

Influence of Static Habitat Attributes on Local and Regional Rocky Intertidal Community Structure

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Abstract Rocky intertidal communities are structured by local environmental drivers, which can be dynamic, fluctuating on various temporal scales, or static and not greatly varying across years. We examined the role of six static drivers (distance to freshwater, tidewater glacial presence, wave exposure, fetch, beach slope, and substrate composition) on intertidal community structure across the northern Gulf of Alaska. We hypothesized that community structure is less similar at the local scale compared with the regional scale, coinciding with static drivers being less similar on smaller than larger scales. We also hypothesized that static attributes mainly drive local biological community structure. For this, we surveyed five to six sites in each of the six regions in the mid and low intertidal strata. Across regions, static attributes were not consistently different and only small clusters of sites had similar attributes. Additionally, intertidal communities were less similar on the site compared with the region level. These results suggest that these biological communities are not strongly influenced by the local static attributes measured in this study. An alternative explanation is that static attributes among our

regions are not different enough to influence the biological communities. This lack of evidence for a strong static driver may be a result of our site selection, which targeted rocky sheltered communities. This suggests that this habitat may be ideal to examine the influence of dynamic drivers. We recommend that future analyses of dynamic attributes may best be performed after analyses have demonstrated that sites do not differ in static attributes.

Keywords Static drivers · Rocky intertidal community structure · Habitat attributes

Introduction

Rocky intertidal communities naturally experience and are resilient to a large range of physical conditions, which is not surprising considering they cycle between submersion in water and exposure to air on a regular basis. Some physical conditions are driven by dynamic forces and fluctuate on various temporal scales (e.g., temperature, salinity, nutrients, etc.), whereas others are static (*sensu* Meager et al. 2011) and do not greatly fluctuate from year to year (substrate, beach slope, exposure to wave action, etc.). Although static attributes typically change minimally over time scales of at least years to decades, they can vary greatly among spatial scales of regions, local sites, and even within a site (i.e., the various intertidal strata) and can influence biological community structure. We have previously documented that intertidal communities in the northern Gulf of Alaska vary with tidal stratum, but high variability in zonation patterns among sites within each region reduced the generality of this pattern (Konar et al. 2009). In that study, significant interactions were found in the algal and invertebrate community between regions and sites (nested within region) and depth. Currently,

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the specific role of static habitat attributes in driving community structure throughout the northern Gulf of Alaska is unclear. Because the relative importance of environmental drivers is difficult to define due to the high number of potential factors and the interactions among them (Little and Kitching 1996), we start here with an attempt to better understand the role of static attributes. Understanding how and on which spatial scales (regional, local, intertidal stratum) static attributes structure intertidal communities will help narrow future studies to the most important community drivers.

Possible static attributes that may influence rocky intertidal community structure in high-latitude systems include distance to freshwater, tidewater glacial presence, exposure to ocean swell, fetch (distance to next land mass), beach slope, and substrate composition. Freshwater entering the nearshore from rivers can lower local ocean salinity, increase sedimentation, and play a role in structuring rocky intertidal communities (Held and Harley 2009; Law et al. 2013). Given equally sized rivers with similar discharge and tributaries, the closer a community is to a river the more the community will be impacted. Lower salinity can affect the physiology and behavior of invertebrates (Garza and Robles 2010; Montory et al. 2014). These impacts can increase during flood events (Nishijima et al. 2013). In addition to salinity, increased sedimentation from rivers can be deleterious to marine organisms. Specifically for algae, sediments can prevent the settlement of algal propagules and can smother newly settled individuals (Schiel et al. 2006; Deiman et al. 2012). Algal grazer efficiency and general diversity can also decrease, and overall community composition can change in areas with increased sedimentation (Spurkland and Iken 2012; Pulfrich and Branch 2014).

Similar to river discharge, glacial discharge lowers salinity and increases sedimentation but it can also lower water temperature (Beszczyńska-Möller et al. 1997; Spurkland and Iken 2012). Changes in water temperature can influence various processes, including feeding and metabolic and population growth rates and changes to species-specific interactions (Sanford 1999; Kordas et al. 2011). For example, a slight decrease in water temperature dramatically reduced the effects of a keystone predator, the sea star *Pisaster ochraceus*, on its principal mussel prey in Oregon, suggesting far-reaching impacts on the structure of these rocky communities initiated by environmental drivers (Sanford 1999).

Intertidal communities are also structured by exposure to waves (Dayton 1971; Ricciardi and Bourget 1999; Pulfrich and Branch 2014; Bloch and Klingbeil 2015). For example, species turnover rates (Bloch and Klingbeil 2015) and algal palatability (Long et al. 2013)

have been correlated with measures of wave exposure. Similarly, high species richness has been found at sites with high wave variability (deJuan and Hewitt 2013). Beach slope and composition of the substrate also can have large ramifications on the structure of intertidal communities by influencing recruitment, disturbance, thermal stress, and survival (Ricciardi and Bourget 1999; Gedan et al. 2011; Bloch and Klingbeil 2015). For example, substrate size can impact community structure by mediating the thermal stress experienced by species with larger rocks remaining cooler than smaller rocks (Gedan et al. 2011).

