

Local habitat and regional oceanographic influence on fish distribution patterns in the diminishing kelp forests across the Aleutian Archipelago

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Abstract Fish distributions can be influenced by changes in their local habitat features and regional oceanographic conditions, both of which can occur at different spatial scales. Currently, the coastal waters throughout the Aleutian Archipelago are dominated by two discrete habitats types, kelp forests and urchin barrens, both of which span known U.S. biogeographic breaks near Buldir and Samalga Passes. These passes roughly divide the western Aleutians from the central Aleutians, and the central Aleutians from the eastern Aleutians, respectively, and have been suggested as important breaks for demersal fishes and deep marine fauna due to corresponding changes in ocean conditions. This study assessed how local habitat features compare to regional oceanographic conditions in how they influence nearshore fish assemblages throughout the Aleutian Archipelago. We hypothesized that these assemblages would differ markedly between the kelp forests and urchin barrens, and that local habitat features such as forest size and the abundance of understory kelps and turf algae are more important to assemblage structure than large-scale oceanographic conditions. To explore these hypotheses, 32 kelp forests and 24 non-

forested urchin barren areas occurring on 15 Aleutian islands were surveyed for fish assemblage structure and habitat characters using scuba. Within the kelp forests, both the interiors (middles) and the margins (edges) of the forests were sampled for comparison. In general, fish assemblages did not significantly differ between kelp forests and urchin barrens in the western and central Aleutian Islands. Across all three regions, we found that of 26 habitat characters considered, five (density of the stipitate kelp *Agarum*, the percent bottom covers of understory foliose algae and encrusting coralline algae, and the availability of gravel and bedrock) together provided the best correlation with the observed variation in the fish assemblages, but this appeared to be due to the greater influence of these in the eastern Aleutians where the abundance of *Agarum* is greatest. However, the relationship between these habitat characters and fish assemblage structure was weak across the archipelago and not statistically significant in any of the regions. Implications of these analyses suggest that a further reduction in kelp forests may not impact fish assemblages in the western and central Aleutians. However, this is likely an artifact of these forests already being in a diminished state, with most of the kelp forests having been replaced by urchin barrens, and thus the impacts to the fish assemblages have presumably already occurred. However, this may be different in the eastern Aleutians where kelp forests remain more abundant and where the influence of *Agarum* appears strongest. In addition, while nearshore fish assemblages were not significantly different on the opposing sides of Buldir Pass, they were significantly different on the opposing sides Samalga Pass, suggesting that variation in large-scale oceanographic

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conditions around this pass were important drivers of differences in fish assemblages. However, if ocean properties, such as temperature and salinity, change around Buldir Pass in the future, then corresponding differences in the fish assemblages may develop.

Keywords Fish · Kelp forests · Urchin barrens · Habitat drivers · Oceanographic biogeographic breaks

Introduction

Many fish species use nearshore rocky habitats as permanent and/or transient homes to reproduce, nurse, feed and avoid predators (Adreani et al. 2004; Erisman and Allen 2006; Johnson et al. 2010; Freeman and Creese 2011). In the ecosystems of the North Pacific Ocean, these habitats include kelp forests (defined here as rocky reefs dominated by canopy-forming kelps) and urchin barrens (defined here as rocky reefs devoid of foliose macroalgae but with abundant herbivorous sea urchins). Within these two habitat types, larger reefs that are characterized by greater habitat complexity typically support a greater richness and abundance of fish species (Hackradt et al. 2011), with vegetated habitats tending to support the highest recruitment, greatest densities, and most species (Pérez-Matus et al. 2007; Cote et al. 2013; Krug and Steele 2013; but for exceptions see Angel and Ojeda 2001; Irigoyen et al. 2011). In addition, the type of vegetation (e.g., canopy-forming kelps versus understory algae) and the specific location within the kelp forests (e.g., interiors versus margins) can further influence the composition of fish assemblages as shown by Pérez-Matus and Shima (2010) and Efir and Konar (2013). As a result, loss of kelp forest vegetation generally results in decreased fish abundance and diversity (Bodkin 1988; Siddon et al. 2008), though increased fish recruitment has been observed in some cases (Levin 1993; Siddon et al. 2008). When changes in fish abundance have occurred, it has been postulated that the fishes are responding to local features of the reef itself, though little is known about the relative importance of physical versus biological reef characters in structuring their assemblages. Regardless, the relationship between habitat vegetation and fish assemblage structure suggests that long-term persistence of some fishes may rely on the continued presence and/or resilience of the vegetation (Bodkin 1988; Carr 1989). However, it remains unclear how nearshore fish assemblages in the Aleutian

Archipelago associate with different physical and biological habitat characteristics over broad spatial scales, how these patterns are impacted by large-scale changes in ocean conditions such as those on opposing sides of biogeographic breaks, or if these patterns vary as a function of widespread kelp loss.

The need for a better understanding of how local habitat characteristics influence fish assemblages in the Aleutian Archipelago centers on observations that the region's kelp forests have been greatly reduced due to overgrazing by sea urchins (Estes et al. 1998). Consequently, most of the nearshore rocky reefs of the Aleutian Islands, specifically in the central and western regions of the archipelago, are currently dominated by urchin barrens, although some kelp forests persist in isolated locations that are scattered among the islands (Konar et al. 2014). The fish assemblages in these habitats have previously been described (Simenstad et al. 1977), with the dominant rock greenling, *Hexagrammos lagocephalus*, generally being substantially more abundant in kelp forests than in urchin barrens (Reisewitz et al. 2006). Likewise, fish assemblages in other areas of Alaska differ between the interiors versus margins of the kelp forests (Efir and Konar 2013), suggesting that they may similarly vary in the kelp forests of the Aleutian Archipelago. Finally, and similar to observations in seagrass meadows and coral reefs, the size of the forests may influence fish assemblages, with larger reefs typically supporting greater fish abundances (Wong et al. 2005; Jelbart et al. 2007; Hackradt et al. 2011). However, it remains unclear how these different sources of potential variation compare in their importance to structuring fish assemblages in the Aleutian Archipelago.

In addition to small-scale heterogeneity in local habitat characteristics, large-scale variation in oceanographic conditions, such as those occurring on opposing sides of biogeographic breaks, can also influence patterns of fish distribution, as has been observed in 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 breaks have been identified based on differences in the physical attributes of the 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). In the Aleutian

Archipelago specifically, U.S. biogeographic breaks have been suggested at Samalga and Buldir Passes based on differences in demersal fish and deep marine faunal communities, both of which have been attributed to changes in ocean conditions (Hunt and Stabeno 2005; Logerwell et al. 2005). In general, identifying biogeographic breaks is important so that we can better understand how large-scale oceanographic factors influence species distribution across broad spatial scales, and these two breaks are hypothesized to be important to the fish assemblages in the Aleutian Archipelago.

Whether kelp forest fishes associate more strongly with local habitat characteristics such as variation in the physical and biological features of the reefs, or differences in oceanographic conditions such as those observed between the opposing sides of biogeographic breaks is unclear. Consequently, a better understanding of these relationships will help us to predict how fish assemblages may respond to future changes in the physical and biogenic characteristics of the reef versus oceanographic climate. As such, the three primary objectives of this study were to 1) compare fish assemblage structure between the kelp forests and urchin barrens of the Aleutian Archipelago and evaluate if these assemblages differ between the interiors and margins of the kelp forests, 2) describe the physical and biological habitat characteristics of the reefs at these same locations and determine which of these habitat characteristics are most important in structuring the fish assemblages, and 3) evaluate if the fish assemblages vary between the opposing sides of known biogeographic breaks at Samalga and Buldir Passes. Once compiled, these data will be used to address two overarching hypotheses: 1) The coastal fish assemblages of the Aleutian Archipelago vary most strongly in accordance with local habitat features such as the presence of kelp forests and the abundance of macroalgae, and 2) Differences in overlying oceanographic conditions, such as observed on opposing sides of biogeographic breaks, are important to these coastal fish assemblages, but less so than variation in local habitat features.

