

TEMPORAL TRENDS OF TWO SPIDER CRABS (BRACHYURA, MAJOIDEA) IN NEARSHORE KELP HABITATS IN ALASKA, U.S.A.

BY

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ABSTRACT

Pugettia gracilis and *Oregonia gracilis* are among the most abundant crab species in Alaskan kelp beds and were surveyed in two different kelp habitats in Kachemak Bay, Alaska, U.S.A., from June 2005 to September 2006, in order to better understand their temporal distribution. Habitats included kelp beds with understory species only and kelp beds with both understory and canopy species, which were surveyed monthly using SCUBA to quantify crab abundance and kelp density. Substrate complexity (rugosity and dominant substrate size) was assessed for each site at the beginning of the study. *Pugettia gracilis* abundance was highest in late summer and in habitats containing canopy kelp species, while *O. gracilis* had highest abundance in understory habitats in late summer. Large-scale migrations are likely not the cause of seasonal variation in abundances. Microhabitat resource utilization may account for any differences in temporal variation between *P. gracilis* and *O. gracilis*. *Pugettia gracilis* may rely more heavily on structural complexity from algal cover for refuge with abundances correlating with seasonal changes in kelp structure. *Oregonia gracilis* may rely on kelp more for decoration and less for protection provided by complex structure. Kelp associated crab species have seasonal variation in habitat use that may be correlated with kelp density.

RÉSUMÉ

Pugettia gracilis et *Oregonia gracilis* sont parmi les espèces de crabes les plus abondants dans les lits (ou forêts) de varech en Alaska et ont été suivis dans deux habitats de varech différents dans la baie de Kachemak, Alaska, U.S.A., de juin 2005 à septembre 2006, de façon à mieux comprendre leur répartition au cours du temps. Les habitats incluent les forêts de varech avec des espèces de sous-canopée seulement et des forêts de varechs avec à la fois des espèces de canopée et de sous-canopée, qui ont été étudiés chaque mois en utilisant le SCUBA pour quantifier l'abondance des crabes et la densité de varech. La complexité du substrat (rugosité et taille dominante du substrat) a été évaluée pour chaque site au début de l'étude. L'abondance de *Pugettia gracilis* était la plus

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élevée à la fin de l'été et dans les habitats de canopée, tandis que *O. gracilis* présentait une plus grande abondance dans les habitats de sous-canopée, à la fin de l'été. Les migrations de grande échelle ne sont probablement pas la cause de la variation saisonnière des abondances. L'utilisation de la ressource comme microhabitat peut expliquer les différences de variation temporelle entre *P. gracilis* et *O. gracilis*. *Pugettia gracilis* peut dépendre plus fortement de la complexité structurelle de la couverture algale pour s'y réfugier, avec des abondances corrélées aux changements saisonniers de la structure du varech. *Oregonia gracilis* peut dépendre du varech plus pour la décoration et moins pour la protection fournie par la structure complexe. Les espèces de crabes associées au varech présentent des variations saisonnières dans l'utilisation de leur habitat qui pourraient être en corrélation avec la densité du varech.

INTRODUCTION

Nearshore kelp beds are among the most productive and diverse ecosystems on earth and provide critical habitat for fishes, mammals, and invertebrates (Steneck et al., 2002). Crabs are important trophic links in kelp habitats and can influence food web dynamics by acting as consumers and as a key food source (Hines, 1982; Polis & Strong, 1996). Fish, mammal, and invertebrate species have been described in kelp habitats (Dayton, 1985; Steneck et al., 2002), however, information on temporal variation of many principle component crustacean species is lacking, especially in Alaskan waters. In high latitudes with seasonal extremes, kelp beds can be variable in terms of kelp density, distribution, and species composition. Documenting temporal variation of abundant crab species will aid in understanding food web dynamics in these ecosystems.

