using scuba surveys and light traps to measure habitat variables and quantify crab zoeae and megalopae. A total of 10,016 crabs belonging to seven families were identified. Four species comprised the majority (97%) of the total crab assemblages and included Cancer oregonensis, Fabia subquadrata, Telmessus cheiragonus, and Pugettia gracilis. Peak abundances occurred in summer but varied on small temporal scales with species. No single bay-wide variable determined the appearance of all species. Depending on species, appearance may be influenced by seasonality of environmental variables. Spatially, highest abundances occurred in habitats with less structural complexity. Spatial differences in crab abundance may have resulted from variability on large scale physical transport mechanisms and not kelp-mediated flow alterations.

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Introduction

Crabs may have significant ecological importance in marine food web dynamics as key consumers and a food source for other organisms (Hines 1982; Polis and Strong 1996). Seasonality of larval crab recruitment to nearshore habitats may be important in shaping the spatial distribution of adult populations (Quijon and Snelgrove 2005). Documenting larval crab distribution in time and space is valuable in determining the natal origin of post-larval cohorts and may aid in understanding dispersal patterns and population connectivity.

Species with lengthy planktonic larval periods are capable of transport over large distances and may recruit into spatially separate communities (Queiroga and Blanton 2005; Park et al. 2007). Some larval species remain nearshore, while others are carried offshore until they return as megalopae to settle in suitable coastal environments (Lough 1974; Paula et al. 2001; Mace and Morgan 2006) where they live as juveniles and adults. Because most crab larvae and post-larvae are unable to swim against horizontal currents because of high energetic costs or physical limitations, the return to nearshore habitats is likely aided by shoreward currents (Paula et al. 2001; Johnson and Shanks 2002). Transport mechanisms such as tides, internal waves, wind patterns, upwelling events, and density-driven currents are thought to transport invertebrate larvae (Shanks 1995a, 1995b; Paula et al. 2001; Johnson and Shanks 2002; Miller and Shanks 2004; see Queiroga and Blanton 2005 for review). The effects of large scale biotic variables such as biogenic structure, predation, food availability, and behavior on temporal and spatial variation of nearshore larval and post-larval abundance are relatively less understood (see Roughgarden et al. 1988; Wolanski and Hamner 1988; Duggins et al. 1990).

Physical and biological variables are strongly correlated with season and temporal variability of larval dispersal and may influence when certain species appear in the water column. The appearance of many brachyuran species coincides with oceanic conditions that are favorable to their survival (high food availability, light, temperature) (Fisher 2006). However, seasonal timing on small temporal scales within favorable environmental conditions is less understood. Larval timing may vary by species as a way of optimizing specific environmental conditions (Park and Shirley 2005).

Biogenic structure may influence the spatial orientation and distribution of crab larvae. Mid-water structure provided by kelps can add habitat and complexity (Foster and Schiel 1985), influence predator-prey interactions (Norderhaug et al. 2005), support higher fish densities (Hamilton and Konar 2007), and alter flow regimes and hydrodynamic processes on small spatial scales (Eckman et al. 1989, 2003). Understory and canopy kelps affect small-scale current regimes by producing drag forces inhibiting water flow and particle transport in these habitats (Jackson and Winant 1983; Eckman et al. 1989). Kelp beds also dampen high frequency variance and slow low frequency wave propagation of internal waves (Jackson 1984; Rosman et al. 2007). Edge effects created by a strong flow gradient may interact with impinging waters limiting the penetration into dense canopy stands (Jackson and Winant 1983; Jackson 1984, 1986, Duggins et al. 1990; Gaylord et al. 2007). Larval dynamics in these areas are likely to be influenced by these kelp-mediated alterations in flow regimes. Because crab larvae may be pelagic for months and rely on physical transport mechanisms, local changes in hydrodynamic processes could alter their local assemblages.

Nereocystis luetkeana is the predominant canopy kelp in south-central Alaska. It provides structure on the surface of the water, where blades can grow to 11 m. Although adults provide little mid-water structure, juvenile *N. luetkeana* found in beds are typically of various heights, which results in mid-water structure throughout the water column (Daly, personal observation). The multi-bladed structure of *N. luetkeana* can alter flow regimes (Koehl and Wainwright 1977; Hurd and Stevens 1997), which could possibly lead to localized alterations in larval and post-larval crab assemblages. The added structure may also harbor higher planktivore densities and provide protection from predators or influence settling behavior of post-larvae.

