KELP FORESTS AND BARREN GROUNDS: PHLOROTANNIN PRODUCTION AND HOLDFAST COMMUNITY STRUCTURE IN THE ALEUTIAN DRAGON KELP, *EUALARIA FISTULOSA*

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A

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Abstract

The canopy forming kelp *Eualaria fistulosa* inhabits two organizational states throughout the Aleutian archipelago, kelp forests and barren grounds. Urchin abundance and behavior determines which state dominates in any given area. Sporophyll phlorotannin content and holdfast epibiont fauna were investigated at multiple islands along the Aleutian archipelago to determine how the organizational state affects the production of secondary metabolites and the taxon richness, abundance and biomass of holdfast communities. Barren ground sporophylls had higher phlorotannin content than kelp forest sporophylls, although grazing rates on sporophylls from each state did not differ during *in situ* grazing experiments. The taxon richness, abundance and biomass of holdfast communities were similar between kelp forests and barren grounds at all islands, although these communities varied among islands and were mostly driven by holdfast volume. These results suggest that physical differences such as light and nutrient availability in the kelp forest structure between organizational states may be responsible for differences in phlorotannin content, but that these differences are not reflected in the holdfast community structure. It appears that barren ground holdfast communities are remnants of a once forested area.

Dedication Page

This thesis is dedicated to Eveline Blanka Schuster.

Born July 30, 1946

Died May 23, 1994

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Acknowledgements

Without the opportunities provided by my advisor Dr. Brenda Konar I would not be a graduate student, and this work would not have been accomplished. The idea for this study came from a conversation between Brenda and Dr. James Estes while I was a volunteer working in the Aleutian Islands. At the time I was simply glad to be diving and counting sea urchins. Since then I've found a world of opportunity in marine science that I never thought existed even a few years ago. I would also like to thank Dr. Rolf Gradinger for great advice when I needed it.

My graduate committee members, Drs. Katrin Iken and Ken Coyle, were instrumental in the lab work associated with this project. Katrin taught me to extract phlorotannins, gave good advice when I needed it and sparked my interest in chemical ecology. Ken's taxonomic knowledge was invaluable to my amphipod identifications. Max Hoberg and Heloise Chenelot sparked my interest in marine invertebrates and gave me the taxonomic knowledge, and patience, necessary to take on a project of this magnitude.

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Introduction[1]

Kelp forests are highly structured habitats that support a diverse faunal community. In temperate regions, kelp forests create complex physical structure at the surface, midwater and benthic levels, providing food and shelter for a diverse fauna of fish (Deza and Anderson 2010) and invertebrates (Arkema et al. 2009). In some regions, kelp forests can be found in an alternate stable state, which is most often a deforested community dominated by sea urchins and encrusting coralline algae (Konar and Estes 2003; Gagnon et al. 2004; Wright et al. 2005). This alternate state, known as a barren ground, can persist for years and often requires a major disturbance or a decline in herbivore abundance to allow the kelp forest state to return (Ebeling et al. 1985; Gagnon et al. 2004). In general, sea urchin abundance and behavior will determine which state will dominate a specific area at any given time (Harrold and Reed 1985; Scheibling et al. 1999; Konar and Estes 2003). Typically, abundant urchins that are actively grazing on intact kelp will create and maintain barren grounds. In contrast, fewer inactive urchins that are well fed on algal drift will not actively graze kelp forests and kelp forests will remain.

This study was carried out in the well-documented stable state kelp forest/barren ground system of the Aleutian archipelago (Estes and Duggins 1995; Estes et al. 1998; Konar and Estes 2003; Estes et al. 2004). Aleutian kelp forests are dominated by the canopy forming kelp *Eualaria fistulosa* and understory kelps of the genera *Saccharina, Agarum* and *Laminaria*. Historically, the sea otter (*Enhydra lutris*) has controlled the abundance of sea urchins (*Strongylocentrotus polyacanthus*) in the Aleutians, inhibiting the development of barren grounds (Estes and Palmisano 1974). Sea otter populations in the Aleutians rapidly declined in the 1990's (Doroff et al. 2003), releasing sea urchins from predation pressure and allowing their population numbers to drastically increase (Estes et al. 1998). Currently, most islands of the Aleutian archipelago are dominated by

[1] For submission to *Marine Biology*

a mosaic of large barren grounds with very high urchin densities and small patches of shallow-water kelp forests that are devoid of urchins (pers obs).

Despite the extreme grazing pressure in Aleutian barren grounds, some *Eualaria fistulosa* sporophytes can be found in this habitat (Edwards and Konar 2012), although they only persist for one generation of this biannual species and are much less abundant than in the kelp forest patches. Although mechanical exclusion of grazing urchins through whiplashing of the reproductive sporophylls may explain *E. fistulosa*'s persistence (Konar 2000), kelps may also use chemical mechanisms to deter grazing (Steinberg et al. 1995; Iken 2012). Most brown algae produce phlorotannins, polymers of phloroglucinol (Johnson and Mann 1986; Molis et al. 2006) that have been shown to be unpalatable to some grazers (Van Alstyne 1988; Peckol et al. 1996; Amsler and Fairhead 2006). Phlorotannin production can be induced by grazing (Winter and Estes 1992; Molis et al. 2006), although other factors such as light intensity (Cronin and Hay 1996; Pavia and Toth 2000) and nutrient availability (Arnold et al. 1995; Cronin and Lodge 2003) have been shown to also influence phlorotannin production. Phlorotannins are presumably costly to produce (Targett and Arnold 1998) and it has been suggested that, like other secondary metabolites, they are allocated preferentially to tissues that contribute the most to an individual's fitness, such as reproductive structures (Van Alstyne et al. 1999a; Toth and Pavia 2007). In *E. fistulosa,* the reproductive structures (i.e., sporophylls) surrounding the base of the alga just above the holdfast are the first tissue encountered by urchins as they approach the sporophyte. I hypothesized that barren ground sporophytes may be producing high levels of phlorotannins in their sporophylls to deter urchin grazing, thus also protecting the holdfast communities from grazing disturbance. Holdfast communities may or may not be influenced by phlorotannin levels in the sporophylls.

Holdfasts tend to support the most diverse epifaunal community associated with any macroalgal part (Christie et al. 2003). The holdfast attaches individual kelp to hard substratum and, in *Eualaria fistulosa*, is formed by intertwining haptera that grow from

the meristematic tissue at the base of the stipe (Bartsch et al. 2008). These holdfasts provide spatially complex habitat for a very diverse macrofaunal assemblage of mobile and sedentary invertebrates (Smith et al. 1996). Numerous descriptive and experimental studies have used kelp holdfast communities to investigate ecological questions about community structure in relation to habitat size and habitat fragmentation (Ojeda and Santelices 1984; Goodsell and Connell 2002; Blight and Thompson 2008). The abundance and diversity of kelp holdfast communities is directly related to the size of the habitat, in this case the holdfast volume (Thiel and Vasquez 2000; Tuya et al. 2011). In physically static habitats, colonization follows successional patterns in which early colonizers are replaced or outcompeted by later colonizers (Farrell 1991; Bram et al. 2005). Biogenic habitats that grow throughout their life time are not as space limited as abiotic habitats and display a different pattern of colonization in which early colonizers may co-exist with later colonizers (Ojeda and Santelices 1984). Thus, in kelp holdfasts, differences in community structure can be a product of holdfast volume.

Since biogenic habitats are created by living organisms, they are sensitive to a variety of environmental drivers. For example, natural processes such as storms and herbivory are common in nearshore areas and can lead to habitat fragmentation, isolating communities once part of a larger, contiguous habitat (Ebeling et al. 1985; Gagnon et al. 2004). Fragmentation can result in subsequent changes in the diversity and abundance of organisms utilizing biogenic habitats (Cranfield et al. 2004; Anderson et al. 2005; Reed and Hovel 2006). In kelp forests, fragmentation can create a mosaic of rich algal assemblages surrounded by bare substratum (Witman and Dayton 2000). In this bare matrix, individual kelp sporophytes can survive.

In this study I investigated the following hypotheses in kelp forests and adjacent barren grounds at 14 islands spanning 1400 km of the Aleutian archipelago. I first hypothesized that the phlorotannin content of *Eualaria fistulosa* sporophylls would be higher in barren grounds than in kelp forests because of the higher urchin abundance at barren states. Second, I expected that urchin grazing rates would be lower on

phlorotannin-rich barren ground sporophylls than on sporophylls from kelp forest individuals. I further hypothesized that the taxon richness and abundance of *E. fistulosa* holdfast communities would be higher in kelp forests than in the adjacent barren grounds because of the dense macroalgal matrix in kelp forests, and would also vary among islands because of differences in the dispersal ability of invertebrates along the large geographic range in this study. Finally, I hypothesized that holdfast volume would be the most important environmental variable in predicting holdfast community structure.

