



Biological correlates of sea urchin recruitment in kelp forest and urchin barren habitats

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ABSTRACT: Shifts between the alternate stable states of sea urchin barren grounds and kelp forests correspond to sea urchin density. In the Aleutian Archipelago, green sea urchins *Strongylocentrotus polyacanthus* are the dominant herbivores that graze kelp forests. Sea urchin recruitment is an important driver that influences sea urchin density, particularly in the absence of top-down control from a keystone predator such as the sea otter *Enhydra lutris*. To understand how the biological community may influence patterns of sea urchin recruitment, we compared sea urchin recruit (size ≤ 20 mm) densities with biomass of other benthic organisms in both barren ground and kelp forest habitats at 9 islands across the Aleutian Archipelago. Patterns of biological community structure between the 2 habitats did not explain patterns of sea urchin recruits; however, the same 10 specific taxa were found to correlate with sea urchin recruits in each habitat. Taxa that showed strong positive correlations included *Codium*, *Constantinea*, *Schizymenia*, and hydrozoans, while strong negative correlations were observed with *Pachyarthron* and *Pugettia*. Weak positive correlations were observed with *Alcyonidium* and ascidiaceans in both habitats, while weak variable relationships were detected with *Polysiphonia* and *Corallina* between habitats. The observed species-specific relationships may be due to small sea urchin displacement by larger conspecifics, larval responses to settlement cues, post-settlement survival via biogenic refugia, or potentially predation. These potential species-specific interactions were apparent, regardless of habitat, and it can be inferred that they would be preserved in the presence or absence of keystone predation.

KEY WORDS: Kelp forest · Nearshore habitats · Recruitment · Species interaction · Urchin barrens

1. INTRODUCTION

Sea urchins are often the key herbivore causing the transition between the alternate stable states of kelp forest (high fleshy macroalgal cover and low urchin density) to barren ground (low fleshy macroalgal cover and high urchin density) habitats on temperate rocky reefs (Estes & Duggins 1995, Gagnon et al. 2004, Filbee-Dexter & Scheibling 2014). Habitat shifts towards sea urchin barrens have been reported across temperate latitudes globally (Johnson et al. 2011, Ling et al. 2015, Krumhansl et al. 2016). Sea

urchins can have important effects on marine habitats, as they heavily graze fleshy macroalgae and cause bioerosion of biogenic reef habitats (Steneck et al. 2017, Rasher et al. 2020). They also provide a key food source for upper trophic levels, such as the sea otter *Enhydra lutris* in the north Pacific (Watt et al. 2000, Larson et al. 2015). Urchin demographics influence the role that urchins play in an ecosystem as a herbivore or as prey. Demographic factors such as size, fecundity, and recruitment will affect population density, grazing rates, and movement (Himmelman 1986, Dumont et al. 2006). While effects that

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urchins can have on habitat and ecosystem structure and the role that they play in food webs are well known, the drivers of sea urchin demographics are complex. Sea urchin demographics may be influenced by environmental gradients (Ebert 2010, Ling et al. 2015) and can vary greatly across regions due to environmental forcing on sea urchins through ontogeny (Estes & Duggins 1995). Recruitment and post-settlement survival is a fundamental process in sea urchin demographics.

Biological drivers can have a strong influence on sea urchin recruitment through multiple pathways that influence post-settlement distribution, growth, and survival. Sea urchin growth and age structure can be influenced by the algal cover on which they are feeding (Ling et al. 2019). Additionally, the whipping action of kelps, particularly *Desmarestia viridis* and *Eualaria fistulosa*, can physically prevent sea urchins from overgrazing (Konar et al. 2014). Globally, top-down control of sea urchin demographics via predation has long been recognized (Pederson & Johnson 2006, Fagerli et al. 2014, Sheppard-Brennand et al. 2017). In the Aleutian Archipelago of Alaska, the precipitous decline of sea otters in the late 1990s and early 2000s, likely due to killer whale predation (Estes et al. 1998), has allowed us to examine how benthic ecosystems function in the absence of keystone predators. Here, the presence of both barren ground and kelp forest habitats across the Aleutian Archipelago offers an ideal opportunity to investigate how biological features influence sea urchin recruitment within these 2 habitats. Kelp forests are believed to be more biodiverse and productive than barren grounds, with a large amount of food available to sea urchins that can survive. The obvious differences in community structure between kelp forest and barren ground habitats are likely to drive differences in sea urchin recruitment, which may differ between kelp forest and barren grounds (Himmelman 1986) due to differences in pre- and post-settlement processes that regulate growth and survival of newly recruited sea urchins (Rowley 1989).

Here, we ask how the surrounding biological community influences patterns of sea urchin recruitment and whether taxa that are correlated with recruits differ between kelp forest and barren ground habitats. We hypothesized that given the different community structures between barren grounds (low fleshy macroalgal cover

and high urchin density) and kelp forests (high fleshy macroalgal cover and low urchin density), there would likely be different biological correlates of sea urchin recruitment. However, if there were similar species associated with sea urchin recruitment in both habitats, this would suggest overarching species interactions that are key drivers to sea urchin recruitment, regardless of habitat state.