Pugettia gracilis Dana, 1851 and *Oregonia gracilis* Dana, 1851 are among the most abundant crab species in Alaskan kelp habitats and rely on kelp for food and protection from predators. *Pugettia gracilis* is a small majoid found in the North Pacific Ocean from Monterey, California, U.S.A. to the Aleutian Islands, Alaska, U.S.A. It is commonly found on rocks and algae on the outer coast and in inshore waters. *Oregonia gracilis* is a small majoid ranging from Monterey, California, U.S.A. to the Bering Sea and is also found in Japan. It is commonly found on mixed composition bottoms and relies heavily on decoration for protection from predators. Both species are important trophic links in nearshore ecosystems by acting as a food source for many taxa including octopuses, sea otters, and a wide variety of fishes. Despite their ecological importance, little is known about the biology of these two spider crab species in Alaskan waters.

The objective of this study was to gain insights to the basic ecology of *Pugettia gracilis* and *Oregonia gracilis* by documenting temporal trends in abundance in two different kelp habitats (kelp beds with understory kelp species only and kelp beds with understory and canopy kelp species) in Kachemak Bay, Alaska, U.S.A. We hypothesized that *P. gracilis* and *O. gracilis* have similar temporal variation in

both habitats and that abundance of *P. gracilis* and *O. gracilis* is highest in summer months.

MATERIAL AND METHODS

Study area

This study was conducted at six sites in Kachemak Bay, located in lower Cook Inlet, Alaska, U.S.A. (fig. 1, 59°30'N 151°30'W). Kachemak Bay has a large tidal range with fluctuations of up to 10 m. Temperatures typically range from approximately 2°C in winter to 12°C in late summer. Glacial discharge influences surface salinity in summer months, however deep water salinity remains relatively stable at approximately 31 throughout the year. Sites selected were based on structural habitat characteristics (substrate complexity, kelp density), which were measured during site selection in May 2005. Three sites contained canopy and understory kelp species and three sites contained understory kelp species only. All sites were separated by at least 1 km and were approximately 2800 m² in area and 10 m in depth to eliminate these factors as covariates (Daly & Konar, 2008). Sites were surveyed (see below) monthly for 16 months beginning in June 2005.

Habitat surveys

Average substrate size and rugosity were measured along nine 30 m transects at each site in May 2005 and September 2006 to quantify substrate complexity (Hamilton & Konar, 2007; Daly & Konar, 2008). Substrate size was determined by measuring the diameter of the substrate 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 one-meter-long polyvinylchloride (PVC) bar with several 5 mm chain links attached to one end (Hamilton & 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.

Kelp assemblages were measured monthly from June 2005 to September 2006 to document seasonal variation in kelp density using transects and quadrats and SCUBA techniques (Daly & Konar, 2008). To quantify understory kelps, 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.

