



A swath across the great divide: Kelp forests across the Samalga Pass biogeographic break



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ABSTRACT

Biogeographic breaks are often described as locations where a large number of species reach their geographic range limits. Samalga Pass, in the eastern Aleutian Archipelago, is a known biogeographic break for the spatial distribution of several species of offshore-pelagic communities, including numerous species of cold-water corals, zooplankton, fish, marine mammals, and seabirds. However, it remains unclear whether Samalga Pass also serves as a biogeographic break for nearshore benthic communities. The occurrence of biogeographic breaks across multiple habitats has not often been described. In this study, we examined if the biogeographic break for offshore-pelagic communities applies to nearshore kelp forests. To examine whether Samalga Pass serves as a biogeographic break for kelp forest communities, this study compared abundance, biomass and percent bottom cover of species associated with kelp forests on either side of the pass. We observed marked differences in kelp forest community structure, with some species reaching their geographic range limits on the opposing sides of the pass. In particular, the habitat-forming kelp *Nereocystis luetkeana*, and the predatory sea stars *Pycnopodia helianthoides* and *Orthasterias koehlerii* all occurred on the eastern side of Samalga Pass but were not observed west of the pass. In contrast, the sea star *Leptasterias camtschatica dispar* was observed only on the western side of the pass. We also observed differences in overall abundance and biomass of numerous associated fish, invertebrate and macroalgal species on opposing sides of the pass. We conclude that Samalga Pass is important biogeographic break for kelp forest communities in the Aleutian Archipelago and may demark the geographic range limits of several ecologically important species.

1. Introduction

The geographic distribution of species can be marked by either gradual decreases in their abundance as they approach their range limits or by abrupt stoppages as they encounter biogeographic breaks. Sudden stops, or breaks, in species distributions are commonly attributed to their physiological limitations and/or physical barriers to dispersal. In marine systems, small-scale habitat heterogeneity can drive local patterns of variation in species distributions, while distinct changes in physical parameters associated with oceanographic boundaries, such as ocean salinity and temperature, can result in establishing biogeographic breaks that set species range limits and drive conspicuous large-scale differences in community structure (Blanchette and Gaines, 2007). Examples of large-scale oceanographic boundaries that result in biogeographic breaks in marine ecosystems occur globally,

with well-documented examples in areas such as Baja California, MEX (Pondella et al., 2005), California, USA (Horn and Allen, 1978; Sivasundar and Palumbi, 2010), the northeast Pacific Ocean (Doyle et al., 2002), the Galapagos Archipelago (Edgar et al., 2004), and Victoria, AUS (Colton and Swearer, 2012). These biogeographic breaks have been largely identified based on differences in the physical attributes of rocky and/or coral reefs (Riginos and Nachman, 2001; Doyle et al., 2002; Pelc et al., 2009), ocean circulation patterns (Pelc et al., 2009), and seawater temperatures (Doyle et al., 2002; Pondella et al., 2005), and generally coincide with abrupt changes in biological communities. Consequently, identifying biogeographic breaks can be important to understanding how large-scale oceanographic conditions influence patterns of species distribution and community structure across broad spatial scales.

Biogeographic breaks along coastal margins commonly occur at

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oceanographic boundaries characterized by persistent up-welling or down-welling, at water mass borders, near prominent geographic features, or in proximity to freshwater inputs. Such areas constrain the dispersion of marine organisms and have been demonstrated for a number of regions (e.g., Cowen et al., 2006; Diehl et al., 2007). For example, larval settlement rates of several invertebrate species are positively correlated to temperatures associated with particular water masses off the coast of California (Gosnell et al., 2014), but they may be reduced in areas of persistent upwelling (Connolly and Roughgarden, 1999). This can have important consequences to the biological communities that occupy these habitats and the services they provide. On nearshore subtidal rocky reefs, kelp forests are recognized as productive and dynamic ecosystems that support high biodiversity, protect the shore from erosion by ocean waves, and provide numerous other ecosystem services (reviewed in Schiel and Foster, 2015). Consequently, forest-forming kelps are ecosystem engineers (Jones et al., 1994), and changes in their distribution and abundance can lead to altered patterns of community assemblages, food web dynamics, carbon uptake and storage, and larval delivery to the shore (reviewed in Schiel and Foster, 2015). The continuity of kelps, and other macroalgae, along coastal regions has been strongly associated with the strength and direction of ocean currents, seawater temperatures, and hydrodynamic forces (Dayton et al., 1984; Dayton, 1985; Edwards, 2004; Coleman et al., 2011). In this way, the distribution of these habitat-forming species may be restricted by biogeographic breaks, thus shaping corresponding nearshore benthic communities (Murray and Littler, 1981; Huovinen and Gómez, 2012). However, while these patterns are clear for many coastal areas, they are poorly resolved across the Aleutian Archipelago.

The Aleutian Archipelago is characterized by a 1900-km chain of volcanic mountains stretching from the Alaska Peninsula, USA to the Kamchatka Peninsula, RUS, dividing the Pacific Ocean from the Bering Sea. The width of the continental shelf below this archipelago varies considerably, ranging from approximately 100 km near the Alaskan Peninsula, 25 km near Samalga Pass, and less than 10 km on the north side of the islands (Hunt and Stabeno, 2005). Passes between the islands allow for the transfer of water between the Pacific Ocean and the Bering Sea (Stabeno et al., 2005). These passes vary in both depth (165–1155 m) and area (1.0–45.7 km²) (Fig. 1; Hunt and Stabeno, 2005). Three major ocean currents feed the waters around the Aleutian Islands and flow through the passes. Specifically, the Alaska Coastal Current (ACC) originates in south-eastern Alaska and flows westward along the Gulf of Alaska, diverting northward into the Bering Sea from False Pass to Samalga Pass in the eastern Aleutian Archipelago (Stabeno et al., 2004; Ladd et al., 2005; Fig. 1). The Alaskan Stream (AS) forms southeast of Kodiak Island from the Alaska Current and flows westward along the shelf break providing most of the water flowing around the Archipelago from Samalga Pass to Near Strait (Reed and Stabeno, 1993; Ladd et al., 2005), after which it breaks off, forming meanders and eddies (Thomson, 1972). The AS provides most of the water flowing through the passes from Samalga Pass to Near Strait (Reed and Stabeno, 1993; Ladd et al., 2005). Finally, the Aleutian North Slope Current (ANSC) flows eastward along the north side of the Archipelago starting at Amchitka Pass, mixing with the Alaska Stream as water flows between the passes (Stabeno and Reed, 1994; Reed and Stabeno, 1999). Varying influences of the ACC versus the AS, along with longitudinal differences in mixing depth and Bering Sea influence, result in a strong front in water properties at Samalga Pass. Waters to the east of Samalga Pass are warmer, fresher, and more nitrate poor than waters to the west (Ladd et al., 2005). Consequently, these water masses, along with variations in shelf sizes, pass depths, and other environmental characteristics influence the distribution of numerous taxa in this region (Hunt et al., 1998; Sinclair and Zeppelin, 2002; Coyle, 2005; Logerwell et al., 2005). For example, inshore-foraging seabirds

occur more frequently where the shelf is widest and therefore the foraging area is greatest (Springer, 1991; Springer et al., 1996). While select passes in the Aleutian Archipelago have been established as biogeographic breaks for some pelagic, offshore and deep water taxa, the role of these passes as biographic breaks for nearshore benthic ecosystems has not otherwise been documented.