2. MATERIALS AND METHODS

At 9 islands in the Aleutian Archipelago, from Chuginadak in the east to Attu in the west (Fig. 1), a total of 360 benthic community quadrats were examined from both habitats, barren ground or kelp forest, in August 2016 and 2017. At each island, 4 sites were established, 2 within each habitat type that best represented these habitats based on the presence or absence of consistently dense subcanopy kelps across the entire area to be sampled (see Metzger et al. 2019 for details on community structure within both types of habitats). While some limited fleshy macroalgae were found in barrens, there was an obvious lack of kelp species (primarily *Eualaria*, *Thalassiosiphon*, and *Saccharina*) and an abundance of sea urchins. All sites were in approximately 6 to 8 m water depth, on rocky benches along exposed shorelines. At each site, divers using SCUBA scraped all mobile and sessile epibiota from each of 10 haphazardly placed 0.25 m² quadrats into a fine mesh pillow case. All invertebrates and macroalgae were returned to the shipboard laboratory for species identification and quantification of total wet biomass (g). All organisms were visually identified to the finest taxonomic resolution possible with the aid of light micro-

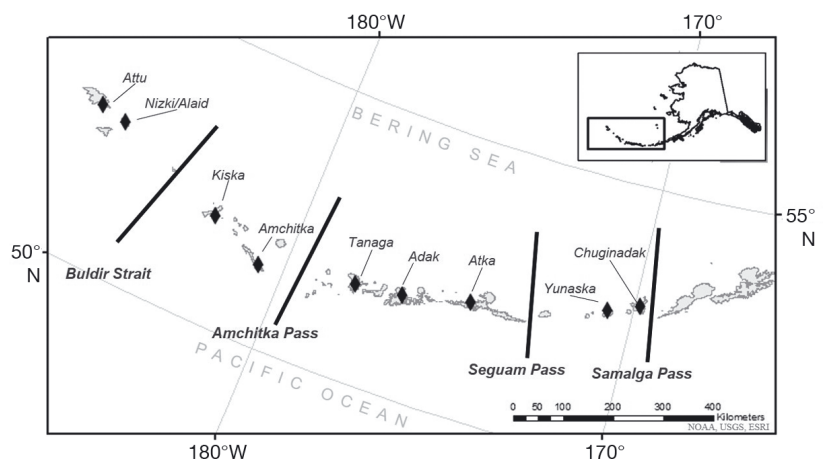


Fig. 1. The Aleutian Archipelago with study islands. (♦) Benthic community sampling sites

scopes and species keys. Test diameters of all sea urchins were measured to the nearest mm using calipers to determine size frequencies within each quadrat.

Data used in this study were initially analyzed for overall community structure differences between habitats (Metzger et al. 2019) and then archived with the Biological & Chemical Oceanography Data Management Office as epibenthic community abundance (Edwards & Konar 2018a) and biomass (Edwards & Konar 2018b). Our analyses used PRIMER v7 and PERMANOVA+ (PRIMER-e, Quest Research; Anderson et al. 2008, Clarke et al. 2014, Clarke & Gorley 2015). Individual sea urchin sizes were assigned a size class (Recruit: ≤ 20 mm, Small: 21–35 mm, Medium: 36–54 mm, or Large: ≥ 55 mm; Estes & Duggins 1995, Brady & Scheibling 2006, Scheibling & Hatcher 2013) and standardized to a proportional scale (from 0.0 to 1.0) among all samples for analyses. Each size bin was treated as an ordered variable and a Bray-Curtis (with 0.01 dummy variable added) similarity matrix was constructed to compare similarity in size distributions between habitats and among islands. Recruits were then selected and used to construct another Bray-Curtis (with 0.1 dummy variable added) similarity matrix of recruit densities by quadrat to test for similarities in the densities of recruits among samples. From the same quadrats, biomass of the surrounding biological community (fleshy and upright coralline macroalgae and invertebrates) was fourth-root transformed, to down-weight dominant taxa and allow for consideration of the full biological community. The biomass data were then constructed into a Bray-Curtis (with 0.01 dummy variable added) similarity matrix to test for similarities in the biomass of the surrounding biological community. Samples were the quadrat level data ($n = 180$ per habitat) from each of ten 0.25 m^2 quadrats per site. The permutational multivariate analysis of variance (PERMANOVA) design was Habitat (Kelp, Barrens), Islands (Attu, Semichis [Nizki/Alaid], Kiska, Amchitka, Tanaga, Adak, Atka, Yunaska, and Chuginadak), Habitat $\times$ Islands, Site(Island), Quadrat(Site). Quadrat data were ordinated by non-metric multidimensional scaling (nMDS) to visualize similarity in sea urchin recruitment among all quadrats across all islands, by habitat. Bubble plots were imposed on points in nMDS space to depict relative differences in sea urchin recruit densities and vector plots show the correlated community taxa driving separation among points in nMDS space. Differences between habitats for both the recruit densities and the surrounding community were separately tested by a 2-way crossed permutational ANOVA

(PERMANOVA; McArdle & Anderson 2001) with Habitat treated as a fixed factor and Island treated as a random factor. A similarity percentage analysis (SIMPER) was used to determine the community taxa most important in explaining the dissimilarity in community structure between habitats. A distance based linear regression (DistLM; Anderson et al. 2008) analysis was used to statistically determine the community taxa that were significantly correlated with sea urchin recruit densities, using the fourth-root transformed community biomass by quadrat as the predictor variable worksheet. DistLM and nMDS were constructed for barren ground and remnant kelp forest habitats independently, to determine taxa that were significantly correlated with sea urchin recruits in both habitats.