In Alaska, seasonality and the potential effects of habitat on spatial distribution are poorly understood for most crab early-life history stages. This study had two facets: (1) to compare temporal variability among species in the zoeal and megalopal stages; and (2) to compare abundances of crabs in early-life history stages among species in different habitats over time. We hypothesized that (1) temporal variability of zoeae and megalopae is different among predominant crab species; and (2) abundances of predominant species in the early-life history stages are different among habitat types over time.

Materials and methods

Study area

This study was conducted in Kachemak Bay, located in lower Cook Inlet, Alaska (Fig. 1, 59°30'N, 151°30'W). This estuarine bay has a large tidal range with fluctuations of up to 10 m. The southern part of the bay is strongly influenced by oceanic input from the Gulf of Alaska. Surface and deep-water currents are counter clockwise, moving water from the Gulf of Alaska into Kachemak Bay along the southern shore and exit along the northern shore (Baird and Pegau 2006).

Nine sites were selected in Kachemak Bay based on structural habitat characteristics including substrate size and rugosity, which were measured during site selection in May 2005. Three sites had a kelp canopy and understory community, three sites only contained a kelp understory community, and the remaining three sites were sand. All sites were separated by at least 1 km and were the same approximate size (approximately 2,800 m²) and depth (approximately 10 m) to eliminate these factors as covariates. Sites were surveyed (see below) monthly for 16 months beginning in June 2005. Physical characteristics (temperature, salinity) were measured in September 2006.

Habitat surveys

Kelp densities were measured monthly from June 2005 to September 2006 to document seasonal variation. The only canopy kelp was N. luetkeana, while understory kelps included Laminaria spp., Saccharina spp., Agarum clathratum, Costaria costata, and Cymathaere triplicate. To quantify understory kelps at each site, individuals were identified and counted in six randomly placed 0.25 m² quadrats along three 30 m transects. Because all understory kelp species are structurally similar in Kachemak Bay (in size and overall shape), they were grouped as understory for statistical analyses. Since canopy kelp are rare compared to understory species, all canopy individuals within each 30 m² transect were enumerated. Juvenile canopy kelp can be the same height as understory kelp so only individuals contributing to the canopy (approximately 2 m above understory) were counted as canopy kelp. Smaller canopy juveniles (<2 m) were considered understory.

Fig. 1 Map of Kachemak Bay, Alaska showing site locations



151°30'W

Average substrate size and rugosity were measured along nine 30 m transects at each site in May 2005 and September 2006 to quantify habitat complexity. Substrate size was determined by measuring the diameter of the dominant substrate type at six random points along each transect. Rugosity is defined as the contour distance along the bottom per meter of horizontal distance and was measured using a 1 m-long polyvinylchloride (PVC) bar with several 5 mm chain links attached to one end (Hamilton and Konar 2007). At six random points along each transect, the bar was placed horizontally so that the chain links draped over the substrate. The chain was then measured per meter of horizontal distance. Rugosity and substrate size values for each site were averaged to determine values for each site. Sites were selected so kelp containing sites had similar substrate complexity. Substrate rugosity in sand was assumed to be one.

Larval and post-larval crab surveys

Light traps were used to collect larval and post-larval crabs at each site. Each trap was constructed of a 19-L, translucent water jug with side openings for planktonic organisms to enter and a PVC pipe with 330 μ m mesh on the bottom. Two battery powered LED dive flashlights (PrincetonTec, Attitude[®]) inside the jug attracted larval organisms (Reyns and Sponaugle 1999; Roegner et al. 2003; Miller and Shanks 2004; Herter 2006). Planktonic organisms that enter the trap cannot easily exit because openings are funnel-shaped and point inward. Traps were attached to a mooring line 6 m above the seafloor. Traps emit light for only a few meters so each trap was separated by at least 5 m to ensure independent replicates. Traps were retrieved via the mooring line, plankton were collected on mesh at the bottom of the trap, and samples were preserved for later analysis. Larval and post-larval crabs were counted and identified to the lowest possible taxonomic level (Hart 1935, 1960; Lough 1974; Adams 1979; Haynes 1981; DeBrosse et al. 1989; Ko 1998; Shanks 2001; McLaughlin et al. 2005). Three traps were deployed monthly for two days at each site for 16 months during neap tide. In summer (June until mid September 2005) traps were deployed weekly.