1.1. Samalga Pass

Samalga Pass (169°W) is recognized as a major oceanographic boundary and pelagic biogeographic break in the Aleutian Archipelago. Despite being narrower (29 km) and shallower (200 m) than many passes in the central Aleutian Archipelago, Samalga Pass demarks the western boundary of the ACC (Mordy et al., 2005). As a result, regions to the east of Samalga Pass may be considered under the coastal influence of the ACC, while regions to the west may be characterized by the oceanic influences of the AS and ANSC (Ladd et al., 2005). Additionally, Samalga Pass exhibits frequent upwelling and eddy formation that may contribute to abrupt differences in productivity and species distributions (Hunt and Stabeno, 2005; Mordy et al., 2005; Stabeno and Hristova, 2014). Consequently, the pass marks a transition where many offshore species, such as demersal fish and deep water faunal communities, reach their range limits and where the structure and productivity of pelagic food webs markedly differ on opposing sides of the pass (Sinclair and Zeppelin, 2002; Coyle, 2005; Hunt and Stabeno, 2005; Jahncke et al., 2005; Logerwell et al., 2005). The pass also coincides with a transition in the community structure of many species of coastal fishes, in particular cods and greenlings (Konar et al., 2015), and marks where the forest-forming bull kelp, *Nereocystis luetkeana*, experiences its western range limit (Miller and Estes, 1989). Three explanations have been suggested to explain these abrupt changes in ecosystems at Samalga Pass: 1) differences in pass width and depth to the east and west; 2) water masses with differing physical and chemical properties to the east and west; and 3) an east to west change from large land masses on a wide continental shelf to small land masses on a narrow shelf (Hunt and Stabeno, 2005). While Samalga Pass has been documented to be a biogeographic break, the influence of this pass on nearshore ecologically important kelp forest communities has yet to be determined. To address this knowledge gap, we compare kelp forest community structure on both sides of Samalga Pass and look for evidence of a biogeographic break in this community.

1.2. Aleutian kelp forests

Large kelp forests are relatively rare in the Aleutian Archipelago west of Samalga Pass, and where they are present they are dominated by a single canopy-forming species, *Eualaria fistulosa* (algal nomenclature as in <http://www.algaebase.org/>). Instead, urchin barrens (i.e., areas that are devoid of most foliose macroalgae and have high densities of sea urchins) dominate the coastal rocky reefs throughout this region (Estes and Duggins, 1995). In contrast, east of Samalga Pass, urchin barrens are rare and the kelp forests are larger and dominated by two canopy-forming species, *E. fistulosa* and *Nereocystis luetkeana* (Miller and Estes, 1989). The presence or absence of urchin barrens is dictated by overgrazing by green sea urchins (*Strongylocentrotus* spp.; invertebrate nomenclature from <http://www.marinespecies.org/>) that has occurred following the widespread loss of their primary predator, the northern sea otter, *Enhydra lutris* (kenyonii) (Estes and Duggins, 1995; Estes et al., 1998). Below the surface kelp canopies, several species of benthic perennial macroalgae occur, including the stipitate kelps *Agarum clathratum*, *A. clathrus*, various species of *Laminaria* (including *L. longipies*, *L. setchellii*, and *L. yezoensis*), numerous species of foliose and coralline red algae, and the pulvinate green alga, *Codium* spp. Other than the two canopy-forming kelp species (*E. fistulosa* and *N. luetkeana*) and the brown, acid-bearing alga, *Desmarestia viridis*, annual species of large

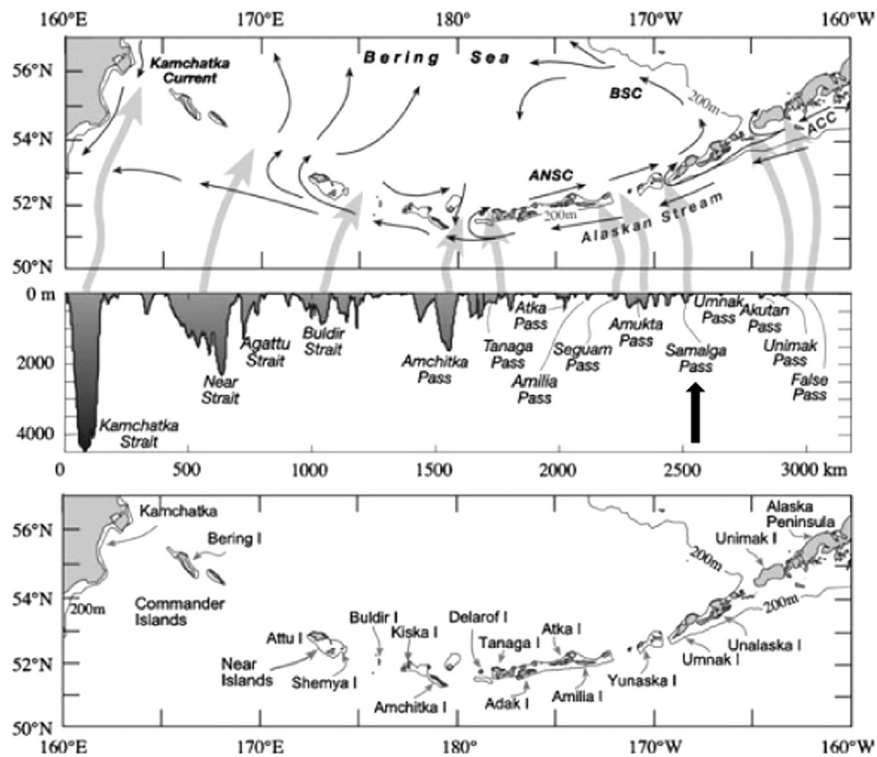


Fig. 1. Map of the Aleutian Archipelago showing major ocean currents (top panel), inter-island passes (middle panel), and islands (bottom panel). Vertical black arrow on the middle panel shows the location of Samalga Pass where this study focused. Figure modified from Hunt and Stabeno (2005).

macroalgae are rare. The most abundant families of shallow reef fishes in these forests include cods (Gadidae), greenlings (Hexagrammidae), rockfish (Scorpaenidae), and sculpins (Cottidae) (Simenstad et al., 1977; Konar et al., 2015). Rich macroinvertebrate assemblages of ascidians, bivalves, gastropods, crustaceans, and echinoderms can be found on Aleutian rocky reefs with particular guilds (i.e., suspension feeders and grazers) being closely associated with productive kelp bed habitats (Estes and Duggins, 1995). While the literature has recognized multiple biogeographic breaks within the Aleutian Archipelago, we focus on Samalga Pass in this study because of the evidence of stark contrasts for other parts of the ecosystem. Consequently, our sampling design divided the archipelago into two geographic regions, the eastern side of Samalga Pass and the western side.

2. Methods

Four islands (Tanaga, Adak, Atka and Chuginadak) were sampled west of Samalga Pass, and three islands (Umnak, Anangula and Unalaska) were sampled east of the pass during a research cruise aboard the *RV Oceanus* in July 2016 (Fig. 2). At each island, two rocky reef sites located at or near established long-term kelp forest monitoring sites were sampled for kelp forest community structure using scuba. The sites were separated by hundreds of meters to several kilometers, depending on forest availability and accessibility. Kelp forest sampling sites were all located on flat rocky reefs and in water depths of $4.8\text{ m} \pm 2.0$ (mean \pm SE) on the west side of the pass and $6.0\text{ m} \pm 0.6$ on the east side of the pass. Although this $\sim 1.2\text{ m}$ difference in average depth is statistically significant (t -test, $p < 0.05$), we believe it ecologically insignificant as there was considerable overlap in site depths between the two sides of the pass (sites ranged from 1.5 m to 8.5 m west of the pass and from 3.3 m to 8.2 m east of the pass), and given the typical large (10 m) winter swells and approximately 2 m tidal range that this region experiences.