3. RESULTS

Patterns of sea urchin size frequency distributions were variable between habitats and among islands (Fig. 2). Standardized sea urchin size frequencies did not significantly differ between habitats ($p(\text{perm}) = 0.06$, $\text{pseudo-}F = 2.4$); however, the interaction between habitat and island was significant ($p(\text{perm}) = 0.001$, $\text{pseudo-}F = 8.0$) suggesting that random effects, by island, influenced the differences in size distributions among islands. Generally, and as expected, sea urchins occurred at higher densities in the barren ground habitat than in the kelp forest habitat. Sea urchins also varied in density among islands. Islands with the highest densities (Kiska, Amchitka, and Tanaga) featured a mode over recruit sea urchin sizes, while those with moderate densities (Adak, Atka, Yunaska, and Chuginadak) featured a primary mode over the small and medium sea urchin sizes. Attu and the Semichi Islands had the lowest sea urchin densities, and the mode was focused on large sea urchins, which were uncommon at most other islands. Densities of large and small sea urchins were significantly different among islands and in quadrats with higher large urchin densities, sea urchin recruit densities were significantly lower ($p(\text{perm}) < 0.05$; Fig. 3). While some islands had significantly higher sea urchin recruit densities, sea urchin recruits were observed in both habitats at all islands.

Community structure as measured by biomass differed significantly between barren ground and kelp forest habitats ($p(\text{perm}) = 0.003$, $\text{pseudo-}F = 11.5$) at all islands ($p(\text{perm}) < 0.001$), despite a significant interaction term between habitat and island ($p(\text{perm}) = 0.001$, $\text{pseudo-}F = 9.4$). In total, 170 identified taxa

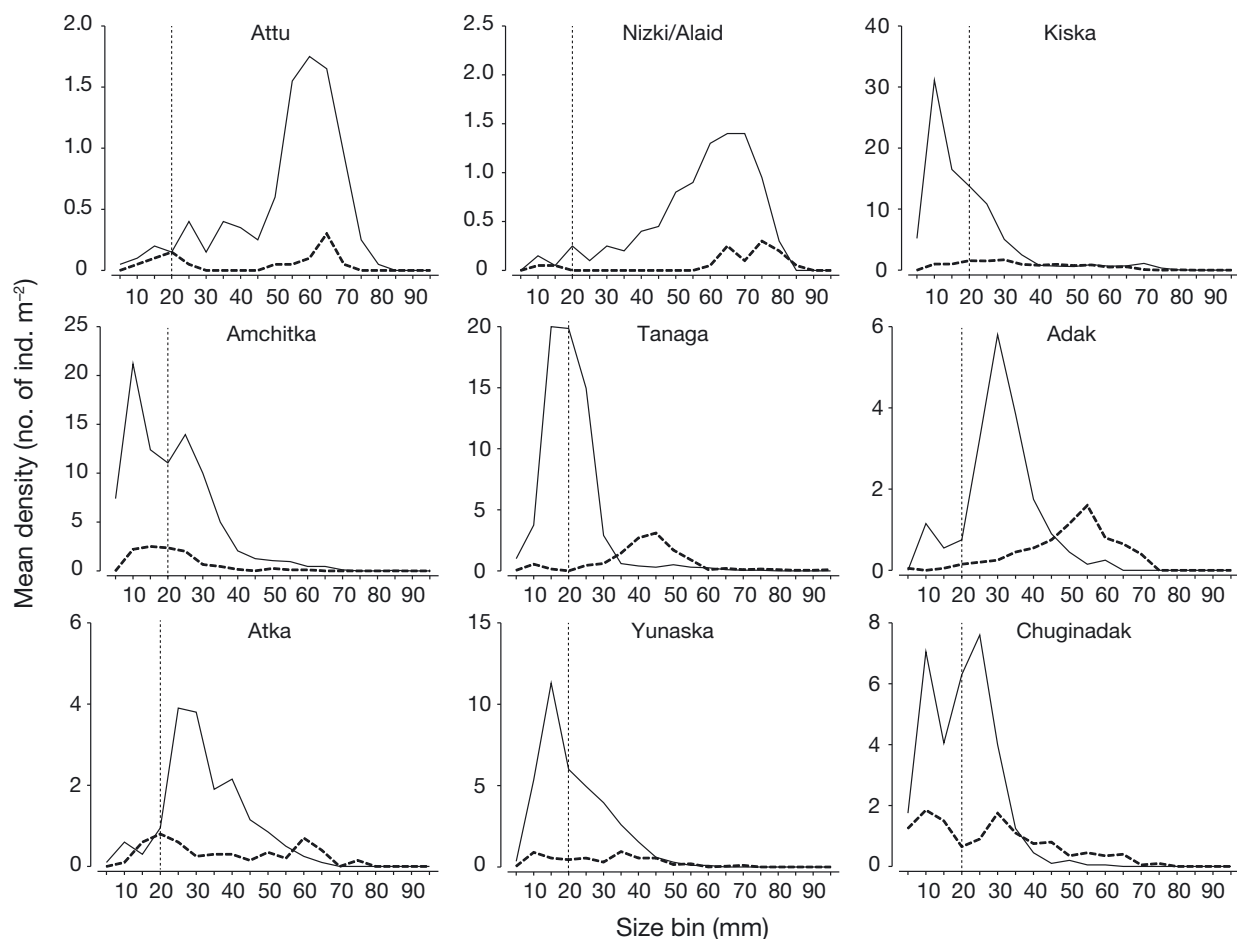
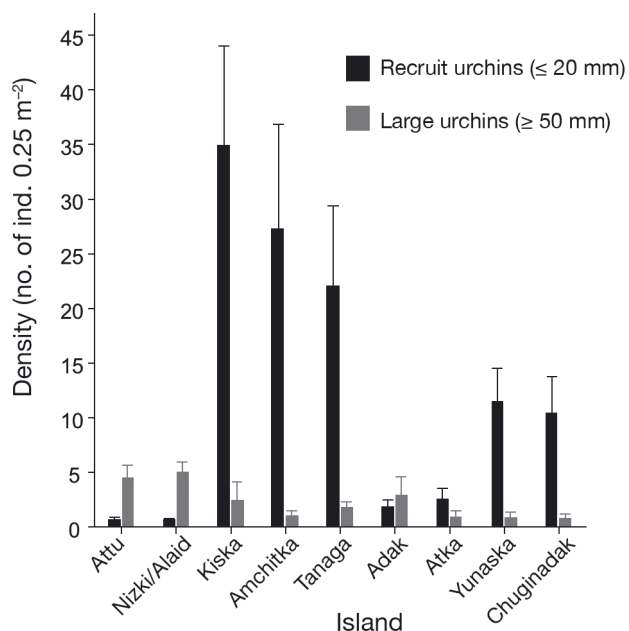