Although many static drivers may influence which species survive at different locations (stratum and sites) in the intertidal, the available species pool from the general geographic region also will determine which species are able to settle. The assembly of species within a site is determined by a process involving the dispersal of species from a regional pool and then filtered by local dynamic and static environmental drivers (Mittelbach and Schemske 2015). Typically, communities are less similar at the local scale (between sites) compared with the regional scale because local processes will differ among sites within a region (Edwards 2004; Konar et al. 2015). It has been suggested that there are different regulating processes operating at different spatial scales. In some cases, regional processes can be important in structuring communities at the local scale (Rivadeneira et al. 2002). For example, El Niño resulted in the near-complete loss of giant kelp over hundreds to thousands of kilometers (regional scale) but the level of recovery of kelp varied at multiple smaller spatial scales, including local (Edwards 2004). Understanding the role that static drivers play in filtering species at various spatial scales will enable us to better define the role of temporally variable dynamic drivers in structuring intertidal communities, which are of concern because these are the drivers being influenced by climate change.

This paper seeks to determine how and on which spatial scales rocky intertidal communities may be structured by static habitat attributes. Specifically, we examine how mid and low intertidal communities at 31 sites within six regions across the northern Gulf of Alaska vary depending on their distance to freshwater, tidewater glacial presence, wave exposure, fetch, beach slope, and substrate composition. As such, we assess mid and low intertidal community structure across sites and regions in the northern Gulf of Alaska and describe the static habitat attributes at these same locations. These data are used to address the hypotheses that (1) intertidal community structure is less similar at the local scale compared with the regional scale, coinciding with static

drivers being more variable on smaller scales (sites within regions) than larger scales (across regions), and (2) static attributes drive local biological community structure.

Materials and Methods

Study Area

Six regions around the Gulf of Alaska (GOA) were surveyed (Fig. 1). In 2012, Western Prince William Sound (WPWS), Eastern Prince William Sound (EPWS), Kenai Fjords National Park (KEFJ), Katmai National Park and Preserve (KATM), and Kachemak Bay (KBAY) were sampled. In 2013, the same regions were sampled except that Northern Prince William Sound (NPWS) was sampled instead of EPWS. Prince William Sound, centered at approximately

60° N, 147° W, is a sub-arctic embayment having characteristics of a small inland sea with abundant freshwater inputs. Within the sound, NPWS contains glaciated fjords with deep open water basins to >870 m depth. In EPWS, the tidal glacial influences are less pronounced, leaving a coast generally characterized by sedimentary formations and nutrient-rich watersheds. In WPWS, an archipelago forms a network of islands and passes stretching from the northern sound down to the open Gulf and production is driven by a portion of the Alaska Coastal Current. KEFJ (60° N, 150° W) is located along the southeastern side of the Kenai Peninsula in south central Alaska. It is glacially fed by the Harding Icefield, one of the largest ice caps in the USA, and is characterized by steep glacial fjords and lagoons sheltered by moraines. KATM (59° N, 155° W) is located on the Alaska Peninsula. Storms, wind mixing, and terrestrial inputs result in high productivity in KATM. KBAY is located north of the Gulf of Alaska at 60° N and 151° W. The bay is a large estuary that