Methods

Study Sites

Sporophyll and holdfast samples were collected from *Eualaria fistulosa* in summer 2009 at four islands along the Aleutian archipelago (Fig. 1, Table 1) at Chuginadak, Adak, Tanaga and Little Kiska. At Atka only holdfasts were collected. In addition, *E. fistulosa* sporophylls were also collected at three other islands, Unalaska, Rat and Shemya. At each island, a site was defined as a kelp forest with understory and visually having low urchin abundance bordered by a barren ground with little understory and visually having high urchin abundance, with the barren grounds having remnant *E.fistulosa* individuals. Due to logistical constraints, sporophylls for feeding experiments were collected at only five islands in 2010, Unalaska, Tanaga, Rat, Amchitka and Shemya (Table 1). Feeding experiments with these sporophylls were prepared during ship transit to other study locations and were then carried out *in situ* in barren grounds at the following ten islands, Yunaska, Seguam, Atka, Adak, Tanaga, Skagul, Rat, Kiska, Alaid and Agattu. All sites were similarly exposed to swell and wave action, and consisted primarily of a hard substratum between 5 and 10 m deep.

Sampling Methods

At each site, one holdfast and three sporophylls were collected from seven *Eualaria fistulosa* sporophytes in the kelp forest and seven in the barren ground using SCUBA. Individual sporophytes were haphazardly selected within their respective habitat and sporophylls and holdfasts were collected by removing the main blade at the top of the stipe, leaving holdfast and sporophylls in place. Then a fine mesh bag (< 0.5 mm) was placed over the holdfast and the haptera were pried from the substrate with a knife. Three sporophylls from each plant were frozen for later phlorotannin extractions and other sporophylls discarded.

The holdfast community was retained for analysis as follows. Each bag containing a holdfast was rinsed onto a 1.0 mm mesh screen, the contents of which plus the holdfast were placed in a jar and fixed in a 4% formaldehyde-seawater solution buffered with hexamethylenetetramine. Approximately eight weeks later, holdfasts were rinsed in fresh water over a 1.0 mm sieve and transferred to 50% isopropyl alcohol for preservation. Each holdfast was dissected and all organisms were identified to the lowest taxonomic level possible, counted and weighed to the nearest milligram while damp. To investigate relationships between holdfast volume and the holdfast community, displacement volume was determined to the nearest milliliter for each holdfast after the removal of all fauna.

To determine the influence of targeted environmental variables on holdfast community composition, habitat data were collected adjacent to each sampled holdfast by visually estimating coralline and total foliose algal percent cover and counting urchin abundance in three haphazardly placed 0.25 m^2 quadrats. Along with these habitat data, latitude, longitude, holdfast volume and sporophyll phlorotannin content were assigned to each holdfast.

Urchin Feeding Experiments

To test whether urchin grazing rates were different on *Eualaria fistulosa* sporophylls collected in kelp forests or barren grounds, a series of *in situ* feeding experiments were conducted. Due to low urchin densities in kelp forests, experiments were carried out only in urchin barrens at ten islands (Table 1). At each island, two treatments consisted of three to four either kelp forest or barren ground sporophylls (total sporophyll weight per treatment ~15-30 g) attached to the center of a brass bar that weighted the treatments to the seafloor. Controls for autogenic weight change of sporophylls consisted of the same number as above of either kelp forest or barren ground sporophylls enclosed in 10 cm x 10 cm plastic cages with 3 mm mesh sides, also attached to brass bars. Each treatment and control consisted of four replicates (n= 16 experiments per site). Treatments and controls were haphazardly placed in the barren area at each site for one hour. To determine sea urchin grazing rates, sporophylls were weighed before and after the one hour exposure. Weight changes (1 g accuracy) in treatments were adjusted in a paired design by those determined for controls. Additionally, 75-150 urchins were collected haphazardly after each experiment from the same area and urchin test size was measured (1 mm accuracy) to determine size frequency of the urchins at each site.

Phlorotannin Purification and Quantification

To compare *Eualaria fistulosa* phlorotannin content in kelp forests and barren grounds, sporophyll phlorotannin extracts were prepared according to the 2, 4-dimethoxybenzaldehyde (DMBA) assay of Stern et al. (1996). This colorimetric assay uses a species-specific standard curve to determine phlorotannin content from absorbance values following the methods of Ragan and Glombitza (1986) as modified by Steinberg and van Altena (1992). For the standard, approximately 140 g of sporophyll tissue, representing tissue from all islands, was homogenized in 0.5 L 80% methanol (MeOH) and extracted in the dark at 0°C for 24 h. The extract was centrifuged to remove precipitates and rotary evaporated at 35°C. Dried extract was re-dissolved in 0.25 L 80% MeOH and adsorbed onto microcrystalline cellulose. The cellulose was packed onto a

column and eluted with toluene to remove pigments, then washed with 2:1 acetone:water to obtain the phlorotannin fraction (Stern et al. 1996). The acetone solution was dried under reduced pressure, re-dissolved in water and freeze dried for 24 h. The dried extract was weighed and dissolved in 80% MeOH to create a purified phlorotannin stock solution of 50 μg/μL. The standard curve was determined using 1.25 μg/μL, 2.50 μg/μL, 3.75 μg/μL, 6.25 μg/μL, and 12.50 μg/μL aliquots from the phlorotannin stock solution.

For determination of phlorotannin concentrations in sporophylls, a total of ~0.25 g tissue subsampled from the three sporophylls collected from each *Eualaria fistulosa* (n=7 per site and state) were homogenized (Fischer Scientific Power Gen 500) and extracted in 80% MeOH water at 0°C for 24 h. The colorimetric working reagent was prepared daily by mixing equal volumes of DMBA (2% by mass in glacial acetic acid) and hydrochloric acid (16% by volume in glacial acetic acid). Phlorotannin concentrations were measured on a solution of 2.5 mL of working reagent, 10 μL of *N*, *N*-dimethylformamide and 400 μL of either sporophyll extract or known concentrations of purified phlorotannins for standard curves. Absorbance was determined at 510 nm after 60-min incubation of the reaction mixture at 30°C. A blank of 400 μL 80% (MeOH) was used to account for color formation in the absence of phlorotannins.

Statistical Analyses

To test whether *Eualaria fistulosa* phlorotannin content varied at each site between kelp forests and barren grounds, or amongst the five islands, a two-factor ANOVA was used. Unpaired 2-sample t-tests were used to investigate the differences in phlorotannin content between kelp forests and barren grounds at each island individually. An unpaired 2-sample t-test was also used to compare urchin grazing rates between *E. fistulosa* sporophylls collected from kelp forests and barren grounds. Significance level for these analyses was set at α=0.05.

Abundance and biomass data from holdfast communities were standardized to holdfast volume and fourth-root transformed in order to down weigh the contributions of quantitatively dominant species to the similarities calculated among samples. Multi-dimensional scaling ordinations (MDS) based on Bray-Curtis similarity matrices were calculated with the software package PRIMER-E (Plymouth Routines in Multivariate Ecological Research, 6.0) to visually represent multivariate differences between kelp forest and barren ground holdfast communities. A one-way analysis of similarity (PRIMER-E: ANOSIM) tested for differences between these communities as well as differences in the holdfast communities among islands. The similarity percentage (SIMPER) analysis in PRIMER-E was used to identify the taxa contributing most to the similarity within island holdfast communities and dissimilarity among island holdfast communities. A single-factor ANOVA tested whether holdfast volume varied between kelp forests and barren grounds at each island. Regressions on taxon richness, abundance and biomass versus holdfast size were analyzed using the R statistical package version 2.14.1.

To quantify the influence of environmental variables on holdfast communities, the BIO-ENV test in PRIMER-E was used. This test finds the best match between the multivariate among-sample patterns of an assemblage and the environmental variables associated with those samples. The environmental variables used in this analysis included holdfast volume, phlorotannin content, coralline and foliose algal cover, urchin density, latitude and longitude.

Results

Phlorotannin Content

In general, *Eualaria fistulosa* sporophylls from kelp forests had significantly lower mean phlorotannin content (3.08 ± 0.25% dry weight (dw)) than tissue from barren grounds (3.79 ± 0.19% dw) (Table 2). There was, however, also a significant interaction between

habitat type and island (Table 2). At the seven islands sampled for sporophyll tissue, phlorotannin content was significantly lower in kelp forests than barren grounds at four islands. At one island, kelp forest sporophylls had significantly higher phlorotannin content than those from barren grounds, and at two islands there was no difference in phlorotannin content between kelp forest and barren ground sporophylls (Fig. 2). Sporophylls from islands in the central Aleutian archipelago had higher phlorotannin content in barren grounds than in kelp forests, while sporophylls from islands at the east and west ends of the archipelago did not (Fig. 1 and 2). The individuals with maximum (7.53% dw, barren) and minimum (0.53% dw, forest) phlorotannin contents were both observed at Chuginadak Island towards the eastern end of the study area. Holdfast volume was not correlated with phlorotannin content (Linear Regression, $r^2 = 0.03$, $F_{1,2} = 0.08$, $P = 0.70$).