Statistical analysis

Statistical analyses were performed using linear models and multivariate approaches with STATISTICA v.6 and PRIMER v.6 (Statsoft, Tulsa, OK, USA). Multidimensional scaling (MDS) analysis (Field et al. 1982) was used to examine habitat variability among sites. Data were ranked and Euclidian distance calculated (Trainor and Church 2003). Repeated measures analysis of variance (ANOVA) was used to determine significance in kelp density among habitats over time, while one-way ANOVA tested for differences in substrate complexity, temperature, and salinity. Repeated measures ANOVA was used to test for significance in overall larval and post-larval abundance and dominant species among habitats over time. Post hoc comparisons (Tukey's Honestly Significant Difference) were also used to determine significance in temporal variation of crab abundance and habitat variables among habitats. Significance was determined with an alpha level of 0.05.

Results

Habitat

Sites were grouped by habitat similarity using four variables: substrate rugosity, substrate size, understory kelp density, and canopy kelp density (Multi-dimensional scaling (MDS) analysis, Fig. 2). All kelp sites grouped separately from sand sites indicating that substrate complexity was dissimilar between kelp and sand sites. Within all kelp sites, the three canopy sites grouped separately from the understory sites suggesting heterogeneity in kelp communities (Fig. 2, MDS analysis).

Canopy density was significantly different among habitats with canopy sites having significantly more canopy than sand (Tukey's HSD, P < 0.0001) and understory (Tukey's HSD, P < 0.0001) sites. Canopy sites had a mean canopy density of 5.29 \pm 0.71 stipes 60 m⁻², while understory sites had a mean canopy density of 0.31 \pm 0.12 stipes 60 m⁻². No canopy was found at sand sites. Also, canopy density at the canopy sites had a strong interaction with seasonality



Fig. 2 Multi-dimensional scaling (MDS) plots of sites calculated from Euclidean distance on ranked canopy density, understory density, substrate rugosity, and substrate size variables. Sand (*open triangle*), understory (*open square*), canopy (*filled square*)

(Tukey's HSD, P < 0.0001) as *N. luetkeana* is an annual species.

Understory density was significantly different among habitats with all habitats being significantly different from each other. Canopy sites had the highest overall understory mean density of 4.45 ± 0.017 stipes 0.25 m^{-2} , followed by understory sites with a mean density of 3.04 ± 0.122 stipes 0.25 m^{-2} . Sand sites had very little understory (0.08 ± 0.142 stipes 0.25 m^{-2}).

Substrate rugosity was significantly different among habitats with kelp sites being similar but significantly different than sand sites (Tukey's HSD, P < 0.0001). No significant changes in substrate complexity occurred over time (ANOVA, P = 0.292). No significant differences in temperature (ANOVA, P = 0.965) and salinity (ANOVA, P = 0.690) were found among sites.

Crab larvae and post-larvae

A total of 10,016 early-life history crabs belonging to seven families were caught in the light traps. Most crabs were identified to species, although some (Table 1) were assigned to higher taxonomic levels. The most abundant species included *Cancer oregonensis*, *Fabia subquadrata*, *Telmessus cheiragonus*, and *Pugettia gracilis*; these four species comprised the majority (97%) of the total assemblages (Table 1). Several majid individuals were unidentifiable and were grouped as Majidae. All lithodid crabs were grouped as such and pagurids were excluded. Some individuals were unidentifiable due to poor preservation and were classified as unknown.

Assemblages were strongly seasonal with peak abundances in late summer. In general, megalopae had a maximum slightly later than zoeae with very few

 Table 1 Crab species caught with light traps during the 16-month study

| Family, species name, common name | Larval | Total | |
|--|--------|-----------|--------|
| | Zoeae | megalopae | |
| Cancridae | | | |
| Cancer oregonensis (pygmy rock crab) | 1,476 | 4,545 | 6,021 |
| Cancer magister (Dungeness crab) | 7 | 26 | 33 |
| Pinnotheridae | | | |
| Fabia subquadrata (mussel crab) | 3,135 | 43 | 3,178 |
| Cheiragonidae | | | |
| Telmessus cheiragonus (helmet crab) | 180 | 172 | 352 |
| Majidae | | | |
| Pugettia gracilis (graceful kelp crab) | 66 | 132 | 198 |
| Chionoecetes bairdi (Tanner crab) | 2 | 6 | 8 |
| <i>Oregonia gracilis</i> (graceful decorator crab) | 24 | 4 | 28 |
| Unknown majid | 43 | 0 | 43 |
| Lithodidae | | | |
| Unknown lithodid | 60 | 0 | 60 |
| Xanthidae | | | |
| Lophopanopeus bellus (black-clawed crab) | 11 | 41 | 52 |
| Unknown | | | |
| Unknown | 11 | 22 | 33 |
| Grapsidae | | | |
| Hemigrapsus spp. (shore crab) | 8 | 2 | 10 |
| Total | 5,023 | 4,993 | 10,016 |