Methods

Study area

The Aleutian Archipelago consists of more than 300 volcanic islands that extend approximately 1,900 km

from the Alaska Peninsula, USA in the east to the Kamchatka Peninsula, RUS in the west. The archipelago further defines the border between the Bering Sea to the north and the Pacific Ocean to the south. From the Islands of Four Mountains (169°W) west, the region's kelp forests are dominated by a single canopy-forming species, *Eualaria fistulosa*, and urchin barrens are abundant. East of these islands urchin barrens are rare and the kelp forests are dominated by two canopy-forming species, *E. fistulosa* and *Nereocystis leutkeana* (Miller and Estes 1989). Below these canopies, several species of understory kelps and benthic macroalgae occur along the substrate, primarily *Agarum clathratum*, *A. clathrus*, various species of *Laminaria* and *Saccharina*, and numerous foliose and coralline red algae. However, other than the two canopy-forming species (*E. fistulosa* and *N. leutkeana*) and the brown acid-bearing alga (*Desmarestia* spp.), annual species of large macroalgae are rare. In addition, understory kelps other than *A. clathratum* (hereafter simply *Agarum*) are rare in the central and western Aleutians due to overgrazing by green sea urchins (*Strongylocentrotus droebachiensis*) that has occurred following the widespread loss of their primary predator, the northern sea otter (*Enhydra lutris*) (Estes and Duggins 1995; Estes et al. 1998). The most abundant families of shallow reef fishes include gadids (Gadidae), greenlings (Hexagrammidae), rockfish (Scorpaenidae), and sculpins (Cottidae) (Simenstad et al. 1977). While the literature has recognized multiple biogeographic breaks within the Aleutian Archipelago, in this study, we focus on two primary ones that occur in the U.S.; at Samalga Pass (169°W) and at Buldir Pass (176°E). Consequently, our sampling design divided the archipelago into three geographic regions (roughly corresponding to the eastern, central and western Aleutians) that also reflect possible distributional changes in demersal fish assemblages (Logerwell et al. 2005).

Fish surveys

To quantify the fish assemblages throughout the Aleutian Archipelago and investigate if they associate differently with kelp forest versus urchin barren habitats, scuba surveys were conducted at 32 kelp forests and 24 urchin barrens occurring on 15 Aleutian Islands in late June and early July of 2009 and 2010 (Fig. 1). Specifically, four kelp forests and four urchin barrens were surveyed in the western Aleutians, 20 kelp forests

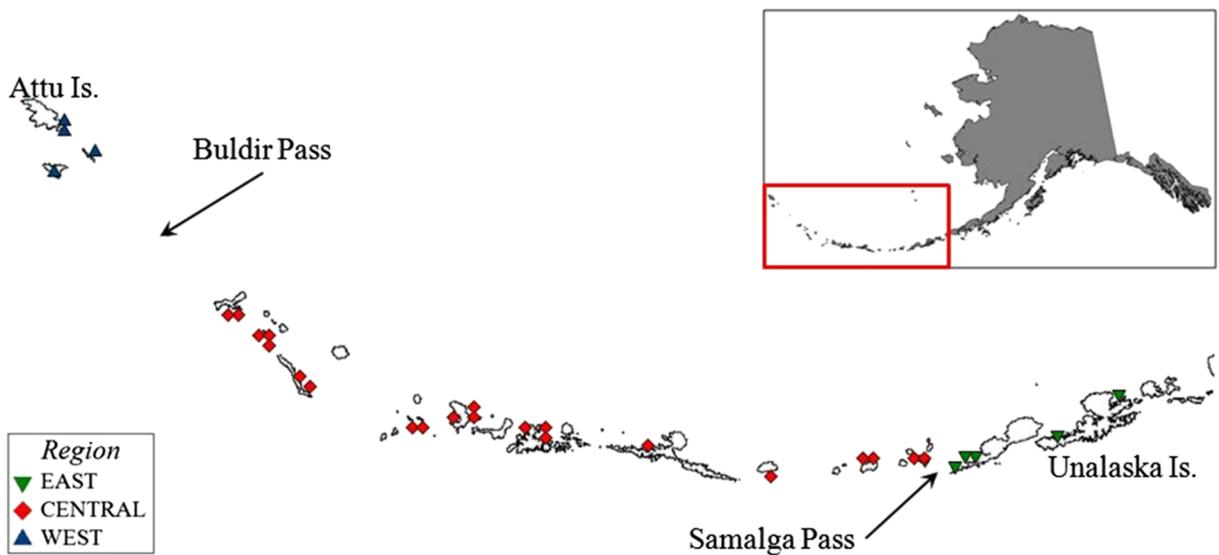


Fig. 1 Map of the Aleutian Archipelago showing 15 study sites. Green downward facing triangles are sites in the east, red diamonds are central sites, and blue upward facing triangles are sites

and 20 urchin barrens were surveyed in the central Aleutians, and eight kelp forests and no urchin barrens were surveyed in the eastern Aleutians (at the time of this study, urchin barrens were not observed in the eastern Aleutians). Because of the large distances between the eastern and western regions of the archipelago and the limited time available to sample in each year, we could not sample all sites in each year of the study but rather sampled the eastern and western regions in different years. However, we did sample different islands in the central Aleutians in each year of the study and saw no discernable changes in community structure (authors personal observation). Also, research done at specific kelp forests during these same cruises suggested that there was little, if any, variability in community structure over the 2–3 years that they were monitored (Konar et al. 2014). For these reasons, we combined years for the analyses. To foster independence among sample sites on each island, the kelp forests and urchin barrens were chosen at random and were separated by hundreds of meters to several kilometers, depending on forest availability. Also, to examine if fish assemblages differ between the interiors and the margins of the kelp forests, two locations were sampled within each of the kelp forests; one in the interior of the forest and one along the offshore edge of the forest. To again foster independence among transects, their starting positions were chosen at random and separated by tens to hundreds of meters. At each location and within each habitat, fish

in the west. The locations of the two biogeographic breaks at Buldir and Samalga Passes are noted with arrows

assemblages were surveyed along two - 2 m × 2 m × 50 m transect corridors (sample area = 200 m³ per transect), one of which extended along the benthos to a height of two meters and the other of which ran through the midwater, four to six meters above the first transect. Specifically, a team of two divers surveyed each transect on SCUBA, and identified and counted all juvenile and adult fishes (excluding larvae) that occurred within each of the transect corridors. Data for the benthic and midwater transects were combined to provide a single estimate of fish abundance at each location.

Habitat surveys

To examine if site-specific characteristics of the physical and/or biogenic habitat were responsible for variation in the observed spatial patterns in fish assemblages, habitat surveys were conducted along each of the benthic transects in each habitat type described above to estimate the abundance of understory and canopy-forming algae, the percent cover of substrate-occupying organisms, and the availability of different substrate types, and to characterize bottom topography, measure overall kelp forest size and depth, and determine oceanographic characters such as seawater salinity and temperature. Specifically, following the fish surveys at each site, a 0.25 m² quadrat was placed on the benthos every 10 m along the transect corridor ($n=6$ per transect) and the percent covers of the different substrate types were estimated within each of

the quadrats using a modified Wentworth scale (Wentworth 1922); where the substrate was visually categorizing into sand (<2 mm grain size (gs)), gravel (2–6 mm gs), cobble (6–100 mm gs), boulder (10 cm–1 m gs), and bedrock (>1 m gs). Also within each quadrat, all understory algae and canopy-forming species less than 2 m tall were identified and counted, and the percent cover of the different substrate-occupying organisms was estimated. These organisms included encrusting coralline algae, foliose red and green algae, brown algae in the genus *Desmarestia*, and numerous sessile invertebrates. Canopy-forming kelps over 2 m tall, which are less abundant than understory algae, were identified to species and counted along each transect. Substrate topography (hereafter rugosity) was measured adjacent to each quadrat using a 1.5 m long chain attached at one end to a 1 m PVC bar, where the chain contoured the substrate for a linear distance of one meter and the length of chain required to cover that distance was recorded. The resulting ratio of chain length vs. the 1 m linear distance was a measure of seafloor topography (Hamilton and Konar 2007). To estimate the size of each kelp forest, the surface canopy of each forest was mapped using a small boat and portable Garmin Oregon 300c GPS. The GPS track line data were uploaded into ArcGIS software (ESRI Software Inc., Redland, CA) and the area of the projected polygons was calculated. Water temperature and depth were recorded along each transect within the forests using an Oceanic Versa Pro dive computer. Salinity was measured using an Atago ATC-S/Mill-E hand-held refractometer on bottom water samples that were collected along each benthic transect. In all, 26 habitat characters were described at each site.

