INFLUENCE OF ENVIRONMENTAL ATTRIBUTES ON INTERTIDAL COMMUNITY STRUCTURE IN GLACIAL ESTUARIES

By

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A Thesis Submitted in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in

Marine Biology

University of Alaska Fairbanks

May 2021

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Abstract

High-latitude coastal environments are experiencing dramatic changes due to climate warming. Increased glacier discharge rates modulate downstream environmental conditions in coastal watersheds. These fast-changing environments are predicted to influence the structure of nearshore marine communities. Here, rocky intertidal community structure, recruitment of key organisms, and environmental correlates were examined at nine watersheds in two regions (Kachemak Bay and Lynn Canal) that bookend the Gulf of Alaska, which were separated by approximately 1000km. Each watershed was part of a gradient in each of the regions that spanned 0-60% glacial coverage. Percent cover, biomass surveys, and recruitment of intertidal organisms, along with environmental monitoring of salinity, temperature, dissolved oxygen, river discharge, turbidity, and nutrient loading were completed from April – September 2019 in each watershed. Biological community structure and variance were analyzed by taxa and by ecological group (i.e., primary producer, filter feeder, omnivore, grazer, predator) and then in relation to the local environmental spatiotemporal profiles. In general, larger watersheds with more glacial coverage and river discharge resulted in higher cover of primary producers and less cover of filter feeders. This pattern was more apparent in the region with more oceanic influence as compared to the other region located within an inlet. In relation to specific environmental drivers, salinity was negatively correlated with primary producer cover ($r = -0.52$), but positively associated with barnacle cover ($r = 0.40$). Additionally, turbidity was positively correlated with primary producer biomass ($r = 0.50$), but negatively correlated with mussel cover ($r = -0.30$). In contrast, there was a positive relationship among mussel recruitment and discharge and turbidity. There was variability in within-ecological group response between regions that could be a response to local circulation and oceanic influences. Barnacles were the main filter feeder species driving patterns in the more saline region located close to the open ocean, while mussels drove patterns in the other less oceanic region. As glaciers recede, environmental conditions, such as salinity, will increase and turbidity will decrease, which may alter future intertidal community assemblages dominated by filter feeders.

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Introduction

Coastal ecosystems are an intermediary environment for a suite of hydrological, geological, and biological processes occurring between the land and sea (Saintilan et al. 2016). The complex interaction of terrestrial and pelagic subsidies (e.g., nutrients, sediments, larvae) can modulate the abundance of key species and ecological processes in nearshore environments (Smith & Hollibaugh 1993, Palumbi 2003). High-latitude coastal ecosystems are experiencing dramatic changes in environmental conditions due to climate warming and increasing glacial ablation (Arendt et al. 2002, Bliss et al. 2014, IPCC 2019). Globally, glacial retreat affects mountain slope stability and run-off seasonality with impacts on water resources, agriculture, and habitat availability (IPCC 2019). Locally, it is predicted that changes in watershed glacial coverage and melt will coincide with changes in riverine discharge, directly modulating downstream estuarine dynamics including changes in ecological relationships, biogeochemical processing, and biological community structure (O'Neel et al. 2015).

Increased glacial melt can modify downstream environmental variables in local estuaries, such as temperature, salinity, pH, dissolved oxygen, light availability, nutrient concentrations (NH_4, NO_2, NO_3, PO_4, and $SiOH_4$), and sedimentation rates by changing the composition of riverine discharge from associated watersheds (Hood & Berner 2009, Arimitsu et al. 2016). In addition, differences in glacial coverage across watersheds can result in a highly variable gradient of terrestrial organic matter and glacial sediment altering biogeochemical fluxes and estuarine productivity (Fellman et al. 2010, Arimitsu et al. 2018). Heavily glaciated watersheds tend to be associated with colder and more turbid river discharge, with accompanying organic matter (OM) from microbial production on the glacier surface and petrogenic OM from the weathering of sedimentary rock as the glacier moves. The dissolved organic matter (DOM) from these processes are more bioavailable to other heterotrophic microorganisms downstream as compared to degraded plant detritus or particulate organic matter (POM) in non-glacial systems, which is more refractory and less available for stimulating bacterial production in the water column (Fig. 1; Hood et al. 2009, Fellman et al. 2010, Spencer et al. 2014). Glaciated systems can contain greater concentrations of rock-derived nutrients than rain-fed systems, including phosphorus and iron, which can increase downstream primary productivity in the nearshore water column (Fig. 1; Smith & Hollibaugh 1993, Hood & Scott 2008). Differences in physical and hydrological conditions associated with glacial versus rain-fed watersheds can influence the structure and function of downstream benthic inter- and subtidal communities (Milner et al. 2017, Cauvy-Fraunié & Dangles 2019) by altering metabolic demand and energy allocation of organisms due to differences in food sources and/or stress produced by the aforementioned environmental changes (Brockington & Clarke 2001).

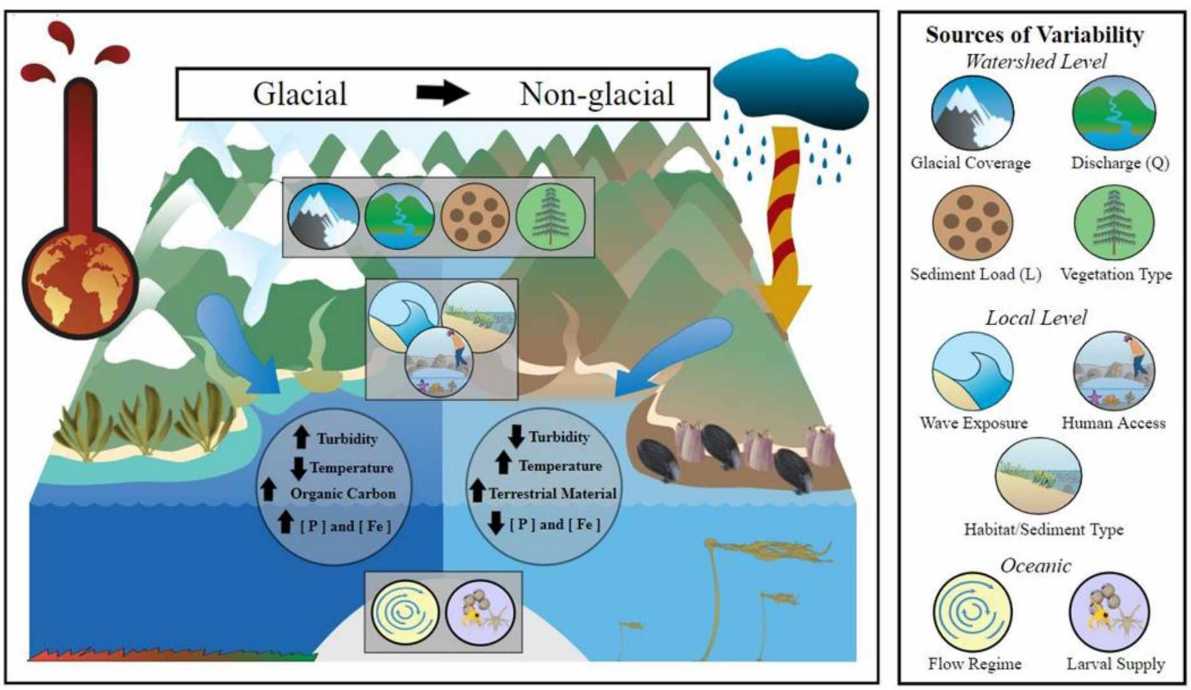

Figure. 1 Conceptual diagram depicting the downstream effects of glacial to non-glacial input into estuaries as a result of increased global temperature, decreased snowfall, and increased

rainfall. The predicted changes in local environmental drivers across the glacial gradient are represented by the arrows and are found within the marine coastal environment in circles. The smaller circular icons contained within the squares represent the sources of variability to an estuarine ecosystem (site), and the predicted biological responses of the local fauna and flora, as represented by the presence of the organisms' icons (primary producers, filter feeders, turf algae, and bull kelp, top to bottom respectively).

Temperature, salinity, irradiance, sedimentation, tidal flux, and dissolved oxygen often define bio-zones within an estuary and create energetic thresholds that delineate potential habitats suitable to marine organisms (Helmuth et al. 2006a, Elliott & Whitfield 2011, Pratt et al. 2014, Kroeker et al. 2019). Glacial melt is expected to alter coastal habitats and associated nearshore communities through changes in these environmental variables by creating more favorable or undesirable conditions for local organisms. Nevertheless, multiple sources of variability exist that can contribute to local ecological processes in non-glacially and glacially influenced estuaries at varying levels across the entire geomorphic transition zone (Fig. 1). This includes variability at the watershed level (i.e., watershed size, discharge, sediment load, glacial coverage, and vegetation type), which dictates the amount and type of material entering an estuary. Wave exposure, elevation, substrate type, and human access are other key sources of variability for coastal rocky shores at the intertidal site level (Menge & Branch 2001, Harley & Helmuth 2003, Alestra & Schiel 2015), along with oceanic sources (i.e., flow rate, flow direction, larval supply) (Fig. 1). Fluctuations in these variables can influence food condition, growth, reproduction, recruitment success, and spatial distribution of ecological groups across a gradient of glacial and non-glacially influenced systems (Clarke 1987, Sokolova et al. 2012, Deutsch et al. 2015).

Rocky intertidal habitats are common in estuaries. They can be biologically diverse and productive systems that respond to changes in their local environment at relatively short timescales, acting as indicators of climate change (Barry et al. 1995, Helmuth et al. 2006b, Kordas et al. 2011, Harley et al. 2012). Intertidal algae have shown reduced growth and survival under increased temperature and suspended sediment load, but enhanced growth under high nutrient conditions (Alestra & Schiel 2015, Graiff et al. 2015). Previous studies reported decreased growth and recruitment in subtidal sub-arctic algae in areas of increased glacial discharge, often associated with decreased salinity and irradiance (Spurkland & Iken 2012, Traiger & Konar 2017). In contrast, subtidal barnacles can thrive in more glaciated watersheds, often showing spatial dominance, possibly due to a lack of competition (Ørberg et al. 2018, Traiger & Konar 2018). These subtidal trends occur where light tends to be the limiting factor; however, the intertidal is more often space and food-limited, thus shifting key environmental drivers (Menge & Branch 2001, Helmuth et al. 2006b). Filter feeding species, such as barnacles and mussels, tend to feed on a combination of phytoplankton, detritus, and terrestrial organic matter (Sarà et al. 2007), while also exhibiting increased growth and fitness in more exposed, higher flow environments (Sanford et al. 1994, Steffani & Branch 2003, Blanchette et al. 2007). Primary productivity is often linked to irradiance, where greater light availability enhances phytoplankton production and food conditions for consumers in the water column, which is predicted to be more pronounced at non-glacial systems (Pratt et al. 2014). Irradiance is not anticipated to be a limiting factor for benthic primary producers (i.e., macroalgae) in the intertidal; instead, an increase in nutrient load from glacial systems is hypothesized to enhance biomass production in glacially influenced assemblages (Fig. 1). Ultimately, changes in these environmental variables and their interactions have the potential to disrupt the bounds of tolerance and energy balance of estuarine organisms, to the benefit of some marine species and detriment of others (Kroeker et al. 2016, 2019).