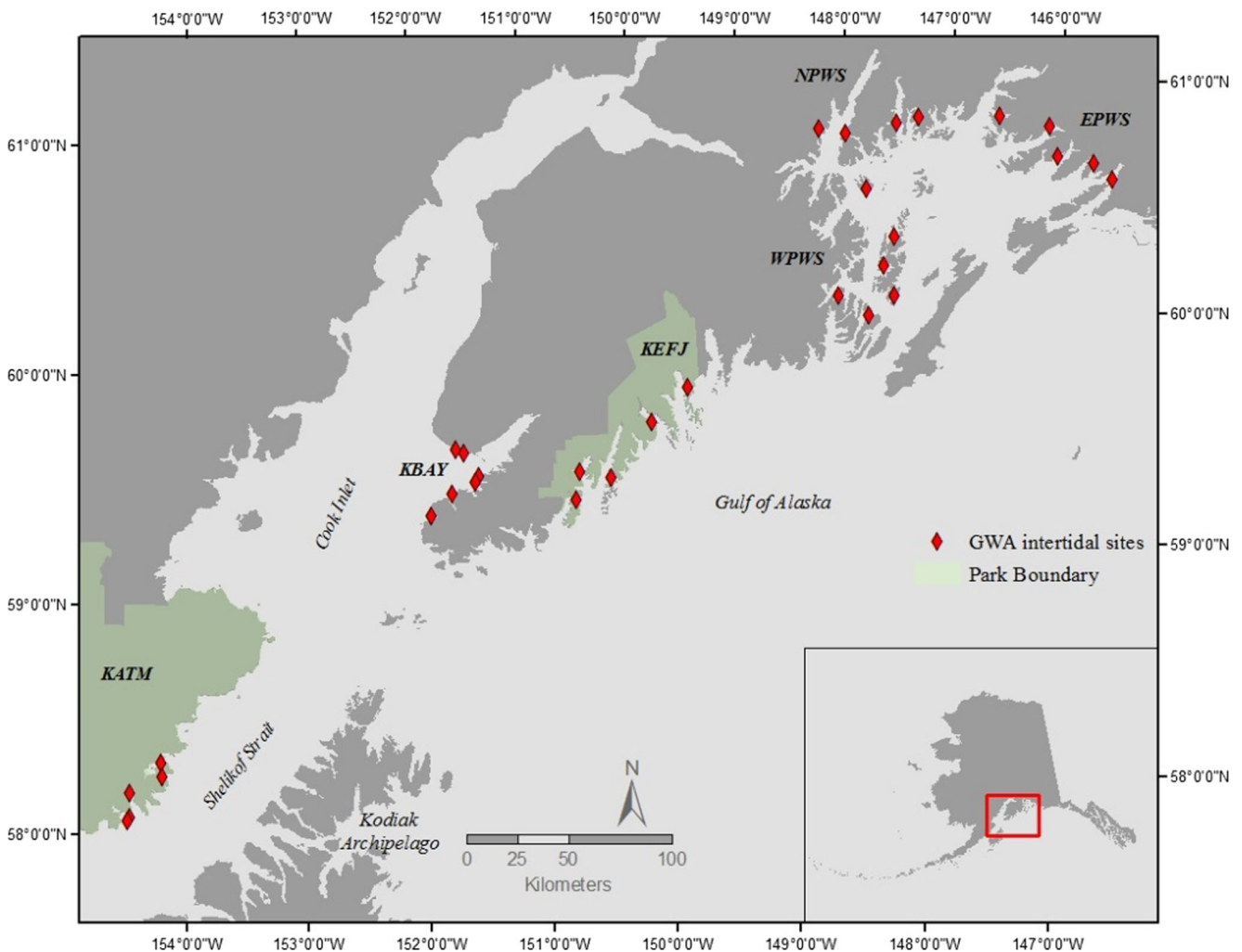


Fig. 1 Map showing study sites within the northern Gulf of Alaska: Northern Prince William Sound (NPWS), Western Prince William Sound (WPWS), Eastern Prince William Sound (EPWS), Kenai Fjords (KEFJ), Kachemak Bay (KBAY), and Katmai (KATM)

can be divided into an inner and outer bay. The outer bay is largely free of glacial influence, whereas several points of glacial discharge from the Harding Icefield enter the inner bay.

Sampling Procedure

Sites were initially chosen based on their slope (not vertical), substrate, and extent (at least 100 m continuous rocky habitat). All sites were also relatively protected from high wave exposure and were associated with freshwater sources, although to varying degrees. Five sites were sampled in the summer in each region except in KBAY where a sixth site was added in both years. Sites were sampled in the mid and low intertidal strata (approximately at +1.5 and +0.5 m, respectively, relative to mean lower low water (MLLW)). In addition, an exception occurred in 2012 in KBAY, when one site was only sampled in the low intertidal stratum.

Static habitat attributes used in this analysis included distance to the nearest freshwater source, tidewater glacial presence by region, exposure to wave action, fetch, beach slope, and substrate type (i.e., percent of bedrock, boulder, cobble, gravel, mud/sand; categories according to the Wentworth scale). For the analysis, data layers were rasterized for glaciers, shoreline, and freshwater sources and were all based on an equal number and size of pixels (50 m × 50 m pixel size) to standardize distance measures. Freshwater sources (stream outflow and tidewater glacier locations) were obtained from the National Hydrography Dataset (NHD), a comprehensive set of digital spatial data that includes marine and coastal information created in the early 2000s for Alaska. Using ArcGIS Spatial Analyst Cost Distance tool (ESRI, Redlands, CA), distances from sites to the nearest freshwater source within each region were calculated only across water bodies, excluding land masses. This includes only those sources of flowing water that appear on USGS maps and excludes small freshwater discharges on beaches and static bodies of water. We recognize that although the distance to a freshwater source and tidewater glacial presence are static elements, the discharge rates of these two sources are variable over seasonal and annual scales. These discharge rates should therefore be included in future analyses of the influence of dynamic attributes. However, the presence and distance of these sources were still deemed important in the static habitat attribute setting.

Exposure was determined from the ShoreZone Alaska web site (<http://alaskafisheries.noaa.gov/mapping/szflex/index.html?T=SZ@L=B>), where locations are classified based on the Biological Wave Exposure classifications of protected, semi-protected, or semi-exposed. Fetch is another commonly used proxy for the wave exposure of a shore (Burrows et al. 2008; Mieszkowska et al. 2013; Tam and Scrosati 2014) and provides a continuous scale of potential wave energy. In this study, fetch was calculated by creating vertices every 10° for

360° centered on each study site (i.e., spoke pattern) to a length of 200 km. Vertices were clipped once a land mass was encountered. A sum of the remaining vertices' distances was used to estimate the total potential fetch at each site. Two land resolutions, or buffers, were created to evaluate the effect of small rocks or islets on any particular site: 200 and 5000 m. All land masses that fell within the buffers were erased for the respective distance fetch measurements. This allowed calculation of fetch distance after removing potentially non-effective barriers to wave energy. Slope (in degrees) was measured at each site in all regions for every 1 m rise in elevation at five equally distanced points along each transect (at mid and low stratum). Slopes for the low and mid strata were then calculated at each site as a mean of the five slope measurements for the 0–1 and 1–2 m rises, respectively. Substrate type was visually estimated as percent substrate cover within each quadrat and the mean calculated for each stratum at each site. Substrate categories used the Wentworth scale and included percent of bedrock, boulder, cobble, gravel, mud/sand.

Biological sampling generally followed Gulf Watch Alaska protocols (http://www.evostc.state.ak.us/Store/Proposal_Documents/2196.pdf) in the mid and low intertidal strata (approximately at +1.5 and +0.5 m, respectively, relative to MLLW). In addition, an exception was in 2012 in KBAY, when one site was only sampled in the low intertidal stratum. At each site, the intertidal community was visually quantified at randomly placed quadrats along a 50-m transect in both strata for percent cover of sessile invertebrates and algae, which were identified to the lowest feasible taxonomic level (as low as species but sometimes phyla). This sampling was completed in one of two ways, depending on the type of long-term monitoring that is conducted in each region. At all sites except for those in KBAY, cover was determined within 12 0.25 m² quadrats in each stratum, which were systematically positioned along the transects based on a random start point uniquely selected each year. Within quadrats, the presence of algae and sessile invertebrates was determined at 25 systematically placed points, and the percent cover was calculated based on the proportion of points occupied by each taxa. In KBAY, percent cover of the overstory kelp layer (i.e., primarily species of *Alaria*, *Hedophyllum*, *Laminaria*, and *Saccharina*), if present, and the top layer of sessile invertebrates and algae were visually estimated from ten randomly placed 1 m² quadrats. Data from the kelp layer and the underlying layer were combined and their abundances re-standardized to 100 %. Because all taxa occurring within multiple layers were recorded at the non-KBAY sites, only the overstory kelp layer and the first, uppermost layer underneath kelp were included in this analysis.