To determine kelp forest community structure at each site, we used a suite of sampling methods to quantify abundance and/or biomass of

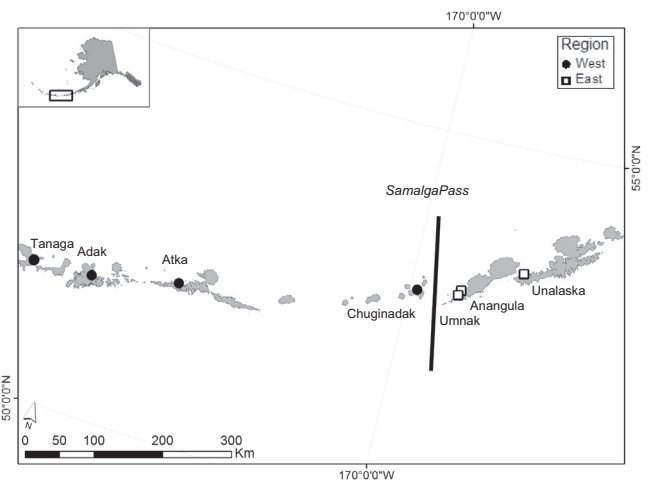


Fig. 2. Map of Aleutian Islands where the kelp forest surveys were done. Four islands were sampled on the west side of Samalga Pass (black circles) and three islands were sampled on the east side of the pass (white squares).

kelp forest inhabitants. Specifically, abundances of canopy-forming kelps, forest-associated fishes, and rare but conspicuous mobile invertebrates were estimated along three 10 m long \times 2 m wide transects (hereafter “swaths”) within each site using scuba. To foster independence among swaths within each site, their starting positions were separated by tens of meters and they were run in opposite directions. Within each swath, all canopy-forming kelps and benthic and midwater fishes were quantified visually by trained divers. All conspicuous motile invertebrates were collected and brought back to the ship for abundance and biomass determination. The rest of the benthic community, which included sessile and small motile invertebrates, understory kelps, and all other macroalgae, were quantified within ten 0.25 m² quadrats that were placed at randomly determined

positions along each of two 30 m transects within each site (independent from swath transects). Specifically, within each of these quadrats, the percent bottom cover of bare substrate (rock), non-geniculate encrusting coralline algae (*Clathromorphum* spp.), pulvinate green algae (*Codium* spp.), and sessile invertebrates (suspension feeders that could not be effectively cleared from the substrate), were estimated visually. Following this visual estimation, all epibenthic algae and invertebrates occurring in the first five quadrats sampled along each transect were scraped from the substrate, placed in fine mesh collection bags and transported to the ship for processing. Onboard the ship, all organisms were identified to the lowest possible taxonomic level, counted (if the species occurs as a discrete individual) and/or weighed using hanging spring scales to determine their biomass. Invertebrate and algal species that could not be identified on the ship were preserved in a 10% formalin solution or pressed for later identification, respectively.

2.1. Statistical analyses

All statistical analyses were done in PRIMER ver. 6. Prior to multivariate community analyses, all data were square root transformed (Clarke and Warwick, 2001) and resemblance matrices based on Bray-Curtis similarities were generated for each data stream (swath counts, percent cover estimates, and benthic scrapes). To avoid potential biases from the different sampling methods (that is, if some methods better represented certain taxa), we chose to analyze the data generated for each sampling method separately. This resulted in separate data sets for the swath-based fish and canopy-forming kelp abundance, swath-based motile invertebrate abundance and biomass, quadrat-based invertebrate abundance and biomass, quadrat-based kelp abundance and macroalgal biomass, and quadrat-based percent cover. For each data set, similarities among sites on either side of Samalga Pass were displayed with non-dimensional scaling (nMDS) plots, and were quantitatively compared using three-factor nested PERMANOVAs, with Region considered as a fixed factor, and Island nested within Region, and Site nested within Island considered as random factors. The relative amount of variability associated with each factor (ω^2) was estimated by isolating its variance component and dividing it by the total variance in the statistical model according to the methods described in Graham and Edwards (2001). The relative importance of each taxa in driving differences between opposing sides of the pass was then determined for each data set using SIMPER analyses.

3. Results

The swath-based surveys identified ten fish species and two canopy-forming kelp species across all study sites (see Appendix S1). While significant differences were found in these assemblages among sites within islands (PERMANOVA: Pseudo-F = 1.455, df = 7, P = 0.031), the greatest difference was observed between the two regions (i.e., between the opposing sides of the Samalga Pass) (Pseudo-F = 5.165, df = 1, P = 0.027; Fig. 3; Table 1). In contrast, no differences were observed among islands within each region (Pseudo-F = 1.538, df = 5, P = 0.064). The taxa most important to driving the differences between the opposing sides of the pass were the canopy-forming kelps *Eualaria fistulosa* and *Nereocystis luetkeana*, and kelp greenlings, *Hexagrammos decagrammus* (Table 2). Further, while *E. fistulosa* and *H. decagrammus* were each observed on both sides of Samalga Pass, *E. fistulosa* was more abundant west of the pass and *H. decagrammus* was more abundant east of the pass (Fig. 4). In contrast, *N. luetkeana* was only observed east of the pass. Additionally, the swath surveys identified 40 invertebrate taxa, of which 28 were echinoderms, five were crustaceans, five were gastropods, and two were classified as “other” (see Appendix S1 and S2). Similar to fish and canopy-forming kelp assemblages, abundance-based invertebrate as-

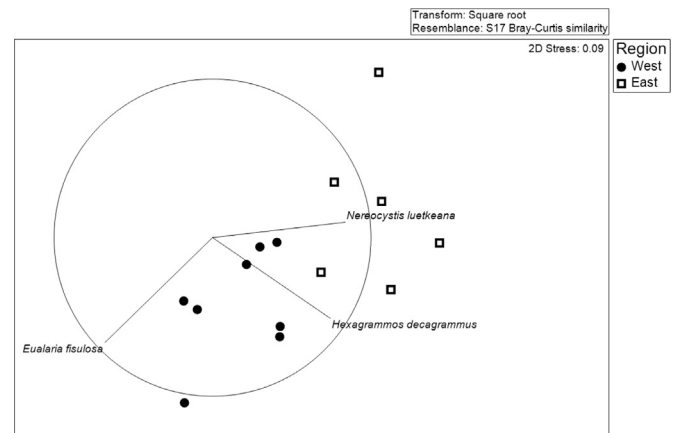


Fig. 3. nMDS plot showing similarities in the assemblages of canopy-forming kelps and kelp-associated fishes based on their abundances in the swath surveys. Each point represents one kelp forest and is designated by shape and fill as to its eastern or western position relative to Samalga Pass. Vectors identify the species most important in the dissimilarities between the two regions based on SIMPER Analyses (see Table 2).

semblages varied significantly among sites within islands (PERMANOVA: Pseudo-F = 3.092, df = 7, P = 0.001) and between the opposing sides of Samalga Pass (Pseudo-F = 5.206, df = 1, P = 0.03; Fig. 5a), but not among islands within each region (Pseudo-F = 0.963, df = 5,7, P = 0.554; Table 1). Likewise, biomass-based invertebrate assemblages also varied significantly among sites within islands (PERMANOVA: Pseudo-F = 2.366, df = 7, P = 0.001) and between the opposing sides of Samalga Pass (Pseudo-F = 4.556, df = 1, P = 0.027; Fig. 5b), but not among islands within each region (Pseudo-F = 1.095, df = 5, P = 0.364). The taxa most important in driving differences in invertebrate abundance between the opposing sides of the pass included the hairy triton (*Fusitriton oregonensis*) and the sea star *Leptasterias camtschatica dispar*, which were more abundant west of the pass, and the sea stars *Henricia vermilion*, *Pycnopodia helianthoides*, *Orthasterias koehleri*, and *Ceramaster arcticus*, which were all more abundant east of the pass (Figs. 5a and 6a; Table 2). Lastly, the most important species contributing to the differences in invertebrate biomass between the opposing sides of the pass were again *F. oregonensis* and *L. dispar*, as well as the large gumboot chiton, *Cryptochiton stelleri*, which all had greater biomass to the west, and *P. helianthoides* and *O. koehleri*, which had greater biomass to the east (Figs. 5b and 6b; Table 2). Indeed, *L. dispar* was observed only to the west of Samalga Pass, while *O. koehleri* and *P. helianthoides* were observed only to the east of the pass.