Bold indicates the predominant species

individuals caught in winter. Strong seasonality occurred in overall abundances with no significant differences among habitats (Repeated measures ANOVA, Table 2). However, pair wise comparison indicated overall megalopae abundance was significantly higher at sand sites than canopy sites (Tukey's HSD, P = 0.0416). Differences in zoeal and megalopal abundances between sand and understory or understory and canopy sites were not significant.

The predominant species varied over time in both earlylife history stages (Fig. 3). *Cancer oregonensis* was the most abundant species (60% of total observed) with maximum zoeae during mid summer (July) followed by highest megalopal abundances shortly thereafter. *Fabia subquadrata* was second in abundance (31.7% of total observed) with maximum zoeae in late July in both 2005 and 2006, followed by very small numbers of megalopae. *Telmessus cheiragonus* (3.5% of total observed) had large isolated numbers of zoeae in April and megalopae in August through September. *Pugettia gracilis* (2% of total observed) had highly pulsed numbers of zoeae and megalopae appearing throughout the summer with highest abundance in late July and early August. All of the most abundant species varied over time in both early-life history stages (Repeated measures ANOVA, P < 0.001) (Table 2).

The predominant species also had spatial variation; however this was not significant for most species (Fig. 4; Table 2). *Telmessus cheiragonus* and *Fabia subquadrata* were the only species in which abundance varied significantly between habitats. *T. cheiragonus* zoea and megalopae were significantly higher at sand sites than canopy sites (Tukey's HSD, P = 0.0449 and 0.0454). *Fabia subquadrata* megalopae were significantly higher at sand sites than canopy sites (Tukey's HSD, P = 0.0211). Pooled across habitat types, the abundance of all predominant species differed significantly over time, with most species occurring in summer. *Fabia subquadrata* megalopae was the only species that had significant habitat by time interaction (Table 2).

Discussion

Environmental variables including tides, temperature, salinity, light, phytoplankton blooms, and predation are seasonally pulsed and may serve as cues for larval release (Morgan 1987; Shirley and Shirley 1989; Starr at al. 1990; Morgan 1995; Park and Shirley 2005; Fisher 2006). Kachemak Bay has extreme daily tidal fluctuations (up to approximately 10 m) and severe seasonal variations in temperature, salinity, and light/dark regimes. In this study, differences in larval and post-larval abundance existed seasonally and among species. Telmessus cheiragonus and P. gracilis larvae appeared in the water column earliest in the year compared to other species, with high numbers of zoeae occurring in mid-April, when water temperature was approximately 5°C. In Japan, Telmessus spp. first appears in the middle of March (Ueda et al. 1999), while Pugettia spp. appear when a minimum temperature of 13°C is reached (Kornieko and Korn 2004). Water temperature in Kachemak Bay reaches a maximum of 13°C in late summer, much later than when P. gracilis first appeared. Interestingly, P. gracilis and T. cheiragonus have similar ranges, occurring from Alaska to Monterey, California (Jensen 1995). Thus far, Telmessus spp. and Pugettia spp. have been largely studied at lower latitudes (Ueda et al. 1999; Kornieko and Korn 2004), where temperatures are warmer. This study suggests that Telmessus spp. and Pugettia spp. larvae can tolerate low temperatures, which may give a competitive advantage in high latitudes where windows of favorable conditions are narrow. In comparison to Telmessus spp. and Pugettia spp., C. oregonensis and F. subquadrata were first observed in late June 2005 and 2006 and occur from Alaska to southern California (Jensen 1995). Larval C. oregonensis were also observed in