To ensure comparability between the two methods (KBAY and all other regions), both methods were completed and then compared in both intertidal strata at the KBAY sites in 2015. For this, the same five random quadrats along each transect for

Table 1 PERMANOVA results testing differences in the biological data by tidal height, method, and quadrat nested in tidal height. Differences in the biological communities are based on Bray-Curtis similarities of square root transformed percent cover data. Bold values are significant

Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i> (perm)
stratum	1	8126.7	8126.7	4.2796	0.013
method	1	1681.9	1681.9	2.3996	0.068
quadrat (stratum)	18	37,947	2108.2	1.4152	0.059
stratum × method	1	1148	1148	1.668	0.15
qu (st) × me	13	9065.7	697.36	0.46814	0.998
Res	25	37,241	1489.7		
Total	59	99,197			

each stratum at every site were assessed using both methods. These data were then square root transformed and a Bray-Curtis similarity matrix was constructed. A three-factor permutational ANOVA/MANOVA (PERMANOVA; factors were tidal height, quadrat nested in height, and the sampling method) demonstrated that the two methods did not yield significantly different results within quadrats at either of the tidal strata (Table 1). This enabled us to compare communities sampled with both methods across regions in subsequent analyses.

Data Analyses

All statistical analyses were done in PRIMER v. 7. Data for static habitat attributes were checked for correlations among each other (at 90 % or greater) using bivariate draftsman plots and Spearman rank correlations. The highest correlation was between bedrock and boulder ($\rho = -0.84$). Because of the lack of meaningful correlations, all attribute data were retained in the analysis, square root transformed, and then normalized to a common measurement scale. To normalize data, PRIMER subtracts the mean and divides by the standard deviation over all samples, which makes the variance along all axes similar. A resemblance matrix of similarities among all sample site pairs based on habitat attributes was then created on the transformed and normalized data using Euclidean distances. To determine if there were differences in regions based on the static habitat attributes, a mean of the mid and low strata slopes and substrate type were calculated for each site. A resemblance matrix based on Euclidean distances of the transformed and normalized habitat attribute data was then created among all sample site pairs (Clarke et al. 2014). A similarity profile analysis (SIMPROF) analysis was used to determine grouping of sites based on static attributes. This analysis objectively identifies group members from a classical hierarchical

agglomerative clustering method. The clustering results of the SIMPROF were overlaid on the non-metric multi-dimensional scaling (nMDS) of the sites as described by their static attributes. To test for differences among regions, a one-factor PERMANOVA was used. In addition, the highest ranked static habitat attributes (from the BEST BIOENV routine; Clarke et al. 2014) were overlaid as vectors on the static attribute cluster nMDS plots to assess which drivers separated the clusters at each stratum. Lastly, a CLUSTER analysis was conducted separately for each stratum on the static habitat attributes of each site and the resulting static groupings were superimposed on the nMDS plots that were based on the biological communities to compare community groupings by static habitat characteristics.

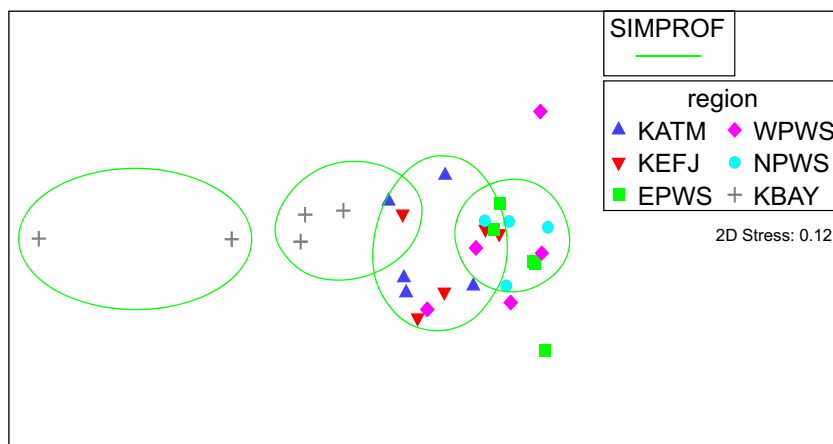
All biological percent cover data were square root transformed, and a resemblance matrix created based on Bray-Curtis similarities (Clarke et al. 2014). Quantitative differences in biological community structures were examined between the 2 years, among the six regions, and among the different sites within each region separately for each stratum. A three-factor mixed-model nested PERMANOVA was used, with year and region as fixed factors, and site nested within region as a random factor. A second PERMANOVA was completed with the KBAY data removed to determine if results were similar. The relative differences in biological communities between regions and sites were evaluated graphically with nMDS for each stratum separately. A SIMPER analysis was conducted on each stratum to determine the primary taxa contributing to community structure in each region.

In addition, the overall relationships between the static habitat attributes and the biological communities for each stratum were evaluated using the BEST BIOENV routine and a subset of variables identified that maximized the rank correlations between these data. This was done by comparing the Bray-Curtis and Euclidean distance resemblance matrices of the biological and environmental data, respectively, to determine if any environmental drivers correlated with the biological communities.