Receding glaciers are a global concern with far reaching consequences on regional hydrological regimes that impact not only local biodiversity and ecosystem services, but can also be a potential threat to human society by limiting water for consumption, agriculture, and hydropower (Bliss et al. 2014, Marzeion et al. 2014, Milner et al. 2017, IPCC 2019). Glacier mass loss in Alaska is among the highest globally (~75 $\pm$ 11 Gt/year; Larsen et al. 2015), with consequential influence on the magnitude and timing of freshwater discharge into the Gulf of Alaska (GOA). This freshwater discharge modulates the Alaska Coastal Current and acts as a primary driver of planktonic organisms, nutrients, and sediments across the GOA and to nearshore ecosystems (Neal et al. 2010, Larsen et al. 2015). The rocky intertidal in Alaskan glacially influenced watersheds is spatially dominated by the brown alga *Fucus distichus,* the red alga *Odonthalia floccosa*, the mussel *Mytilus trossulus,* and the barnacles, *Semibalanus balanoides* and *Balanus glandula*; an assemblage highly representative of intertidal communities globally (O'Clair & Zimmerman 1986, Menge & Branch 2001). The perennial macroalgae, *Fucus* and *Odonthalia* provide shelter and nutrition to herbivorous consumers, such as limpets (*Lottia* spp.) and periwinkles (*Littorina* spp.) (Klinger & Fukuyama 2011). Other ephemeral algal species occur throughout the year, competing for space in the mid- to upper intertidal (O'Clair & O'Clair 1998, Konar et al. 2009). The filter-feeding invertebrates, *Mytilus*, and *Semibalanus* and *Balanus* (henceforth mussels and barnacles), consume a wide variety of OM, detritus, and plankton found in the water column. Higher-trophic level predators, including sea stars and predatory whelks, as well as sea otters (*Enhydra lutris*), bears (*Ursus* spp.), and birds feed on these species in the GOA (Carroll & Highsmith 1996a, Smith & Partridge 2004, Coletti et al. 2016). Locally, intertidal community structure is regulated by a combination of top-down and bottom-up forcing (Menge et al. 1997), and the regional species pool, which is also predicted to respond to climate change (Helmuth et al. 2002, Milner et al. 2017).

In the present study, the relationship between estuarine intertidal communities and key environmental variables was examined along a gradient of glacial to non-glacial watersheds in two regions, Kachemak Bay and Lynn Canal located within Southcentral and Southeast GOA, respectively (Fig. 2). This gradient is based on watershed characteristics including watershed size and relative watershed glacial cover (0-60%). Although the intertidal communities in both regions are estuarine by definition, the regions differ based on their oceanic influence, local circulation patterns, and regional species pool. Kachemak Bay (KB) experiences a strong flow of GOA water from the Alaska Coastal Current with local upwelling at the mouth that travels counterclockwise along the bay creating different marine conditions on the inner and outer part of the bay (Muench et al. 1978, Johnson 2021). Lynn Canal (LC) is located approximately 100 km from the open ocean in interconnected passages influenced by land runoff and local climate (Bruce et al. 1976). This nested regional study design allows for the identification of glacial-driven patterns across estuaries within nearshore assemblages.

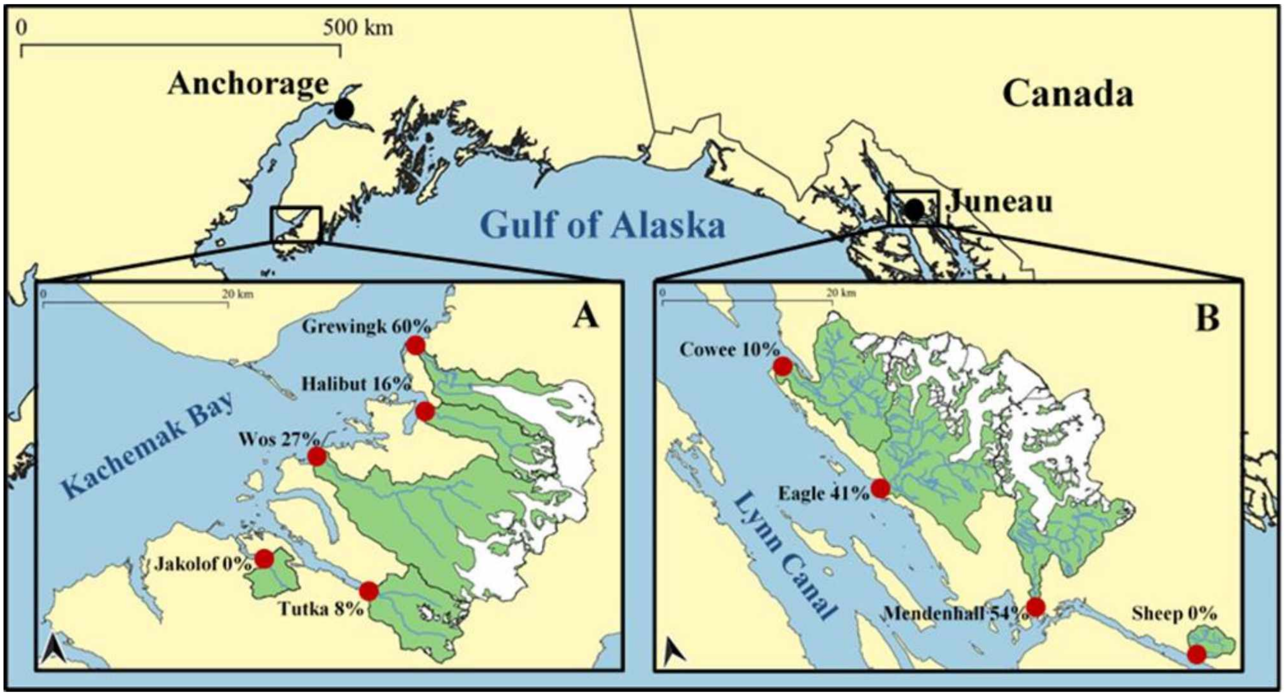

Figure. 2 Map of the Gulf of Alaska study regions (insets) and intertidal sites (red circles). Watersheds are outlined in black within each region. The white area represents the glacial coverage and green is vegetation. Note that the intertidal site of Eagle is located downstream of the convergence of the Eagle and Herbert Rivers. Thus, the associated watershed border contains both the Eagle and Herbert watersheds.

The hypotheses tested were that (1) community patterns and environmental trends across sites along the glacial gradient will be similar between regions and over season (a depiction of similar estuarine processes), (2) spatial coverage and biomass of primary producers (focus on the highest contributors *Fucus* and *Odonthalia*) will be positively correlated with increasing glacial coverage, nutrient load, and turbidity, and (3) spatial coverage, biomass, and recruitment of filter feeders (mussels and barnacles), will be negatively correlated with glacial coverage and turbidity.

Materials & Methods

Two distinct study regions in the GOA, Kachemak Bay (KB-5 sites) and Lynn Canal (LC-4 sites), located within the coastal areas of Southcentral and Southeast Alaska, respectively, were chosen, because they each exhibit a gradient of glacial to non-glacial estuarine ecosystems (Fig. 2). Glaciation was determined by estimating the percentage of glaciated area from the total watershed area (Table 1). In LC, daily mean discharge was measured upstream at each watershed using pressure transducers and at established USGS discharge gauges. The Eagle site receives freshwater discharge from two large glacial rivers: Herbert and Eagle. Herbert River has a stream gauge with daily flow data. Eagle River is ungauged; however, because the two watersheds are similar in size, elevation range, and glacier coverage (Fellman et al., 2014), discharge was estimated for Eagle River by weighting the discharge for Herbert River to the area of the Eagle River watershed. Thus, total freshwater discharge to the intertidal was estimated as Total Q = (Herbert Q) + (Herbert Q*0.8004), where Q is discharge in m^3/day. In KB, an Acoustic Doppler Current Profiler (ADCP) or flow rate instrument was used monthly (April to September 2019) to estimate the amount of freshwater entering the estuaries. Monthly sampling in conjunction with associated river height gauges was used to approximate daily mean discharge values. In each watershed, one intertidal site was located on the outflow side of a river mouth to capture the greatest riverine discharge influence.

Table 1. Percent of glaciation based on the 2019 glacial and watershed areas for each site in the two study regions (Kachemak Bay and Lynn Canal).

Estuarine Intertidal Site	Percent Glaciated (%)	Glacial Area (km^2)	Watershed Area (km^2)
Kachemak Bay			
Jakolof	0	0.0	18.9
Tutka	8	5.0	66.0
Halibut	16	9.0	55.6
Wosnesenski	27	69.0	257.0
Grewingk	60	67.0	111.5
Lynn Canal			
Sheep	0	0.03	15.5
Cowee	10	12.2	119.2
Eagle	41	52.8 + 64.2	127.1 + 158.7
Mendenhall	54	123.6	228.2

Intertidal community structure was assessed monthly (April – September 2019) using two methods along a fixed horizontal transect, ranging from 30-50m in length, depending on the extent of continuous habitat at each site. Ten randomly placed quadrats ($0.0625m^2$) were scraped, at approximately 1-m distance, and at alternating sides along the transect, to collect all individuals (excluding barnacles) for biomass estimates. These samples were immediately processed in the laboratory, or frozen at -18°C until processing could be done, i.e., species identified and weighed (g wet mass including shells). Percent cover of all sessile organisms and densities of mobile species were quantified in ten randomly placed quadrats ($0.25\ m^2$) at alternating sides along the transect. Substrate was also measured within these quadrats to determine the site's average substrate type based on the Wentworth scale (i.e., mud, sand, gravel, cobble, boulder, and bedrock; Wentworth 1922). Slope (percent) was also measured at each site using a compass inclinometer or level rod starting at Mean Lower Low Water (MLLW) and ending at the permanent transect (Dornbusch 2010). Substrate type and slope were considered static environmental variables in further analyses, as they do not vary greatly from month to month.

Dynamic environmental variables (i.e., dissolved oxygen, temperature, salinity, and conductivity, turbidity) were measured once monthly at each site using a YSI Pro2030 shortly after low tide at nearshore 0-5m, 50-m, and 100-m offshore from each intertidal site at 1-m and 5-m (if available) water depth. Measurements from the same month were averaged across distances from shore and water depth to represent the mean of potential estuarine environmental conditions at the time of field sampling. Water samples (60mL) were taken at each location to measure average site turbidity and later analyzed on a Hach 2100P TurbidMeter to determine Nephelometric Turbidity Units (NTU). Two 1-L polyethylene bottles were also rinsed (3x), filled with seawater at the nearshore location, and kept refrigerated until analysis for dissolved organic carbon (DOC), total nitrogen (TN), and total dissolved phosphorus (TDP) concentrations. DOC and TN samples were analyzed with a Shimadzu Total Organic Carbon Analyzer (TOC-L-CSH) using high temperature combustion. Total dissolved phosphorus (TDP) was measured using persulfate digestion in combination with the ascorbic acid method (Valderrama 1981). The nutrient concentrations were later multiplied with discharge to determine specific (watershed area normalized) instantaneous mass flux of a nutrient into an estuarine site. This allowed for direct comparison of nutrient export efficiency among watersheds (Hood & Scott 2008).

Lastly, invertebrate recruitment (barnacles and mussels) was quantified using standardized larval collectors that were replaced monthly (Navarrete et al. 2008). Barnacle recruitment was quantified using five Plexiglass plates (10 x 10cm) covered in slip resistant tape (3M Safety-Walk™), while mussel recruitment was quantified using five filamentous plastic tuffys (Menge 1991), all approximately at 1-m distance from the transect and secured to rocks with screws. After monthly collection, plates and tuffys were frozen until laboratory processing, when they were rinsed, sorted, and resulting invertebrates identified to larger taxonomic group (genus *Mytilus* or superfamily Balanoidea), and counted via a dissection microscope. Larval collectors were not deployed at the Eagle and Cowee in the LC region due to the regulations of these protected sites by the Alaska Department of Natural Resources.