Fig. 2. Mean size distributions showing summed densities of measured sea urchins in 5 mm size-bins, averaged between sites ($n = 2$), by habitat: barren (solid line) and kelp (dashed line) for each island. The vertical dashed line at 20 mm marks the cutoff for the recruit size class. Note different y-axis scales reflecting differences in abundance among islands (range = <1 –40)



were observed in the benthic biomass scrapes, 116 were observed in barren ground and 148 were observed in kelp forest habitats. Among all taxa, 27 explained 70% of the observed dissimilarity between barren ground and kelp forest habitats (Table 1). Taxa that contributed at least 5%, individually, to dissimilarity between habitats were the kelps *Thalassiophyllum* (7.15%), *Eualaria* (6.34%), and *Saccharina* (4.66%), and sea urchins *Strongylocentrotus* (4.62%). Most taxa driving the dissimilarity between habitats occurred in greater biomass in kelp forests, except for *Strongylocentrotus*, the green alga *Codium*, the upright coralline alga *Pachyarthron*, the rock jingle *Pododesmus*, and the limpet *Lottia*, which occurred in greater biomass in barren grounds (Table 1).

Fig. 3. Mean density (no. of ind. 0.25 m^{-2}) of recruit and large sea urchin size classes averaged among sites by island ($n = 4$, 2 of each habitat). Error bars show SD

Table 1. Results from SIMPER analysis for dissimilarity of fourth-root transformed community biomass between barren ground and kelp forest habitats. Average fourth root biomass of each taxa and the calculated dissimilarities (average dissimilarity and dissimilarity/SD) show differences between habitats. Untransformed biomass values are shown for reference. The percent variation explaining the dissimilarity for each taxon is provided individually and cumulatively, up to a cut-off of 75 % cumulative variation explained

Taxa	Urchin barren average biomass		Kelp forest average biomass		Avg. diss.	Diss./SD	Indiv. %	Cumul. %
	4th root ($^4\sqrt{g}$)	Untrans. (g)	4th root ($^4\sqrt{g}$)	Untrans. (g)				
<i>Thalassiophyllum</i>	0.01	1.00×10^{-8}	0.81	4.30×10^{-1}	6.00	1.16	7.15	7.15
<i>Eualaria</i>	0.01	1.00×10^{-8}	0.70	2.40×10^{-1}	5.31	0.94	6.34	13.49
<i>Saccharina</i>	0.00	0.00×10^0	0.53	7.89×10^{-2}	3.91	0.74	4.66	18.16
<i>Strongylocentrotus</i>	0.91	6.86×10^{-1}	0.76	3.34×10^{-1}	3.88	1.10	4.62	22.78
<i>Odonthalia</i>	0.01	1.00×10^{-8}	0.47	4.88×10^{-2}	3.63	1.10	4.32	27.10
<i>Acarnus</i>	0.08	4.10×10^{-5}	0.44	3.75×10^{-2}	3.25	1.18	3.88	30.98
<i>Ptilota</i>	0.01	1.00×10^{-8}	0.36	1.68×10^{-2}	2.71	0.79	3.23	34.21
<i>Halichondria</i>	0.03	8.10×10^{-7}	0.36	1.68×10^{-2}	2.63	0.79	3.13	37.34
<i>Desmarestia</i>	0.04	2.56×10^{-6}	0.29	7.07×10^{-3}	2.31	0.71	2.75	40.09
<i>Codium</i>	0.19	1.30×10^{-3}	0.18	1.05×10^{-3}	2.25	0.75	2.68	42.76
<i>Laminaria</i>	0.00	0.00×10^0	0.27	5.31×10^{-3}	1.98	0.54	2.37	45.13
Ascidiacea	0.10	1.00×10^{-4}	0.25	3.91×10^{-3}	1.97	0.91	2.35	47.48
Hydrozoa	0.16	6.55×10^{-4}	0.22	2.34×10^{-3}	1.86	0.99	2.22	49.70
<i>Styela</i>	0.02	1.60×10^{-7}	0.25	3.91×10^{-3}	1.80	0.81	2.15	51.85
<i>Constantinea</i>	0.14	3.84×10^{-4}	0.18	1.05×10^{-3}	1.78	0.84	2.12	53.97
<i>Leptasterias</i>	0.05	6.25×10^{-6}	0.21	1.94×10^{-3}	1.64	0.86	1.96	55.93
<i>Agarum</i>	0.00	0.00×10^0	0.18	1.05×10^{-3}	1.56	0.38	1.86	57.78
<i>Pugettia</i>	0.05	6.25×10^{-6}	0.18	1.05×10^{-3}	1.46	0.81	1.74	59.52
<i>Tonicella</i>	0.08	4.10×10^{-5}	0.11	1.46×10^{-4}	1.21	0.71	1.44	60.97
<i>Pachyarthron</i>	0.11	1.46×10^{-4}	0.07	2.40×10^{-5}	1.18	0.65	1.41	62.37
<i>Musculus</i>	0.02	1.60×10^{-7}	0.14	3.84×10^{-4}	1.10	0.69	1.31	63.68
<i>Alcyonidium</i>	0.02	1.60×10^{-7}	0.15	5.06×10^{-4}	1.06	0.46	1.26	64.94
<i>Pododesmus</i>	0.09	6.56×10^{-5}	0.06	1.30×10^{-5}	1.02	0.44	1.21	66.15
<i>Lottia</i>	0.12	2.07×10^{-4}	0.04	2.56×10^{-6}	1.00	0.67	1.20	67.35
<i>Turnerella</i>	0.06	1.30×10^{-5}	0.09	6.56×10^{-5}	1.00	0.55	1.19	68.54
<i>Polysiphonia</i>	0.04	2.56×10^{-6}	0.10	1.00×10^{-4}	0.99	0.45	1.18	69.73
<i>Henricia</i>	0.01	1.00×10^{-8}	0.12	2.07×10^{-4}	0.91	0.57	1.08	70.81
<i>Schizymenia</i>	0.09	6.56×10^{-5}	0.05	6.25×10^{-6}	0.90	0.58	1.08	71.96
Porifera	0.03	8.10×10^{-7}	0.10	1.00×10^{-4}	0.86	0.54	1.03	72.98
<i>Mikamiella</i>	0.02	1.60×10^{-7}	0.10	1.00×10^{-4}	0.83	0.53	0.99	73.97
<i>Dermaturus</i>	0.04	2.56×10^{-6}	0.09	6.56×10^{-5}	0.78	0.60	0.93	74.90