Analyses

All statistical analyses were done in PRIMER ver. 6 and SYSTAT ver. 12. Prior to analyses, data on fish abundances were 4th root transformed to down weight the effects of overly abundant species and account for the importance of rarer species, thereby integrating their contributions and focusing attention on patterns within the whole assemblage (Clarke and Warwick 2001). Next, a resemblance matrix of similarities in fish assemblages among all sample site pairs was created based on Bray-Curtis similarities on the transformed data. Following this, data for habitat characteristics, which include estimates of physical factors such as the availability of different substrate types, bottom rugosity, reef

depth, water temperature and salinity, and of biogenic factors such as the abundances of different habitat-forming understory algae and canopy-forming kelps, the percent cover of benthic algae and invertebrates, and of overall forest size were checked for multivariate normality using bivariate draftsman plots and square root transformed. The habitat data were then normalized and a resemblance matrix of similarities in habitat characteristics among all sample site pairs was created based on Euclidean distances on the transformed data. Because interpretation of Euclidean distances for environmental variables is most effective if the data are approximately multivariate-normally distributed, our choice of a square-root transformation was based on how it corrected for problems associated with multivariate normality. This ultimately resulted in different transformations for the fish and habitat variables, with each based on the individual needs of the corresponding similarity measures used, as suggested for this type of analysis by Clarke and Ainsworth (1993).

Since both habitat types (kelp forests and urchin barrens) were observed in the western and central Aleutians but only kelp forests were observed in the eastern Aleutians, our data were not orthogonal with respect to this important variable. Consequently, we adopted an iterative strategy for analyzing our data in which we examined hypotheses related to habitat type that included data from only two regions separately from hypotheses relating to more general Aleutian-wide fish assemblages or of specific difference between locations within the forests, both of which included data from all three regions. First, the relative differences in overall fish assemblages among three regions (eastern vs. central vs. western Aleutians) were evaluated graphically with an nMDS plot based on Bray-Curtis similarities. Additionally, quantitative differences in fish assemblages among the three regions and the different islands within each region were examined with a two-factor nested PERMANOVA, with Region considered as fixed factor and Island nested within Region considered as a random factor. Following the identification of significant differences in fish assemblages among the three regions (see Results), differences between specific pairs of regions were examined with permutation post hoc tests. The amount of variation explained by each of these factors was determined by calculating the ‘magnitude of effects’ associated with each factor according to their variance components (Graham and Edwards 2001). The relative importance of each fish species to

the differences among regions was then determined using a Similarity Percentage (SIMPER) analyses on the fish assemblage data. Next, the relative differences between the two habitat types (kelp forests vs. urchin barrens) within just the western and central regions of the Aleutians were evaluated graphically with an nMDS plot that was based on Bray-Curtis similarities. Following this, quantitative differences in fish assemblages among the two regions and the different islands within each region, and between the two habitat types were examined with a three-factor nested PERM ANOVA, with Region and Habitat type considered as fixed factors, and Island nested within Region considered as a random factor. The amount of variation explained by each of these factors was determined by calculating the ‘magnitude of effects’ associated with each factor according to their variance components. Lastly, relative differences in fish assemblages between locations within the forests (interiors vs. margins) across all three regions were examined with an nMDS plot that was based on Bray-Curtis similarities. Quantitative differences in these assemblages were examined among regions, islands within each region, and between locations within the kelp forests with a three-factor nested PERMANOVA, with Region and Location within the forests considered as fixed factors, and Island nested within Region considered as a random factor. The amount of variation explained by each of these factors was determined by calculating the ‘magnitude of effects’ associated with each factor according to their variance components. Following identification of a significant Region X Location interaction (see [Results](#)), differences in fish assemblages between the interiors and margins of the forests were examined within each region separately using separate two-factor PERM ANOVAs, with Island and Location within the forest considered as fixed factors. This last test, while similar to the first PERMANOVA that explicitly tested hypotheses relating to how spatially variable the fish assemblages were in general regardless of local habitat type, differed in that it considered only kelp forests and focused on hypotheses relating to how location within the forests impacted these assemblages.

The overall relationships between the 26 measured habitat characters and the fish assemblages were evaluated across all three geographic regions to identify the habitat variables that provided the best match between the among-site patterns in fish assemblages and the among-site patterns in habitat variables. The rationale

here is that the degree to which these two data sets match should reflect the degree to which the chosen habitat variables ‘explain’ the observed patterns in fish assemblages (Clarke and Warwick 2001). This involved examining all combinations of habitat variables to identify a subset of variables that maximized the rank correlations (i.e., provided the ‘best’ fit) between the similarity matrix of fish abundances (based on Bray-Curtis distances) and a similarity matrix of the different habitat variables (based on Euclidean distances). To do this, a resemblance matrix based on 4th root transformed fish abundance data was created to determine among-site similarities in fish assemblages. Next, a resemblance matrix based on square root transformed and normalized habitat data was created for the habitat variables. Following this, the subset of habitat variables that best described the observed patterns in fish assemblages was identified using the BIO-ENV procedure in Primer-E on the ranked correlations between all site pairs. A ‘global BEST match permutation test’ was used to test for significance of the fit between the matrices based on the best habitat characters and the fish assemblages. Next, and because the other analyses identified significant variation among the three regions, the relationships between the 26 habitat characters and the fish assemblages were examined within each region separately using individual BIO-ENV procedures, and the subset of habitat variables that best described the observed patterns in fish assemblages were identified for each region. Each of these included ‘global BEST match permutation tests’ to test for significance between the selected habitat characters and the fish assemblages.

Results

Twenty-five fish taxa were observed across all reefs surveyed in this study. These fish assemblages were highly variable among the three geographic regions (PERMANOVA: $p=0.053$) and the different islands within each region ($p=0.002$) (Figs. 2 and 3; Table 1). However, most of the spatial variability (79 %) in the fish assemblages was observed at the smallest spatial scale examined (among sites within each island), with less variability observed among islands within each region (14 %) or among regions themselves (7 %). This indicated that variation in the fish assemblages followed a hierarchical scaling pattern, with most of the variability observed at small spatial scales and the