Univariate and multivariate statistical analyses were performed to determine differences in community structure among sites and between regions, as well as explore correlations among environmental and biological variables across the glacial gradient. Biological patterns were analyzed with respect to both taxa and combined ecological groups (e.g., filter feeder, primary producer, grazer; Table 2) to examine broader community patterns between regions. Common indices (i.e., species richness, Pielou's evenness, Shannon and Simpson diversity index) were used to examine patterns of diversity across the glacial gradient and between regions (Morris et al. 2014). Faunal percent cover and biomass data were square-root transformed to examine community structure using ecological groups. All similarities in community structure were calculated using Bray-Curtis resemblance matrices. The non-metric multidimensional scaling (NMDS) matrix was visualized using *ggplot2* in R (Wickham 2016), then with fitted ecological group and scaled environmental vectors using the 'envfit' function in the *vegan* package

(Oksanen et al. 2020). Significance level in all statistical analyses was α = 0.05. Pearson correlations were also used to examine the univariate relationship between raw percent cover/biomass data and each environmental variable sampled.

Table 2. Species that comprise each ecological group for the community composition methodology. Community composition methods included percent coverage measured via quadrat sampling and biomass collections in the field.

	Community composition method	
Ecological group	Percent coverage	Biomass
Filter feeder	*Mytilus trossulus, Balanus glandula* *Semibalanus balanoides*	*Mytilus trossulus*
Primary producer	*Fucus distichus* *Odonthalia flocossa*	*Fucus distichus* *Odonthalia flocossa*
Other algae	*Savoiea bipinnata, Endocladia muricata, Gloiopeltis furcata, Mazzaella spp., Palmaria hecatensis, Cryptosiphonia woodii, Ulva spp., Acrosiphonia spp., Mastocarpus papillatus, Desmarestia aculeata Melanosiphon intestinalis, Scytosiphon lomentaria,* & Filamentous diatoms	*Ulva spp., Mastocarpus papillatus, Monostroma grevillei, Desmarestia aculeata Melanosiphon intestinalis* & Filamentous algal complex (including *Savoiea bipinnata, Acrosiphonia spp., Urospora neglecta Pylaiella littorallis* & Filamentous diatoms)
Grazer		*Lottia spp., Littorina spp., Lacuna vincta* & *Mopalia spp.*
Omnivore		*Gnorimosphaeroma oregonense, Pentidotea wosnesenskii* & *Pagurus spp.*
Predator		*Nucella spp., Onchidoris bilamellata, Emplectonema gracile* & *Amphiporus formidabilis*

A Principal Components Analysis (PCA) was carried out for each region to determine the dynamic environmental variables that best correlated with glacially influenced sites across seasons. The few missing data points (n = 20/432, or 4.6% of dynamic environmental variables) were estimated via regression or imputation (R package ‘Hmisc’, Harrell 2020) dependent on data type. PERMANOVA and SIMPER multivariate statistical analyses were performed using PRIMER v7 to test for differences among spatiotemporal estuarine factors and identify ecological groups/species that contribute most to those differences. The intertidal biological PERMANOVA design function for this analysis included Region (fixed, 2 levels: LC, KB), Site (random, nested within Region, 9 levels), and Month (fixed, 6 levels: April, May, June, July, August, September).

Glacial discharge level based on site variability was included as an additional estuarine factor for analysis (Fig. 3). Spatial differences included a no, low, and high glacial discharge factor based on the glacial cover, and the range and median of daily mean discharge at each site (Fig. 3B). Jakolof and Sheep were classified as no glacial discharge sites due to their 0% glacial cover and small discharge. Low glacial discharge sites included Tutka, Halibut, and Cowee, which showed small discharge medians and ranges. The largest watersheds with the greatest glacial coverage and discharge variability were classified as high glacial discharge, which included Wosnesenski (or Wos), Grewingk, Eagle, and Mendenhall. Sub-seasonal analysis consisting of two-month intervals were also used to examine similarities in community structure between regions over time through the glacial melt season (1) April and May, (2) June and July, and (3) August and September. Thus, a second PERMANOVA design function including Region (fixed, 2 levels: LC, KB), Glacial discharge level (random, nested in Region, 3 levels), and Season (fixed, 3 levels) was used to examine variability in community structure by species composition and ecological groups, as well as variability among the dynamic environmental profiles.

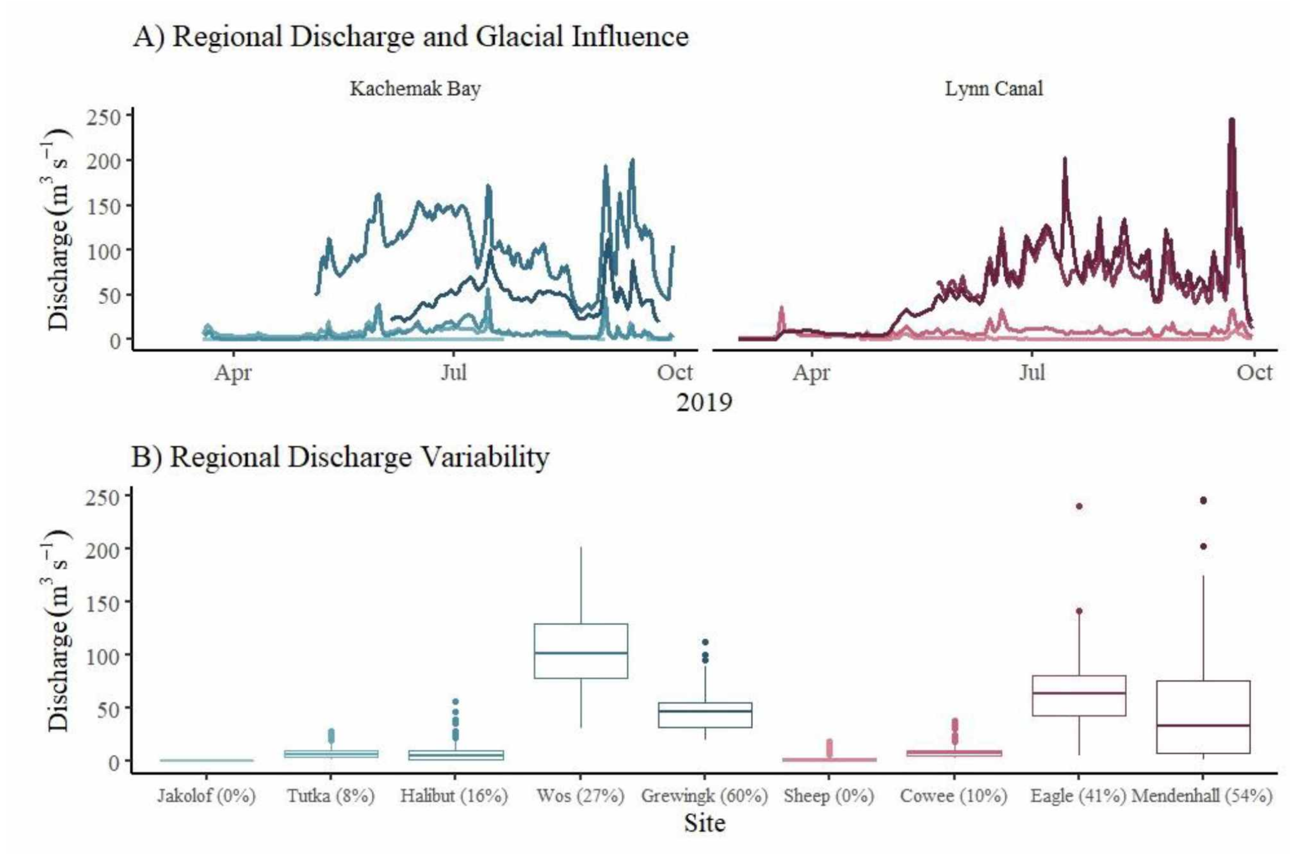

Figure. 3 Spatiotemporal variability of daily discharge across regions and sites (A). Percentages refer to the site's glacial coverage. The blue colors represent the region of Kachemak Bay and red colors represent Lynn Canal. Each region's color gradient represents increasing glacial coverage from light to dark color tones. Summary statistics of daily discharge were used to determine no, low, and high glacial discharge sites (B). Jakolof and Sheep were classified as no glacial discharge sites (0%) for Kachemak Bay and Lynn Canal, respectively. Low glacial discharge (<20%) sites included Tutka, Halibut, and Cowee. The largest watersheds with the greatest glacial coverage were also in the high glacial discharge (>20%) category, including Wos, Grewingk, Eagle, and Mendenhall.

Results

Spatial organization of estuarine intertidal communities across a glacial gradient

The GOA intertidal community showed strong regional differences in species composition (Table S1, PERMANOVA $p < 0.05$); however, this regional distinction was lost when ecological groups were used to examine community composition (Fig. 4A, B; Table S2). There was a significant effect of site nested within region for species and group analyses and for both percent cover and biomass (Tables S1, S2). Both regions showed distinct grouping of percent cover data by glacial discharge when examining ecological groups (Fig. 4C, E; Tables S3A, S4A). However, only biomass (Fig. 4D, F) showed significant community differences over time (Tables S3B, S4B; PERMANOVA, $p < 0.05$). In general, sites were more tightly clustered (i.e., more similar) using percent cover data than biomass, most likely linked to the biomass-seasonal effect.