Patterns of similarity in sea urchin recruit occurrence among all quadrats were correlated with specific invertebrate and macroalgal taxa in both barren ground and kelp forest habitats (Fig. 4). While overall benthic community structure differed between habitats and sea urchin recruits were correlated with slightly different taxa between habitats, 10 taxa were significantly correlated in both habitats ($p < 0.05$, Table 2). Of the 10 significantly correlated taxa, the geniculate coralline alga *Pachyarthron* and the crab *Pugettia* showed strong negative correlations with sea urchin recruits, while the green alga *Codium*, the fleshy red algae *Constantinea* and *Schizymenia*, and hydroids exhibited strong positive correlations (Fig. 4). While significantly correlated in both habitats, the *Alcyonidium* bryozoan, the Ascidiacea tunicates, the filamentous red alga *Polysiphonia*, and geniculate coralline alga *Corallina* all showed weaker correla-

tions with sea urchin recruits than the aforementioned taxa. *Alcyonidium* and Ascidiacea generally showed positive correlations with sea urchin recruits. *Polysiphonia* and *Corallina* exhibited mixed correlations with sea urchin recruits, dependent on habitat; where correlations with *Polysiphonia* were negative and *Corallina* somewhat neutral in barren grounds, while in kelp forests, correlations with *Corallina* were negative and *Polysiphonia* slightly positive (Fig. 4).

4. DISCUSSION

Variability of sea urchin demography can be influenced by patterns of recruitment over space and time. Our results suggest that specific taxa can play an important role in shaping patterns of sea urchin recruitment through potentially positive or negative