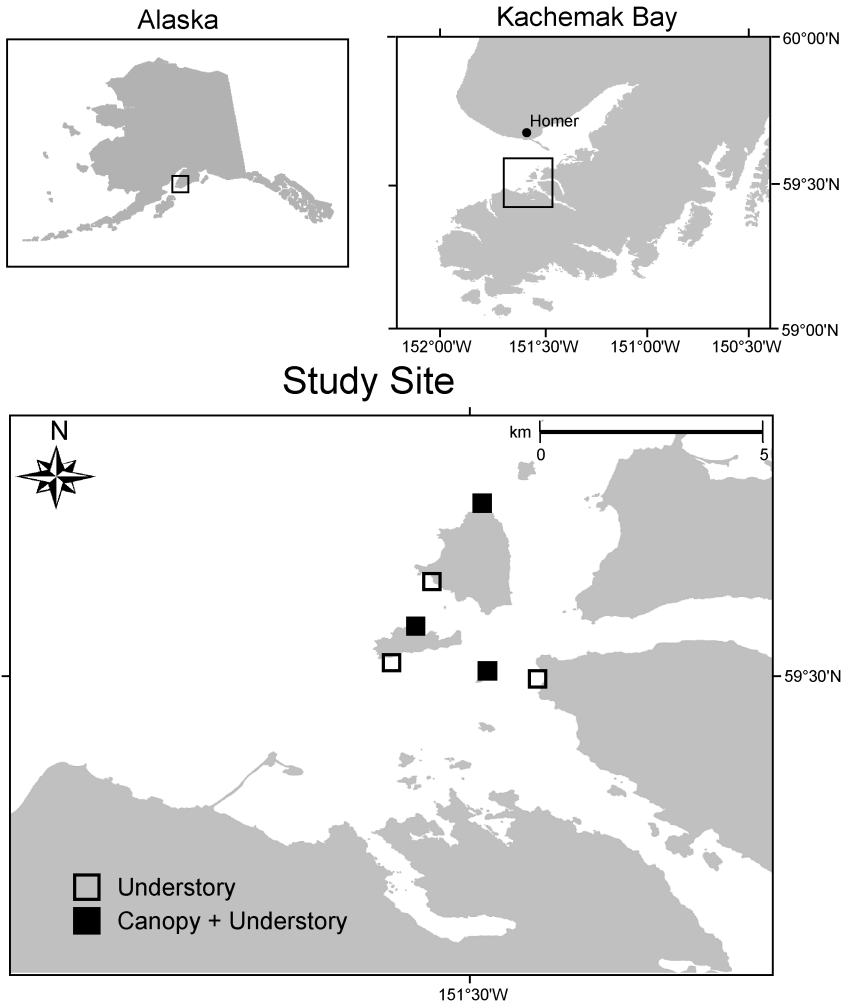


Fig. 1. Map of Kachemak Bay, Alaska, U.S.A., showing site locations.

Crab surveys

Benthic SCUBA surveys were used to quantify temporal and spatial distribution of crabs. At each site, three $30\text{ m} \times 1\text{ m}$ random transects at a depth of approximately 10 m were visually surveyed monthly from June 2005 to September 2006. In addition, six 0.25 m^2 quadrats were randomly placed along each transect to assess highly cryptic individuals.

Statistical analysis

A repeated measures analysis of variance (ANOVA) and post-hoc comparisons (Tukey's Honestly Significantly Different) were used to determine significance

in temporal variation of kelp density, substrate complexity, and crab abundance between habitats. Significance was determined with an alpha level of 0.05.

RESULTS

Habitat

Average (\pm SE) substrate rugosity was similar between canopy (1.31 ± 0.02) and understory (1.35 ± 0.02) sites, however, average (\pm SE) substrate size (diameter) was higher at canopy habitats (84.75 ± 4.49 cm) than understory habitats (50.99 ± 4.27 cm) ($P < 0.001$) (fig. 2) (Daly & Konar, 2008). The only canopy kelp was *Nereocystis luetkeana* (Mertens) Postels & Ruprecht, while understory kelps included *Laminaria* spp., *Saccharina* spp., *Agarum clathratum* Dumortier, *Costaria costata* (Agardh) Saunders, and *Cymathaere triplicate* (Postels & Ruprecht) Agardh. At all sites, kelp density had seasonal variability with highest densities in summer and lowest densities in winter (fig. 3).

Juvenile and adult crabs

A total of 332 crabs belonging to four families were observed in SCUBA surveys. Most crabs were identified to species. The most abundant species included *Pugettia gracilis* and *Oregonia gracilis*, which made up the majority (91%) of the crabs observed (table I). *Oregonia gracilis* had a significant habitat \times time interaction with highest abundances seen in understory habitats in August 2005, however, there were no main effects for time or habitat (fig. 4, table II). Distribution of *Pugettia gracilis* was temporally variable with highest densities in

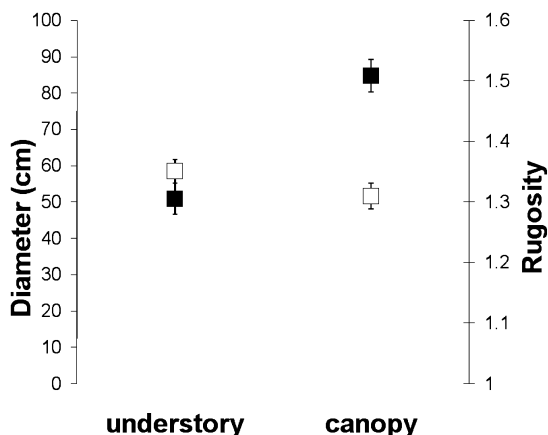


Fig. 2. Substrate complexity at understory and canopy sites. Solid squares indicate substrate size; open squares indicate substrate rugosity. Vertical bars are ± 1 SE.