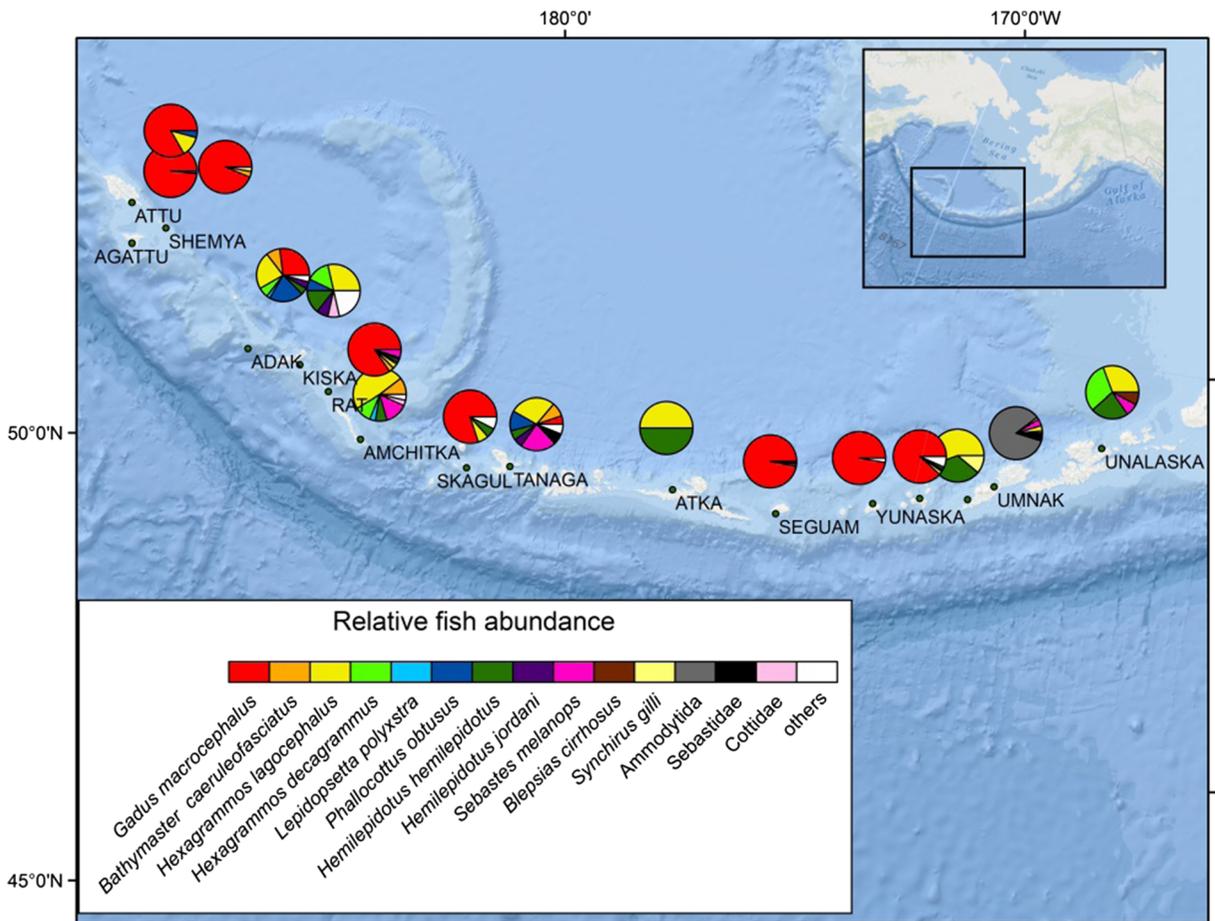


Fig. 2 Map of the Aleutian Archipelago showing relative differences in the proportional species composition within the fish assemblages observed on the different inlands sampled in 2009 and 2010. Data reflect all fish observed in both kelp forests and urchin barrens

least amount of variability observed at large spatial scales. Consequently, although significant differences were observed among the regions, the only significant differences observed between specific pairs of regions were between the western and eastern Aleutians (Pair-wise test: $p=0.076$), with little-to-no differences observed between the eastern and central Aleutians ($p=0.131$) or the western and central Aleutians ($p=0.148$, Table 1). The primary taxa responsible for the overall differences among the regions were *Gadus* (gadids) and *Hexagrammos* (greelings), which on average accounted for approximately 25 and 13 % of the differences among the regions, respectively (Table 2A-C).

When the fish assemblages were compared between kelp forests and urchin barrens on the different islands throughout the western and central Aleutians (i.e., regions where these two habitats were both observed), no significant differences were observed between the two

regions (PERMANOVA: $p=0.261$) or among islands within each region ($p=0.407$) (Table 3). Indeed, most of the total variation in assemblage composition was observed among sample sites within each island (95 %), and only a small amount of the variation was observed between the two regions (4 %) or among islands within each region (1 %). Counter to our initial hypothesis, no differences were observed between the kelp forest and urchin barrens ($p=0.584$; Fig. 4), and this factor accounted for very little (<1 %) of the total variation. Further, this lack of differences between the habitats itself did not vary among the different islands within each region (Habitat X Island(Region) interaction: $p=0.936$, < 1 % of the variation explained) or between the two regions (Habitat X Region interaction: $p=0.564$, < 1 % of the variation explained). Consequently, as with the patterns observed when all three regions were considered together without

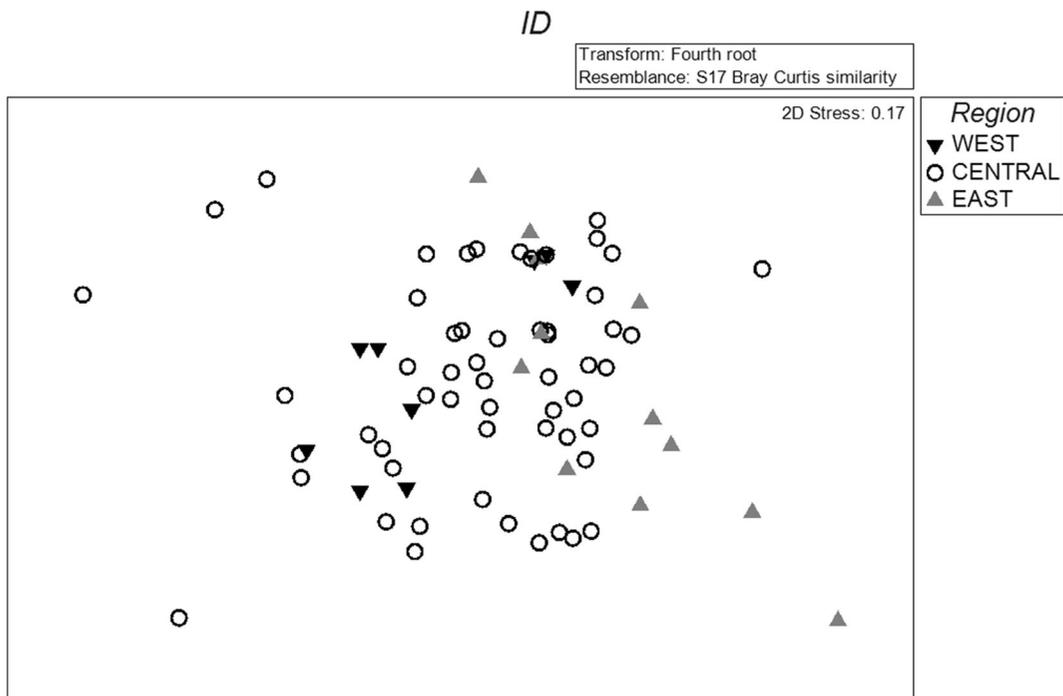


Fig. 3 nMDS plot showing relative (significant) differences in the fish assemblages observed among the three regions of the Aleutian Archipelago. Data are for all fish observed in both urchin barrens

and kelp forests. Each symbol represents a different study. Differences were based on Bray Curtis similarities of the 4th root transformed data

consideration of habitat type, this indicates that the fish assemblages in the Aleutian Islands indeed follow a scaling issue, in which they were most variable at small spatial scale and less variable at larger spatial scales, with very little influence of habitat type.