The quadrat-based sampling identified significant differences in benthic cover of sessile invertebrates and encrusting macroalgae among sites within each island (PERMANOVA: Pseudo-F = 5.901, df = 7, P = 0.001), among islands within each region (Pseudo-F = 2.593, df = 5, P = 0.003), and between the opposing sides of Samalga Pass (Pseudo-F = 5.538, df = 1, P = 0.028; Fig. 7). As with invertebrate abundance and biomass from the swaths, differences between the opposing sides of Samalga Pass explained the largest amount of the variation in benthic cover (Table 1). While all invertebrate and macroalgal taxa were observed on both sides of Samalga Pass, the taxa most important to driving the differences between the opposing sides of the pass included non-geniculate coralline algae (*Clathromorphum* spp.), and various species of suspension/filter feeding invertebrates, which were all more abundant to the west of the pass (Fig. 8; Table 2). In contrast, bare substrate was more common to the east of the pass.

The quadrat-based scrapes identified 37 species of macroalgae and 131 species of invertebrates across all study sites (Appendices S1 and S2). When examined separately, abundance of stipitate kelps varied significantly among sites within islands (PERMANOVA: Pseudo-F = 7.767, df = 7, P = 0.001) and between the opposing sides of Samalga

Table 1

PERMANOVA results for each data stream by sampling method. The sources of variation are the factors region [Re], island nested in region [is(Re)], and site nested in island [si(is(Re))], and residual error [Res]. The proportion of total variance explained by each source of variation (ω^2) was calculated by summing the estimated variance components of each source and dividing by the number of sources ($n = 4$).

	Source	df	SS	MS	Pseudo-F	P(perm)	ω^2
Swath	Fish and canopy kelp observational counts						
	Re	1	6281.2	6281.2	5.1657	0.027	26.12
	is(Re)	5	6079.8	1216	1.5382	0.064	7.52
	si(is(Re))	7	5533.4	790.49	1.4554	0.031	8.75
	Res	28	15,208	543.13			57.61
	Total	41	33,102				
	Invertebrate Abundance						
	Re	1	26,430	26,430	5.2058	0.03	26.4
	is(Re)	5	25,386	5077.1	0.96298	0.554	0
	si(is(Re))	7	36,906	5272.3	3.0915	0.001	30.24
	Res	28	47,751	1705.4			43.36
	Total	41	1.36E+05				
	Invertebrate Biomass						
	Re	1	25,064	25,064	4.5565	0.027	23.09
	is(Re)	5	27,503	5500.7	1.0957	0.364	1.94
si(is(Re))	7	35,141	5020.2	2.3665	0.001	23.46	
Res	28	59,398	2121.4			51.51	
Total	41	1.47E+05					
Percent Cover	Re	1	65,524	65,524	5.5377	0.028	25.54
	is(Re)	5	59,100	11,820	2.5935	0.003	11.86
	si(is(Re))	7	31,909	4558.4	5.9012	0.001	12.36
	Res	265	2.05E+05	772.44			50.25
	Total	278	3.61E+05				
Quadrat Clearings	Algal Abundance						
	Re	1	56,115	56,115	5.5114	0.008	28.27
	is(Re)	5	51,235	10,247	1.402	0.17	6.16
	si(is(Re))	7	51,137	7305.3	7.767	0.001	26.69
	Res	124	1.17E+05	940.56			38.88
	Total	137	2.75E+05				
	Algal Biomass						
	Re	1	85,799	85,799	4.8412	0.013	25.15
	is(Re)	5	89,179	17,836	1.6038	0.05	8.44
	si(is(Re))	7	77,811	11,116	6.4453	0.001	23.63
	Res	124	2.14E+05	1724.6			42.78
	Total	137	4.67E+05				
	Invertebrate Abundance						
	Re	1	48,820	48,820	3.4272	0.038	14.01
	is(Re)	5	71,425	14,285	1.8231	0.008	8.93
	si(is(Re))	7	54,833	7833.2	3.5006	0.001	15.51
	Res	125	2.80E+05	2237.7			61.55
	Total	138	4.55E+05				
	Invertebrate Biomass						
	Re	1	72,887	72,887	5.6189	0.008	22.9
	is(Re)	5	65,039	13,008	2.0812	0.001	8.83
	si(is(Re))	7	43,736	6248.1	2.8044	0.001	10.5
	Res	125	2.78E+05	2227.9			57.78
	Total	138	4.60E+05				

Pass (Pseudo-F = 5.511, df = 1, P = 0.008; Fig. 9a), but not among islands within each region (Pseudo-F = 1.402, df = 5, P = 0.170; Table 1). Similarly, macroalgal assemblages based on species' biomass also varied significantly among sites within each island (PERMANOVA: Pseudo-F = 6.445, df = 7, P = 0.001), among islands within each of the regions (Pseudo-F = 1.604, df = 5, P = 0.05), and between opposing sides of the pass (Pseudo-F = 4.841, df = 1, P = 0.013; Fig. 9b; Table 1). The differences between opposing sides of the pass again explained the largest amount of the variation in kelp abundance. This was similar to overall macroalgal biomass, where differences between opposing sides explained most of the variance in macroalgal biomass, and variation among islands within each region explained the least variance. While all macroalgae, except for *Nereocystis luetkeana*, were observed on both sides of Samalga Pass, the differences in stipitate kelp abundance between the regions were primarily driven by three taxa; *Agarum*

clathrus, which was more abundant to the west, and *Laminaria longipes* and *Laminaria* spp., which were more abundant to the east (Fig. 10a; Table 2). However, when these kelps were combined with all macroalgae, differences in overall macroalgal biomass between the regions were primarily driven by seven species. Specifically, *A. clathrus*, *A. clathratum*, and *Eualaria fistulosa* were all more abundant to the west, while *Laminaria* spp., *L. longipes*, *Ptilota serrata*, and *Odonthalia setacea* were more abundant to the east (Fig. 10b; Table 2). Similarly, invertebrate abundance also varied significantly among sites within each island (PERMANOVA: Pseudo-F = 3.501, df = 7, P = 0.001), between opposing sides of Samalga Pass (Pseudo-F = 3.472, df = 1, P = 0.038; Fig. 11a), and among islands within each of the regions (Pseudo-F = 1.823, df = 5, P = 0.008; Table 1). While all invertebrates identified within the quadrats were observed on both sides of the pass, the taxa that best described differences in the

Table 2

Breakdown of average dissimilarity between the east and west of Samalga Pass into contributions from each taxa; taxa are ordered in decreasing contributions. Only taxa contributing at least 5% are included.