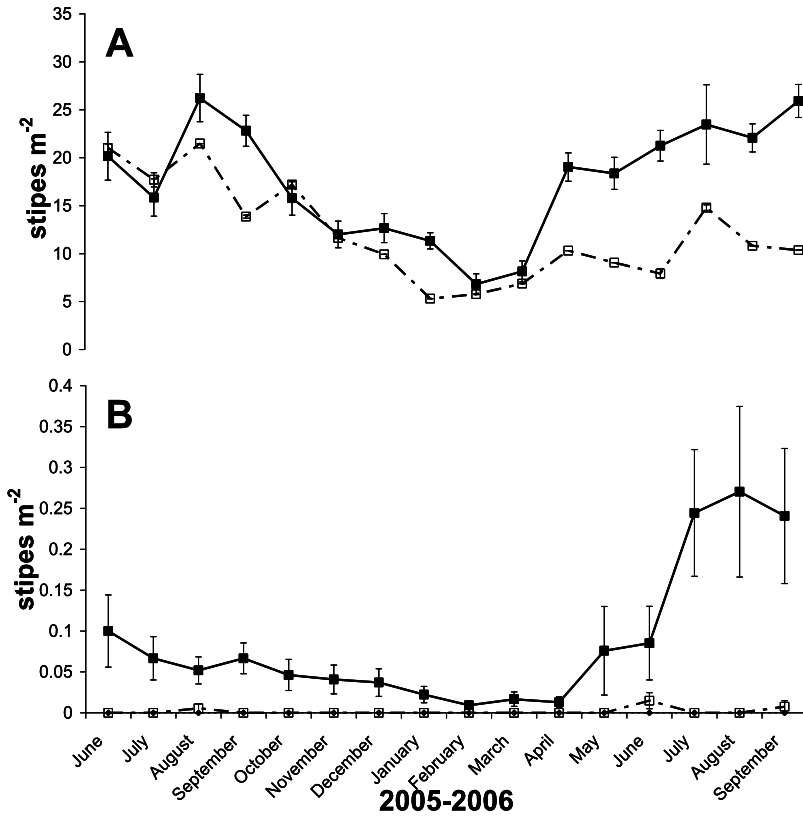


Fig. 3. A, understory kelp; and, B, canopy kelp density (stipes m^{-2}). Solid lines indicate canopy sites; open lines indicate understory only sites. Vertical bars are ± 1 SE.

late summer (fig. 4, table II). Abundance of *P. gracilis* was higher in canopy sites than understory ($P < 0.001$) (table II).

DISCUSSION

Pugettia gracilis had temporal variation in abundance. Temporal variability in crab distribution may be determined by seasonal behavior and migrations on various spatial scales. *Pugettia gracilis* was most abundant in late summer with numbers decreasing throughout the winter. Little is known about the migration patterns of this species; however, migrations most likely occur at small spatial scales. If this species had a large scale spatial migration in winter, no crabs would be expected once the environmental threshold was reached. However, *P. gracilis* was observed in low densities in winter suggesting temporal variability of this species was a function of changes in microhabitat use, not large scale migrations

TABLE I
Crab species observed using SCUBA surveys; **bold** indicates the most abundant species

Family, species name, common name	Understory	Canopy	Total
Majoidea			
<i>Pugettia gracilis</i> Dana (graceful kelp crab)	41	146	187
<i>Oregonia gracilis</i> Dana (graceful decorator crab)	74	41	115
<i>Hyas lyratus</i> Dana, 1851 (Pacific lyre crab)	1	1	2
Cancridae			
<i>Cancer oregonensis</i> (Dana, 1852) (pygmy rock crab)	11	9	20
Unknown	2	0	2
Cheiragonidae			
<i>Telmessus cheiragonus</i> (Tilesius, 1812) (helmet crab)	2	2	4
Lithodidae			
<i>Rhinolithodes wosnessenskii</i> Brandt, 1848 (rhinoceros crab)	1	0	1
<i>Phyllolithodes papillosus</i> Brandt, 1848 (heart crab)	0	1	1
Total observed	132	200	332