Mar Biol (2008) 153:1055-1064

Table 2 Repeated measures ANOVA results for predominant species

| Species | Source | Zoeae | | | | Megalopae | | | | | |
|----------------|-----------------------|----------|-----|---------|--------|-----------|----------|-----|---------|--------|---------|
| | | SS | df | MS | F | Р | SS | df | MS | F | Р |
| C. oregonensis | Time | 17799.4 | 20 | 889.97 | 4.052 | <0.0001 | 110720.7 | 20 | 5536.04 | 1.932 | 0.0144 |
| | Habitat | 912.9 | 2 | 456.45 | 2.108 | 0.1234 | 10508.5 | 2 | 5254.27 | 2.084 | 0.1264 |
| | Habitat \times Time | 9672.8 | 40 | 241.82 | 1.117 | 0.2989 | 70433.0 | 40 | 1760.82 | 0.698 | 0.9152 |
| | Error | 60186.7 | 278 | 216.50 | | | 711145.4 | 282 | 2521.79 | | |
| F. subquadrata | Time | 76241.5 | 20 | 3812.07 | 6.305 | <0.0001 | 22.75103 | 20 | 1.14 | 4.844 | <0.0001 |
| | Habitat | 3207.8 | 2 | 1603.88 | 1.835 | 0.1615 | 1.05073 | 2 | 0.53 | 2.283 | 0.1038 |
| | Habitat \times Time | 33429.3 | 40 | 835.73 | 0.956 | 0.5499 | 16.78601 | 40 | 0.42 | 1.824 | 0.0029 |
| | Error | 246443.9 | 282 | 873.91 | | | 64.88889 | 282 | 0.23 | | |
| T. chieragonus | Time | 551.4 | 20 | 27.57 | 17.153 | <0.0001 | 294.778 | 20 | 14.74 | 3.061 | 0.0001 |
| | Habitat | 10.6 | 2 | 5.28 | 1.988 | 0.1389 | 16.280 | 2 | 8.14 | 2.121 | 0.1218 |
| | Habitat \times Time | 102.8 | 40 | 2.57 | 0.968 | 0.5307 | 190.961 | 40 | 4.77 | 1.244 | 0.1596 |
| | Error | 749.4 | 282 | 2.66 | | | 1082.381 | 282 | 3.84 | | |
| P. gracilis | Time | 17.6 | 20 | 0.88 | 2.041 | 0.0087 | 208.2619 | 20 | 10.41 | 11.133 | <0.0001 |
| | Habitat | 2.0 | 2 | 0.98 | 2.004 | 0.1367 | 1.9238 | 2 | 0.96 | 0.674 | 0.5107 |
| | Habitat \times Time | 21.7 | 40 | 0.54 | 1.113 | 0.3041 | 38.1093 | 40 | 0.95 | 0.667 | 0.9390 |
| | Error | 137.4 | 282 | 0.49 | | | 402.6931 | 282 | 1.43 | | |
| Combined | Time | 130529.4 | 20 | 6526.47 | 5.738 | <0.0001 | 124745.3 | 20 | 6237.26 | 2.145 | 0.0054 |
| | Habitat | 1523.0 | 2 | 761.50 | 0.522 | 0.5941 | 11719.5 | 2 | 5859.77 | 2.302 | 0.1019 |
| | Habitat \times Time | 54302.5 | 40 | 1357.56 | 0.930 | 0.5952 | 74931.0 | 40 | 1873.28 | 0.736 | 0.8793 |
| | Error | 411709.2 | 282 | 1459.96 | | | 717780.2 | 282 | 2545.32 | | |

Repeated measures ANOVA was used for predominant species to test for effects of time, habitat variability, and a habitat time interaction *Bold* indicates statistical significance ($\alpha \le 0.05$)

June in southeastern Alaska (Park and Shirley 2005), and in Puget Sound and had optimum development at $10-15^{\circ}$ C temperatures (Sulkin and McKeen 1994). These temperatures are similar to those recorded in mid to late summer in Kachemak Bay. Little is known about physical tolerances of *F. subquadrata*.

Kelp habitats can create different environments for crab larvae and post-larvae in terms of structure and hydrodynamic processes. Other field studies have demonstrated that kelp habitats can significantly affect localized hydrodynamics (Jackson and Winant 1983; Jackson 1984, 1986; Eckman et al. 1989; Duggins et al. 1990; Eckman et al. 2003; Gaylord et al. 2006, 2007; Rosman et al. 2007). Added structure may produce a strong flow gradient at kelp bed edges, reducing penetration of particles (larvae). It was demonstrated that 20-70% of arriving waters reached the center of a canopy kelp bed suggesting that kelp structure could potentially filter incoming water (Gaylord et al. 2007). Limited passage of barnacle larvae through canopy kelp beds has been observed, however predation by planktivorous fish was the likely cause and not a kelpmediated alteration in flow (Gaines and Roughgarden 1987). Kelp bed size can influence flow modification (Gaylord et al. 2007). For example, larger (kilometer-scale) canopy kelp beds have been reported to dampen current velocities to a greater extent than smaller beds (200 m \times 300 m) (Gaylord et al. 2007). Currents have been shown to penetrate through smaller canopy kelp beds (few 100 m) as opposed to being diverted around them (Gaylord et al. 2006). The beds surveyed in the present study were smaller in comparison (tens of meters wide) and comprised of a species that may provide less biogenic structure.