	Taxa	West Av. Abund	East Av. Abund	Av. Diss	Diss/SD	Contrb%	Cum.%
Swath	Fish and canopy kelp observational counts		Average dissimilarity = 35.3%				
	<i>Eualaria fistulosa</i>	8.9	5.7	16.9	1.5	47.8	47.8
	<i>Nereocystis luetkeana</i>	0.0	0.9	4.9	3.8	13.7	61.5
	<i>Hexagrammos decagrammus</i>	0.3	0.6	3.2	1.1	9.1	70.6
	Invertebrate Abundance		Average dissimilarity = 81.2%				
	<i>Leptasterias camtschatica dispar</i>	1.5	0.0	8.1	1.9	10.0	10.0
	<i>Fusitriton oregonensis</i>	1.1	1.0	6.3	0.9	7.7	17.8
	<i>Henricia vermillion</i>	0.3	1.1	6.1	1.4	7.6	25.3
	<i>Pycnopodia helianthoides</i>	0.0	0.8	5.1	1.2	6.2	31.6
	<i>Orthasterias koehleri</i>	0.0	0.8	4.8	2.1	5.9	37.5
	<i>Ceramaster arcticus</i>	0.3	0.7	4.1	1.1	5.0	42.5
	Invertebrate Biomass		Average dissimilarity = 83.3%				
	<i>Pycnopodia helianthoides</i>	0.0	0.8	20.8	1.6	25.0	25.0
	<i>Orthasterias koehleri</i>	0.0	0.3	8.6	2.7	10.3	35.3
	<i>Cryptochiton stelleri</i>	0.3	0.2	7.0	1.1	8.3	43.6
	<i>Fusitriton oregonensis</i>	0.3	0.1	6.3	0.8	7.6	51.3
	<i>Leptasterias camtschatica dispar</i>	0.3	0.0	5.9	1.5	7.0	58.3
	Percent Cover	<i>Clathromorphum</i> spp.	3.6	1.2	8.2	1.8	32.4
Suspension Feeders		4.8	3.2	6.8	1.4	26.6	58.9
Bare Substrate		1.7	2.8	4.4	1.5	17.1	76.1
Quadrat Clearings	Algal Abundance		Average dissimilarity = 70.2%				
	<i>Laminaria</i> spp.	0.2	2.9	23.2	3.4	33.0	33.0
	<i>Laminaria longipes</i>	1.2	2.6	22.5	1.4	32.0	65.1
	<i>Agarum clathrus</i>	1.0	0.6	7.6	1.3	10.8	75.9
	Algal Biomass		Average dissimilarity = 67.2%				
	<i>Laminaria</i> spp.	0.1	0.9	13.5	4.9	20.1	20.1
	<i>Agarum clathrus</i>	0.6	0.3	7.6	1.4	11.3	31.4
	<i>Eualaria fistulosa</i>	0.8	0.5	6.4	1.6	9.6	41.0
	<i>Laminaria longipes</i>	0.1	0.3	5.5	1.1	8.2	49.2
	<i>Ptilota serrata</i>	0.1	0.4	5.4	1.4	8.1	57.3
	<i>Agarum clathratum</i>	0.2	0.1	4.0	0.7	6.0	63.2
	<i>Odonthalia setacea</i>	0.2	0.3	3.5	1.3	5.2	68.4
	Invertebrate Abundance		Average dissimilarity = 65.8%				
	<i>Musculus niger</i>	1.2	3.4	7.5	1.5	11.4	11.4
	<i>Strongylocentrotus</i> spp.	2.3	0.4	5.9	1.7	9.0	20.4
	Invertebrate Biomass		Average dissimilarity = 70.9%				
	<i>Strongylocentrotus</i> spp.	0.1	0.5	11.3	2.3	16.0	16.0
	<i>Halichondria</i> spp.	0.1	0.3	5.5	1.3	7.7	23.7

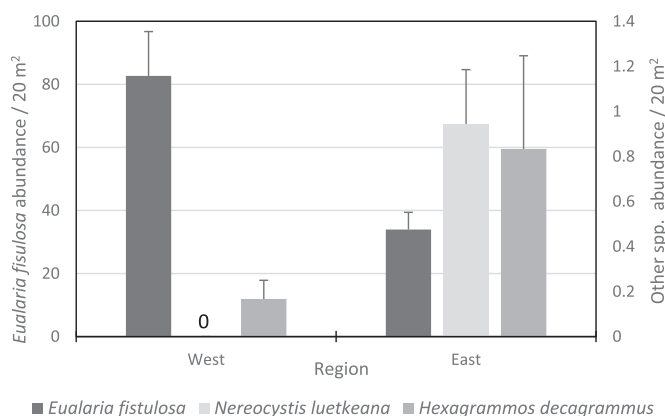


Fig. 4. Average abundance (means + se) of the canopy-forming kelps, *Eualaria fistulosa* and *Nereocystis luetkeana*, and the kelp greenling, *Hexagrammos decagrammus*, in the regions west and east of Samalga Pass based on swath observation data. These three species each contributed $\geq 5\%$ to the overall dissimilarities in assemblages between the opposing sides of Samalga Pass, as determined by SIMPER analyses. Means and errors are based on the average counts on island to the west (N = 4) and east (N = 3) of the pass. Note that *N. luetkeana* was absent west of Samalga Pass (indicated by the 0).

invertebrate abundances between opposing sides of the pass included the mussel, *Musculus niger*, which was more abundant to the east, and urchins, *Strongylocentrotus* spp., which were more abundant to the west (Fig. 12a; Table 2). Likewise, invertebrate biomass also varied significantly among sites within each island (PERMANOVA: Pseudo-F = 2.804, df = 7, P = 0.001), among islands within each region (Pseudo-F = 2.081, df = 5, P = 0.001), and between opposing sides of the pass (Pseudo-F = 5.619, df = 1, P = 0.008; Fig. 11b; Table 1). Lastly, while all invertebrates found to significantly influence patterns of biomass were observed on both sides of the pass, the taxa that best explained biomass differences between the opposing sides of the pass included *Strongylocentrotus* spp., and the sponge *Halichondria* spp., which both had greater biomass to the west (Fig. 12b; Table 2).

4. Discussion

This study demonstrated that Samalga Pass is an important biogeographic break for shallow water benthic communities inhabiting kelp forests in the eastern Aleutian Islands. In particular, the forest-forming kelps *Eualaria fistulosa* and *Nereocystis luetkeana* differed in their abundances on opposing sides of the pass, with the most striking difference being the complete absence of *N. luetkeana* to the west of the pass. This is consistent with a report by Miller and Estes (1989), who

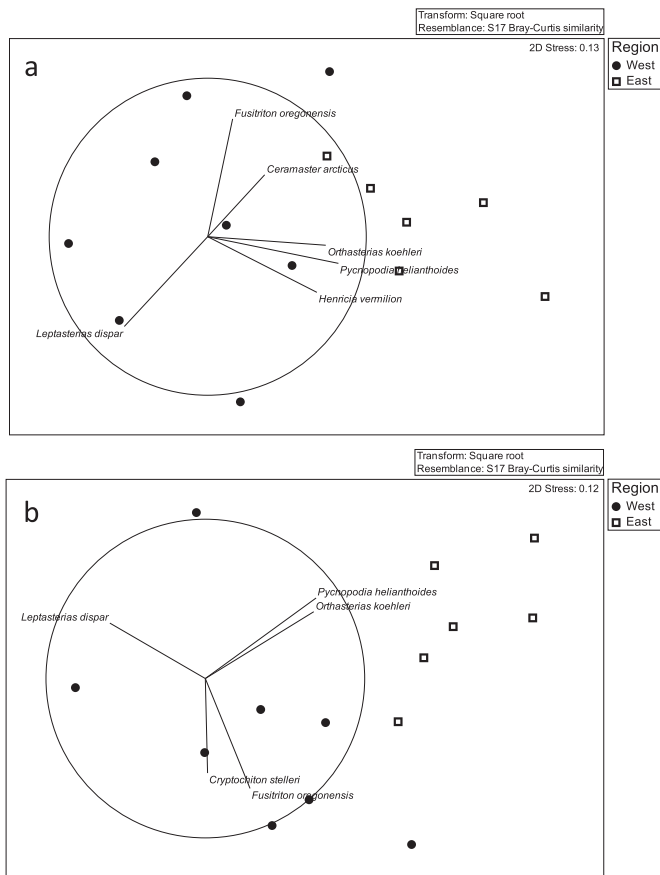


Fig. 5. nMDS plots showing similarities in the assemblages of large mobile invertebrates observed in the swath surveys based on a) abundance and b) biomass. Each point represents one kelp forest and is designated by shape and fill as to its eastern or western position relative to Samalga Pass. Vectors identify the species most important in the dissimilarities between the two regions based on SIMPER Analyses (see Table 2).