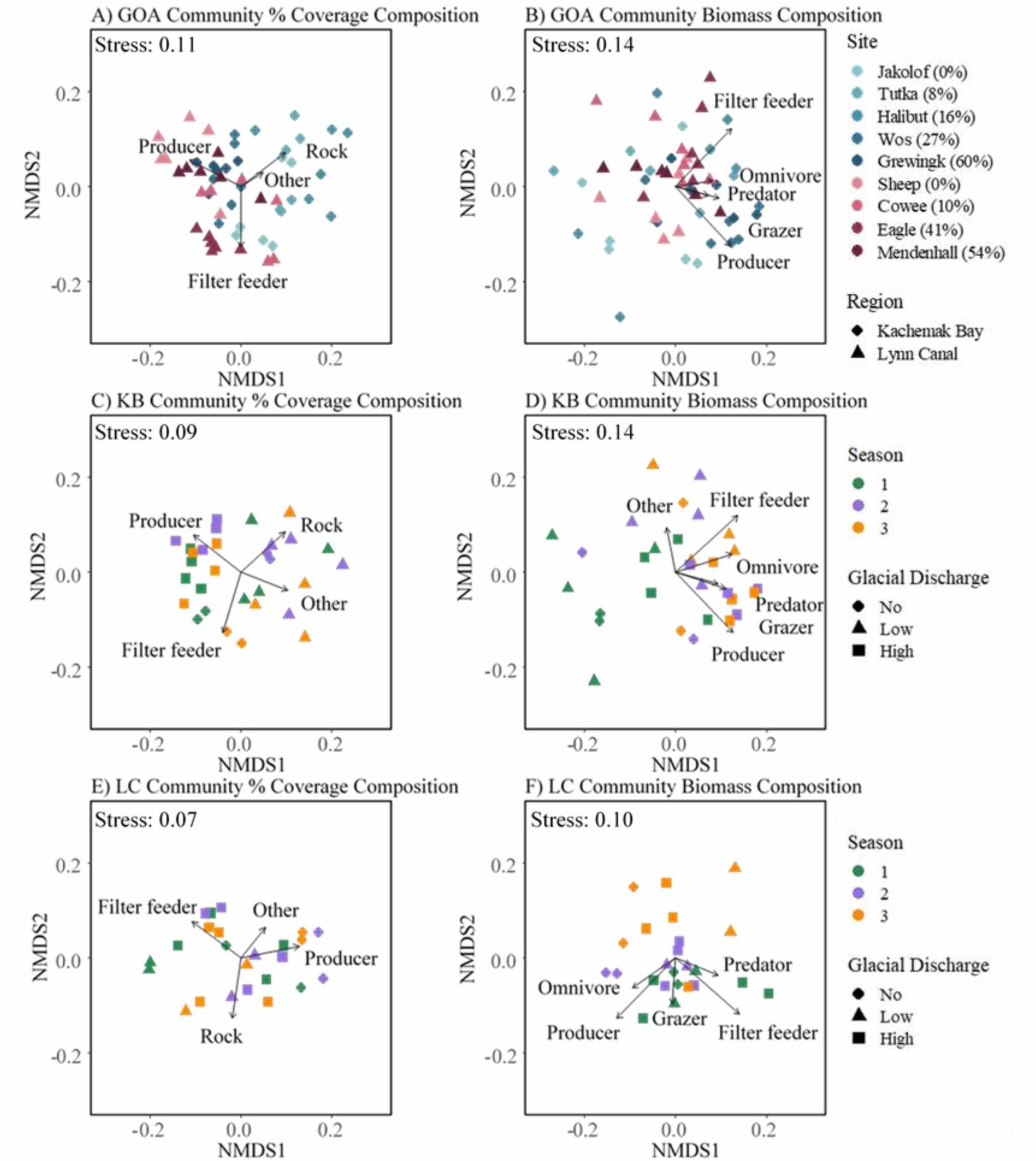

Figure 4. Intertidal community Non-metric multidimensional scaling (NMDS) ordinations of percent coverage (A, C, E) and biomass (B, D, F) across a glacial gradient with ecological group vectors (p-value < 0.05). The stress value reflects how well the ordination summarizes the

observed distances among the samples. Ecological group arrows (or vectors) associate with the samples of their respective direction and those with a longer segment are more strongly correlated with the data than those with a shorter segment. The GOA composition is colored by site and shapes represent the different regions (A, B). The blue colors represent the region of Kachemak Bay (circles) and red colors represent Lynn Canal (triangles). Each region's color gradient represents increasing glacial coverage from light to dark tones. Kachemak Bay and Lynn Canal compositions are colored by season and shapes represent the different glacial discharge levels (C, D, E, F). Data for all ordinations were based on ecological groups as listed in Table 2.

The watersheds with high glacial discharge in KB were associated with primary producer coverage (Fig. 4C). In contrast, the non-glacial discharge site in KB was associated with filter feeders, specifically barnacle cover (Fig. 4C, Fig. 5). Bare rock was associated with the low glacial sites (Fig. 4C, Fig. 5). Mussels, as the only filter feeder collected for biomass, was the greatest contributor to community biomass at all glacial discharge levels across both regions (Tables S5, S6). Differences in the LC region where due to an association of primary producers with both the highest and the non-glacial discharge sites (Fig. 4E, Fig. 5). The other high glacial LC site was associated with filter feeders (Fig. 4E), with an almost equal contribution of barnacles and mussels (Fig. 5, Tables S7, S8).

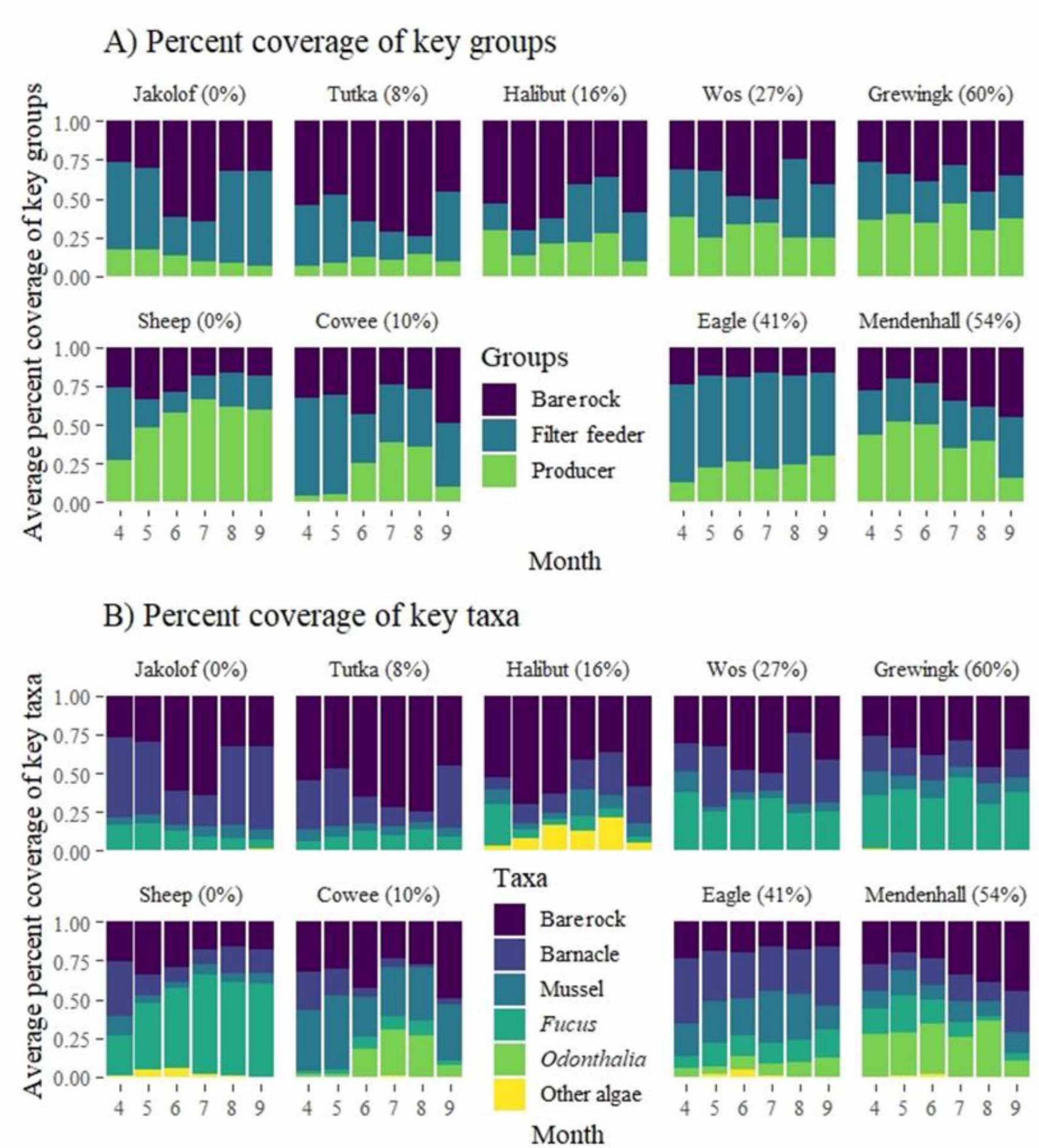

Figure 5. Average proportional mean percent coverage of ecological groups (A) and key taxa (B) across the glacial gradient. Ecological groups are based on Table 2. The top row in each panel is Kachemak Bay and the lower row is Lynn Canal. Purple represents bare rock coverage, blue tones represent filter feeder taxa and green colors represent primary producers. Other algae less abundant algal species are represented in yellow.

Some species and ecological groups coincided with the glacial gradient, but these patterns were not always consistent between the two regions (Fig 5). In KB, there was an increase in the proportional coverage of primary producers as glacial coverage increased, while barnacle cover was greatest at the non-glacial site (Fig. 5A). The brown alga *Fucus* was the largest contributor to percent cover after bare rock in the high KB glacial sites (Wos and Grewingk; Fig. 5B; Tables S7, S8). Barnacle cover was the largest contributor after bare rock in low (Halibut, Tutka) glacial discharge sites (Fig. 5B; Tables S7, S8). Mussels and the red alga *Odonthalia* were not strong spatial contributors in any of the KB sites (Fig. 5B; Table S7). In LC, a mix of primary producers (*Odonthalia* and *Fucus*) increased along with glacial coverage, except at the non-glacial coverage site of Sheep, where *Fucus* was the greatest primary producer contributor (Fig. 5B, Tables S7, S8). Average proportional mussel cover increased as glacial coverage decreased in LC, except in the non-glacial discharge site (Fig. 5B, Table S7). However, these patterns were not detected in LC when examining filter feeders together (Fig 5A). Barnacles did not show a trend along the glacial gradient in LC (Fig. 5B, Tables S7, S8). No clear patterns of community diversity were observed when examining species richness, evenness, or various diversity indices (Table 3).

Table 3. Common diversity indices of each study site separated by region (Kachemak Bay and Lynn Canal) The various indices were used to examine community patterns across the glacial gradient and between regions. Species richness represents the average number of species and Pielou's evenness describes the relative abundance of the different species. The Shannon diversity index is more sensitive to the measure of richness, while Simpson is more sensitive to evenness.

Estuarine Intertidal Site	Glacial Cover	Total species	Species richness	Pielou's evenness	Shannon diversity index	Simpson diversity index
		Kachemak Bay				
Jakolof	0	21	4.288	0.315	0.959	0.560
Tutka	8	18	3.476	0.293	0.847	0.472
Halibut	16	27	5.255	0.327	1.079	0.555
Wosnesenski	27	14	2.376	0.299	0.788	0.506
Grewingk	60	21	3.875	0.305	0.929	0.546
		Lynn Canal				
Sheep	0	16	3.106	0.337	0.936	0.546
Cowee	10	17	3.207	0.293	0.831	0.404
Eagle	41	21	3.805	0.244	0.744	0.347
Mendenhall	54	14	2.646	0.407	1.073	0.562

Spatiotemporal variability of filter feeder recruitment

At most sites in both regions, mussel recruitment was greatest during June and July and started to decline in August (Fig. 6A). Monthly riverine discharge showed a positive correlation with mussel recruitment (Fig. 6B; $r = 0.58$, $p = 0.0003$). Discharge was also highly associated with turbidity, and recruitment also correlated with turbidity across the regions (Pearson correlation, $r = 0.434$, $p = 0.009$). At most sites in both regions, barnacle recruitment peaked earlier in May (Fig. 6C). While the Mendenhall high glacial discharge site in LC showed high barnacle recruitment, this pattern was not mirrored in KB (Fig. 6D). Invertebrate recruitment trends did not reflect community patterns across the glacial gradient. For example, mussel recruitment increased with glacial discharge and turbidity, whereas adult mussel cover decreased with turbidity and glacial coverage (Fig. 5, 6).