Urchin Feeding Experiments

There was no difference in grazing rates on sporophylls collected from the two stable states (Unpaired t-test, $t_{10} = 1.28$, $P = 0.22$). Grazing rates were negligible at some islands; therefore, only islands where urchins consumed more than 0.5 g/hr of sporophyll tissue were used to compare grazing rates between kelp forest and barren ground sporophylls. Urchin size and grazing rates varied among islands (Table 3).

Holdfast Communities in Kelp Forest and Barren Ground Habitats

Eualaria fistulosa holdfasts contained 61 taxa representing 10 phyla combined for kelp forest and barren ground habitats (Table 4). From 68 holdfasts, a total of 17,984 organisms were counted with a total biomass of 168.1 g. Amphipods and polychaetes were the most species-rich groups. Nemerteans, polychaetes, amphipods and other arthropods accounted for 78% of total abundance, while nemerteans, polychaetes, cnidarians and flatworms accounted for 71% of total biomass.

Mean taxon richness (forest: 19.9 ± 1.6 taxa, barren: 19.9 ± 1.3 taxa) was very similar between the two states. MDS ordinations representing holdfasts from all islands combined showed no visible difference between kelp forest and barren ground holdfast communities in either abundance or biomass (Fig. 3). An ANOSIM test supported this conclusion ($R = 0.016$, P = 0.11% and $R = 0.016$, P = 0.11% for abundance and biomass, respectively). Mean abundance (forest: 2.20 ± 0.01 ind/mL, barren: 2.25 ± 0.01 ind/mL) and mean biomass (forest: 0.003 ± 0.001 g/mL, barren: 0.003 ± 0.001 g/mL) were also similar between the two states.

When islands were analyzed separately using an ANOSIM test, four of five islands did not show significant differences between kelp forest and barren ground holdfast communities (Chuginadak: $R = 0.185$, P = 0.03%; Atka: $R = 0.097$, P = 0.07%; Tanaga: $R = 0.146$, P = 0.04%; Little Kiska: $R = 0.113$, P = 0.1%). At Adak, the kelp forest and barren ground holdfast communities were significantly different (ANOSIM $R = 0.394$, $P < 0.01$). Dissimilarity between kelp forest and barren ground holdfast communities at Adak was driven by several different taxa, with most contributing less than 5% to the total dissimilarity.

When island holdfast community composition was compared with both stable states combined per island, MDS ordination separated the five islands into slightly overlapping groups (Fig. 4). An ANOSIM test between holdfast communities among islands was significant ($R = 0.409$, $P < 0.01$). The taxa that contributed the most to holdfast community differences among islands were gammarid amphipods, polychaetes, tanaids, flatworms and nemerteans (SIMPER, Table 5). The taxa contributing most to similarities in holdfast communities within islands were gammarid amphipods, polychaetes, flatworms and nemerteans (SIMPER, Table 5). Holdfast volume was positively correlated with the similarity percentage at each island (Linear Regression, $r^2 = 0.77$, $F_{1,3} = 14.23$, P = 0.03), indicating that islands with larger holdfasts had more homogenous holdfast communities than islands with smaller holdfasts.

Holdfast volumes ranged from 5-415 mL and were significantly different among islands (ANOVA, $F_{(4,65)} = 11.49$, $P < 0.001$), but showed no significant difference between kelp forests and barren grounds within islands (Table 6). Taxon richness, abundance and biomass were correlated with holdfast volume (Fig. 5). Taxon richness increased rapidly with increasing size of the holdfasts up to about 100 mL of holdfast volume. In larger holdfasts the increase in taxon richness was slower. BIO-ENV analysis attributed 49% of the variation in holdfast community structure to holdfast volume alone. Other habitat variables, including phlorotannin content, coralline and foliose algal cover, urchin density, latitude and longitude each contributed less than 1% to community structure.

Discussion

Kelp forests and barren grounds in the Aleutian archipelago form a mosaic of alternate stable states with very different biological and physical landscapes. The forcing factor between stable states in the Aleutians is grazing activity by the sea urchin, *Strongylocentrotus polyacanthus* (Estes and Duggins 1995; Estes et al. 1998), which is found in low densities in kelp forests and extremely high densities in barren grounds. Phlorotannin content was higher in barren ground sporophylls than in kelp forest sporophylls, indicating that the differences in the state of the community, and thus grazing pressure, may be influencing *Eualaria fistulosa's* production of secondary metabolites. Despite the stark differences reported in macroalgal and urchin community structures between kelp forest and barren grounds (Konar and Estes 2003), there was no difference in *E. fistulosa* holdfast community structure between the two states in this study. As in other studies where the relationship between holdfast size and the holdfast community was investigated, holdfast volume was the most accurate predictor of community taxon richness, abundance and biomass (this study; Ojeda and Santelices 1984; Smith et al. 1996; Thiel and Vasquez 2000).

Phlorotannins were examined in this study to determine whether the difference in urchin abundance between Aleutian kelp forests and barren grounds was reflected in the allocation of secondary metabolites to reproductive tissues in *Eualaria fistulosa.* Since kelps have been shown to produce phlorotannins in response to grazing (Hammerstrom et al. 1998; Lüder and Clayton 2004), and urchin abundances are much higher in barren grounds, I hypothesized that phlorotannin content would be higher in barren ground sporophytes than kelp forest sporophytes. Accordingly, phlorotannin content was higher in barren ground sporophytes (3.78% dw) than in kelp forest sporophytes (3.08% dw) and was well within the range of results reported for other Laminariales, e.g. *Laminaria hyperborea* in Norway 2.5% dw (Norderhaug et al. 2003), *Macrocystis pyrifera* in California 1.02 - 1.04% dw (Van Alstyne et al. 1999b) and *Agarum clathratum* and *Saccharina groenlandica* in Alaska 1.0 – 5.0% dw (Dubois and Iken 2012). As in several brown algae in other northern areas (Toth and Pavia 2000; Pavia et al. 2003), *E. fistulosa* phlorotannin content in the Aleutians showed variation within populations (islands) and between populations, indicating that production of secondary metabolites is a phenotypically plastic trait. This plasticity can be modulated by light availability (Cronin and Hay 1996), exposure to nutrients (Arnold et al. 1995), and grazing pressure (Pavia and Brock 2000).

Physical and chemical factors such as light availability (Cronin and Hay 1996) and exposure to nutrients (Arnold et al. 1995) can induce the production of phlorotannins. Sporophytes of *Eualaria fistulosa* persisting in barren grounds are sparsely distributed compared to the dense sporophytes occurring in kelp forests, and are thus presumably under less competition for light (Clark et al. 2004) and may also be exposed to greater currents, and more nutrients (Jackson 1998; Hurd 2000), than sporophytes in kelp forests. Barren ground sporophytes produce up to three times as many zoospores as kelp forest sporophytes (Edwards and Konar 2012), indicating that more resources (i.e., sunlight and nutrients) are available to sporophytes in barren grounds than in kelp forests. I suggest that these additional resources could contribute to the differences in phlorotannin content observed in this study.

Grazing pressure is often evoked as an important driver of plant chemical defense mechanisms. In particular, the optimal defense theory (ODT) postulates that the allocation of defensive secondary metabolites to different tissue types corresponds with the tissue's contribution to overall fitness and the risk of attack by grazers (Pavia et al. 2002; Pavia and Toth 2008). Thus, tissues that contribute the most to an organism's fitness are better protected from herbivores that are sensitive to the defensive secondary metabolites, such as phlorotannins. Sporophylls as reproductive tissue are important to the organism's fitness, and while the differential distribution of phlorotannins to various thallus parts was not investigated in this study, the intertidal kelp *Alaria nana,* which has very similar morphology to *Eualaria fistulosa*, produced higher phlorotannin content in reproductive than vegetative tissues (Pfister 1992). Chemical defenses can also be induced by grazing activity (Amsler 2001; Jormalainen and Honkanen 2008), although phlorotannin induction in response to herbivory has had mixed experimental support, with responses differing among algal and herbivore species (Toth and Pavia 2002; Amsler and Fairhead 2006; Fairhead et al. 2006). Strong grazing pressure in urchin barrens might force phlorotannin production, but inducible defenses are mostly linked to small mesograzers such as gastropods and amphipods that are non-lethal to the plant (Toth and Pavia 2007). In contrast, larger grazers such as urchins typically consume the alga before induction can take place (Iken 2012). Therefore, in the Aleutian archipelago, where grazing pressure is mostly exerted by large sea urchin grazers (Estes et al. 1998), inducible defense may not be an efficient mechanism to deter herbivory.