described the geographic extent of *N. luetkeana* being Samalga Pass. While they speculated that this range limit resulted from light limitation to the west side of the pass, we find it surprising that *N. luetkeana* has not extended beyond Samalga Pass, especially given that reproductive sporophytes have regularly been observed floating on the ocean surface and/or cast ashore as beach wrack as far west as the Semichi Islands, which are 1300 km away, during 20 years of research cruises to this region by our team (authors pers. obs.). While it is possible that the spores of these drifting individuals do not remain viable long enough to reproduce once they reach these islands, we believe it is unlikely that this can account for the total lack of *N. luetkeana* west of the pass given that only 29 km separates the closest island on the west side of the pass (Chuginadak) from the large *N. luetkeana* forests on the closest island on the east side of the pass (Umnak). Also, the spores of other kelp species have been observed to remain viable over the course of several months as the kelps drift as far as 1000 km (Hobday, 2000a, 2000b; Macaya et al., 2005), which is easily enough time to allow dispersal across the pass. Instead, we postulate that the colder ocean temperatures west of the pass due to influence from the ACC (Ladd et al., 2005) may not be conducive for spore or gametophyte success, given the narrow abiotic tolerances of many kelp gametophytes (Deysner and Dean, 1986; Carney and Edwards, 2006; Fejtek et al., 2011). Regardless of the reason why *N. luetkeana* does not extend to the west of the pass, our data show stark differences in distribution and abundance of the forest-forming kelps, as well as in the assemblages of kelp forest fishes, benthic algae, and sessile and motile invertebrates, between the opposing sides of the pass. Indeed, when regional (i.e., cross-pass) variability in each of these assemblages was compared to

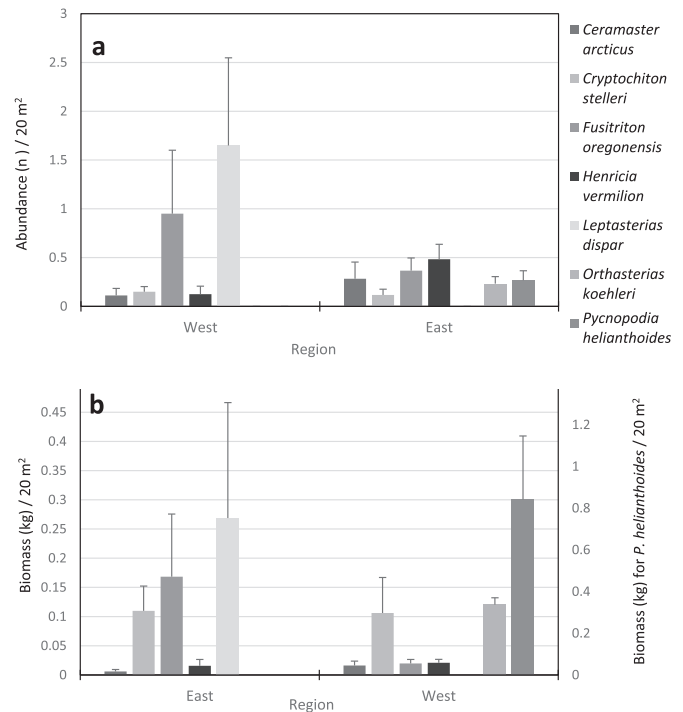


Fig. 6. Average (+ se) a) abundance and b) biomass of the primary motile invertebrate species responsible for the dissimilarity in community assemblages between the west and east of Samalga Pass. These seven species each contributed $\geq 5\%$ to the overall dissimilarities between the opposing sides of the pass, as determined by SIMPER analyses of swath observation data. Means and errors are based on the average counts on island to the west (N = 4) and east (N = 3) of the pass.

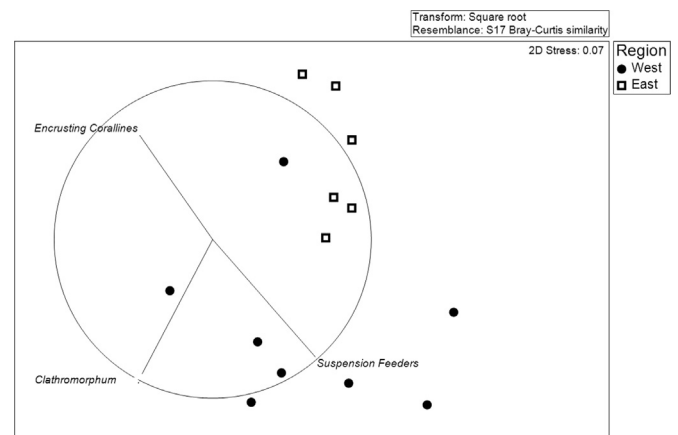


Fig. 7. nMDS plot showing similarities in the assemblages of organisms observed in the quadrat visual surveys that make up the primary substrate bottom cover. Each point represents one kelp forest and is designated by shape and fill as to its eastern or western position relative to Samalga Pass. Vectors identify the taxa most important in the dissimilarities between the two regions based on SIMPER Analyses (see Table 2).

the geographic variability observed among sites within each island, the assemblages were either comparably variable at the region and site level, or significantly more variable at the regional level. This is counter to expectations that the least amount of variation should occur at the largest scale examined and the most variation at the smallest scale examined (Weins, 1989; Edwards, 2004). Although we found evidence of significant within-island variation in Aleutian kelp forest communities, the preponderance of evidence for variability explained at the regional level suggests that Samalga Pass serves as a biogeographic break driving corresponding differences in the kelp forest communities.

In addition to *Nereocystis luetkeana* and *Eualaria fistulosa*, other macroalgae and bare substrate also were observed to differ markedly

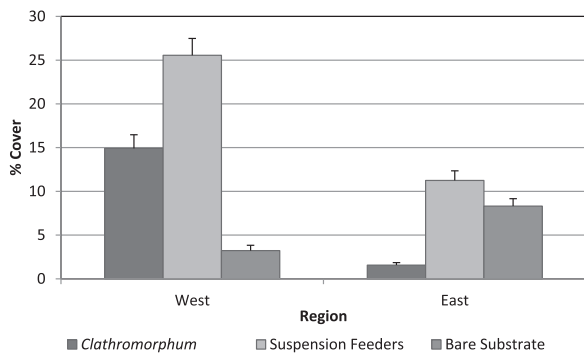


Fig. 8. Average percent bottom cover (+ se) of *Clathromorphum* spp., suspension feeders, and bare substrate on islands in the regions west and east of Samalga Pass. These three groups each contributed $\geq 5\%$ to the overall dissimilarities in bottom cover between the opposing sides of Samalga Pass, as determined by SIMPER analyses of benthic scraping data. Means and errors are based on the averages on island to the west (N = 4) and east (N = 3) of the pass.