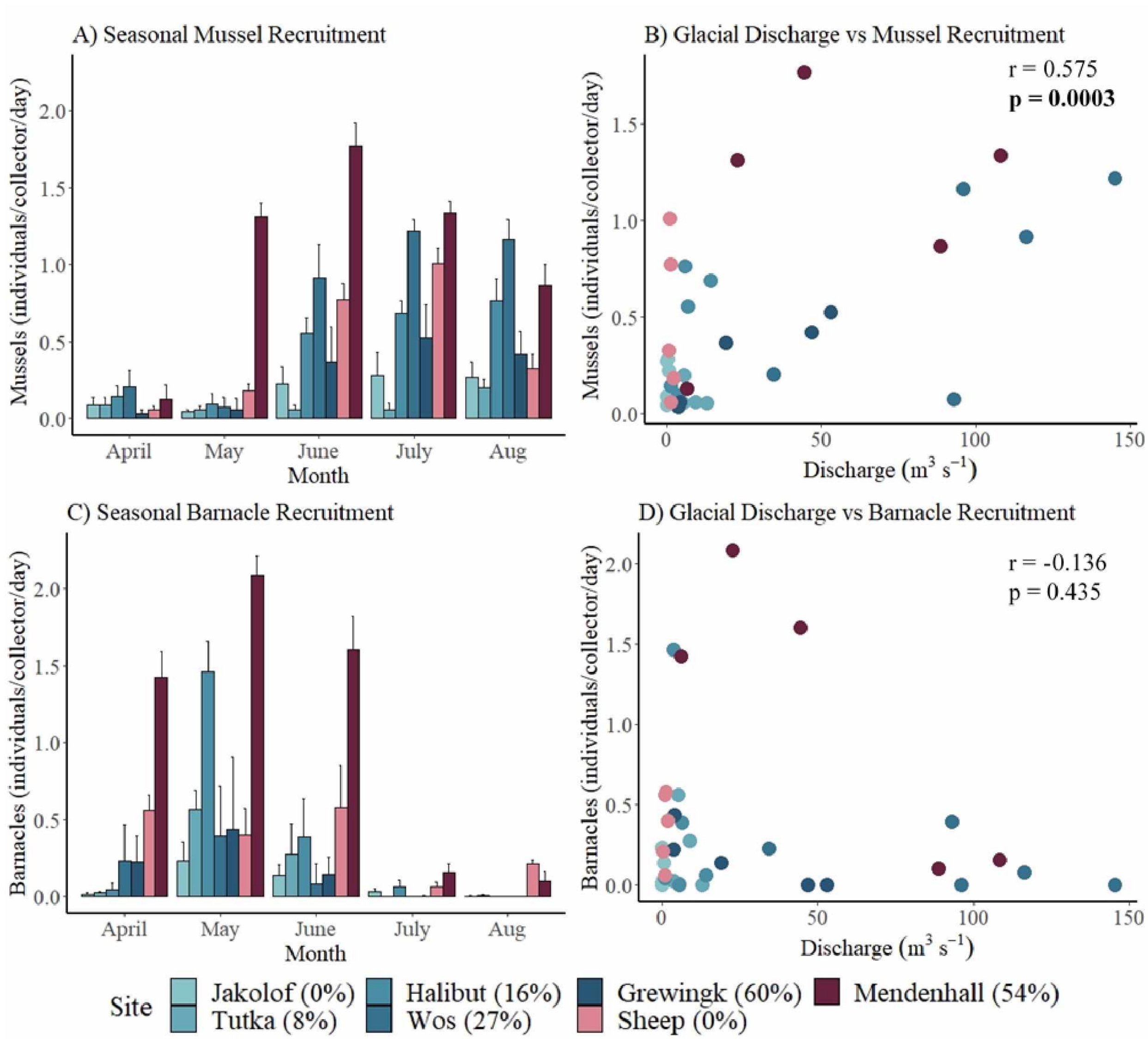

Figure 6. Spatiotemporal variability of mussel and barnacle recruitment in relation to month and site/region (A, C). Each month contains an average of approximately 30 days of larval collector deployment, thus only five months of data. Pearson correlations (r) examining the relationship

between the monthly glacial discharge index and recruitment of mussels (B) and barnacles (D). Bold p-values represent a significant correlation at $\alpha = 0.05$.

Dynamic environmental trends between regions

Environmental variables were significantly different among glacial discharge levels and across seasons, but patterns were similar between the two regions (Fig. 7, 1S, 2S; Tables 4 and S9). The PCA of both regions reflects the PERMANOVA results by showing a separation of sites among season 1 and seasons 2 and 3, as well as between high and no to low glacial discharge sites (Fig. 7). Dissolved oxygen and salinity showed a negative association with temperature that occurred seasonally in both regions as indicated by opposing vectors (Fig. 7). Water temperature increased throughout the season, peaked in July, and began to decline in August and September, whereas, salinity and dissolved oxygen gradually decreased over this time period (Fig. 1SA-C). Riverine discharge, along with turbidity and all nutrient fluxes, was associated with the high glacial discharge sites (Fig. 7). In general, the largest watersheds with the greatest discharge had the highest turbidity values and nutrient loads, except at Sheep where turbidity and nutrient loads were high compared to other no and low glacial sites (Fig. 1SD, 2S; Table 4).

Table 4. Mean +/- 1 standard deviation of dynamic environmental variables across sites for the entire sampling period. Temperature, salinity, dissolved oxygen (DO), and turbidity were sampled via water collection or YSI sampling approximately 5, 50, 100 m offshore from each intertidal site. Nutrient flux was estimated from 5m nearshore water samples and multiplied by discharge.

Estuarine Intertidal Site	Temp (°C)	Salinity	DO (mg/L)	Turbidity (NTU)	C Flux (kg/s)	N Flux (kg/s)	P Flux (kg/s)
	Kachemak Bay						
Jakolof	9.9 ± 2.8	30.7 ± 0.8	11.4 ± 1.3	2.5 ± 0.9	0.01 ± 0.01	0.001 ± 0.0	0.15 ± 0.22
Tutka	9.6 ± 3.1	29.0 ± 3.0	12.2 ± 1.1	3.4 ± 2.5	0.08 ± 0.03	0.01 ± 0.01	1.53 ± 1.08
Halibut	10.0 ± 3.0	29.8 ± 2.9	11.2 ± 0.7	4.2 ± 2.7	0.10 ± 0.08	0.01 ± 0.01	1.30 ± 0.70
Wosnesenski	10.0 ± 2.8	28.4 ± 3.5	10.9 ± 1.5	9.9 ± 8.6	0.46 ± 0.26	0.06 ± 0.03	6.87 ± 5.27
Grewingk	10.4 ± 3.4	28.3 ± 3.3	10.9 ± 0.7	3.1 ± 1.5	0.24 ± 0.19	0.02 ± 0.01	2.29 ± 1.18
	Lynn Canal						
Sheep	9.8 ± 2.7	22.6 ± 5.9	12.0 ± 2.4	2.9 ± 2.5	0.09 ± 0.06	0.01 ± 0.01	1.00 ± 0.68
Cowee	10.8 ± 4.2	25.5 ± 6.4	10.7 ± 1.2	2.2 ± 1.6	0.07 ± 0.02	0.01 ± 0.01	0.75 ± 0.39
Eagle	11.0 ± 4.4	25.2 ± 5.7	11.4 ± 1.4	1.8 ± 1.7	0.27 ± 0.12	0.01 ± 0.01	2.62 ± 1.07
Mendenhall	10.6 ± 3.7	24.2 ± 4.9	11.2 ± 1.3	5.8 ± 4.0	0.30 ± 0.14	0.02 ± 0.01	2.71 ± 1.05

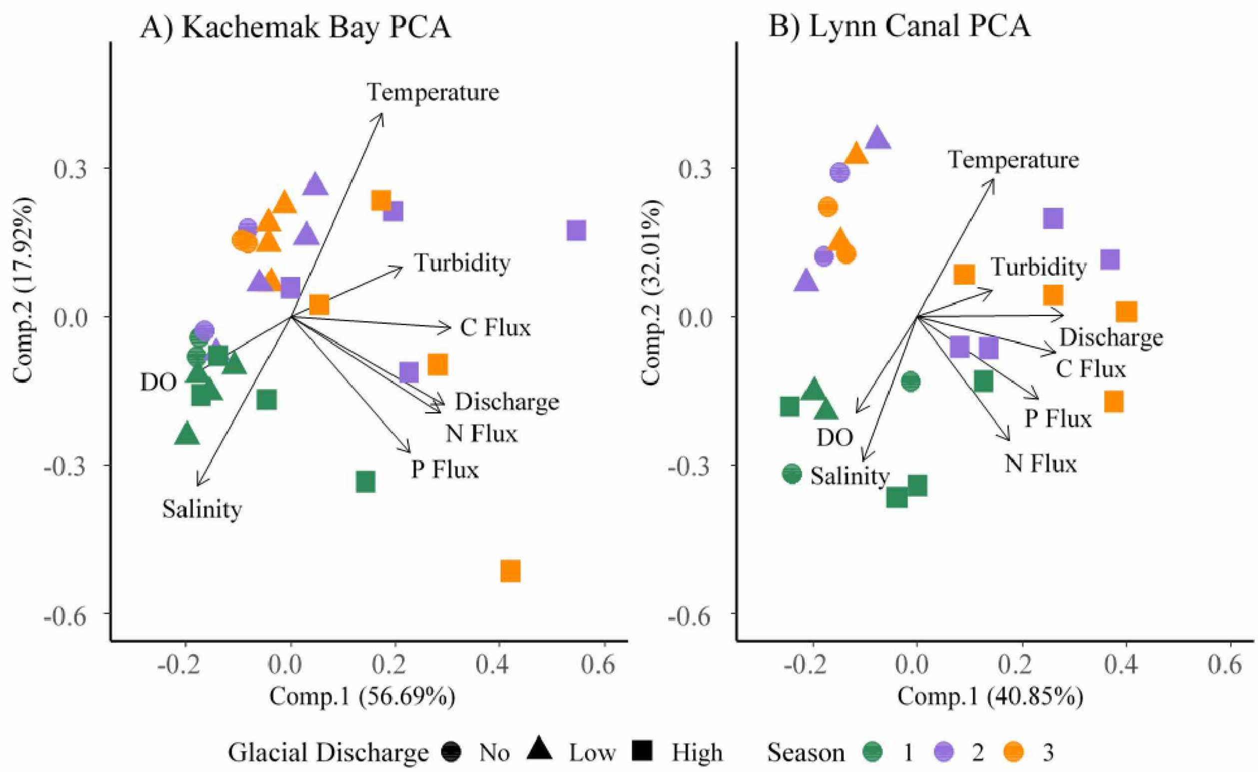

Figure 7. Principal Components Analysis (PCA) of dynamic environmental variables between the regions of Kachemak Bay (A) and Lynn Canal (B) comparing discharge and bi-monthly seasonal variability. Environmental variable arrows (or vectors) associate with the samples of their respective direction and those with a longer segment are more strongly correlated with the data than those with a shorter segment. Principal components (Comp. 1, Comp. 2) represent the directions of the data that explain a maximal amount of variance.

Relationship between environmental variables and biological groups

When examining environmental parameters with the multivariate community data, the static environmental variables (Table 5) contributed more to the percent cover community structure (Fig. 8A, C, E) than the biomass community structure (Fig. 8B, D, F). The cover data demonstrated that sites correlating with primary producers (Fig. 4A) also correlated with mud and gravel substrates (Fig. 8A). In contrast, sites correlating with filter feeders (Fig. 4A) also correlated with boulder and bedrock substrates (Fig. 8A). The low and mid KB glacial discharge sites correlated with cobble, slope, and complexity for percent cover (Fig. 8C). High glacial discharge sites in KB with increased primary producers (Fig, 4C, mostly *Fucus* Fig. 5B) associated with gravel, sand, discharge, nitrogen, and carbon flux (Fig. 8C). In LC, filter feeder cover (Fig. 4E) associated with boulder and bedrock substrates (Fig. 8E), while producer cover (Fig. 4E) associated most closely with mud (Fig. 8E). In contrast to percent cover, biomass associated more with dynamic environmental variables. Specifically, biomass at the KB high glacial discharge sites were associated with riverine discharge, turbidity, carbon, and nitrogen flux (Fig. 8B, 8D), while filter feed biomass in LC was associated with salinity, boulder, and bedrock (Fig. 4F, 8F). Fewer dynamic environmental variables were associated with community biomass patterns in LC than in KB (Fig. 8D, F).