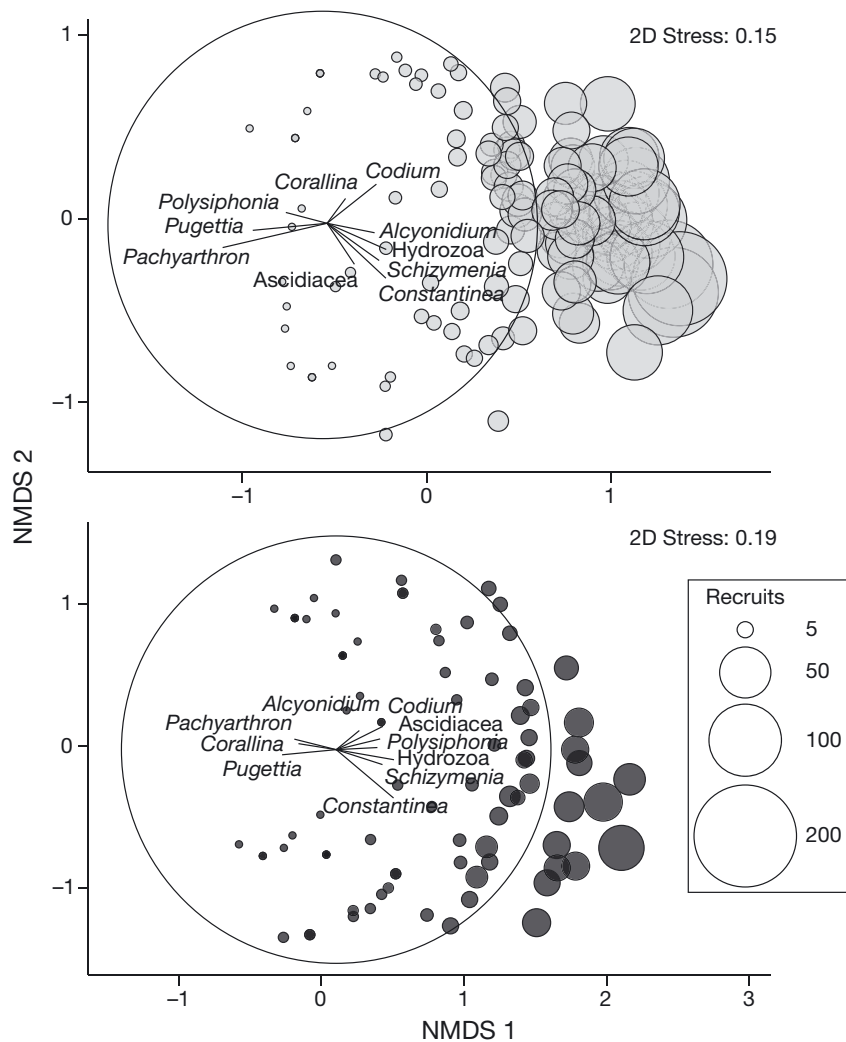


Fig. 4. nMDS plot of similarity of sea urchin recruit similarities (zero-corrected Bray-Curtis) by quadrat for barren ground (top) and kelp forest (bottom) habitats. Bubble plot shows densities (no. of ind. 0.25 m^{-2}) of sea urchin recruits (test diameter $\leq 20 \text{ mm}$). Vectors show the strength of correlations with taxa significantly correlated in both habitats by DistLM (Table 2) and the circle represents a unit of 1.0 correlation strength

interactions with sea urchin recruits that are likely more pronounced in the absence of the keystone predator in the system, sea otters. By examining correlations between other benthic taxa and sea urchin recruits at the quadrat level in 2 alternate stable state habitats, barren grounds and kelp forests, our findings pinpoint which taxa are key biological correlates with sea urchin recruitment. We rejected our initial hypothesis that the taxa driving patterns of sea urchin recruits would differ between barren ground and kelp forest habitats, because although some of the correlated taxa differed, the taxa most strongly correlated with sea urchin recruits were similar in both habitats, suggesting species-specific interactions that

are not habitat-specific. Also, despite differences in sea urchin abundance between habitats, it was puzzling that patterns of standardized sea urchin size distributions did not significantly differ between habitats; however, this pattern varied among islands such that there was a strong interaction between habitat and island (as seen in Fig. 2 for 6 of the 9 islands) and suggests that local processes likely shaped patterns of growth and survival among samples.

Densities of sea urchin recruits were different between habitats and among islands; however, where they occurred, sea urchin recruits were positively associated with the encrusting green alga *Codium*, the red algae *Constantinea* and *Schizymenia*, and hydrozoan invertebrates. In contrast, sea urchin recruits were negatively associated with the geniculate coralline alga *Pachyarthron* and the decorator crab *Pugettia*. Sea urchin recruit densities also were inversely correlated with large sea urchins (Fig. 3). This study has pinpointed correlations between specific community taxa and sea urchin recruits, which may be indicative of a causative relationship.

4.1. Correlations with macroalgae

The encrusting green alga *Codium* occurred in dense patches in both kelp forests and barren grounds. Despite the potential for being overgrazed, *Codium* is one of the few macroalgae that persists and thrives in barren grounds (Metzger et al. 2019). The association between sea urchin recruits and *Codium* could be due to several possible relationships. *Codium* could be a food source for sea urchins, as they have been documented to consume it; however, *Codium* is not a very nutritious resource for sea urchins (Trowbridge 1995, Suskiewicz & Johnson 2017). Perhaps sea urchin recruits are instead feeding on the biofilm that occurs on the surface of the *Codium* and not relying on the alga for nutrition (Zhang et al. 2014). *Codium* can also produce dimethylsulfoniopropionate (DMSP, Lyons et al. 2010) as a chemical defense strategy; however, DMSP can also act as a chemical attractant to sea

Table 2. DistLM results for community biomass of taxa that were determined to be significantly correlated ($p < 0.05$) with sea urchin recruits in both barren ground and kelp forest habitats, out of the full community ($n = 170$ taxa). The proportion of explained variation (Prop. exp. var.) shows the contribution of each taxa to the amount of explainable observed variation for each habitat, independently

Taxa	Kelp forest			Barren ground		
	pseudo- F	p	Prop. exp. var.	pseudo- F	p	Prop. exp. var.
<i>Alcyonidium</i>	4.038	0.008	2.22 %	4.338	0.003	2.38 %
Asciacea	6.915	0.001	3.74 %	2.816	0.017	1.56 %
<i>Codium</i>	3.031	0.020	1.67 %	4.516	0.001	2.47 %
<i>Constantinea</i>	7.569	0.001	4.08 %	3.870	0.006	2.13 %
<i>Corallina</i>	3.469	0.011	1.91 %	3.098	0.009	1.71 %
Hydrozoa	6.960	0.001	3.76 %	5.153	0.001	2.81 %
<i>Pachyarthon</i>	2.965	0.022	1.64 %	17.818	0.001	9.10 %
<i>Polysiphonia</i>	3.160	0.014	1.74 %	2.641	0.016	1.46 %
<i>Pugettia</i>	3.673	0.012	2.02 %	9.075	0.001	4.85 %
<i>Schizymenia</i>	4.702	0.001	2.57 %	4.907	0.002	2.68 %