Flow studies in kelp forests have dealt mainly with the canopy kelp *Macrocystis pyrifera*, which has broad, leafy blades along the entire length of its stipe creating midwater structure throughout the water column.

In the present study, spatial variability in abundance occurred for all crab species. Because there was no significant difference in zoeal abundance among habitats, kelp structure was probably not the principle agent behind variability. Canopy densities and physical morphology of *Nereocystis luetkeana* may be too low and provide too little structure to affect the hydrodynamics enough to influence larval distributions. Differences in spatial distributions are most likely determined by large scale physical transport mechanisms and not differences in flow at small scales. Interestingly, sand sites had significantly higher combined megalopal abundances than canopy sites. **Fig. 3** Cancer oregonensis (**a**), Fabia subquadrata (**b**), Telmessus cheiragonus (**c**) and Pugettia gracilis (**d**). Temporal variation in larval and postlarval abundances (crabs trap⁻¹). Solid lines indicate megalopae, dashed lines indicate zoeae. Scales differ for each species. Error bars are +1 standard error



Predation pressure may influence larval and post-larval abundance. Kelp beds are extremely productive and diverse ecosystems that support many kinds of planktivores. Based on their abundance, feeding rates, prey, and position in the water column, fish are an important predator of organisms in the size range of crab larvae and post-larvae (Gaines and Roughgarden 1987). Studies have also suggested that spines of crab zoeae have been selected to prevent



Fig. 4 Cancer oregonensis (**a**), Fabia subquadrata (**b**), Telmessus cheiragonus (**c**) and Pugettia gracilis (**d**). Habitat use by predominant species (crabs $trap^{-1}$). Scales differ for each species. Different letters

are significantly different between habitats for individual species. Error bars are +1 standard error

predation by small fishes and not other organisms (Morgan 1989). Increased fish densities in kelp habitats may significantly impact larval crab distribution and explain trends of lower larval abundance.

Sampling bias may have influenced light trap efficiency. Traps might be expected to sample more effectively in winter as ambient light levels are lower due to shorter daylight hours. However, overall organism abundance was lower in winter suggesting that seasonal differences in abundance are most likely due to life history traits. Between habitats, trap effectiveness may explain differences in abundance. Trap visibility, the added trap structure and differences in predation may have affected catch efficiency. The increased structure of *N. luetkeana* could obstruct the traps from larval view. Because sand sites had no kelp, traps may have been more visible to megalopae. Also, megalopae may be less likely to leave the canopy structure to enter traps. In sandy areas with no mid-water structure, megalopae may be more attracted to the added

trap structure. Increased predation could be determining lower megalopal abundances in kelp habitats, as fish abundance was higher in kelp habitats (Daly, personal observations).

This study supports the importance of documenting temporal and spatial variability and habitat structure for larval and post-larval crabs. Other locations of comparable latitude may have similar trends in larval dynamics. The dramatic seasonality of environmental variables may regulate the timing of larval hatching. Temporal variability among species was most likely due to species specific tolerances to several physical and biological variables. No single bay-wide trend determining the appearance of all species was apparent. Spatial distribution was variable between species. The general trend was that highest zoeal and megalopal abundances occurred in habitats with the least structural complexity. Spatial differences in abundance probably resulted from large scale physical transport mechanisms overriding any small scale macroalgal influences. The canopy density observed probably was insufficient to alter small scale hydrodynamics enough to affect local assemblages of early-life history stage crabs. Larval and post-larval crab appearance was species specific and varied on small temporal and spatial scales.

Future studies on larval dynamics and recruitment in kelp beds may prove useful in understanding adult population distributions in these habitats. A flow rate comparison between inner and outer canopy kelp habitats might aid in understanding the effects of kelp structure on local hydrodynamics. Standardizing structure via artificial kelp would further elucidate kelp effects on flow regimes. Focusing on a single crab species using a short, concentrated sampling effort may be helpful to understand small scale temporal variation and kelp structure effects on spatial larval and post-larval crab distribution.

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