Table 5. Mean +/- 1 standard deviation of static environmental variables across sites for the entire sampling period. Slope was only measured once at each site; thus, no standard deviation is available. Each substrate type was estimated while completing community sampling inside each quadrat. Slope (percent) was also measured at each site using a compass inclinometer or level rod starting at Mean Lower Low Water (MLLW) and ending at the intertidal transect.

Estuarine Intertidal Site	Slope	Mud (% cover)	Sand (% cover)	Gravel (% cover)	Cobble (% cover)	Boulder (% cover)	Bedrock (% cover)
	Kachemak Bay						
Jakolof	26.85	2.6 ± 2.8	1.6 ± 1.6	19.1 ± 15.0	32.2 ± 17.8	25.0 ± 15.5	19.0 ± 40.12
Tutka	16.69	0.0 ± 0.0	0.0 ± 0.0	37.0 ± 22.4	49.5 ± 20.5	13.5 ± 21.2	0.0 ± 0.0
Halibut	21.4	2.0 ± 2.0	0.2 ± 0.6	14.1 ± 9.2	48.7 ± 26.7	33.5 ± 27.9	1.5 ± 4.7
Wosnesenski	13.26	0.0 ± 0.0	5.3 ± 4.4	23.3 ± 11.9	28.9 ± 13.9	36.0 ± 17.1	6.5 ± 14.1
Grewingk	1.1	8.4 ± 9.4	1.0 ± 2.1	82.9 ± 9.6	7.7 ± 6.1	0.0 ± 0.0	0.0 ± 0.0
	Lynn Canal						
Sheep	5.24	42.8 ± 32.6	5.1 ± 16.9	24.5 ± 24.0	18.5 ± 13.5	9.1 ± 20.4	0.0 ± 0.0
Cowee	1.75	2.8 ± 5.7	63.7 ± 22.8	2.3 ± 3.9	1.4 ± 2.0	24.3 ± 25.4	5.4 ± 14.9
Eagle	10.51	12.8 ± 18.8	0.0 ± 0.0	1.1 ± 2.3	26.0 ± 25.2	56.0 ± 33.6	4.1 ± 12.9
Mendenhall	6.99	32.4 ± 16.8	0.0 ± 0.0	27.7 ± 18.4	26.2 ± 12.7	13.7 ± 17.9	0.0 ± 0.0

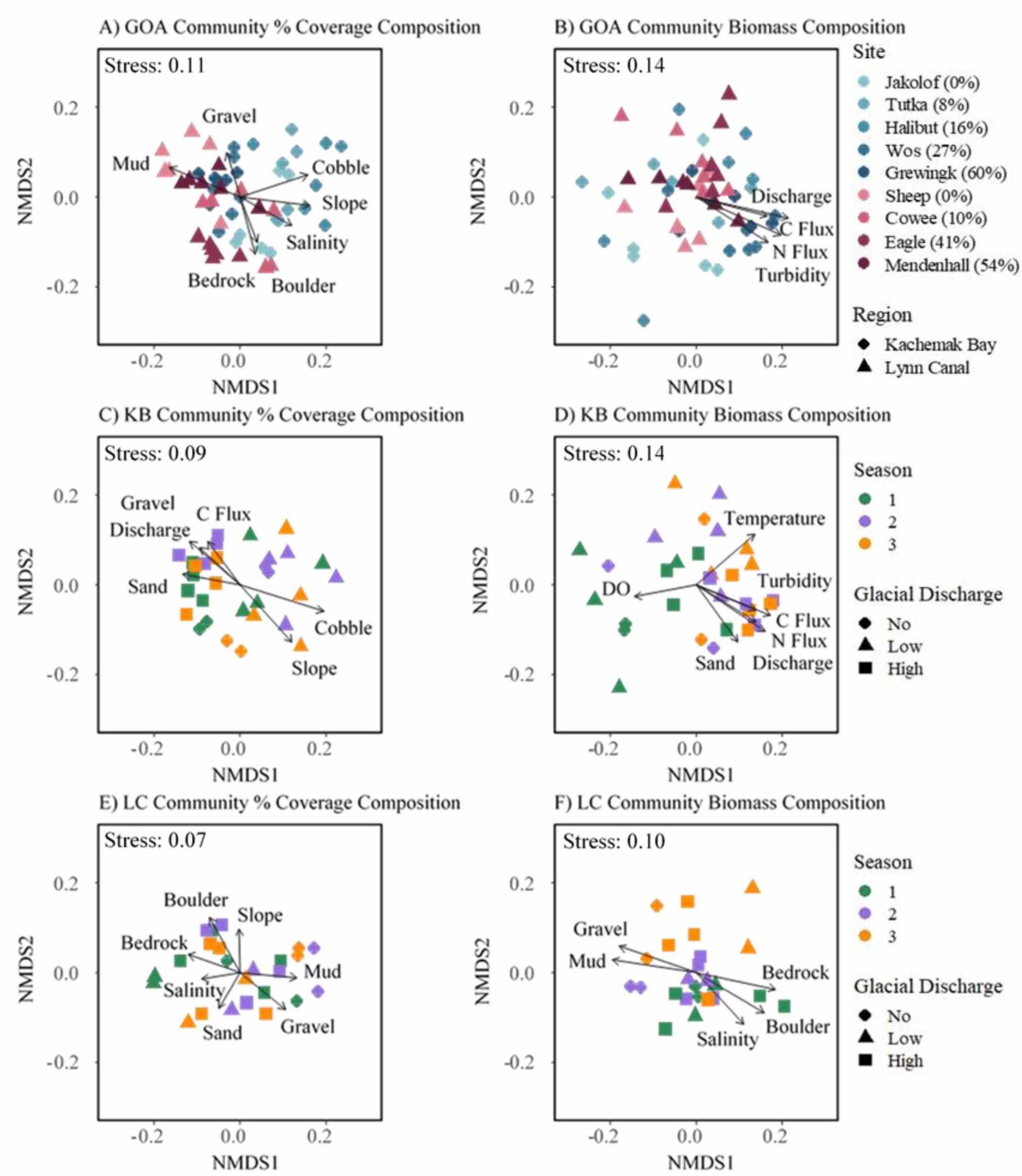

Figure 8. Intertidal community Non-metric multidimensional scaling (NMDS) ordinations of percent coverage (A, C, E) and biomass (B, D, F) across a glacial gradient with static and dynamic environmental vectors (p-value < 0.05). Data for all ordinations were based on

ecological groups as listed in Table 2. The stress value reflects how well the ordination summarizes the observed distances among the samples. Environmental vectors associate with the samples of their respective direction and those with a longer segment are more strongly correlated with the data than those with a shorter segment. The GOA composition is colored by site and shapes represent the different regions (A, B). The blue colors represent the region of Kachemak Bay (circles) and red colors represent Lynn Canal (triangles). Each region's color gradient represents increasing glacial coverage from light to dark tones. Kachemak Bay and Lynn Canal compositions are colored by season and shapes represent the different glacial discharge levels (C, D, E, F).

The univariate analyses confirmed the biological and environmental relationships found using multivariate analysis. There was a positive correlation between turbidity and primary producer biomass (Fig. 9A), and a negative correlation between salinity and primary producer cover (Fig. 9B). In contrast, barnacle cover was positively correlated with salinity (Fig. 9C), and mussel cover was negatively correlated with turbidity (Fig. 9D). Lastly, there was a positive relationship between producer biomass with grazer biomass, as well as grazer biomass with predator biomass (Fig. 9E, F).

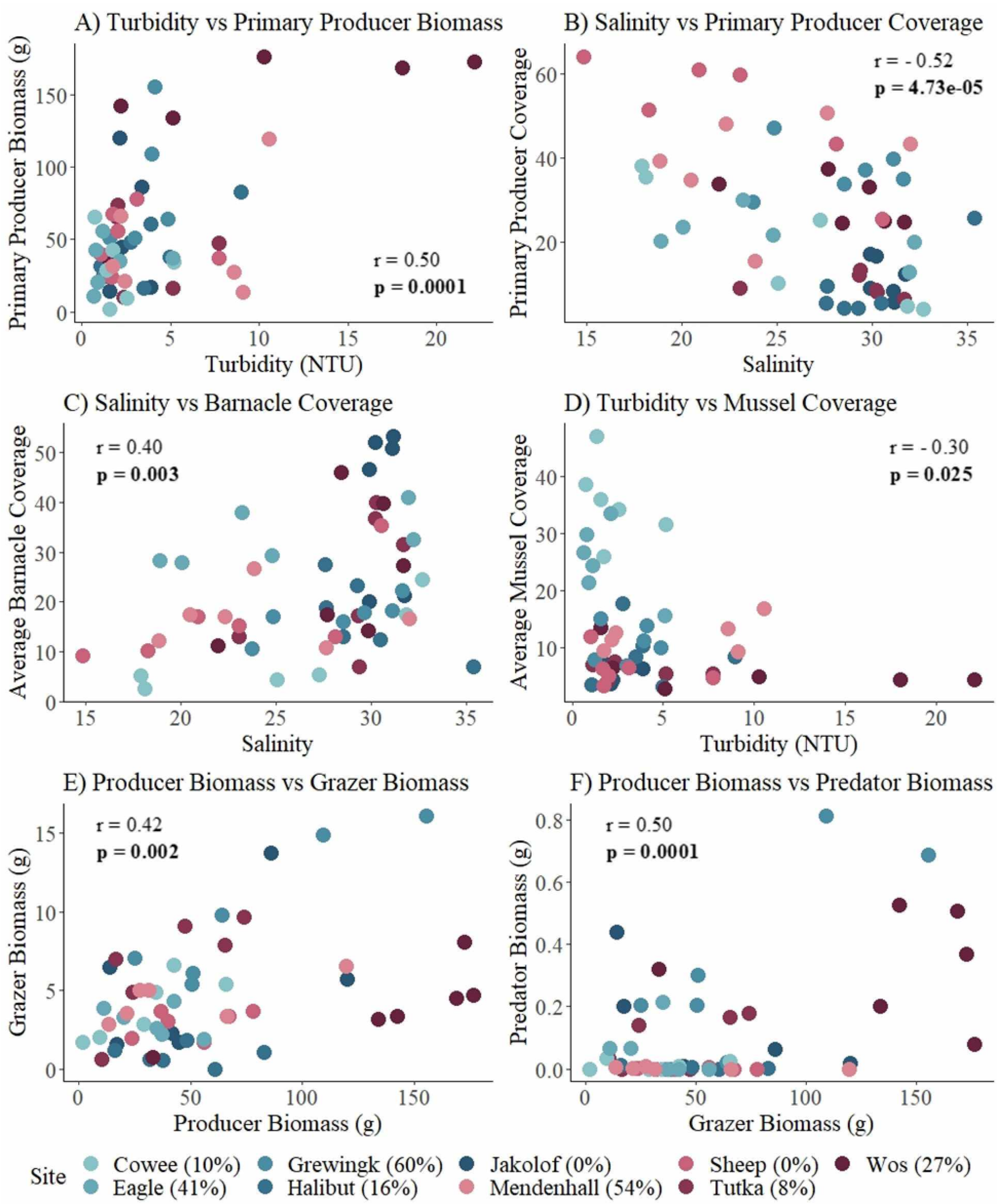

Figure 9. Significant Pearson correlations (r) examining the relationship between monthly environmental variables and ecological groups/species based on Table 2. Bold p-values represent a significant correlation at α = 0.05. The blue colors represent the region of Kachemak Bay and

red colors represent Lynn Canal. Each region’s color gradient represents increasing glacial coverage from light to dark tones.