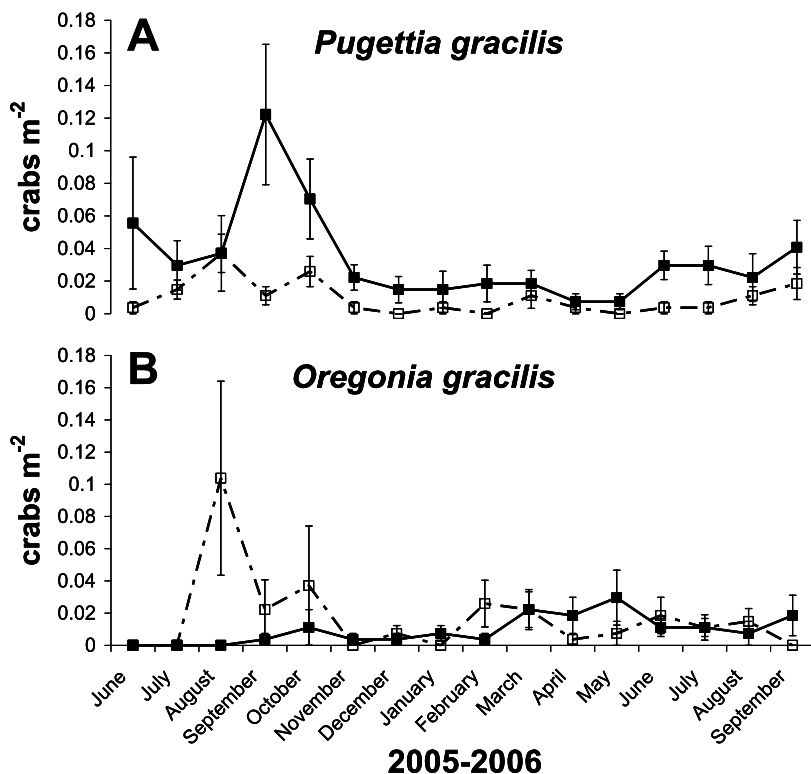


Fig. 4. A, *Pugettia gracilis* Dana, 1851; and, B, *Oregonia gracilis* Dana, 1851 abundance (crabs m⁻²). Solid lines indicate canopy and understory habitat; dashed lines indicate understory only habitat. Vertical bars are ± 1 SE.

TABLE II

Repeated measures ANOVA results for juvenile and adult *Pugettia gracilis* Dana and *Oregonia gracilis* Dana. **Bold** indicates statistical significance (α less than or =0.05)

Species	Source	SS	df	MS	F	P
<i>P. gracilis</i>	Time	71.0	15	4.73	3.200	<0.001
	Habitat	38.3	1	38.28	20.490	<0.001
	Habitat × Time	44.1	15	2.94	1.574	0.090
	Error	239.1	128	1.87		
<i>O. gracilis</i>	Time	38.6	15	2.57	1.524	0.106
	Habitat	3.7	1	3.78	2.002	0.160
	Habitat × Time	51.0	15	3.40	1.800	0.042
	Error	241.8	128	1.89		

by all individuals. Other spider crabs may undergo spatial migrations (Wicksten & Bostick, 1983), although Hines (1982) could find no seasonal movement of tagged spider crabs in Monterey Bay, California, U.S.A. However, seasonal effects may be more pronounced at higher latitudes where variations in temperature, salinity, and light and dark regimes can be more intense. *Pugettia* spp. eat kelp almost exclusively (Hines, 1982), thus moving to deeper waters with less food would not be beneficial, although some crab species can go long periods (>6 months) without eating (Schultz & Shirley, 1997). Relatively constant year round brooding activity has been documented for several spider crabs species such as *Loxorhynchus crispatus* Stimpson, 1857, *Pugettia producta* (J. W. Randall, 1840), *Mimulus foliatus* Stimpson, 1860, *Pugettia richii* Dana, 1851, and *Scyra acutifrons* Dana, 1851 (cf. Boolootian et al., 1959; Knudsen, 1964; Hines, 1982) suggesting that reproductive cycles may not be solely responsible for temporal variation in behavioral modifications of *P. gracilis*. However, other spider crab species such as *Maja squinado* (Herbst, 1788) are known to carry out an autumn migration to deep waters when nearing sexual maturity (González-Gurriarán et al., 2002; Corgos et al., 2006), although seasonal variation in juvenile and adult *M. squinado* distribution may also be caused by shifts in habitat utilization (González-Gurriarán & Freire, 1994).