When the fish assemblages within just the kelp forests were examined across all three geographic regions of the archipelago, they did not vary significantly among regions (PERMANOVA: $p=0.157$, 4 % of the variation explained) but did vary among the different islands within each region ($p=0.001$, 18 % of variation explained) (Table 4). Further, because we found significant differences in the fish assemblages among regions when all habitats were considered (discussed above), a priori post hoc test of differences in the assemblages between specific pairs of regions were done, and these revealed that marginal differences were observed between the western and eastern Aleutians (Pair-wise test: $p=0.076$), but not between the western and central Aleutians ($p=0.148$) or the central and eastern Aleutians ($p=0.131$; Table 4). More importantly, and contrary to our initial predictions, the assemblages did not differ between locations (interiors vs. margins) in the forests ($p=0.546$, < 1 % of variation explained) (Fig. 5;

Table 4), a pattern that was consistent in all three regions (Region X Location interaction: $p=0.925$, < 1 % of the variation explained) and on the different islands within each region (Island(Region) X Location interaction: $p=8.818$, < 1 % of the variation explained). Further, and as with habitat-independent patterns in the fish assemblages, the greatest amount of variation (78 %) was again observed among sample sites within each island. The primary species responsible for the differences among the three regions were again *Gadus* and *Hexagrammos*, which varied depending on the specific regions being compared but on average accounted for approximately 25 and 14 % of the similarity in the resemblance matrix, respectively (Table 5A–C). This indicates that the fish assemblages within just the kelp forests of the Aleutian Archipelago followed a similar scaling issue to that observed when both kelp forest and urchin barrens were considered, in that they were most variable at the smallest scale examined (i.e., among sites within each island), followed by the intermediate scale (i.e., among islands within each region), and then by the largest scale (i.e., among regions), with very little influence of location within the habitat. Further, when the fish assemblages in the kelp forests were examined

Table 1 (A) PERMANOVA results testing differences in fish assemblages among Regions and Islands nested within Regions. Differences are based on Bray-Curtis similarities of 4th root

transformed abundance data. (B) Post-hoc permutation tests of the significant Region factor. Data are for all Aleutian fish regardless of habitat

| A: PERMANOVA | | | | | | |
|-------------------|--------|----------|--------|----------|---------|----------------|
| Source | df | SS | MS | Pseudo-F | P(perm) | mag effect (%) |
| Region | 2 | 14,791 | 7395.5 | 1.8116 | 0.053 | 7 % |
| Island(Region) | 13 | 61,958 | 4766.0 | 1.8867 | 0.002 | 14 % |
| Res(=sites) | 64 | 1.62E+05 | 2526.1 | | | 79 % |
| B: Post-hoc tests | | | | | | |
| Comparison | t | P(perm) | | | | |
| West v East | 1.5428 | 0.076 | | | | |
| West v Central | 1.3056 | 0.148 | | | | |
| East v Central | 1.2863 | 0.131 | | | | |

within each region separately, they again did not vary between locations within the forests in any of the regions (PERMANOVAs: western, $p=0.695$; central $p=0.689$; eastern, $p=0.584$). In contrast, results were mixed when assessing differences in the assemblages between locations within the forests when examined across the different islands within each region separately. Specifically, the relative influence of location within the forests varied among the islands in the western Aleutians (Location X Island(Region) interaction: $p=0.035$), but not in the eastern ($p=0.968$) or central ($p=0.515$) Aleutians, but again the effect of location within the forest was not significant for any of the comparisons.

Of all 26 habitat variables that were considered in this study, only five were found to provide the ‘best’ fit with the observed patterns in fish assemblages when examined across all sites in the Aleutian Archipelago. Specifically, these were *Agarum* density and the percent bottom cover of understory and encrusting algae, and the availability of gravel and bedrock (BIO-ENV: $\rho=0.114$). Interestingly, and in contrast to our hypotheses, forest size was not considered as one of the important factors. In fact, including forest size or any of additional habitat variables reduced the overall fit between the habitat and fish resemblance matrices, suggesting they were not important to the fish assemblages. However, even when considering only these five best variables, no significant relationship was observed between the resemblance matrix based on fish assemblages and the resemblance matrix based on the habitat variables ($p=0.49$), indicating that the relative differences and/or similarities in fish assemblages between sites was not attributed to corresponding generalizable differences and/

or similarities in local habitat characters, but rather was due either to large-scale (regional) oceanographic factors or that the important habitat drivers of the fish assemblages themselves varied among the different regions. Indeed, when each region was examined separately, the habitat variables that provided the best fit with the fish assemblages differed depending on which region was considered, but none of these were significantly correlated to patterns in fish assemblages in any of the regions. Specifically, the habitat variables that provided the best fit in the eastern Aleutians included *Agarum* density (BIO-ENV: $\rho=0.295$), but these were not significantly correlated with fish assemblages ($p=0.24$). In contrast, in the western and central Aleutians, no subset of variables could be identified that provided a better fit with the fish assemblages than other sets of variables (western, maximum $\rho=0.86$; central, maximum $\rho=0.143$), and none were significantly correlated with patterns in fish assemblages (western, $p=0.07$; central, $p=0.86$).

Discussion

The organization of biological communities can be influenced by physical and biological factors that operate on a wide variety of spatial and temporal scales (Levin 1992). Consequently, to understand the primary factors responsible for structuring species assemblages, it is often helpful to identify the scales at which these assemblages are most variable and thus are most strongly influenced by their environments (Edwards 2004). Throughout the Aleutian Archipelago, our data suggest

Table 2 Spatial comparison - all habitats

A. SIMPER analyses showing percent contribution of each species to the overall observed differences in fish assemblages between the western and eastern Aleutian Islands of all habitats

| Species | West | Est | Avg Diss | Diss/SD | Conttib% | Cum.% |
|--------------------------------------|-----------|-----------|----------|---------|----------|-------|
| | Avg Abund | Avg Abund | | | | |
| <i>Gadus macrocephalus</i> | 2.53 | 0 | 24.93 | 1.12 | 30.35 | 30.35 |
| <i>Hexagrammos lagocephalus</i> | 0.76 | 0.79 | 9.69 | 0.82 | 11.79 | 42.14 |
| <i>Hemilepidotus hemilepidotus</i> | 0.13 | 0.38 | 6.22 | 0.66 | 7.56 | 49.7 |
| Sebastidae sp. 1 | 0 | 0.4 | 5.66 | 0.51 | 6.89 | 56.59 |
| <i>Phallocottus obtusus</i> | 0.38 | 0.17 | 5.14 | 0.6 | 6.26 | 62.85 |
| <i>Hexagrammos decagrammus</i> | 0 | 0.27 | 5.08 | 0.46 | 6.19 | 69.04 |
| Ammodytidae | 0 | 0.51 | 4.92 | 0.42 | 5.99 | 75.03 |
| <i>Bathymaster caeruleofasciatus</i> | 0.36 | 0.18 | 4.81 | 0.72 | 5.85 | 80.88 |
| <i>Synchirus gillis</i> | 0 | 0.33 | 4.46 | 0.59 | 5.43 | 86.31 |
| <i>Sebastes melanops</i> | 0 | 0.23 | 2.68 | 0.42 | 3.27 | 89.58 |
| <i>Lepidopsetta polyxystra</i> | 0.22 | 0 | 2.14 | 0.48 | 2.6 | 92.18 |

B. SIMPER analyses showing percent contribution of each species to the overall observed differences in fish assemblages between the western and central Aleutian Islands for all habitats

| Species | West | Central | Av.Diss | Diss/SD | Contrib% | Cum.% |
|--------------------------------------|----------|----------|---------|---------|----------|-------|
| | Av.Abund | Av.Abund | | | | |
| <i>Gadus macrocephalus</i> | 2.53 | 0.66 | 26.65 | 1.24 | 35.57 | 35.57 |
| <i>Hexagrammos lagocephalus</i> | 0.76 | 0.72 | 10.74 | 0.66 | 14.33 | 49.9 |
| <i>Bathymaster caeruleofasciatus</i> | 0.36 | 0.27 | 6.23 | 0.74 | 8.32 | 58.22 |
| <i>Phallocottus obtusus</i> | 0.38 | 0.26 | 6.23 | 0.66 | 8.31 | 66.53 |
| <i>Hemilepidotus hemilepidotus</i> | 0.13 | 0.42 | 6.17 | 0.74 | 8.24 | 74.77 |
| <i>Lepidopsetta polyxystra</i> | 0.22 | 0.05 | 2.84 | 0.48 | 3.79 | 78.56 |
| <i>Sebastes melanops</i> | 0 | 0.2 | 2.65 | 0.39 | 3.53 | 82.09 |
| unknown juvenile fish | 0 | 0.19 | 2.41 | 0.34 | 3.22 | 85.31 |
| <i>Hemilepidoyus jordani</i> | 0 | 0.16 | 2.39 | 0.34 | 3.19 | 88.5 |