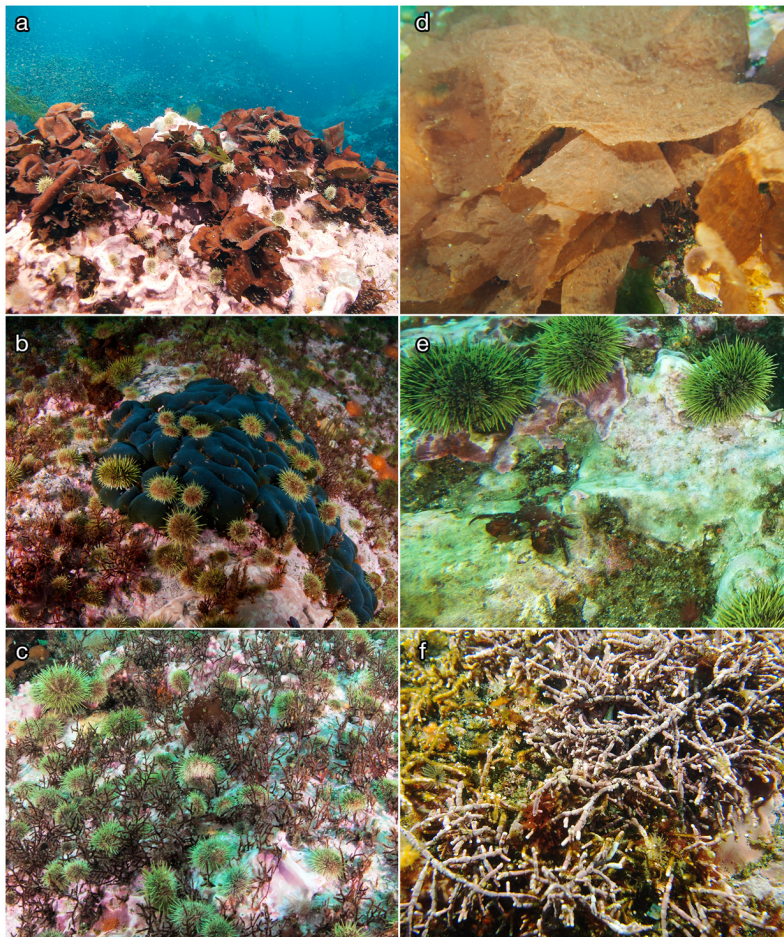


Fig. 5. Some community taxa that were significantly correlated with sea urchin recruits (≤ 20 mm): (a) *Constantinea*, (b) *Codium*, (c) Hydrozoa, (d) *Schizymenia*, (e) *Pugettia* and large *Strongylocentrotus*, and (f) *Pachyarthon*. Photo credits: (a) Shawn Harper (www.seaweedsalaska.com/species.asp?SeaweedID=218), (b,c) Joseph Tomoleoni (USGS-Western Ecological Research Center), (d,f) B. Konar, and (e) Melissa Good (Sea Grant Alaska)

urchins (Van Alstyne et al. 2001, Van Alstyne & Puglisi 2007). It is unknown if the chemical compounds within *Codium* act as an attractant or deterrent to sea urchins. It is likely that sea urchin recruits are using the folds and physical structure of *Codium* beds as a structural refuge from predators and larger conspecifics (Fig. 5b).

The red alga *Constantinea* is a perennial with an erect thallus and a branched cylindrical stipe emerging from a small discoid holdfast that grows up to a height of approximately 15 cm. The circular, cup-shaped blades grow through the winter each year to form an understory canopy over the benthos (Fig. 5a). While several species occur across the northwest Pacific, *Constantinea rosa-marina* was the only species observed in this study, occurring in both kelp forests and in isolated patches in barren grounds. While it is unknown if this alga produces chemical defenses to deter grazing, the robust structure of the stipe may be a structural defense against grazing by sea urchins. *Constantinea* individuals are long-lived perennials, often surviving longer than 15 yr (Klochko & Pisareva 2009) and play an important ecological role by providing persistent sub-canopy habitat over the benthos, even when under intensive grazing pressure (Foreman 1977). The relationship between *Constantinea* and sea urchin recruits remains unclear as it is not understood if the sea urchins are associated with the plant as a food source or as a structural refuge from predation or displacement by larger conspecifics.

Another red alga positively correlated with sea urchin recruits, *Schizymenia*, also has an uncertain relationship with sea urchins. *Schizymenia* is an ephemeral alga and does not feature any robust structure that could resist grazing from or harbor sea urchin recruits. The large, thin, leafy blades often cover patches of the benthos and perhaps sea urchin recruits can find refuge beneath the dense

cover (Fig. 5d) or use *Schizymenia* as a food source. However, some *Schizymenia* species produce compounds that have been extracted for use in antiretroviral therapy treatments in the biomedical field (Nakashima et al. 1987, Anand et al. 2016). It is unknown if these same compounds influence the palatability of *Schizymenia* to sea urchins.

The filamentous red alga *Polysiphonia* poses a puzzling relationship in that it exhibited a negative correlation in barren grounds and a positive correlation in kelp forests. *Polysiphonia* can occur in large, bushy tufts that sweep across the benthos, which in some ways could act as a physical deterrent to organisms that would be whipped away in the surge. The complex structure provided by the fine branching could also offer refuge for sea urchin recruits that seek shelter within the body of the plant. *Polysiphonia* has also been shown to induce metamorphosis in larval sea urchins and act as a refuge for post-larval juveniles (Pearce & Scheibling 1991). In the kelp forest habitats, *Polysiphonia* may play this role for sea urchin recruits, whereas its role in the barren grounds differs under the higher grazing intensity. More research is needed on the relationship between sea urchin recruits and *Polysiphonia* from both habitats to disentangle the observed mixed result.