Crab spatial distributions may be regulated by available habitat. *Pugettia gracilis* had highest abundances at canopy sites. Interestingly, peak abundances of *P. gracilis* occurred at times of highest understory density. Canopy kelp has the ability to dampen ambient current velocities and can buffer physical factors in kelp habitats (Eckman et al., 1989, 2003), however, understory kelp may more directly affect crabs than canopy by providing increased refuge from predators. *Pugettia producta* utilize opportunistic feeding strategies for nearby food searches and do not actively search for distant food sources via chemosensory stimuli (Zimmerfaust & Case, 1982). Most canopy kelp structure is in the water column and not

directly available to crabs. *Pugettia gracilis* was found primarily on the tops of understory macroalgae and exhibited some decorating behavior with pieces of surrounding algae (B. Daly, pers. obs.). In winter, *P. gracilis* may utilize rock crevice refuges for protection from predators when kelp densities are lowest or to avoid being swept away by strong storm surges. Inhabiting substrate crevices would make them less visible to predators, resulting in lower observed winter numbers. Similar seasonal variation has been observed in *Pugettia quadridens* (De Haan, 1850) in eelgrass beds in Kwangyang Bay, Korea (Huh & An, 1998) and other studies have shown kelp structure influences spider crab density, size variability, and microhabitat resource partitioning in central California, U.S.A. (Hines, 1982).

Oregonia gracilis has the most complex decoration of all northern decorator crabs (Jensen, 1995) and covers itself with pieces of algae, invertebrates, and sediment. *Oregonia gracilis* was usually found directly on the substrate and relied heavily on decoration and substrate complexity to conceal itself from predators. Because *O. gracilis* actively uses small pieces of biogenic debris to decorate itself, the three-dimensional structure of kelp may be less critical for avoiding predators. Drift kelp, a major component of *O. gracilis* diet, was observed at all sites. *Oregonia gracilis* feed on drift kelp via a waiting strategy, which minimizes movement and may minimize detection by predators. Some spider crabs use the same algal species for both food and decoration, while others use different algal species for each function (Sato & Wada, 2000). Coordination of camouflage criteria has an effect on microhabitat selection, enabling crabs to exploit alternate spatial refuges and strategies for concealment from predators. Differences in microhabitat resource utilization may account for differences in temporal variation between *P. gracilis* and *O. gracilis*. Kelp structure may have little importance to *O. gracilis*, thus behavior and seasonal abundance may be independent of kelp density.

Predation is an obvious source of mortality and may be responsible for temporal variation in crab density if predator abundance fluctuated seasonally. Common predators in Alaskan kelp beds are fish, octopuses, and sea otters, which are known to take spider crabs as a portion of their diet (Quast, 1968; Love & Ebeling, 1978; Hines, 1982; Vincent et al., 1998; Dodge & Scheel, 1999) suggesting that the general level of predation may be high. The magnitude of predation pressure was not measured; however, fish densities are lowest in winter in Alaskan kelp beds (Hamilton & Konar, 2004). Octopuses and sea otters were present at some sites with highest abundances in summer months. The size of *Pugettia gracilis* and *Oregonia gracilis* does not preclude predation from octopuses, otters, and most fish. As such, it is likely that predation limited overall crab populations similarly if predator density was constant at all sites.

Sampling bias may influence crab observations. SCUBA surveys can underestimate benthic organism densities, especially in complex habitats where individuals are difficult to observe (Coyer et al., 1999). Also, small crabs such as recruits are difficult to observe. As a result, abundances are likely to be underestimated; however, relative comparisons in crab densities should be valid. Seasonal migration is difficult to test, especially with small, cryptic species that are difficult to tag. Additionally, it was not logistically feasible to search a large structurally complex subtidal habitat because numbers of tagged individuals would become quickly diluted.

This study provides insight to the ecology of two abundant crab species in nearshore Alaskan kelp beds. Crab abundance varied seasonally and was likely a result of changes in microhabitat utilization such as moving to rock crevice refuges in winter months for protection from storm surges as kelp density decreases. Resource partitioning in *Pugettia gracilis* and *Oregonia gracilis* (structural refuge and decoration) may be adaptations for minimizing predation and maintaining ecological niches, thus it is not surprising that temporal utilization of the environment varies as resources are elastic in space and time.

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