C. SIMPER analyses showing percent contribution of each species to the overall observed differences in fish assemblages between the western and central Aleutian Islands for all habitats

| Species | East | Central | Av.Diss | Diss/SD | Contrib% | Cum. % |
|--------------------------------------|---------|----------|---------|---------|----------|--------|
| | Av.bund | Av.Abund | | | | |
| <i>Hexagrammos lagocephalus</i> | 0.79 | 0.72 | 11 | 0.83 | 13.76 | 13.76 |
| <i>Gadus macrocephalus</i> | 0 | 0.66 | 8.55 | 0.6 | 10.7 | 24.46 |
| <i>Hemilepidotus hemilepidotus</i> | 0.38 | 0.42 | 8.26 | 0.83 | 10.33 | 34.79 |
| Sebastidaw sp. 1 | 0.4 | 0.07 | 6.36 | 0.54 | 7.95 | 42.74 |
| <i>Hexagrammos decagrammus</i> | 0.27 | 0.12 | 6.18 | 0.52 | 7.73 | 50.47 |
| Ammodytidae | 0.51 | 0 | 5.17 | 0.43 | 6.47 | 56.94 |
| <i>Sebastes melanops</i> | 0.23 | 0.2 | 4.91 | 0.59 | 6.14 | 63.08 |
| <i>Bathymaster caeruleofasciatus</i> | 0.18 | 0.27 | 4.86 | 0.64 | 6.07 | 69.15 |
| <i>Synchirus gillis</i> | 0.33 | 0.02 | 4.75 | 0.62 | 5.94 | 75.09 |
| <i>Phallocottus obtusus</i> | 0.17 | 0.26 | 4.43 | 0.63 | 5.54 | 80.63 |
| unknown juvenile fish | 0 | 0.19 | 2.47 | 0.36 | 3.09 | 83.72 |
| unknown sp. | 0.17 | 0.05 | 2.47 | 0.46 | 3.08 | 86.8 |
| <i>Hemilepidoyus jordani</i> | 0 | 0.16 | 2.44 | 0.36 | 3.05 | 89.85 |
| <i>Blepsias cirrhosus</i> | 0.17 | 0 | 2.05 | 0.4 | 2.56 | 92.41 |

Av. Abund Average Abundance, Av Diss Average dissimilarity, Diss/SD the ratio of dissimilarity to standard deviation, Contrib % Percent contribution

Table 3 (A) PERMANOVA results testing differences in fish assemblages among Regions, Islands nested within Regions, and Habitats (kelp forests vs. urchin barrens). Differences are based on

Bray-Curtis similarities of 4th root transformed abundance data. Data are for all fish in the western and central Aleutians

| A: PERMANOVA | | | | | | |
|----------------|----|---------|--------|----------|---------|----------------|
| Source | df | SS | MS | Pseudo-F | P(perm) | mag effect (%) |
| Region | 1 | 4005.9 | 4005.9 | 1.3094 | 0.261 | 4 % |
| Island(Region) | 1 | 1802.8 | 1802.8 | 0.62413 | 0.584 | <1 % |
| Habitat | 11 | 34226.0 | 3111.4 | 1.0345 | 0.407 | <1 % |
| RexHab | 1 | 1888.0 | 1888.0 | 0.65363 | 0.564 | <1 % |
| Is(Re)xHab | 9 | 25342.0 | 2815.8 | 0.93617 | 0.553 | <1 % |
| Res(=sites) | 17 | 51132.0 | 3007.8 | | | 95 % |

that fish assemblages are currently most variable at the smallest spatial scale we considered (among sample sites within each island), but that variation at intermediate (among islands within each region) and large (among geographic regions) spatial scales is also significant. Surprisingly, this regional-scale variation, which is presumably driven by differences in oceanographic conditions, such as those that occur on the opposing sides of the biogeographic breaks and thus delineate the geographic regions, appears even more important to fish

assemblage structure than whether the fish are inside kelp forests or in urchin barrens. While this supports our general hypothesis that coastal fish assemblages in the Aleutian Archipelago vary based on habitat characteristics, it contradicts our specific predictions that local-scale habitat features such as habitat type (kelp forest versus urchin barren) or location within the habitat (interiors vs. margins of the kelp forests) are more important than regional differences in ocean climate, as has been observed in numerous other studies (e.g.,

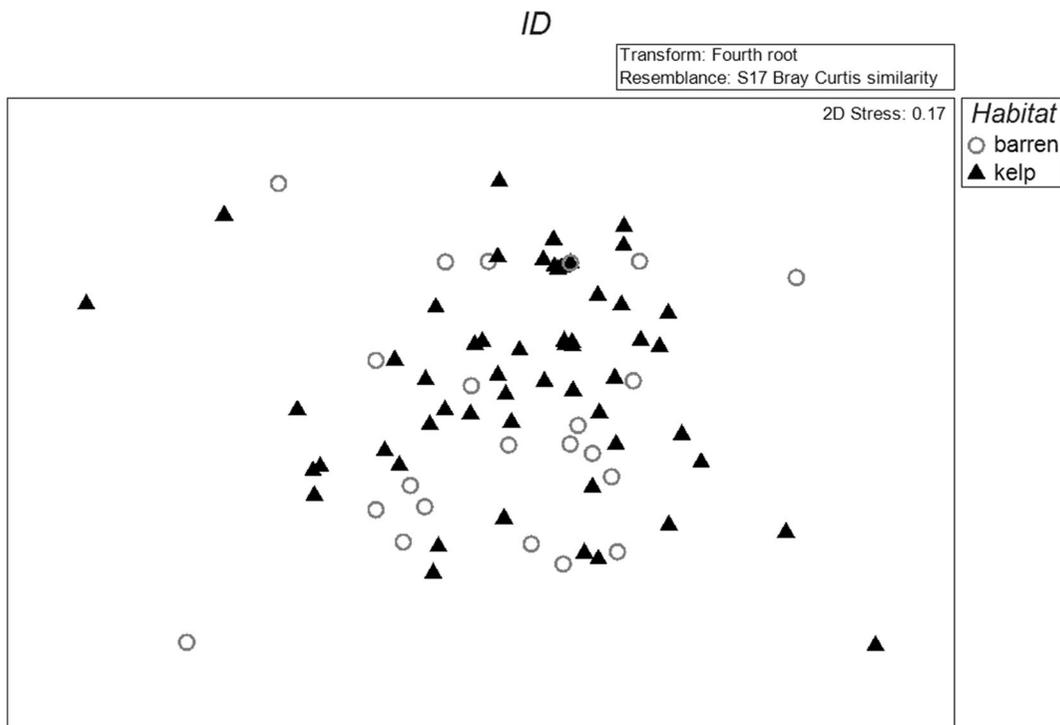


Fig. 4 nMDS plot showing relative (non-significant) differences in the fish assemblages observed between kelp forests and urchin barrens throughout the western and central Aleutian Islands. Each

symbol represents a different study site. Differences were based on Bray Curtis similarities of the 4th root transformed data

Table 4 (A) PERMANOVA results testing differences in fish assemblages among Regions, Islands nested within Regions and Locations within the kelp forests (interiors vs. margins). Differences are based on Bray-Curtis similarities of 4th root transformed

abundance data. (B) A priori post-hoc permutation tests of the significant Region factor. Data are for all fish within just the kelp forests

A: PERMANOVA

| Source | df | SS | MS | Pseudo-F | P(perm) | mag effect (%) |
|----------------|----|--------|--------|----------|---------|----------------|
| Region | 2 | 11,461 | 5730.6 | 1.4124 | 0.157 | 4 % |
| Island(Region) | 13 | 56,630 | 4356.2 | 1.7801 | 0.001 | 18 % |
| Location | 1 | 1740.9 | 1740.9 | 0.82029 | 0.546 | <1 % |
| RexLoc | 2 | 1878.8 | 939.39 | 0.44421 | 0.925 | <1 % |
| Is(Re)xLoc | 13 | 26,690 | 2053.1 | 0.83898 | 0.818 | <1 % |
| Res(=sites) | 26 | 63,625 | 2447.1 | | | 77 % |

B: Post-hoc tests

| Comparison | t | P(perm) |
|----------------|--------|---------|
| West v East | 1.5428 | 0.076 |
| West v Central | 1.3056 | 0.148 |
| East v Central | 1.2863 | 0.131 |