Pachyarthron and *Corallina* are branching geniculate coralline algae that create complex turf habitat over the benthos (Fig. 5f). The relationship with sea urchin recruits may be due to the physical structure of these upright corallines, which makes them more resistant to grazing. Higher biomass of these species was observed in barren grounds, where grazing intensity is likely much greater and reduces the soft-fleshy macroalgal cover. It is likely that the complex structure and thick, calcified cell structure make geniculate coralline algae a non-food source for small sea urchins. *Pachyarthron* was positively correlated with the presence of large sea urchins, which is likely a result of sea urchin grazing in the local area, removing soft-fleshy macroalgae and reducing competition for space. In this sense, the geniculate corallines were more likely to occur where large sea urchins occurred. Thus, the lack of sea urchin recruits may not be due to the corallines, but to the presence of larger conspecifics, which could displace or cannibalize the recruits (LeGault & Hunt 2016). The variable relationship observed between sea urchin recruits and *Corallina* (Fig. 4) could reflect that in a sea urchin barren state, where there is little cover or refuge to be found, geniculate coralline algae can provide adequate cover for sea urchin recruits from predators. *Strongylocentrotus droebachiensis*

has been shown to find refuge from predators in *Corallina vancouveriensis* in Washington (Yiu & Feehan 2017); however, a strong positive relationship was not immediately obvious upon examination across the Aleutian Archipelago. Furthermore, a negative and variable relationship between the geniculate corallines and sea urchin recruits was observed, despite the expectation that geniculate corallines can chemically attract settling sea urchins (Pearce & Scheibling 1990). Since this study reports on correlations, it would be of interest to conduct an *in situ* manipulative experiment with geniculate corallines in the Aleutian Archipelago, to test if patterns indeed differ from those observed in other sea urchin barren systems and account for differences between laboratory and field conditions.

4.2. Correlations with invertebrates

Sea urchin recruits were correlated with several phyla of benthic invertebrates, with mixed relationships, likely due to potential predator–prey interactions. The strong positive correlation between sea urchin recruits and hydrozoans in both habitats is likely indicative of sea urchins using hydroids as a refuge from other predators in the system, whether larger conspecifics, sea stars, or other macroinvertebrates (Fig. 5c). The hydroids observed in this study were erect with alternate branching, often occurring as a benthic canopy layer approximately 5 cm tall. Sea urchin recruits were frequently observed among the hydroids, potentially using the stinging nematocysts as a defensive fortress. Weak positive relationships of sea urchin recruits with the upright, fleshy bryozoan *Alcyonidium* and multiple genera of tunicates, Ascidiacea, could be due to both the biogenic structure offered by these taxa and their potential provisioning of a food source. Sea urchin recruits may be seeking refuge from other predators in the complex structure and could also be feeding on the biofilms or organisms themselves (Zhang et al. 2014).

Crabs are known to prey upon small sea urchins, and in some cases can regulate their demography and ecological role as a grazer (Steneck et al. 2013, Fagerli et al. 2014, Feehan et al. 2014). Our finding that sea urchin recruits showed strong negative correlations with *Pugettia* crabs fits with observations from other systems with *S. droebachiensis* in the Gulf of Maine and Norway (Steneck et al. 2013, Fagerli et al. 2014), and presents a potentially alternative pathway to demographic regulation of sea urchins in the absence of their keystone predator, the sea otter.

However, while *Pugettia* were observed, and negatively correlated in barren grounds, they are unlikely to be able to control sea urchin demographics in such a sea urchin-dominated habitat, but may alter behavior (Hagen et al. 2002). The possible effect of *Pugettia* on sea urchin recruits is likely to be limited to kelp forests, where sea urchins occur in lower densities, the crabs in higher densities, and where the crabs are able to prey upon small, newly settled individuals (Steneck et al. 2013). Such regulation of small sea urchins by mesopredators can be critical in controlling demographics, even in the presence of sea otters, as evidenced by increases in urchins following the loss of *Pycnopodia* due to the recent sea star wasting epidemic in the North Pacific (Burt et al. 2018). We did observe *Pycnopodia* and many other sea stars during this study; however, they were often deeper than our sampling depth and did not generally occur in our surveys and, therefore, did not emerge as significantly correlated with sea urchin recruits.

Sea urchin biomass was not significantly correlated with sea urchin recruits in this study; however, density of large sea urchins was inversely correlated with density of sea urchin recruits. There is evidence that large sea urchins will displace smaller conspecifics in pursuit of food (Narvaez-Diaz 2018) — and even cannibalize small sea urchins (LeGault & Hunt 2016). It could be that the dearth of sea urchin recruits at some islands, such as Attu and Nizki/Alaid, is due to a preponderance of large sea urchins. Large sea urchins are quite mobile and will cover meters of the sea floor per day in search of food, while small urchins may opt for a more sedentary, cryptic lifestyle (Dumont et al. 2004). These ontogenetic shifts in behavior lead to differences in growth, where small sea urchins express slower growth than large urchins due to fewer opportunities to feed on high quality food (Himmelman 1986). The relationship between larger sea urchins and new recruits may also be based on larval supply. Some islands, and even some sites within islands, may differ in the supply of larval sea urchins. While larval supply has not been examined at these islands/sites, it should be noted that for this study, some barren and kelp sites within an island were only tens of meters apart, so larval supply was probably similar.

In the central and western Aleutians, sea urchin recruitment is influenced by patterns of sea urchin size structure, probably in combination with the associated biological community. The findings of this study have revealed that specific species correlate with sea urchin recruitment, which was manifested

in both alternate stable states, barren grounds and kelp forests. To our knowledge, this is the first paper to demonstrate this potential relationship. While patterns of community structure are obviously different between habitats, our findings suggest that within habitat differences in community structure, specifically the preponderance of the specific taxa identified in this study, could influence the ability for temperate reef systems to flip between alternate stable states by shaping patterns of sea urchin recruitment.

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