Discussion

Glacial retreat and melt is a contemporary result of the warming associated with climate change in high-latitude ecosystems. The connective nature of glaciers, watersheds, rivers, and estuaries suggests that upstream changes have impacts on the downstream coastal environment and accompanying marine communities (Valentin et al. 2018, Cauvy-Fraunié & Dangles 2019, Pitman et al. 2020). These linkages were explored in this study by examining a variety of environmental factors that may affect estuaries and their biological communities. The interplay between glacial and non-glacial freshwater riverine discharge and oceanic waters was expected to create a spectrum of estuarine conditions that would also be reflected in the local intertidal communities across the glacial gradient. Some similar community patterns were found across regions when examining ecological groups; however, trends of decreasing filter feeder cover and increasing primary producer cover associated with increased glacial coverage were more apparent in KB than LC. Different filter feeders, barnacles in KB and mussels in LC, created these patterns between the two regions. Specifically, the environmental variables, turbidity and salinity, were correlated with the abundance of ecological groups (primary producers and filter feeders) across the glacial gradient. As glaciers continue to recede, these changes in the environment and resulting ecological community structure could have implications for diversity, food web relationships, and energy transfer.

Intertidal communities have traditionally been described as being regulated by local ecological forces, such as disturbance, competition, and predation (Dayton, 1971; Paine, 1981; Paine, 1984). Ecological subsidies in the form of nutrients and larval propagules also play a role in structuring marine communities (Menge et al. 2003, Palumbi 2003, Shanks & Morgan 2018), which can be often linked to a mosaic of environmental drivers (Kroeker et al. 2016). The delivery of these subsidies is influenced by the regional and local circulation patterns of open and closed coastal systems that differ greatly across latitudes, exposure regimes, and substrate type (Mann & Lazier 1996, Hacker et al. 2019). Our two study regions, which were approximately 1000 km apart, showed distinct salinity patterns most likely linked to local circulation and geography. While both regions, and their respective sites, are considered estuaries, geographically LC is part of a system of interconnected channels and passages located much farther away (approx. 100km) from the open ocean as compared to KB (Bruce et al. 1976). As a result, salinities in LC were generally lower than in KB. Of all the sites, the main biological outlier was the non-glacial discharge Sheep site, which is geographically trapped between two very large glacial watersheds and could be influenced by both watersheds across the tidal cycle. This may explain Sheep's enhanced turbidity and nutrient loads, as well as low salinity, thus resulting in higher than predicted primary producer coverage. In general, sites followed similar temperature and dissolved oxygen trends across time and between regions, which most likely contributed to similar environmental PCAs. These dynamic environmental patterns across the sampling seasons and among different glacial discharge levels were similar among regions, supporting the hypothesis that comparable estuarine processes are driving similar trends in ecological groups across the glacial gradient in both regions. Ultimately, it was the environmental variables turbidity and salinity that were most correlated with ecological group cover and biomass. Primary producers were dominant at less saline, more turbid sites, whereas filter feeders dominated the more saline, less turbid sites. These results support previous studies that have also come to similar conclusions regarding the main drivers (i.e., salinity, turbidity) of rocky estuarine intertidal communities, as well as changes in ecological group cover/biomass across the estuarine salinity gradient (Guerra-García et al. 2006, Giménez et al. 2010, Gomes-Filho et al. 2010).

Primary producers (macroalgae in this case) were the most abundant and spatially dominant at high discharge, highly turbid sites with increased nutrient loads across both regions. Notably, there was a positive univariate relationship between turbidity and primary producer biomass, and a negative relationship between salinity and producer cover. However, there were no univariate relationships between producer biomass/coverage and the various nutrients examined. Glacier-fed rivers have high sediment loads leading to enhanced turbidity in the water column, which includes suspended sediments that are formed as the glacier grinds against rock (Pitman et al. 2020). Glacially influenced meltwater carries important nutrients to coastal ecosystems, where intertidal producers, unlike their subtidal counterparts, can use these nutrients without limitations in light availability, as the hypothesis suggested (Ørberg et al., 2018; Traiger & Konar, 2018). Previous studies have also shown related fucoid species to be more abundant in heavily sedimented and turbid intertidal sites as compared to their seemingly more sensitive kelp relatives (Schiel et al. 2006). Although sediment can prevent fucoid zygote attachment (Schiel et al. 2006), intertidal recruitment success could be increased by releasing zygotes at a time when there is less sediment in the water (e.g., earlier or later in our sampling period).

In general, an increased flux of nutrients was present at high glacial discharge sites and the Sheep site in LC with no glacial cover, characterizing this site as an outlier. These nutrients have the potential to be beneficial to primary producers over time; however, there was no temporal trend or correlation between nutrient load and producer cover/biomass. The lack of correlation could be due to the morphological complexity of *Fucus* and *Odonthalia* as compared to smaller, fast-growing algae (i.e., phytoplankton) that are often stimulated rapidly by increased nutrient availability (Sand-Jensen & Borum 1991, Pedersen & Borum 1996). Instead, these larger, long-living algae typically have lower nutrient requirements (per unit biomass) due to their slower growth rates and could decrease nutrient demand by allocating nutrients to specific tissue type and/or building up internal stores when nutrients are in excess (Nielsen & Sand-Jensen 1990, Duarte 1992). Although this investigation and previous studies showed no direct effect of nutrient enrichment on macroalgal abundance, growth, or coverage (Sfriso et al. 1987, Sand-Jensen & Borum 1991, Pedersen & Borum 1996), the consistently larger nutrient flux associated with high discharge and turbid glacial sites could lend a competitive advantage to intertidal macrophytes that are not light limited. These nutrients, the building-blocks for primary producer growth and production, may become less available over time, as glaciers become smaller shifting environmental conditions, giving filter feeders an advantage in the competition for space in the long term.

Benthic filter feeders were more spatially dominant at low discharge sites, supporting the hypothesis that more saline and less turbid conditions were more favorable for filter feeders at these low glacial discharge sites. The underlying mechanisms driving these patterns could be less sediment in the water column creating more favorable light conditions for plankton production in the water, which is a main food source for these filter feeders (Gili & Coma 1998). High turbid conditions have negatively impacted other species of barnacles and mussels across multiple systems (Loosanoff 1962, Anderson et al. 2004, Gomes-Filho et al. 2010). Another study comparing turbid and non-turbid systems found increased chl-a, phytoplankton, and zooplankton in the less turbid site (Raghunathan et al. 2003), thus potentially linking favorable conditions in the nearshore water column to intertidal community assemblages.

Similar to macrophytes, contrasting patterns in filter feeders were found when comparing trends in subtidal and intertidal communities. Previous studies have shown subtidal filter feeders, specifically barnacles, to be more dominant than macrophytes in sites with heavier sedimentation (Ørberg et al. 2018, Traiger & Konar 2018), while other research has demonstrated a smothering effect that limits invertebrate success (Irving & Connell 2002). However, in the intertidal system, where feeding is limited by the tidal cycle, turbidity and increased sedimentation could have a negative impact on filter feeders by clogging or impeding feeding mechanisms (Jones et al. 2012). Filter feeders can close themselves to prevent sedimentation from impeding physiological processes (i.e., the circulation of water for oxygen and food), thus ultimately reducing feeding time (Anderson et al. 2004). Clear water conditions can increase filtering rates and/or feeding efficiency, by allowing organisms to quickly pass water through the feeding channels and filtering out desired particles (Jones et al. 2012). Thus, filtering and feeding efficiency is especially important for intertidal filter feeder growth and success. Here, filter feeders were generally most abundant in less turbid, no to low glacial discharge sites.

Patterns in marine community structure are often controlled by recruitment via larval dispersal (Keough & Downes 1982, Menge 1991, Hughes et al. 2000). In this study, mussel recruitment was greatest at the high glacial discharge sites. Similar recruitment patterns were observed for barnacles in LC, but not KB (Fig. 6B). In previous studies of boreal systems, barnacles and mussels displayed intense, relatively synchronized annual settlement (Raimondi 1990, Petraitis

1991, Cáceres-Martínez et al. 1993). The estuarine recruitment rates (0-2 ind./d) calculated from our study are considerably smaller compared to similar species in Oregon and California open coast systems (0-50 no./d; Navarrete et al. 2008). Barnacle recruitment peaked in early summer (May) when discharge was still low, which matches previous observations in KB (Carroll 1996), whereas mussel recruitment patterns followed increasing discharge and turbidity trends. Differences in the timing of peak recruitment of barnacles and mussels could be due to variation in reproductive cycles and seasonal spawning cues. The difference in the magnitude of recruitment across sites could be linked to different conditions in the local water column across the glacial gradient. A highly turbid environment may prevent predation of these meroplankton due to limited visibility (Hamner 1995, Thetmeyer & Kils 1995, Kerr et al. 2014). In addition, these planktotrophic groups feed in the water column with less complex feeding structures than their adult counterparts (Jablonski & Lutz 1983). Thus, the increased sediment load in these locations might not impede food availability for the planktonic stage, as it could for the settled adult stage, as originally hypothesized. This study suggests that high discharge sites in both regions were not recruitment-limited, because adult cover was not correlated with recruitment rates. Instead, post-recruitment processes seem to be driving low filter feeder spatial coverage. This ‘uncoupling’ of adult coverage and recruit densities is often linked to competition and predation that can reduce growth and increase mortality (Connell 1985). Recruitment of primary producers may look different from filter feeders. The most common alga *Fucus* settles < 10m from the female due to the negative buoyancy of the zygote (Serrão et al. 1997). Thus, recruitment success of the main producer in this study could be more closely linked to local adult population than the dispersal filter feeder species.

Conclusion

Although the community structure based on species composition was different between the regions examined in this study, some similar patterns were present in each region across the glacial gradient when ecological groups were considered. In general, there was a decrease in primary producer and an increase in filter feeder cover (either mussels in LC or barnacles in KB) as glacial coverage decreased, except at Sheep (0%), which appeared more glacial in terms of its environmental conditions. If a "space-for-time" substitution was employed, it suggests that highly glacial watersheds will become more non-glacial downstream as warming trends continue (Blois et al. 2013). The results from this study predict a shift from a primary producer-dominated community to one dominated by filter feeders as glaciers recede. This transition could influence community functioning, as there could also be a possible concurrent decline of grazers and predators (Tejada-Martinez et al. 2016, Guerry & Menge 2017), which have previously demonstrated a positive relationship with primary producer biomass and most likely rely on the producer's shading to prevent desiccation during low tide (Harley et al. 2012, Watt & Scrosati 2013). Food webs may also shift as a result of receding glaciers, which may create a stronger coupling and transfer of energy between plankton and benthic filter feeders (Gili & Coma 1998). Thus, this study suggests that increased glacial melt from climate change has the potential to accelerate a transition of dominant spatial competitors in downstream estuarine communities, alter local environmental conditions, and impact future intertidal community structure.