To determine whether the observed differences in phlorotannin content influenced urchin grazing rates, urchins were offered sporophylls collected from forests and from barrens. I hypothesized urchin grazing rates would be higher on sporophylls collected from kelp forests than sporophylls collected from barren grounds. However, there was no difference in grazing rates on sporophylls collected from each state, indicating that in this study there was no direct connection between urchin grazing and phlorotannin production, i.e., that phlorotannins may not act as a defensive compound against this grazer (see Amsler and Fairhead 2006). Phlorotannins are often not toxic, but reduce assimilation efficiency

over time, and may have no immediate negative effect on the consumer (Boettcher and Targett 1993). Thus, short *in situ* experiments may not have detected differences in assimilation efficiency that could occur over longer time periods due to higher phlorotannin concentrations in barren ground sporophylls.

Highly variable urchin grazing rates among islands were most likely a product of urchin size, as small urchins graze at lower rates than large urchins (Kasim 2009). At three of four islands where urchins grazed less than 0.5 g/hr, mean test diameter was 20 mm or less, indicating that in the Aleutians, small urchins graze very little and that urchin size at an island could impact the vulnerability of *Eualaria fistulosa* to grazing. Equal grazing rates in kelp forests and barren grounds could also be a product of nutritional limitation in barren grounds, as urchins in barren grounds have little to no algae available for consumption (Konar and Estes 2003). Consequently, barren ground urchins have less caloric content than kelp forest urchins (Stewart and Konar 2012). Since feeding experiments were carried out in barren grounds where urchins are food limited, it is likely that urchins did not strongly discriminate among possible food sources in the feeding experiment, regardless of phlorotannin content. Similar results were reported at the island Shemya (Konar 2000), where barren ground urchins consumed large amounts of experimentally offered *Desmarestia viridis*, a sulfuric acid producing alga that is otherwise often unpalatable to grazers (Thompson 1988). However, when *D. viridis* is naturally occurring (i.e., not experimentally offered) it is not grazed due to its ability to mechanically exclude urchins through whiplash (Konar 2000; Gagnon et al. 2003). Mechanical grazer exclusion is also important in the maintenance of Aleutian kelp forests (Konar 2000) and likely contributes to the persistence of *E. fistulosa* in urchin barrens, as urchins do not approach the sporophyte when sporophylls are in motion (pers obs).

Based on the notion that high phlorotannin content in barren ground kelp could protect these holdfasts from urchin grazers, *Eualaria fistulosa* holdfast communities were investigated to test my hypothesis that the contrasting urchin abundances in the alternate states also influence holdfast community structure. Contrary to my expectations, *E.*

fistulosa holdfast communities were strikingly similar in terms of taxon richness, abundance and biomass between the two states. Though this similarity could be due to insufficient taxonomic resolution, the most likely explanation is the dynamics of the Aleutian stable state system. Grazing pressure can force changes between kelp forest and barren states (Estes and Palmisano 1974; Dayton et al. 1984; Konar and Estes 2003), often resulting in a mosaic of forest and barren habitats (Konar and Estes 2003). In other regions, holdfast fauna have been shown to migrate between habitats when surrounded by a suitable matrix such as understory kelps (Norderhaug et al. 2002; Waage-Nielsen et al. 2003) and if the majority of taxa are mobile. Movement among holdfasts in a kelp forest establishes homogenous communities of organisms in the forest (Norderhaug et al. 2002). In the Aleutians, remnant *Eualaria fistulosa* individuals are currently persisting in some barren habitats that were once kelp beds but have been overgrazed by sea urchins (Edwards and Konar 2012). Individuals of *E. fistulosa* in a kelp forest and remnant individuals remaining in a new adjacent barren after a change in state may, for a certain period of time, have similar holdfast community structure due to migration among holdfasts in the previous forest state (Norderhaug et al. 2002). Since *E. fistulosa* is a biannual species (Edwards and Konar 2012), and because only holdfasts from living individuals were collected, it can be assumed that holdfasts were less than two years old. Most organisms inhabiting *E. fistulosa* holdfasts have a life history longer than that of the holdfast itself, and thus barren ground holdfasts that remain after a change in state may not persist long enough for the holdfast communities to differentiate from those in kelp forests. Similar results have been reported for insect communities inhabiting bracket fungi in fragmented old growth forests where the composition of insect communities was the same in undisturbed and fragmented forests, most likely because the time since fragmentation was not sufficient for communities to differentiate (Komonen 2001).

Taxon richness in *Eualaria fistulosa* holdfasts was higher than values reported for holdfasts of the giant kelp, *Macrocystis pyrifera* in Chile (43 taxa, six phyla: Ojeda and Santelices 1984), where most organisms were identified to family, but lower than in holdfasts of *Ecklonia radiata* in New Zealand (351 taxa, 15 phyla: Anderson et al. 2005)

and *Laminaria hyperborea* in Norway (116 taxa: Norderhaug et al. 2002), where most organisms were identified to species. The lower holdfast diversity in *E. fistulosa* compared with *E. radiata* and *L. hyperborea* holdfast communities may be due to differences in taxonomic resolution, as identification in this study was mostly to family, while the identifications in the other two studies were mostly to species. Invertebrate communities in Aleutian kelp beds can be diverse, with up to 338 taxa (primarily identified to species) identified from the nearshore encrusting coralline habitat (Chenelot et al. 2011), indicating that increased taxonomic resolution in this study could place the diversity of Aleutian kelp holdfast communities on par with those found in New Zealand and Norway. Holdfast communities of *E. fistulosa* were dominated by peracarid crustaceans and vermiform organisms of the taxa Nemertea, Polychaeta and Turbellaria. This was similar to holdfast communities of *E. radiata* from New Zealand (Anderson et al. 2005) and *L. hyperborea* from northern Europe (Norderhaug et al. 2002), where peracarid crustaceans and polychaetes were the most abundant taxa. In contrast, *M. pyrifera* holdfasts from Chile were dominated by decapod crustaceans and echinoderms (Ojeda and Santelices 1984).

Holdfast volume is an important predictor of diversity (Smith et al. 1996; Thiel and Vasquez 2000). Mean holdfast volumes of New Zealand *Ecklonia radiata* (120 mL: Anderson et al. 2005) and United Kingdom *Laminaria hyperborea* (280 mL: Sheppard et al. 1980) are similar to those of *Eualaria fistulosa* (115 mL: this study). Also, the most abundant taxa are the same in the aforementioned kelp species, small mobile organisms such as peracarid crustaceans and polychaetes. Similarities in holdfast communities from different geographic areas seem to be primarily explained by similarities in holdfast volume, as small holdfasts are well suited for small taxa and exclude larger taxa. The extremely large holdfasts of Chilean *Macrocystis pyrifera* (up to 20,000 mL: Ojeda and Santelices 1984) are dominated by a very different set of taxa, including large echinoderms and hermit crabs (Ojeda and Santelices 1984). In *M. pyrifera* holdfasts, cavitation by sea urchins creates large spaces between haptera (Tegner et al. 1995), allowing larger organisms to colonize the holdfast. It is important to note that despite the

unique community structure of large *M pyrifera* holdfasts, smaller *M. pyrifera* holdfasts harbor a community more similar to that in the small holdfasts of *E. radiata, L. hyperborea* and *E. fistulosa* (this study; Ojeda and Santelices 1984). Similar community structure in holdfasts of comparable volume, regardless of geographic area, confirms that holdfast volume is an important predictor of holdfast community structure. Holdfast volumes were similar in kelp forests and barren grounds and may contribute to the similarity in community structure between the two states.

As in other studies of biogenic habitats (Ojeda and Santelices 1984; Kelaher et al. 2001; Komonen 2001), the diversity of *Eualaria fistulosa* holdfast communities reached a plateau as holdfast volume, and thus habitat complexity, increased. Here, holdfast volume explained half of the variation observed in community structure, while other habitat variables such as phlorotannin content, coralline and foliose algal cover, urchin density, latitude and longitude contributed less than 1% each to the variation. The sample discrimination similarity percentages (SIMPER) for each island were correlated with holdfast volume, indicating that large holdfast communities have less variation between samples than small holdfast communities. The impact of this correlation is reflected in the high diversity and similarity of the large Tanaga holdfast communities compared with the low diversity and low similarity of the small Adak holdfast communities. The only site where holdfast communities differed between forests and barrens was Adak Island. This may be due to the small holdfast size and corresponding low overall diversity. In the perennial kelps *Laminaria hyperborea* and *Macrocystis pyrifera,* holdfast volume is a product of age (Lobban 1978; Sheppard et al. 1980). Although the relationship between sporophyte age and holdfast volume has not been investigated in the biannual *E. fistulosa,* age is a likely explanation for the variation seen in holdfast volume and the subsequent differences between forest and barren holdfast communities at Adak Island.