Bodkin 1988; Reisewitz et al. 2006; Efird and Konar 2013). In fact, our data show that local habitat characteristics are largely non-significant in structuring fish assemblages, especially when compared to variation

among the three geographic regions or the islands within each region. This hierarchical scaling pattern is similar to that observed for kelp assemblages along the California, USA and Baja California, MEX coasts

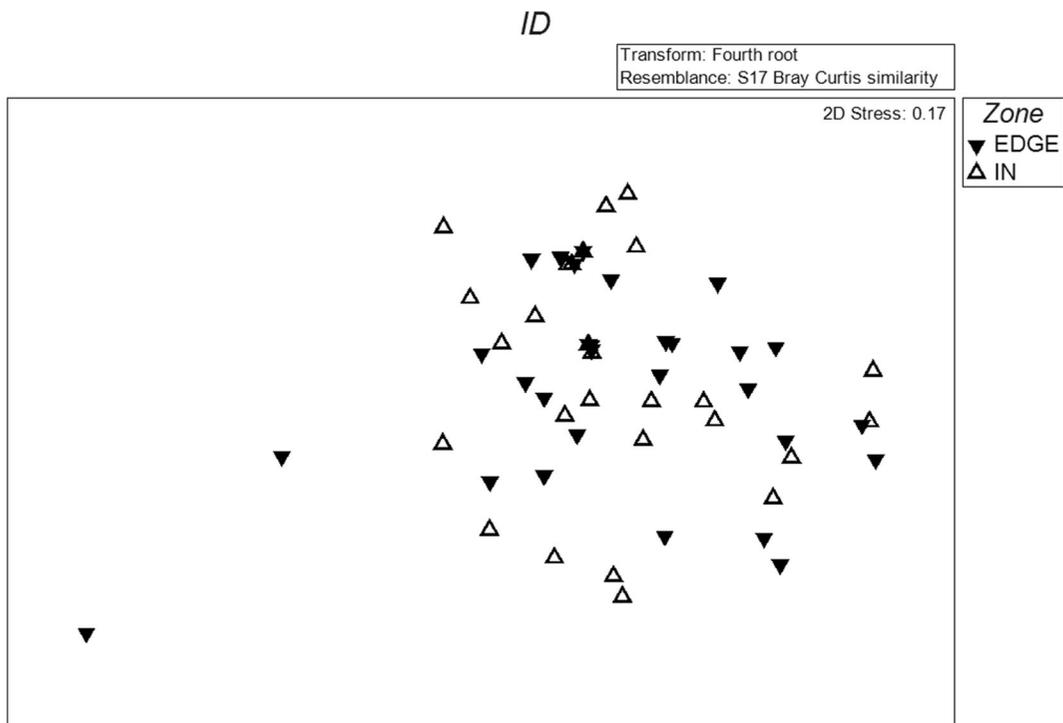


Fig. 5 nMDS plot showing relative (non-significant) differences in the fish assemblages observed between locations (Zones) of the kelp forests throughout all three regions of the Aleutian

Archipelago; IN=interiors and EDGE=margins. Each symbol represents a different study site. Differences were based on Bray Curtis similarities of the 4th root transformed data

Table 5 Kelp Forests - Interiors and margins comparison

A. SIMPER analyses showing percent contribution of each species to the overall observed differences in fish assemblages between the western and eastern Aleutian Islands of all habitats

| Species | West | Est | Avg Diss | Diss/SD | Conttib% | Cum.% |
|-------------------------------|-----------|-----------|----------|---------|----------|-------|
| | Avg Abund | Avg Abund | | | | |
| Gadus macrocephalus | 2.05 | 0 | 22.6 | 0.95 | 28.23 | 28.23 |
| Hexagrammos lagocephalus | 0.83 | 0.79 | 10.05 | 0.86 | 12.56 | 40.79 |
| Hemilepidotus hemilepidotus | 0.16 | 0.38 | 6.51 | 0.64 | 8.13 | 48.92 |
| Sebastidae sp. 1 | 0 | 0.4 | 5.89 | 0.53 | 7.36 | 56.28 |
| Ammodytidae | 0 | 0.51 | 5.56 | 0.42 | 6.94 | 63.22 |
| Phallocottus obtusus | 0.47 | 0.17 | 5.55 | 0.65 | 6.94 | 70.16 |
| Hexagrammos decagrammus | 0 | 0.27 | 5.54 | 0.48 | 6.92 | 77.08 |
| Synchirus gillis | 0 | 0.33 | 4.88 | 0.61 | 6.1 | 83.18 |
| Bathymaster caeruleofasciatus | 0.27 | 0.18 | 4 | 0.68 | 5 | 88.17 |
| Sebastes melanops | 0 | 0.23 | 2.91 | 0.42 | 3.64 | 91.81 |

B. SIMPER analyses showing percent contribution of each species to the overall observed differences in fish assemblages between the western and central Aleutian Islands for within the kelp forest only

| Species | West | Central | Av.Diss | Diss/SD | Contrib% | Cum.% |
|-------------------------------|----------|----------|---------|---------|----------|-------|
| | Av.Abund | Av.Abund | | | | |
| Gadus macrocephalus | 2.05 | 0.79 | 24.38 | 1.15 | 34.15 | 34.15 |
| Hexagrammos lagocephalus | 0.83 | 0.75 | 12.2 | 0.65 | 17.09 | 51.24 |
| Phallocottus obtusus | 0.47 | 0.34 | 8.11 | 0.79 | 11.36 | 62.6 |
| Hemilepidotus hemilepidotus | 0.16 | 0.44 | 7.18 | 0.76 | 10.06 | 72.66 |
| Bathymaster caeruleofasciatus | 0.27 | 0.15 | 4.41 | 0.61 | 6.18 | 78.84 |
| Sebastes melanops | 0 | 0.17 | 2.44 | 0.37 | 3.41 | 82.25 |
| unknown juvenile fish | 0 | 0.19 | 2.43 | 0.35 | 3.4 | 85.65 |
| Hemilepidotus jordani | 0 | 0.14 | 2.38 | 0.36 | 3.34 | 88.99 |
| Cottidae | 0.15 | 0.05 | 2.06 | 0.36 | 2.88 | 91.87 |

C. SIMPER analyses showing percent contribution of each species to the overall observed differences in fish assemblages between the western and central Aleutian Islands for within the kelp forest only.

| Species | East | Central | Av.Diss | Diss/SD | Contrib% | Cum. % |
|-------------------------------|---------|----------|---------|---------|----------|--------|
| | Av.bund | Av.Abund | | | | |
| Hexagrammos lagocephalus | 0.79 | 0.75 | 10.89 | 0.85 | 13.73 | 13.73 |
| Gadus macrocephalus | 0 | 0.79 | 10.71 | 0.67 | 13.51 | 27.24 |
| Hemilepidotus hemilepidotus | 0.38 | 0.44 | 8.44 | 0.84 | 10.64 | 37.88 |
| Sebastidae sp. 1 | 0.4 | 0.02 | 6.02 | 0.54 | 7.59 | 42.47 |
| Hexagrammos decagrammus | 0.27 | 0.1 | 5.93 | 0.52 | 7.48 | 52.95 |
| Phallocottus obtusus | 0.17 | 0.34 | 5.68 | 0.73 | 7.17 | 60.12 |
| Ammodytidae | 0.51 | 0 | 4.97 | 0.41 | 6.27 | 66.39 |
| Synchirus gillis | 0.33 | 0.02 | 4.74 | 0.63 | 5.98 | 72.37 |
| Sebastes melanops | 0.23 | 0.17 | 4.69 | 0.56 | 5.91 | 78.28 |
| Bathymaster caeruleofasciatus | 0.18 | 0.15 | 3.65 | 0.53 | 4.6 | 82.88 |
| unknown sp. | 0.17 | 0.05 | 2.29 | 0.47 | 2.88 | 85.76 |
| unknown juvenile fish | 0 | 0.19 | 1.99 | 0.38 | 2.51 | 88.27 |
| Blepsias cirrhosus | 0.17 | 0 | 1.98 | 0.38 | 2.5 | 90.77 |

Av. Abund Average Abundance, *Av Diss* Average dissimilarity, *Diss/SD* the ratio of dissimilarity to standard deviation, *Contrib %* Percent contribution

(Edwards 2004), but contradicts observations by Reisewitz et al. (2006) who found that at least some Aleutian fish populations are strongly impacted by changes in kelp forest habitat. Further, these results are not atypical in that fish assemblage response to drivers is often mixed depending on the spatial scale that is being examined. In southern and Baja California islands for example, a clustering of warm-water and cold-water fish assemblages has been observed to co-occur, with the distribution of some fish not being explained by latitude or temperature, but this is not consistent across all fish species (Pondella et al. 2005). In fact, similar to our results, that study found that no single pattern explained fish density across all of the islands examined.