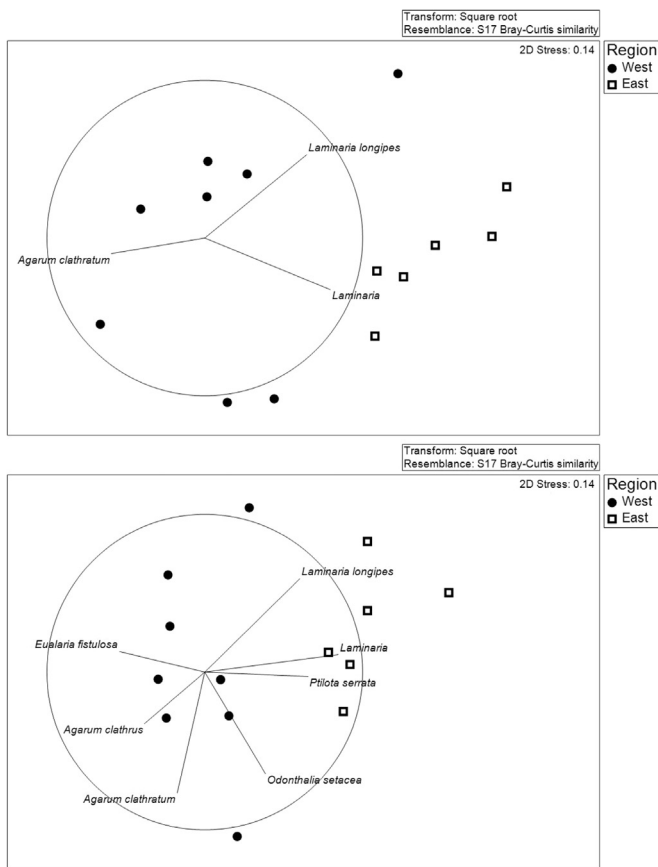


Fig. 9. nMDS plots showing similarities in the assemblages of a) stipitate kelps based on abundance, and b) macroalgae based on biomass. Each point represents one kelp forest and is designated by shape and fill as to its eastern or western position relative to Samalga Pass. Vectors identify the taxa most important in the dissimilarities between the two regions based on SIMPER analyses of benthic scraping data (see Table 2).

between the opposing sides of the pass. The crustose coralline algae, *Clathromorphum* spp., the stipitate kelps, *Agarum clathratum*, *A. clathrus*, *Laminaria longipes*, and *Laminaria* spp., the red algae, *Ptilota serrata*, and *Odonthalia setacea*, and bare substratum were all important in driving differences between the regions. Specifically, *Laminaria* spp. and bare substratum were more abundant east of Samalga Pass. These kelp form dense surface and subsurface canopies and are dominant competitors, which may outcompete other taxa (Vadas, 1968; Dayton et al., 1984). For example, in kelp forest communities in the San Juan Islands, WA, *L. complanata* and *L.*

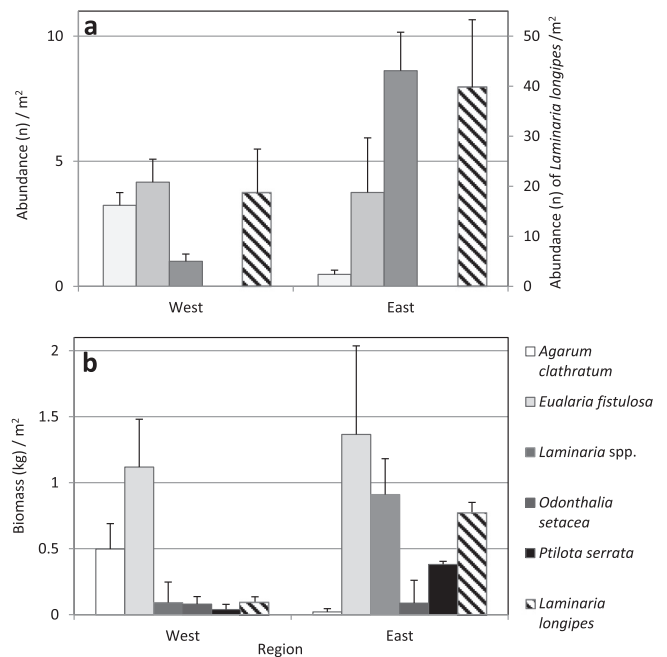


Fig. 10. Average (+ se) a) abundance and b) biomass of the primary taxa responsible for the dissimilarity in macroalgal community assemblages between the west and east of Samalga Pass. These six taxa each contributed $\geq 5\%$ to the overall dissimilarities between the opposing sides of the pass, as determined by SIMPER analyses of benthic scraping data. Means and errors are based on the average counts on island to the west (N = 4) and east (N = 3) of the pass. No abundance data were available for *Odonthalia setacea* and *Ptilota serrata*.

groenlandica were able to establish dense populations under canopies of *N. luetkeana* and thereby replace other sub-canopy species such as *Agarum* spp. (Vadas, 1968). Furthermore, once established, patches of *Laminaria* spp. can be highly stable over time and thereby slow, or even prevent, establishment of other kelp species (Dayton et al., 1984). In contrast to the east, *E. fistulosa*, *A. clathrus*, *A. clathratum*, and *O. setacea* were all more abundant west of Samalga Pass. Given that kelp canopies can strongly influence the establishment and abundance of other macroalgae (Duggins and Dethier, 1985; Reed et al., 1992; Benes and Carpenter, 2015), differences in kelp assemblages may result in marked differences in other kelp forest species. For example, in California, canopies of the giant kelp, *Macrocystis pyrifera* greatly reduce available light (Clark et al., 2004), and experimental removal of these canopies can result in increased growth rates and recruitment of understory species (Duggins and Dethier, 1985; Edwards, 1998). However, different species of kelp can impact their physical environments differently, in turn resulting in varied responses by understory species (e.g., Dayton et al., 1984; Clark et al., 2004) as has been observed for *N. luetkeana* and *E. fistulosa* in other areas of Alaska (Hondelero and Edwards, in press). In the Aleutian Islands, while surface canopies occur on both sides of Samalga Pass, the high densities of *N. luetkeana* east of the pass may result in lower average benthic light levels. Each *N. luetkeana* sporophyte can have 30–60 four-meter long blades, which extend off the plant's buoyant pneumatocyst (Koehl et al., 2008), and thus may provide more shading than *E. fistulosa* (Hondelero and Edwards, in press). This may be significant given some species of *Laminaria* are considered low-light adapted, or “shade plants” (e.g., Luning, 1979), so their tolerance for low light conditions may allow them to dominate under thick surface canopies. Together, the low-light characteristics and competitive dominance of *Laminaria* spp. over other kelps may at least partially explain differences in kelp assemblages on the opposing sides of Samalga Pass.

Together with the forest-forming kelps, forest associated fish assemblages differed on opposing sides of Samalga Pass, with kelp greenlings (*Hexagrammos decagrammus*) being the most important

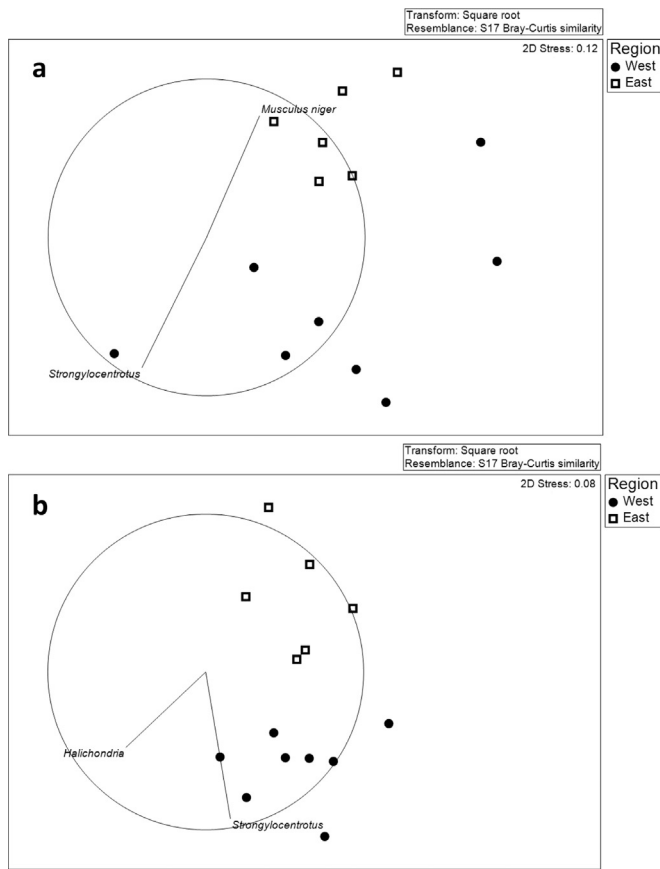


Fig. 11. nMDS plots showing similarities in invertebrate a) abundance, and b) biomass based on benthic scraping data. Each point represents one kelp forest and is designated by shape and fill as to its eastern or western position relative to Samalga Pass. Vectors identify the taxa most important in the dissimilarities between the two regions based on SIMPER analyses (see Table 2).