Results

All static attributes varied to some extent among regions (Appendix 1). When the mid and low strata attributes were averaged to describe each site, some sites clustered within their regions; however, there was much overlap of sites among regions (PERMANOVA pseudo-*F* = 5.482, *P*(perm) = 0.001; Fig. 2). Based on a SIMPROF analyses, two of the KBAY sites clustered together and three KBAY sites clustered with one KATM and one KEFJ site. There was much overlap among the PWS sites with only one WPWS site clustering alone. In general, the mid and the low intertidal strata were

Fig. 2 nMDS plots showing differences in static attribute data for each site color coded by regional association. Data were square root transformed and normalized. A SIMPROF test was used to obtain groupings



characterized by different static attributes (Fig. 3). The mid stratum was most characterized by fetch (200-m buffer), slope at +0.5, tidal glacial presence, and proportional boulder and gravel substrate (rho = 0.630; BEST-BIOENV routine). Tidal glacial presence, beach slope, and proportional rock substrate were most responsible for separating sites in KBAY from those in other regions (Fig. 3a). In the low intertidal, distance to freshwater, exposure, and percent of mud/sand substrate

were the most influential drivers of the site characteristics (rho = 0.499; BEST-BIOENV routine). Tidal glacial presence and proportional rock substrate most separated the KBAY sites from sites in the other regions; however, there was much overlap among KBAY, KATM, and KEFJ in their static attributes (Fig. 3b). In both the mid and low intertidal, regions were significant for the static attributes (Table 2, PERMANOVA).

For the mid intertidal stratum, biological communities were significantly different at the site level (Table 3 top, PERMANOVA). While region was also significant, it was less influential (lower pseudo-*F* value) than site. Year was not significant. In the mid stratum, bare substrate and *Fucus distichus* were important contributors to all regions. Differences were apparent for NPWS and KBAY, which had *Cladophora/Chaetomorpha/Rhizoclonium* complex and *Palmaria* spp., respectively (Electronic Supplementary Material 1; additional data are given in Electronic Supplementary Material 2). In the mid stratum, individual taxa and categories did not have a higher correlation coefficient than that of the entire community (*Odonthalia/Neorhodomela* complex, *Ulva/Monostroma* complex, *Alaria* spp., *Mytilus trossulus*, barnacles, and bare rock were tested

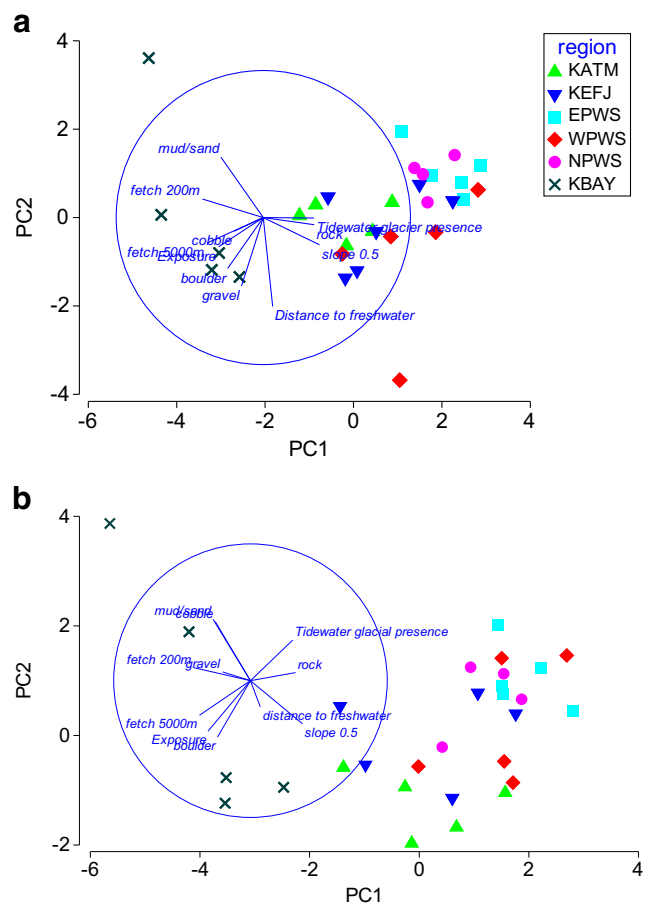


Fig. 3 PCA for each site and year color coded by region for the mid (a), and low tidal stratum (b) with environmental drivers as vectors

Table 2 PERMANOVA results testing differences in the environmental data by region and site (nested in region). Differences in the environmental data are based on Euclidean distance of square root transformed and normalized data. Top: mid strata, Bottom: low strata. Bold values are significant

Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i> (perm)
re	5	159.03	31.806	4.9106	0.001
si (re)	23	148.97	6.477	No test	
Total	28	308			
Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i> (perm)
re	5	146.81	29.362	4.4299	0.001
si (re)	21	139.19	6.6281	No test	
Total	26	286			

Table 3 PERMANOVA results testing differences in the intertidal biological data by year, region, and site (nested in region). Differences in the biological communities are based on Bray-Curtis similarities of square root transformed percent cover data. Top: mid strata, Bottom: low strata. Bold values are significant. Bold values are significant

Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i> (perm)
ye	1	6608.1	6608.1	2.2331	0.054
re	5	2.23E + 05	44,588	4.2963	0.001
si (re)	23	2.52E + 05	10,969	9.8405	0.001
ye × re	3	14,455	4818.3	1.6221	0.066
ye × si (re)	16	47,683	2980.2	2.6735	0.001
Res	541	6.03E + 05	1114.7		
Total	589	1.16E + 06			

Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i> (perm)
ye	1	10,152	10,152	3.0778	0.011
re	5	2.27E + 05	45,421	2.5946	0.001
si (re)	23	4.38E + 05	19,025	17.81	0.001
ye × re	3	18,947	6315.5	1.8994	0.019
ye × si (re)	14	47,027	3359.1	3.1445	0.001
Res	504	5.38E + 05	1068.2		
Total	550	1.30E + 06			

with the highest $\rho = 0.150$ for bare rock; BEST-BIOENV routine). For the low intertidal stratum, significant differences also were associated with site nested within region (Table 3 bottom, PERMANOVA). Here, both region and year were also significant, but again less influential (lower pseudo-*F* values) than site. In the low stratum, no one taxon was an important contributor to all regions. The *Odonthalia/Neorhodomela* complex was unique to KEFJ and *Acrosiphonia* spp. was unique to KBAY (Electronic Supplementary Material 3; additional data are given in Electronic Supplementary Material 2). In the low stratum, the individual taxa and categories that were tested did not have a higher correlation coefficient than that of the entire community (*Odonthalia/Neorhodomela* complex, *Ulva/Monostroma* complex, *Alaria* spp., *Mytilus trossulus*, barnacles, and bare rock were tested with the highest $\rho = 0.401$ for bare rock; BEST-BIOENV routine). Given the differences in sampling between KBAY and the other regions, we repeated the analyses without KBAY, even though our method comparison did not show significant differences between the two methods (Table 1). Overall PERMANOVA results for both mid and low intertidal strata remained the same when KBAY was excluded, with significant site effects (highest pseudo-*F* values) (Table 4).

The biological communities at most sites did not cluster by their regions in the nMDS plots for either intertidal stratum (Fig. 4). The exception to this was seen with the KBAY sites, which formed a fairly distinct regional group in both strata (Fig. 4). Some of the KATM sites also formed a small cluster but only for the low tidal stratum (Fig. 4b). All sites within the

Table 4 PERMANOVA results testing differences in the intertidal biological data by year, region, and site (nested in region) excluding the KBAY sites. Differences in the biological communities are based on Bray-Curtis similarities of square root transformed percent cover data. Top: mid strata, Bottom: low strata. Bold values are significant

Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i> (perm)
ye	1	10,158	10,158	3.828	0.007
re	4	93,240	23,310	2.483	0.002
si (re)	19	1.93E + 05	10,138	8.571	0.001
ye × re	2	9461	4730	1.782	0.089
ye × si (re)	12	31,910	2659	2.248	0.001
Res	452	5.35E + 05	1182		
Total	490	8.84E + 05			

Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i> (perm)
ye	1	13,547	13,547	4.791	0.008
re	4	1.44E + 05	35,953	2.011	0.022
si (re)	19	3.75E + 05	19,733	17.375	0.001
ye × re	2	13,115	6557	2.318	0.018
ye × si (re)	11	31,178	2834	2.496	0.001
Res	426	4.84E + 05	1136		
Total	463	1.08E + 06			

PWS regions and the KEFJ sites strongly overlapped (Fig. 4). By comparison, the only clearly defined groupings of sites when categorized by static attribute clusters were static groups 1 and 3 in the mid intertidal (Fig. 5a). These two static groups combined coincided with the KBAY sites (compare Figs. 4a and 5a). These two static groups were similar in their glacial presence, percent rock, and beach slope. In general, sites from multiple regions shared static attribute groupings (i.e., static attribute groups were spread across regions), especially for the low intertidal stratum. This suggests that except for KBAY mid intertidal, the regions did not consistently differ in the static attributes that were measured in this study.

Discussion

Intertidal communities are assembled by processes operating over various spatial scales. Typically, the species that recruit and survive at the local scale are a subset of the species available from a regional pool that are selected by dynamic and static environmental drivers acting at local scales (deJuan and Hewitt 2011; Mittelbach and Schemske 2015). For example, intertidal species composition often differs depending on substrate grain size (Gedan et al. 2011) and wave energy (Bloch and Klingbeil 2015), both of which are typically relatively homogeneous over small/local scales, but can be highly variable among large regional scales. These local drivers result in a subset of species at the local scale when compared to the regional scale, where all substrate types and wave exposure

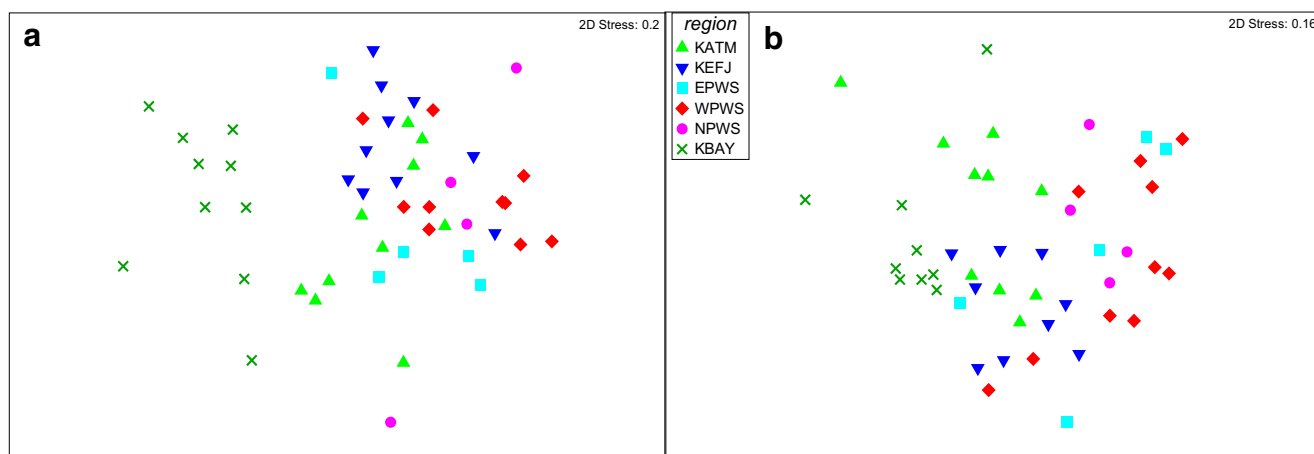


Fig. 4 nMDS plots showing differences in biological data for each site and year color coded by regional association for the mid (a), and low tidal stratum (b). Data were square root transformed

levels are represented and all available species exist within the region. This implies regional differences in species composition would presumably be driven by differences in the proportion of habitats with particular substrate types and wave exposures, which will likely be much less variable than local scale differences among sites.