The observations that the fish assemblages varied significantly among the geographic regions suggested that one of the biogeographic breaks we chose (i.e., Samalga Pass) was important to fish assemblage structure. Samalga Pass is characterized by differences in ocean currents on either side of this pass, with Alaska Coastal Current waters dominating on the eastern side of the pass and Alaska Stream waters dominating on the western side of the pass (Hunt and Stabeno 2005). Consequently, the waters to the eastern side of the pass are generally warmer, less saline, and nutrient-poor relative to the waters to the western side of the pass, which are generally colder, more saline, and nutrient-rich (Ladd et al. 2005; Mordy et al. 2005). Further, Samalga Pass is relatively shallow (200 m) and narrow (approximately 3.9 km² in cross-sectional area) (Hunt and Stabeno 2005) and exhibits a strong discontinuity for cold-water corals, zooplankton, demersal fish, and seabirds (US Fish and Wildlife Service 2000; Coyle 2005; Heifetz et al. 2005; Logerwell et al. 2005). In addition, some fish diets have been shown to change on either side of this pass (Logerwell et al. 2005). Although our analysis did not show any significant differences in ocean temperature or salinity on the opposing sides of Samalga Pass, our measures were collected at one point in time and probably are not a good indicator of the overall long-term oceanographic conditions at this location. In contrast, Buldir Pass is deeper (640 m) and wider (28.0 km² in cross-sectional area) (Hunt and Stabeno 2005) and also exhibits some changes in species distributions on its opposing sides. Specifically, numerous demersal fish species exhibit a reduction in species richness to the west of the pass (Logerwell et al. 2005). However, we observed no significant changes in fish assemblages on the opposing

sides of Buldir Pass. Together, and because it is thought that fish distribution reflects contemporary oceanography and not necessarily historical processes (Pelc et al. 2009), this suggests that Samalga Pass is currently the more significant biogeographic break in the Aleutian Archipelago, especially with regard to variation both fish assemblages and oceanographic conditions.

While our study found no differences in fish assemblages between kelp and barren habitats, these results are contrary to what has been seen in this (Reisewitz et al. 2006) and other (Levin 1991; Pérez-Matus et al. 2007; Cote et al. 2013; Krug and Steele 2013) areas. For example, Reisewitz et al. (2006) found that on four islands in the Aleutian Archipelago, urchin-dominated habitats generally supported more diverse fish assemblages than kelp dominated habitats, but that certain species (e.g., greenlings in the genus *Hexagrammos*) were more strongly associated with the kelp forests. Perhaps our current study did not find similar differences because the majority of the fish we surveyed were adults, and adult fish are less strongly tied to kelp forests than are their juvenile con-specifics (Choat and Ayling 1987; Carr 1989). Differences between these studies could also be attributed to differences in sampling, as Reisewitz et al. (2006) relied on trammel nets that efficiently sampled rock greenlings but perhaps did not as effectively sample other species, while we used diver visual surveys that sample all species with roughly the same efficiency. Reisewitz et al. (2006) postulated that greenlings exhibit diver-averse behavior during underwater censuses, resulting in fish hiding under kelp or otherwise exhibiting cryptic behavior. However, we were careful to look under kelp and in other habitats during our surveys in order to not miss greenlings or other cryptic fish. Lastly, and most importantly, differences between these studies may be due to longer-term temporal changes in the Aleutian Archipelago. Specifically, the current state of Aleutian kelp forests may be such that the forests are now too small to maintain the fish populations that were present during the Reisewitz et al. (2006) study. Certainly these forests are smaller and more lacking in understory foliose algae than they were during Reisewitz's study (Konar and Edwards assisted with that study, personal observation), and these remnant beds may now be equivalent to the barren areas as much of their understory kelps are absent.

Similar to the lack of differences between kelp forest and urchin barrens, we found no differences in fish assemblages between the inner regions and the margins of the kelp forests. This is contrary to what has been observed in other areas of Alaska where fish assemblages differ between locations in the kelp forest (Efird and Konar 2013). It has been suggested that predator avoidance and/or prey availability drive such patterns as oppose to local-scale physical and biological habitat features (Lima and Dill 1990; Smith et al. 2011). For example, the kelp forests studied by Efird and Konar (2013) were bordered by sandy bottom habitats, which may have a different suite of predators than observed in the kelp forests. In contrast, the kelp forests in the Aleutian Archipelago are bordered by urchin barrens, which again exhibited similar fish assemblages. Since similar fishes were found in kelp forests and barrens, it follows that fish predators would be similar in both habitats, so there is likely no predator avoidance advantage in being within the forests. Finally, our study suggested that kelp forest size is not one of the more important habitat variables structuring fish assemblages, but this again may be due to long-term reductions in the overall abundance and complexity of kelp forests that have resulted in the fish assemblages no longer strongly responding to the presence of (or size of, or location in) kelp forests.

Conclusions

Overgrazing by sea urchins has greatly reduced the abundance of kelp forests across the Aleutian archipelago, especially in the western and central regions of the island chain. In addition, climate models predict a dramatic increase in the annual frequency and severity of extreme weather events during the next century, which together with continued grazing, will likely further reduce kelp coverage (Byrnes et al. 2011). Our findings suggest that nearshore fish assemblages throughout the archipelago do not differ significantly between kelp forest and urchin barren habitats, or between locations (interiors versus margins) within the forests. Further, and contrary to previous observations from before the kelp declines, the fish assemblages no longer appear to associate strongly with local habitat characters such as kelp and understory algal abundance, especially in western and central Aleutians where the kelp forests

have largely disappeared. Consequently, we found that a further reduction in kelp forests may not impact fish assemblage composition or abundance in these regions, but this may be an artifact that these forests are already in a diminished state and isolated from one another such that kelp forests now resemble urchin barrens in that many of them largely lack most understory kelp species. However, this may be different in the eastern Aleutians where kelp forests remain more abundant and where the fish assemblages differed from the western Aleutians and where the influence of understory kelps such as *Agarum* appears strongest. In fact, our analyses suggested that *Agarum* density was one of the habitat variables that ‘best’ correlated with fish assemblages when examined across the entire archipelago, but that this was likely the result of high densities of *Agarum* in the eastern Aleutians where this association was strongest, and low density in the western and central Aleutians where this relationship was weak or not observed. Thus, regional differences in the fish assemblages may have been due, at least in part, to corresponding differences in *Agarum* (and other kelps) abundance. In addition, our findings suggest that the larger-scale variation in ocean climate that may occur on opposite sides of biogeographic breaks were important to these fish assemblages in certain regions of the archipelago but not others. Specifically, we have shown that fish assemblages differ significantly on opposing sides of the Samalga Pass, which roughly separates the eastern and central Aleutians, but not on opposing sides of Buldir Pass, which roughly separates the central and western Aleutians. The primary taxa responsible for the observed differences were *Gadus* (gadids) and *Hexagrammos* (greelings). However, if water mass properties change around Buldir Pass in the future, or if grazing reduces the kelp forests in the eastern Aleutians as it did in the western and central Aleutians, then corresponding impacts may be seen in the fish assemblages.

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