Similar to another study in New Zealand across 290 km of coastline (Anderson et al. 2005), Aleutian holdfast communities differed across a large geographic range. In the present study, sites that extended 850 km across five islands had significantly different

holdfast communities. Different invertebrate dispersal ability to migrate or settle in new habitats is often responsible for large-scale variation in distribution patterns (Keever et al. 2009; Nikula et al. 2010). However, in this study, 17 of the 18 taxa contributing four percent or more to the SIMPER dissimilarity between islands were ubiquitous among islands. The broad distribution of important taxa driving differences among islands indicates that it is not presence or absence that most influences differences among islands, but the relative abundance of these taxa. Brooders, specifically the peracarid crustaceans, are a large portion of the taxa driving differences among islands. In marine habitats, brooders recruit to the immediate vicinity of their parents (Thiel 1999), yet many benthic invertebrates have regionally universal distributions (Highsmith 1985). Two mechanisms responsible for distributions of invertebrates living in algal habitats are planktonic larval dispersal and epipelagic dispersal of juveniles and adults by association with algal rafts (Nikula et al. 2010). The broad distribution of brooders in this study cannot be attributed to planktonic larval dispersal, but rafting, and possible long distance migration in the benthos, may explain their presence at all islands. In the Southern Ocean, over 25% of algal rafts contained holdfasts with living organisms, indicating a significant dispersal potential for holdfast organisms via algal rafts (Smith 2002). Planktonic larval dispersal is also common in some of the taxa driving differences among islands, such as the polychaetes (Wilson 1991), ophiuroids (Kasyanov 2001) and nemerteans (Turbeville 2002). The distribution of these taxa across the entire Aleutian archipelago is most likely due to oceanic dispersal of their planktonic larvae.

The dynamics of alternate stable states in the Aleutian archipelago have been extensively studied (Estes and Duggins 1995; Estes et al. 1998; Konar 2000; Konar and Estes 2003; Estes et al. 2004), but this research is the first to investigate *Eualaria fistulosa* phlorotannin content and holdfast communities in the context of an alternate stable state system. The most important generalization from this study is that despite the biological and physical differences between kelp forest and barren ground habitats, and despite the differences in phlorotannin content between the two states, the holdfast community composition is strikingly similar. This is contrary to studies in both terrestrial (Herkert

1994) and marine systems (Eggleston et al. 1998; Reed and Hovel 2006), where habitat fragmentation often increases or decreases diversity and alters the structure of communities utilizing a habitat. Similarities in kelp forest and barren ground holdfast communities indicate that organisms inhabiting kelp holdfasts in barren grounds are most likely remnants of a once forested area, and that the relatively short life history of *Eualaria fistulosa* may prevent the establishment of a unique barren ground holdfast community.

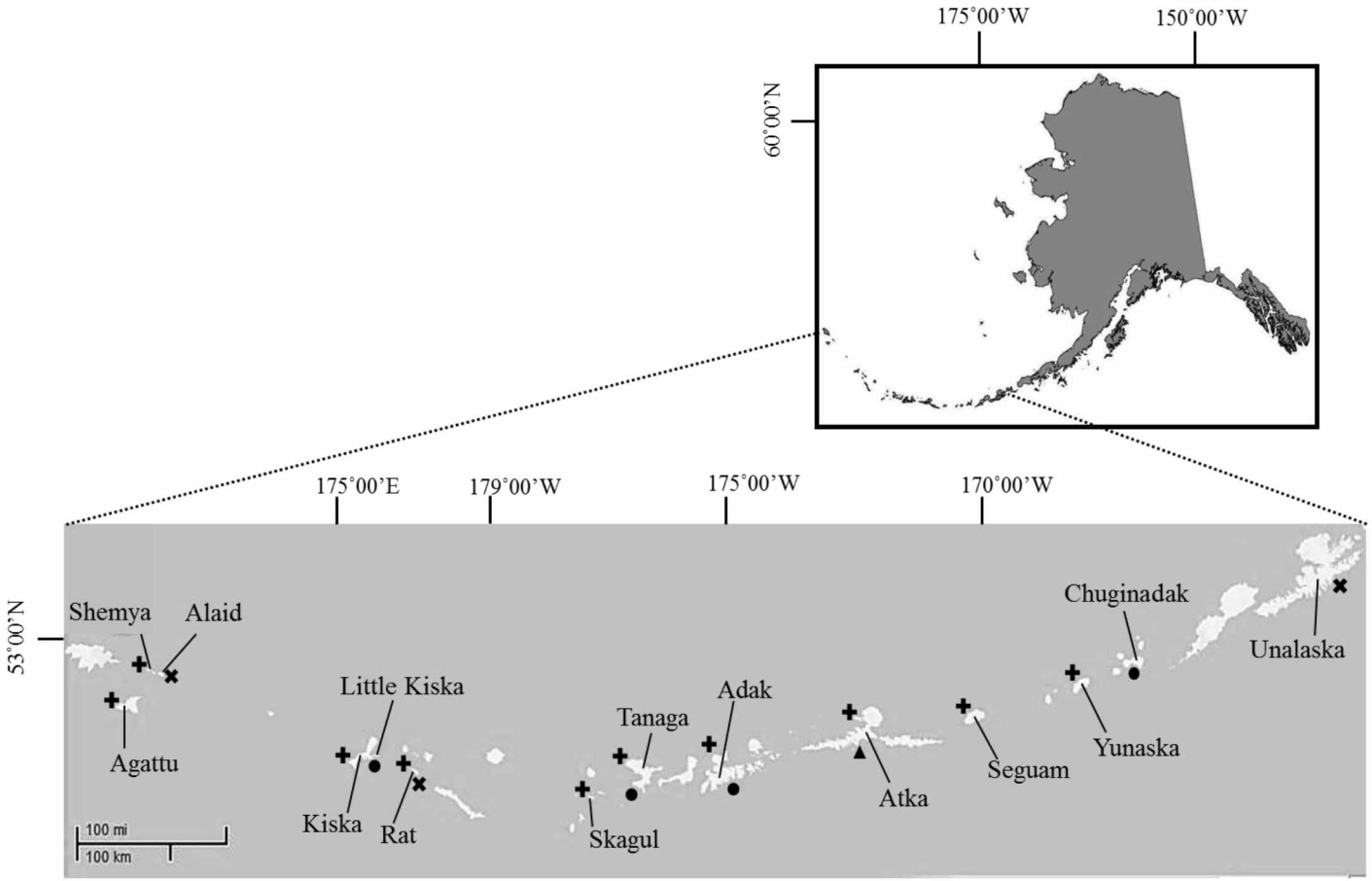

Figure 1. Map of Study Area. Black triangle: only holdfasts collected. Black circles: sporophylls and holdfasts collected in kelp forests and barren grounds. Black **x**: sporophylls collected in kelp forests and barren grounds. Black +: *in situ* feeding experiments in barren grounds.

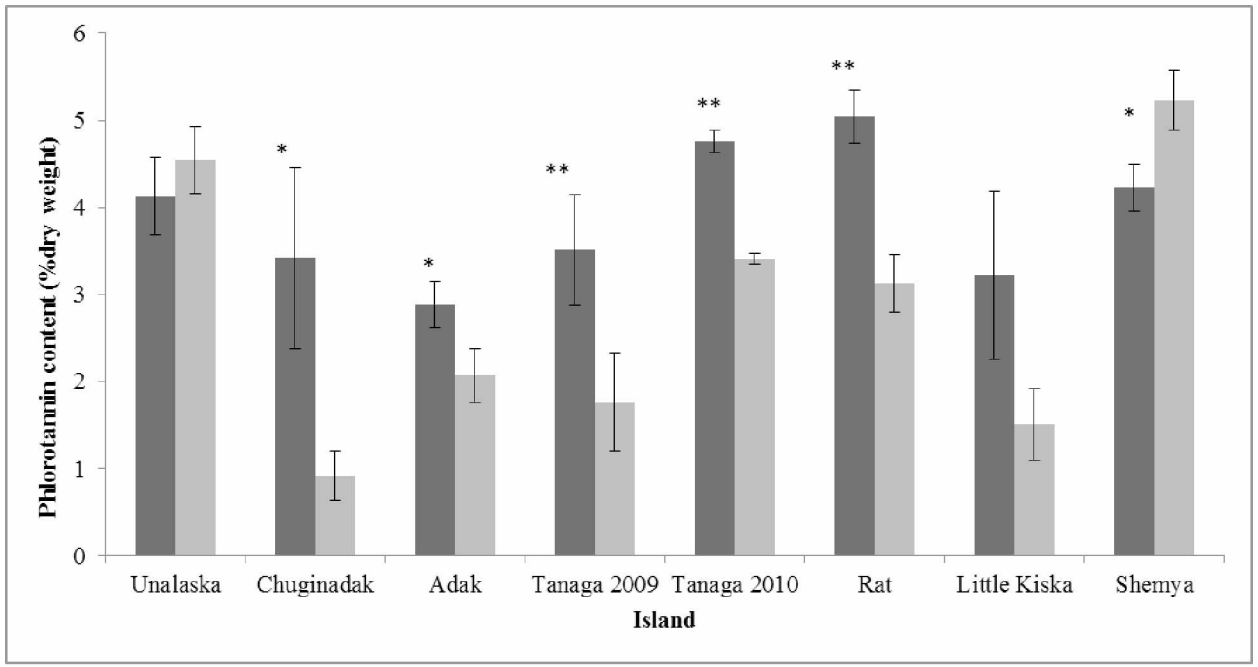

Figure 2. Sporophyll phlorotannin content (% dry weight) in kelp forests and barren grounds at seven islands along the Aleutian archipelago. Kelp forests are represented by light grey columns and barren grounds are represented by dark grey columns. Error bars: ± 1 s.e. * indicates significance at α =0 .05, and ** indicates significance at α = 0.01.