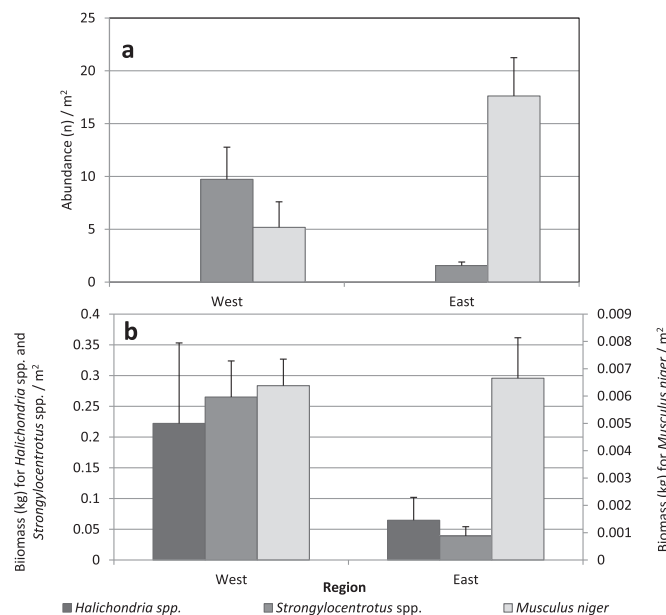


Fig. 12. Average (+ se) a) abundance and b) biomass of the primary taxa responsible for the dissimilarity in invertebrate assemblages between the west and east of Samalga Pass based on benthic scraping data. These three taxa each contributed $\geq 5\%$ to the overall dissimilarities between the opposing sides of the pass, as determined by SIMPER analyses. Means and errors are based on the average counts on island to the west (N = 4) and east (N = 3) of the pass. No abundance data were available for *Halichondria* spp.

fish species in driving cross-pass differences. This agrees with other studies that have found differences in offshore (Logerwell et al., 2005) and nearshore (Konar et al., 2015) fish communities. Indeed, over 63% of the offshore fish species monitored by the US National Oceanographic and Atmospheric Administration in their 2010 trawl survey were either absent on one side of, or differed in abundance across, Samalga Pass (von Szalay et al., 2011). Though the reason for these differences may be related to differences in bathymetry, the connectivity of some fish populations along the Aleutian Archipelago remains unclear (Logerwell et al., 2005). It is clear, however, that for fish species associated with nearshore habitats in the archipelago, the widespread reduction of kelp forests that has occurred over the past few decades in the western Aleutian Islands has resulted in a decrease in some species, such as the rock greenling, *H. lagocephalus* (Reisewitz et al., 2005). Similarly, decreases in kelp frond density significantly decreased the number of kelp associated fish recruits in California kelp forests (O'Connor and Anderson, 2010), and loss of these forests can result in reduced numbers of associated fishes (Bodkin, 1988). Together, these highlight how differences in the structural habitat that kelp forests provide can have significant effects on the abundance and distribution of associated fish species (Hamilton and Konar, 2007; O'Connor and Anderson, 2010; Efrid and Konar, 2014; Konar et al., 2015). Consequently, differences in distribution and abundance of the forest-forming kelps across Samalga Pass are likely a strong determinant of differences in fish communities observed in our study.

In addition to differences in fish and macroalgae, we observed significant differences in sessile and motile invertebrate assemblages on opposing sides of Samalga Pass. Differences in invertebrate assemblages across Samalga Pass are likely due to three factors: 1) the physiological tolerance of a taxa and their tolerance for an ACC or AS dominated oceanographic environment, 2) the potential barriers to dispersal caused by currents and other attributes associated with Samalga Pass, and 3) species interactions between kelp forest community members that may be facilitative or inhibitory for one or multiple taxa. As an example of the latter, the distribution of *Cryptochiton stellari* may be strongly tied to crustose coralline algae such as *Clathromorphum* spp. Chemical cues from coralline algae induce metamorphosis in larval *C. stellari* (Lord, 2011). Not only were *C. stellari* and *Clathromorphum* spp. more abundant west of Samalga Pass, but these taxa are also highly abundant in urchin barren habitats (authors, unpub data), which are more frequently observed west of Samalga Pass (Estes and Duggins, 1995). Further research into the ecologies of these taxa is necessary to determine the mechanisms by which their abundances change across Samalga Pass.

Of the sea stars, *Leptasterias dispar* was only observed to the west of Samalga Pass, and *Orthasterias koehleri* and *Pycnopodia helianthoides* were only observed to the east of the pass. We recognize that this may have resulted from simply missing these species in our sampling, as Jewett et al. (2012) observed both *L. dispar* and *P. helianthoides* at a few other Aleutian Archipelago islands in a separate survey. Further, historical observations from 1987 provide evidence that *P. helianthoides* also occurred slightly west of Samalga Pass around Chuginadak Island (J. Estes pers. obs.), and single individuals of this species have occasionally been observed in the central Aleutians, particularly around the fishing port of Adak Island, since the mid 2000s (authors pers. obs.). At the time of its first discovery in the archipelago, *H. vermilion* was thought to be limited to the east of Samalga Pass (Jewett and Clark, 2011), but our study observed it to the west of the pass. While the reasons for these differences in their cross-pass abundances remain unknown, they might be related to salinity and/or temperature, as the ocean waters east of Samalga are warmer and fresher than they are west of the pass due to influence from the ACC or AS, respectively (Ladd et al., 2005). Regardless, the broad distribution of at least some sea stars observed in our study (e.g., *O. koehleri* and *P. helianthoides*) was not surprising given they are broadcast spawners (Greer, 1962; Miller, 1989), with planktotrophic larvae that have

potential pelagic larval durations in excess of 20 weeks (Strathmann, 1978), which would allow for their dispersal over broad geographic areas. In contrast, other sea stars (e.g., multiple species of the genus *Leptasterias*) brood their young (Chia, 1966; George, 1994), and thus may be limited in their ability to disperse long distances. Whether these differences in larval dispersal are important to their cross-pass differences remains unknown and warrants further investigation.

In this study, we identified significant differences in the distribution and abundance of two forest forming kelps, *Eualaria fistulosa* and *Nereocystis luetkeana* along with differences in the kelp-associated fish, invertebrate, and macroalgal assemblages. These observed community differences could be due to multiple physical and biological features that change at Samalga Pass. Possible explanations include rapid changes in ocean temperatures and/or currents on opposing sides of the pass (Ladd et al., 2005), or that the islands west of Samalga Pass lie beyond the continental shelf and thus have deep water habitats that may provide refuge and/or nursery grounds for some invertebrates. Another possible explanation may be that the predatory sea star, *Pycnopodia helianthoides*, is more common to the east of the pass compared to the west. This sea star exerts strong top-down control on sea urchins and other invertebrates elsewhere in the northeastern Pacific through both predation and behavioral responses (Duggins, 1983; Hagen et al., 2002). The presence of *P. helianthoides*, in concert with differences in environmental conditions may regulate invertebrate distribution patterns on the islands east of the pass. Another top predator, the sea otter, can also have a strong top-down control on kelp forest ecosystems. Sea otters have dramatically declined across the Aleutians, including areas to the east of Samalga Pass (Doroff et al., 2003). Because of this overall decline, it is unlikely that sea otter population levels alone explain the disparity in kelp forest cover and kelp community assemblage across Samalga Pass. While we do not know what specific factor(s) control the current distribution of organisms across Samalga Pass, we have shown that similar to pelagic and offshore communities, kelp forest communities differ across this pass. This finding is significant as it demonstrates a biogeographic break existing for multiple communities, impacting both the offshore and nearshore environments.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.csr.2017.06.007.

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