An extreme example of local scale variability is differences in community composition between intertidal elevations. That is, the characteristic zonation pattern of intertidal communities is similar across many regions (e.g., Knox 2001, except see Harley and Helmuth 2003) but the strata differ greatly at the site level. Many of the differences between the community structures of intertidal strata can be explained by species tolerance to desiccation, which can be mitigated by wave exposure, with mean air exposure time over the daily tidal cycle and relative wave exposure as the most important static environmental drivers (Dayton 1971). Here, we used intertidal stratum as a covariate to account for this expected difference in community composition between intertidal elevations and

concentrated on among site and regional level differences for each stratum. Our study demonstrated that the different regions across the northern Gulf of Alaska were largely overlapping in their intertidal community structure, similar to previous results involving other regions within the Gulf of Alaska (Konar et al. 2009). This contrasts with a study in the Gulf of Maine that found distinct community types in different regions despite the regions sharing many of the same species (Bryson et al. 2014). In Maine, the different community structures probably emerged because of regional differences in coastal oceanography modulating species recruitment.

Our first hypothesis that intertidal community structure is less similar at the local scale compared with the regional scale was supported. This corresponds to the findings of other studies that concluded that environmental processes dominate at larger scales and ecological (dynamic) processes play a more important role at local scales (Konar et al. 2015; Menge et al. 2015). It is possible that within the northern Gulf of Alaska, environmental processes (including static drivers) influence

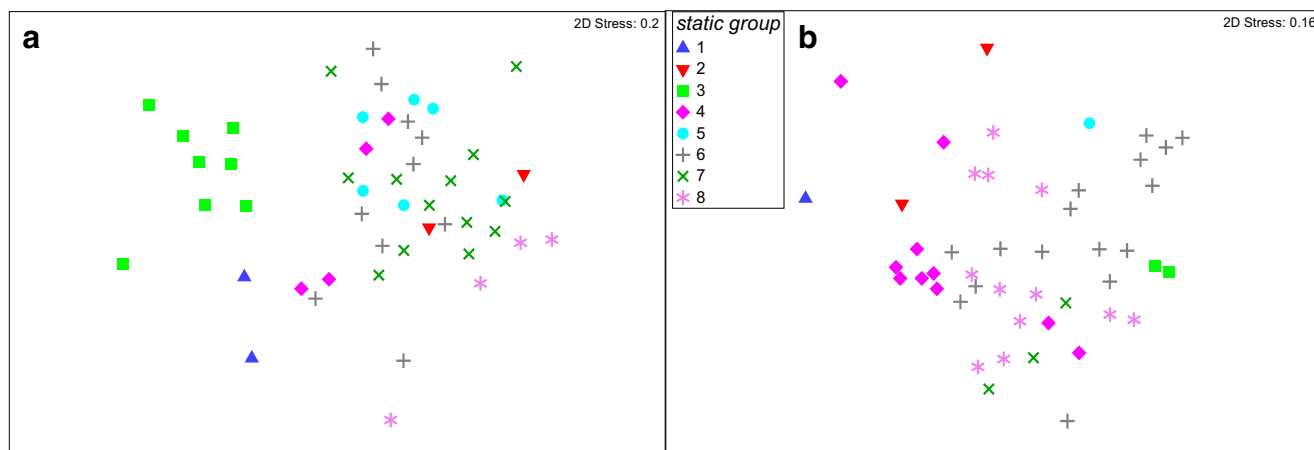


Fig. 5 nMDS plots showing differences in biological data for each site and year color coded by static attribute group for the mid (a), and low tidal stratum (b). Static groups were assigned to a site based on

a cluster analysis on the environmental data each site. Data were square root transformed

all sites similarly but it is the ecological processes that structure communities at the site level and these local processes might be very different among sites within the Gulf of Alaska. The one region where sites did cluster together was in the KBAY mid intertidal stratum. This suggests some degree of connectivity among the KBAY sites that is distinct from the other regions. The static drivers that most influenced the separation of the KBAY sites from the others were glacial presence, percent rock, and beach slope. Although KBAY has no tidewater glaciers, PWS and KEFJ have many of them. Slope was generally less steep at KBAY compared with the other regions, which may result in different interactions with wave exposure. On shores with a gentle slope, waves typically break when their height is approximately half the water's depth (Thornton and Guza 1983) whereas on steep slopes, waves generally break when their height is approximately equal to the local water depth (Galvin 1972). This difference in wave exposure, with presumably higher wave impacts in KEFJ compared with KBAY, may be influencing community structure. Similar to wave action, slope also influences desiccation rates, which will influence mortality, particularly of young individuals (Connell 1972). Lastly, KBAY had less bedrock than the other regions, which may also be contributing to community differences as rock complexity has been regarded as a habitat driver in other studies (Kohn and Leviten 1976; Bloch and Klingbeil 2015). For example, high habitat complexity has been associated with higher community diversity (Eriksson et al. 2006), and we found highest species richness in KBAY in an earlier comparison across Gulf of Alaska regions (Konar et al. 2009).