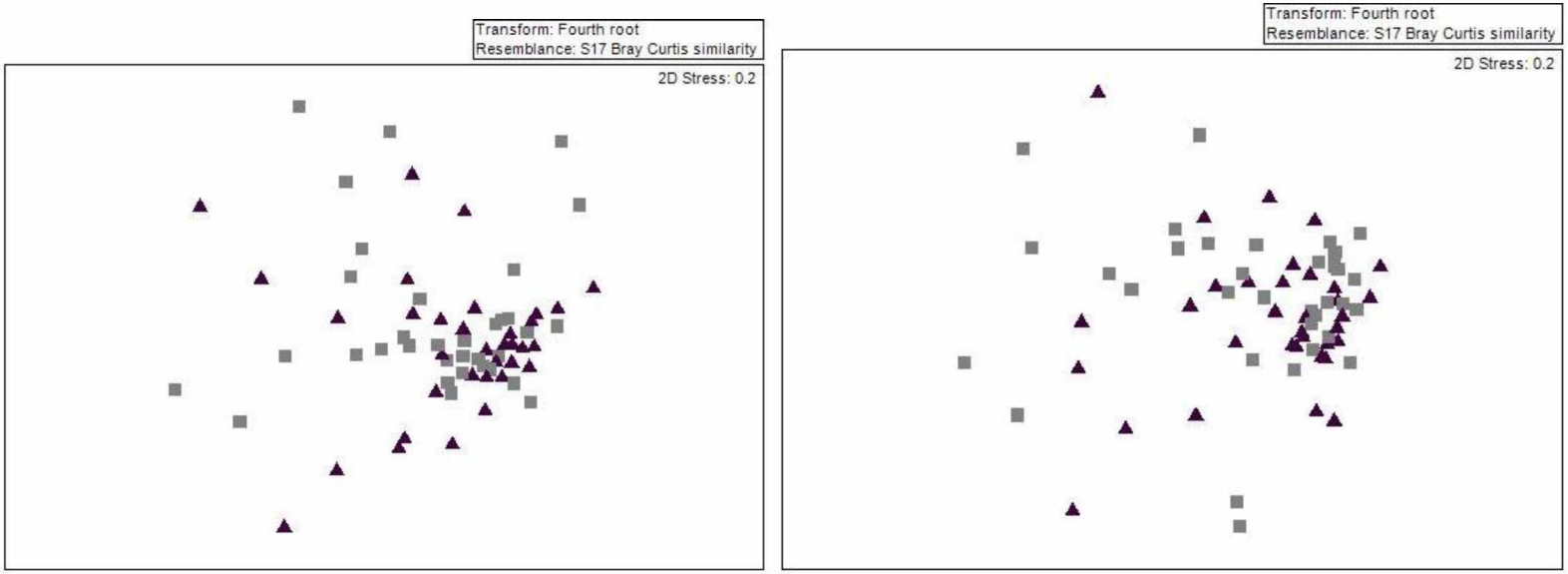

Figure 3: Two-dimensional multidimensional scaling plots using abundance (left) and biomass (right) of 68 holdfasts from kelp forests (grey squares) and barren grounds (black triangles) with all islands combined.

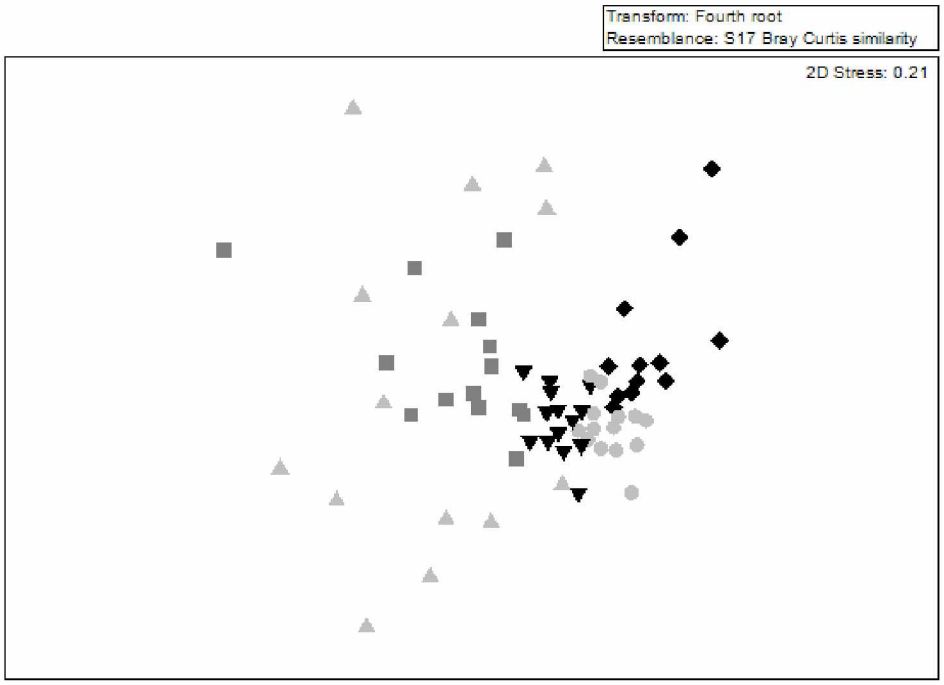

Figure 4. Two-dimensional multidimensional scaling plot of 68 holdfast communities (based on abundance, barren and forest holdfasts combined) from five islands (Chuginadak: light grey circle; Atka: dark grey square; Adak: light grey triangle; Tanaga: black triangle; and Little Kiska: black diamond) along the Aleutian archipelago.

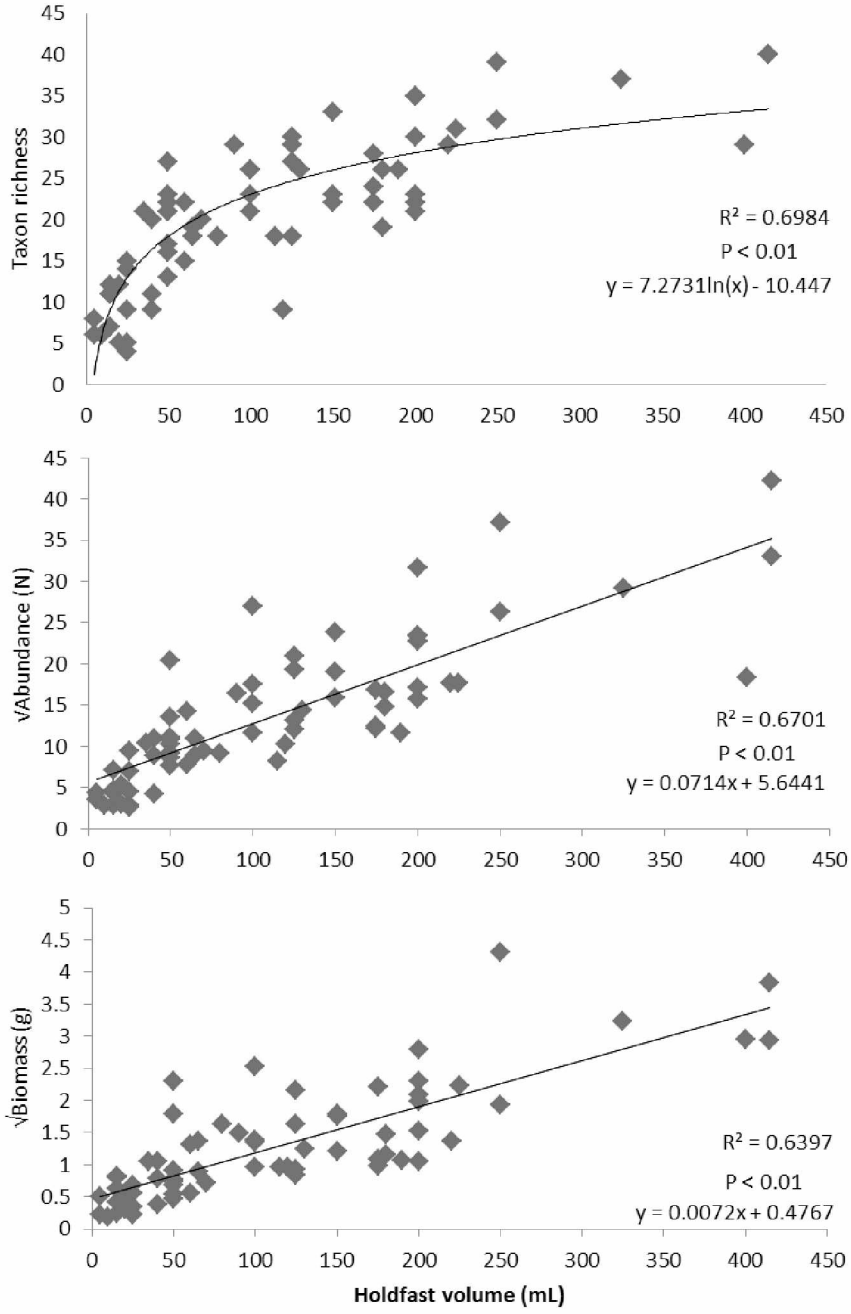

Figure 5: Relationships between holdfast volume (mL) and number of taxa, abundance and biomass for all islands combined. Abundance and biomass were square root transformed to reduce the influence of outliers.

Table 1: Coordinates for collection and experimental sites at 15 islands across the 1400 km study area in the Aleutian archipelago.

	Island	Latitude	Longitude
Holdfasts only collected	Atka	52°10'08"N	174°37'72"W
Holdfasts and sporophylls collected	Chuginadak	52°53'02"N	169°51'34"W
	Adak	51°52'09"N	176°36'55"W
	Tanaga	51°47'19"N	178°04'06"W
	Little Kiska	51°56'55"N	177°38'79"E
Sporophylls collected	Unalaska	53°38'49"N	166°25'44"W
	Rat	51°49'23"N	178°17'25"W
	Shemya	52°42'00"N	174°05'06"E
	Amchitka	51°31’29”N	178°57’17”W
Feeding experiments	Yunaska	52°35'44"N	170°40'27"W
	Seguam	52°16'30"N	172°26'35"W
	Atka	52°08'21"N	174°36'51"W
	Adak	51°52'31"N	176°37'18"W
	Tanaga	51°42'35"N	178°03'03"W
	Skagul	51°36'27"N	178°34'57"W
	Rat	51°47'26"N	178°17'08"W
	Kiska	51°56'15"N	177°36'28"E
	Alaid	52°45'02"N	173°54'26"E
	Agattu	52°23'27"N	173°33'27"E

Table 2: Analysis of variance of the phlorotannin content (% dry weight) in *Eualaria fistulosa* sporophylls collected from kelp forests and barren grounds at seven islands in the Aleutian archipelago.

Source of Variation	df	*MS*	*F*	P
Forest or Barren	1	31.983	37.1796485	< 0.05
Island	6	12.218	14.2030396	< 0.05
Interaction	6	3.144	3.6550860	< 0.05
Residual	56	0.860		

Table 3: Grazing rates (g/hr ± 1 s.e.) and mean test size (mm ± 1 s.e.) of sea urchins at ten islands in the Aleutian archipelago. Due to no difference in grazing rates between kelp forest and barren ground sporophylls, data for the two states were averaged (x = no data collected).

	Yunaska	Seguam	Atka	Adak	Tanaga	Skagul	Rat	Kiska	Alaid	Agattu
Grazing rate	4.8 ± 1.0	4.6 ± 0.4	2.9 ± 0.7	1.3 ± 0.5	0 ± 0	4.3 ± 0.6	0.1 ± 0.1	0.3 ± 0.2	2.3 ± 0.5	0.3 ± 0.2
Size (mm)	29.0 ± 1.5	x	x	40.0 ± 1.0	18.0 ± 0.9	35.0 ± 1.9	10.0 ± 0.4	19.0 ± 0.7	44.0 ± 2.0	45.0 ± 4.0

Table 4: List of invertebrates inhabiting holdfasts in kelp forests (F) and barren grounds (B) at five islands in the Aleutian archipelago. Abundance values are standardized to holdfast volume (ind/mL) and are the means at each island ± 1 s.e.

	Chuginadak		**Atka**		**Adak**		**Tanaga**		**Little Kiska**	
	F	**B**	**F**	**B**	**F**	**B**	**F**	**B**	**F**	**B**
Cnidaria										
Actinaria	0.08 ± 0.02	0.05 ± 0.02	0.01 ± 0.01	0.03 ± 0.02	0.02 ± 0.01	0.01 ± 0.01	0.10 ± 0.01	0.05 ± 0.01	0.02 ± 0.01	0.00 ± 0.00
Stauromedusae	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Turbellaria										
Turbellaria	0.16 ± 0.04	0.05 ± 0.02	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01	0.05 ± 0.00	0.07 ± 0.01
Annelida										
Hirudinea										
Hirudinea indetermined	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Polychaeta										
Acroceridae	0.02 ± 0.00	0.07 ± 0.01	0.00 ± 0.00	0.02 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.02	0.02 ± 0.01
Ampharetidae	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.02 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
Cirratulidae	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.01	0.03 ± 0.02	0.01 ± 0.00	0.00 ± 0.00
Dorvillidae	0.04 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01	0.00 ± 0.00	0.02 ± 0.01	0.03 ± 0.02	0.04 ± 0.02	0.01 ± 0.01	0.02 ± 0.01
Dysponetus pygmaeus (Levinsen, 1879)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01
Exogone sp.	0.07 ± 0.03	0.07 ± 0.03	0.03 ± 0.01	0.05 ± 0.03	0.03 ± 0.03	0.18 ± 0.08	0.27 ± 0.07	0.24 ± 0.10	0.01 ± 0.01	0.05 ± 0.03
Flabelligera	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lumbrineridae	0.06 ± 0.01	0.10 ± 0.04	0.10 ± 0.04	0.06 ± 0.06	0.00 ± 0.00	0.03 ± 0.03	0.04 ± 0.01	0.04 ± 0.02	0.00 ± 0.00	0.01 ± 0.00
Maldanidae	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Nereidae	0.06 ± 0.02	0.02 ± 0.00	0.05 ± 0.02	0.09 ± 0.03	0.04 ± 0.03	0.05 ± 0.02	0.27 ± 0.03	0.27 ± 0.07	0.00 ± 0.00	0.05 ± 0.03
Nereidae juvenile	0.01 ± 0.01	0.01 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01	0.02 ± 0.02	0.04 ± 0.02	0.01 ± 0.00	0.01 ± 0.01	0.01 ± 0.01
Orbiniidae	0.01 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

Table 4 Continued

Phyllodocidae	0.02 ± 0.01	0.03 ± 0.01	0.01 ± 0.01	0.03 ± 0.02
Polynoidae	0.01 ± 0.00	0.00 ± 0.00	0.45 ± 0.09	0.46 ± 0.22
Sabellidae	0.22 ± 0.08	0.01 ± 0.00	0.01 ± 0.01	0.07 ± 0.05
Spionidae	0.00 ± 0.00	0.01 ± 0.00	0.05 ± 0.02	0.01 ± 0.01
Syllidae	0.31 ± 0.07	0.42 ± 0.07	0.15 ± 0.05	0.11 ± 0.05
Terebellidae	0.07 ± 0.02	0.05 ± 0.01	0.08 ± 0.02	0.08 ± 0.05
Nemertea				
Nemertea indetermined	0.17 ± 0.05	0.10 ± 0.02	0.02 ± 0.01	0.08 ± 0.06
Mollusca				
Bivalvia				
Bivalvia indetermined	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Calyptraeidae				
Crepidula sp.	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cephalaspidea				
Cephalaspidea indetermined	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gastopoda				
Gastropoda indetermined	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01
Nudibranchia				
Nudibranchia indetermined	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Patellogastropoda				
Patellogastropoda indetermined	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Polyplacophora				
Polyplacophora indetermined	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Arthropoda (Crustacea)				
Pycnogonida				
Pycnogonida indetermined	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Decapoda				
Canceridae	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

0.02 ± 0.02	0.00 ± 0.00	0.05 ± 0.01	0.03 ± 0.01	0.03 ± 0.01	0.07 ± 0.02
0.07 ± 0.03	0.18 ± 0.05	0.01 ± 0.00	0.02 ± 0.01	0.01 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.05 ± 0.03	0.39 ± 0.10	0.66 ± 0.52	0.02 ± 0.01	0.02 ± 0.01
0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01	0.00 ± 0.00	0.03 ± 0.03	0.01 ± 001
0.07 ± 0.03	0.04 ± 0.03	0.24 ± 0.02	0.22 ± 0.05	0.08 ± 0.03	0.10 ± 0.01
0.02 ± 0.02	0.02 ± 0.01	0.08 ± 0.02	0.10 ± 0.05	0.03 ± 0.01	0.04 ± 0.01
0.02 ± 0.01	0.01 ± 0.01	0.11 ± 0.02	0.21 ± 0.07	0.02 ± 0.01	0.02 ± 0.01
0.02 ± 0.02	0.00 ± 0.00	0.02 ± 0.00	0.01 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.00 ± 0.00
0.03 ± 0.03	0.03 ± 0.01	0.01 ± 0.00	0.02 ± 0.01	0.01 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