In our study, we examined the role of static habitat attributes in structuring communities at both local and regional scales. Our second hypothesis that the static attributes measured in this study would separate local from regional biological community structure was largely unsupported, except for the KBAY mid intertidal communities. Study sites within all regions were relatively sheltered and were in proximity to freshwater sources, which may have contributed to the local and regional similarity we found. If true, static drivers may be a stronger factor for intertidal communities at more diverse types of sites. However, comparing sites with similar static attributes may provide an excellent opportunity to examine dynamic drivers that will vary at different temporal scales at the site and region levels without confounding effects of static habitat attributes. We recommend that future analyses of dynamic attributes may best be performed after analyses have demonstrated that the influence of static attributes does not differ among sites.

Although the static attributes measured here did not play a large role in structuring the intertidal communities, the specific attributes that most influenced structure in the mid and low strata were different. Although no one driver was found to influence both the mid and the low intertidal strata, types of

drivers were similar for both. For example, substrate type is often a driver of community structure (Sousa 1979) and it was a driver for both intertidal strata included here, although different substrate measures were found to be important in each stratum. In the mid intertidal, percent boulder and gravel substrate were important whereas in the low intertidal, it was percent of mud/sand. This difference in substrate importance could be related to various functions that substrate plays for rocky intertidal organisms. For example, larger substrate sizes are more thermally stable, which is more of a concern for organisms in the mid than the low intertidal (Gedan et al. 2011). Similarly, larger substrate sizes are less movable by hydrodynamic forces that are typically strong in mid intertidal regimes, creating a disturbance for intertidal organisms (Gaylord 1999). Likewise, we found wave exposure to be important but it manifested its importance differently depending on tidal stratum. In the mid stratum, fetch (at a 200-m buffer) was important whereas in the low stratum, exposure category was influential. Historically, wave exposure has been believed to be the most important local driver of intertidal community structure (Lewis 1964; Dayton 1971), although this has not been consistently found (Zacharias and Roff 2001). Two additional drivers were found to be important but not in both strata. In the mid stratum, slope was an important driver whereas in the low, it was distance to freshwater. Slope may be important in the mid because it mediates the length of air exposure in that stratum, which is less important to the low intertidal communities that naturally experience shorter exposure times. Similarly, distance to freshwater may be an important driver in the low stratum because this stratum is submerged longer than the mid and communities may be more impacted by freshwater and presumably, the variation in salinity (a dynamic driver) during this extra time of submergence.

Community structure can vary temporally because dynamic drivers fluctuate seasonally and annually (Caffey 1985; Burrows et al. 2012). Dynamic drivers can impact static attributes and biological drivers (Jonsson et al. 2006). For example, waves can change the amount of sand deposition onto rocky intertidal organisms, altering their community structure (Littler et al. 1983). If a habitat has more cobbles than bedrock, these cobbles can be moved in a way that organisms are damaged during times of large waves (Shanks and Wright 1986). Similarly, waves can reduce grazing activity, which can change algal community structure on intertidal benches (Jonsson et al. 2006). While we tried to isolate a set of static drivers, the reality is likely more complicated because some static drivers are directly influenced by dynamic processes. For example, wave exposure and fetch can be numerically measured but the manifestation of these attributes (i.e., through wind and waves) will vary from year to year based on weather and hence may have different impacts on community structure from year to year (Mazzucco et al. 2015). A

longer term study may be able to tease apart the interactions of static and dynamic drivers, but that was beyond the focus of this study. The distinct separation of mid intertidal communities in KBAY from other regions may also be related to alternative drivers not examined in our study including those that may not be static. Within a variety of other potential drivers, top-down predation and differences in grazer density may be contributing to the separation of the KBAY sites. Sea stars, predatory snails, sea otters, and sea ducks, all can have top-down effects and structure communities (Paine 1980; Estes and Duggins 1995; Marsh 1986). In addition, grazers such as limpets, chitons, and sea urchins can have large impacts on algal community structure (Konar and Estes 2003; Salomon et al. 2007; Burgos-Rubio et al. 2015). Similar to biological processes, there may be physical processes that differ among our regions. Although all regions are influenced by glaciers and streams, some physical attributes such as turbidity, dissolved oxygen, and nutrients may be differing. In addition, the level of habitat complexity that was measured at our sites was limited and could be further expanded. Currently, these biological and physical drivers have not been examined or compared among our sites or regions.

Understanding and managing nearshore community resilience requires knowledge about how static and dynamic drivers work together to influence community structure. A better understanding of static drivers will assist in analyzing the role of dynamic drivers that are a concern with changes in climate and ocean chemistry (acidification and freshening). In the future, greater frequency of environmental extremes is likely, including greater fluctuations in large-scale events such as the Pacific Decadal Oscillation or the recent warm Blob in the North Pacific (Peterson et al. 2015). In high latitudes, dynamic drivers such as temperature change, increased glacial melt, river discharge due to permafrost melting, sea-level rise, and increases in the frequency of storms will affect rocky shores and coastal environments in general. It is thought that over the next 25 years, rocky shore communities will change subtly and will be subject to increasing degradation (Thompson et al. 2002). Because the static habitat attributes did not vary greatly among the sites studied here, these regions are ideal to examine community variability in the context of short-term (i.e., variations in salinity, temperature and nutrients), long-term (climate change and the Pacific Decadal Oscillation), and episodic (oil spill and eutrophication) dynamic drivers.

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