Table 4 Continued

Dermaturus mandtii (Brandt, 1850)	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.02 ± 0.01
Lithodidae juvenile	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.04	0.04 ± 0.01
Lithodidae	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pugettia sp. juvenile	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pugettia sp.	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Isopoda				
Isopoda indetermined	0.00 ± 0.00	0.02 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
Flabellifera	0.02 ± 0.01	0.02 ± 0.01	0.03 ± 0.01	0.08 ± 0.04
Janiridae	0.03 ± 0.01	0.04 ± 0.02	0.02 ± 0.01	0.06 ± 0.03
Amphipoda				
Amphipoda indetermined 1	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Amphipoda indetermined 2	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Amphipoda indetermined 3	0.05 ± 0.01	0.05 ± 0.01	0.41 ± 0.11	0.38 ± 0.18
Ampithoidae	0.08 ± 0.03	0.05 ± 0.03	0.18 ± 0.04	0.68 ± 0.49
Caprellidae	0.14 ± 0.06	0.02 ± 0.01	0.01 ± 0.01	0.03 ± 0.03
Lysianassidea	0.02 ± 0.01	0.05 ± 0.02	0.02 ± 0.01	0.00 ± 0.00
Melitidae	0.32 ± 0.07	0.20 ± 0.05	0.10 ± 0.03	0.14 ± 0.07
Metapelloides sp.	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.01 ± 0.01
Pleustidae	0.04 ± 0.02	0.05 ± 0.01	0.05 ± 0.03	0.01 ± 0.01
Pontogeneidae	0.25 ± 0.09	0.40 ± 0.25	0.14 ± 0.04	0.46 ± 0.23
Protomedia sp.	0.00 ± 0.00	0.00 ± 0.00	0.13 ± 0.13	0.00 ± 0.00
Stegocephalidae	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Stenothoidae	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Tanaidae				
Zeuxo normani (Richardson, 1905a)	0.01 ± 0.00	0.00 ± 0.00	0.13 ± 0.05	0.11 ± 0.04
Tanaidae indetermined	0.01 ± 0.01	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00

0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
0.04 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.01 ± 0.01	0.03 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.02 ± 0.01	0.07 ± 0.03	0.08 ± 0.02	0.13 ± 0.04	0.00 ± 0.00	0.00 ± 0.00
0.05 ± 0.03	0.06 ± 0.03	0.05 ± 0.01	0.07 ± 0.02	0.04 ± 0.01	0.03 ± 0.01
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.15 ± 0.06	0.17 ± 0.05	0.19 ± 0.06	0.35 ± 0.08	0.02 ± 0.01	0.03 ± 0.01
0.16 ± 0.08	0.00 ± 0.00	0.24 ± 0.12	0.04 ± 0.02	0.00 ± 0.00	0.00 ± 0.00
0.03 ± 0.03	0.10 ± 0.10	0.01 ± 0.01	0.04 ± 0.04	0.00 ± 0.00	0.03 ± 0.03
0.02 ± 0.02	0.01 ± 0.01	0.01 ± 0.00	0.01 ± 0.00	0.02 ± 0.01	0.02 ± 0.01
0.40 ± 0.20	0.02 ± 0.02	0.84 ± 0.16	0.40 ± 0.12	0.08 ± 0.02	0.08 ± 0.01
0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.02 ± 0.02	0.09 ± 0.03	0.11 ± 0.06	0.13 ± 0.05	0.03 ± 0.02	0.01 ± 0.01
0.13 ± 0.09	0.19 ± 0.07	0.34 ± 0.28	0.08 ± 0.03	0.14 ± 0.03	0.23 ± 0.06
0.00 ± 0.00	0.00 ± 0.00	0.09 ± 0.08	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.10 ± 0.04	0.02 ± 0.02	0.11 ± 0.02	0.02 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

Table 4 Continued

Echinodermata				
Asteroidea juvenile	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Holothuroidea				
Pentamera trachyplaca (Clarke, 1924)	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00
Ophiuroidea	0.01 ± 0.01	0.06 ± 0.01	0.01 ± 0.00	0.00 ± 0.00
Strongylocentrotus polyacanthus (A. Agassiz & H.L. Clark, 1907)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Sipuncula				
Echiura				
Echiurus echiurus (Pallas, 1967)	0.00 ± 0.00	0.02 ± 0.01	0.00 ± 0.00	0.03 ± 0.03
Chordata				
Cyclopteridae	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.03 ± 0.01	0.00 ± 0.00
0.03 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.01 ± 0.01	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.15 ± 0.07	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

Table 5: Percent contribution of individual taxa to the similarity of samples within each island (upper table), and to the differences between pairs of islands (lower table).

Chuginadak	Atka	Adak	Tanaga	Little Kiska
66.01%	**52.91%**	**32.53%**	**67.96%**	**56.98%**
Syllidae 9.03%	Polynoidae 14.08%	Amphipoda 15.07%	*Melita* sp. 7.99%	Syllidae 11.37%
Melita sp. 8.01%	*Zeuxo normani* 9.46%	Polynoidae 13.64%	Nereidae 7.35%	Pontogeneidae 10.92%
Pontogeneidae 5.96%	Amphipoda 9.19%	Pontogeneidae 10.86%	Syllidae 7.17%	Turbellaria 10.55%
Turbellaria 5.80%	Ampithoidae 9.06%	*Melita* sp. 8.68%	Amphipoda 6.70%	*Melita* sp. 8.88%
Nemertea 5.77%	Pontogeneidae 8.08%	*Zeuxo normani* 6.89%	*Exogone* sp. 6.28%	Janiridae 8.56%

	54.16% (R=0.622, P<0.01)	**64.10%** (R=0.417, P<0.01)	**39.71%** (R=0.554, P<0.01)	**45.02%** (R=0.424, P<0.01)
	Polynoidae 5.91%	Turbellaria 4.55%	Sabellidae 4.06%	Lumbrineridae 4.51%
	Turbellaria 4.24%	Syllidae 4.49%	Pontogeneidae 3.71%	Caprellidae 4.50%
Chuginadak	*Zeuxo normani* 4.10%	Lumbrineridae 4.07%	Acroceridae 3.55%	Ampithoidae 4.48%
	Lithodidae juv. 3.86%	Nemertea 3.93%	Caprellidae 3.51%	Ophiuroidea 3.99%
	Nemertea 3.43%	*Melita* sp. 3.93%	*Zeuxo normani* 3.44%	Sabellidae 3.61%
		60.39% (R=0.131, P<0.01)	**49.85%** (R=0.475, P<0.01)	**60.55%** (R=0.602, P<0.01)
		Ampithoidae 5.64%	Sabellidae 5.31%	Polynoidae 5.86%
		Pontogeneidae 4.62%	Polynoidae 4.90%	Ampithoidae 5.58%
	Atka	Lithodidae juv. 4.54%	*Melita* sp. 3.97%	*Zeuxo normani* 4.90%
		Amphipoda 4.51%	*Exogone* sp. 3.80%	Turbellaria 4.34%
		Melita sp. 4.41%	Nemertea 3.53%	Amphipoda 4.32%
			61.94% (R=0.369, P<0.01)	**66.90%** (R=0.326, P<0.01)
			Sabellidae 5.24%	Turbellaria 5.23%
			Melita sp. 4.50%	Phylodocidae 4.35%
		Adak	Nereidae 4.32%	Polynoidae 4.17%
			Exogone sp. 4.23%	Pontogeneidae 4.10%
			Nemertea 3.81%	Amphipoda 4.07%
				49.64% (R=0.612, P<0.01)
				Sabellidae 4.67%
				Flabellifera 4.28%
			Tanaga	Ampithoidae 4.24%
				Nereidae 4.18%
				Exogone sp. 4.07%

Table 6: Mean holdfast volume at five islands in the Aleutian archipelago (mL ± s.e.). P-values are from unpaired two sample t-tests assuming unequal variances.

	Holdfast volume kelp forest	Holdfast volume barren ground	P
Chuginadak	160.00 ± 26.20	112.85 ± 23.75	0.21
Atka	54.29 ± 5.61	82.14 ± 25.93	0.31
Adak	15.00 ± 2.44	37.86 ± 14.79	0.15
Tanaga	247.14 ± 51.33	165.00 ± 27.36	0.18
Little Kiska	107.50 ± 28.51	171.67 ± 50.85	0.29

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