Acknowledgements

I especially thank my advisor B. Konar and committee members K. Iken, A. Kelley for their feedback and support throughout this process. I also thank A. Beaudreau, E. Hood, and L. Munk for assistance and discussions that helped in the preparation of this manuscript. I am indebted to E. Hasan, T. Dorsaz, E. Williamson, B. Zhang, N. Lundstrom, M. Bargas, S. King, E. Whitney, J. Jenckes, A. Dowling, and J. Schloemer for assistance with sample collection and analyses in the laboratory. Lastly, I thank my family and friends for their unconditional love and support. Financial support for this project was provided by Alaska EPSCoR National Science Foundation award #OIA-1757348 and the State of Alaska.

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Appendix

Table S1. Results of a PERMANOVA comparing Gulf of Alaska community percent coverage (A) and biomass (B) structure based on species composition, region, site, month, then region, season, and glacial discharge. Significant *p*-values (α = 0.05) are in boldface. High values of *Pseudo-F* indicate the magnitude of variance explained by that factor.

A. Gulf of Alaska percent coverage community structure based on species composition

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Region	1	4518.1	4518.1	4.31	**0.026**
Month	5	770.7	154.2	2.26	0.015
Site (region)	7	7331.7	1047.4	15.37	**0.001**
Region x Month	5	186.9	37.2	0.54	0.822
Residual	35	2383.8	68.1		
Total	53	15212.0			

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Region	1	3678.0	3678.0	2.48	0.145
Season	2	602.5	301.3	2.90	0.036
Glacial Discharge (region)	4	6309.7	1577.4	19.46	0.001
Region x Season	2	252.9	126.5	1.21	0.325
Glacial Discharge (re) x Season	8	843.6	105.5	1.30	0.203
Residual	36	2917.3	81.0		
Total	53	15212.0			

B. Gulf of Alaska biomass community structure based on species composition

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Region	1	5021.1	5021.1	3.92	**0.029**
Month	5	1311.3	262.3	1.27	0.243
Site (region)	7	8951.9	1278.8	6.20	**0.001**
Region x Month	5	3391.0	678.2	3.29	0.001
Residual	35	7212.9	206.1		
Total	53	26066.0			

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Region	1	4070.1	4070.1	2.77	0.183
Season	2	687.28	343.6	1.49	0.195
Glacial Discharge (region)	4	6217.3	1554.3	5.98	0.001
Region x Season	2	2629.2	1314.6	5.74	0.007
Glacial Discharge (re) x Season	8	1816.6	227.1	0.87	0.663
Residual	36	9360.2	260.0		
Total	53	26066.0			

Table S2. Results of a PERMANOVA comparing Gulf of Alaska community percent coverage (A) and biomass (B) structure based on ecological groups (Table 2), region, site, month, then region, season, and glacial discharge. Significant *p*-values ($\alpha = 0.05$) are in boldface. High values of *Pseudo-F* indicate the magnitude of variance explained by that factor.

A. Gulf of Alaska percent coverage community structure based on ecological group

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Region	1	1440.6	1440.6	2.06	0.118
Month	5	627.6	125.5	2.07	0.047
Site (region)	7	4901.1	700.2	11.56	**0.001**
Region x Month	5	577.3	115.5	1.91	0.051
Residual	35	2120.2	60.6		
Total	53	9640.8			

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Region	1	1186.8	1186.8	1.38	0.250
Season	2	621.8	310.9	3.94	0.039
Glacial Discharge (region)	4	3661.7	915.4	11.01	0.001
Region x Season	2	583.0	291.5	3.69	0.018
Glacial Discharge (re) x Season	8	628.9	78.6	0.95	0.535
Residual	36	2992.8	83.1		
Total	53	9640.8			

B. Gulf of Alaska biomass community structure based on ecological group

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Region	1	862.9	862.9	1.22	0.354
Month	5	916.8	183.4	1.29	0.249
Site (region)	7	4962.6	708.9	5.01	**0.001**
Region x Month	5	2856.8	571.4	4.04	0.001
Residual	35	4948.5	141.4		
Total	53	14713.0			

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Region	1	780.9	780.9	1.09	0.264
Season	2	492.1	246.0	1.51	0.215
Glacial Discharge (region)	4	3018.3	754.6	4.16	0.001
Region x Season	2	2343.6	1171.8	7.19	0.002
Glacial Discharge (re) x Season	8	1292.7	161.6	0.89	0.614
Residual	36	6528.7	181.4		
Total	53	14713.0			

Table S3. Results of a PERMANOVA comparing Kachemak Bay community percent coverage (A) and biomass (B) structure based on ecological group (Table 2), site, and month, then glacial discharge and season. Significant *p*-values ($\alpha = 0.05$) are in boldface. High values of *Pseudo-F* indicate the magnitude of variance explained by that factor.

A. Kachemak Bay percent coverage community structure based on ecological groups

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Site	4	2978.9	744.7	11.68	**0.001**
Month	5	472.4	94.5	1.48	0.235
Residual	20	1274.9	63.7		
Total	29	4726.2			
Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Glacial Discharge	2	2437.0	1218.5	16.24	**0.001**
Season	2	613.5	306.8	4.85	0.051
Glacial Discharge x Season	4	249.7	62.4	0.83	0.584
Residual	21	1576.0	75.1		
Total	29	4726.2			

B. Kachemak Bay biomass community structure based on ecological groups

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Site	4	3843.4	960.8	6.11	**0.001**
Month	5	2715.9	543.2	3.45	**0.001**
Residual	20	3144.9	157.3		
Total	29	9704.2			
Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Glacial Discharge	2	2286.1	1143.0	4.94	**0.001**
Season	2	1924.6	962.3	6.45	**0.047**
Glacial Discharge x Season	4	574.6	143.7	0.62	0.823
Residual	21	4856.7	231.3		
Total	29	9704.2			

Table S4. Results of a PERMANOVA comparing Lynn Canal community percent coverage (A) and biomass (B) structure based on ecological group (Table 2), site, and month, then glacial discharge and season. Significant *p*-values ($\alpha = 0.05$) are in boldface. High values of *Pseudo-F* indicate the magnitude of variance explained by that factor.

A. Lynn Canal percent coverage community structure based on ecological groups

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Site	3	1922.2	640.7	11.37	**0.001**
Month	5	706.5	141.3	2.51	**0.041**
Residual	15	845.3	56.4		
Total	23	3474.0			
Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Glacial Discharge	2	1224.7	612.4	6.48	**0.002**
Season	2	593.5	296.7	3.13	0.114
Glacial Discharge x Season	4	379.2	94.8	1.00	0.460
Residual	15	1416.8	94.5		
Total	23	3474.0			

B. Lynn Canal biomass community structure based on ecological groups

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Site	3	1119.2	373.1	3.10	**0.006**
Month	5	1223.5	244.7	2.04	**0.04**
Residual	15	1803.6	120.2		
Total	23	4146.4			
Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Glacial Discharge	2	732.2	366.1	3.28	**0.02**
Season	2	1012.5	506.2	2.86	**0.049**
Glacial Discharge x Season	4	718.1	179.5	1.61	0.112
Residual	15	1671.9	111.5		
Total	23	4146.4			

Table S5. Average biomass (± 1 SD; including shell) and percent contribution (Contrib.) of discriminating (or individual) taxa for biomass community structure by site over the entire sampling season in each region using SIMPER analysis.

	Average biomass (g) ± 1 SD	Contrib. (%)	Cum. (%)
Kachemak Bay			
Jakolof (0%) Low			
Mytilus trossulus	46.3 ± 62.5	43.09	43.09
Fucus distichus	53.5 ± 67.8	39.70	82.79
Lottia spp.	3.3 ± 5.4	8.50	91.29
Tutka (8%) Mid			
Mytilus trossulus	90.1 ± 98.4	51.85	51.85
Fucus distichus	35.4 ± 82.3	29.71	81.57
Littorina spp.	4.9 ± 8.6	11.58	93.15
Halibut (16%) Mid			
Mytilus trossulus	85.9 ± 113.3	44.41	44.41
Fucus distichus	37.5 ± 103.0	32.25	76.76
Filamentous algal complex	10.4 ± 20.5	16.48	93.24
Wos (27%) High			
Fucus distichus	137.8 ± 202.1	45.80	45.80
Mytilus trossulus	94.8 ± 118.5	41.82	87.62
Littorina spp.	3.2 ± 5.7	6.04	93.66
Grewingk (60%) High			
Mytilus trossulus	95.8 ± 71.0	45.69	45.69
Fucus distichus	68.3 ± 114.7	33.61	79.30
Littorina spp.	6.0 ± 6.0	10.68	89.98
Lynn Canal			
Sheep (0%) Low			
Mytilus trossulus	68.1 ± 77.6	43.02	43.02
Fucus distichus	50.4 ± 66.7	37.06	80.08
Littorina spp.	2.3 ± 1.7	8.31	88.39
Cowee (10%) Mid			
Mytilus trossulus	111.3 ± 83.2	59.91	59.91
Odonthalia floccosa	11.0 ± 25.8	12.85	72.76
Fucus distichus	19.5 ± 77.0	11.64	84.40
Eagle (41%) High			
Mytilus trossulus	153.3 ± 150.2	53.65	53.65
Fucus distichus	15.5 ± 32.9	17.88	71.54
Odonthalia floccosa	18.2 ± 31.7	13.27	84.81
Mendenhall (54%) High			
Mytilus trossulus	83.9 ± 40.4	46.92	46.92
Odonthalia floccosa	19.2 ± 29.9	19.41	66.33
Fucus distichus	27.5 ± 55.1	15.16	81.49

Table S6. Average biomass (± 1 SD; including shell) and percent contribution (Contrib.) of discriminating (or individual) taxa for biomass community structure by glacial discharge level over the entire sampling season in each region using SIMPER analysis.

	Average biomass (g) ± 1SD	Contrib. (%)	Cum. (%)
Kachemak Bay			
Low Glacial Discharge			
Mytilus trossulus	51.1 ± 65.8	43.09	43.09
Fucus distichus	53.9 ± 71.8	39.70	82.79
Lottia spp.	3.4 ± 5.7	8.50	91.29
Littorina spp.	1.6 ± 3.9	5.85	97.13
Mid Glacial Discharge			
Mytilus trossulus	91.7 ± 111.6	51.41	51.41
Fucus distichus	40.6 ± 99.5	33.70	85.11
Filamentous algal complex	6.3 ± 16.4	4.82	89.93
Lottia spp.	0.8 ± 1.0	3.69	93.62
High Glacial Discharge			
Mytilus trossulus	99.5 ± 98.0	44.69	44.69
Fucus distichus	106.9 ± 169.1	39.39	84.08
Littorina spp.	4.8 ± 6.2	8.24	92.32
Lottia spp.	2.1 ± 3.3	4.91	97.23
Lynn Canal			
Low Glacial Discharge			
Mytilus trossulus	68.1 ± 77.6	43.02	43.02
Fucus distichus	50.4 ± 66.7	37.06	80.08
Littorina spp.	2.3 ± 1.7	8.31	88.39
Lottia spp.	0.7 ± 0.9	3.94	92.33
Mid Glacial Discharge			
Mytilus trossulus	111.3 ± 83.2	59.91	59.91
Odonthalia floccosa	11.0 ± 25.8	12.85	72.76
Fucus distichus	19.5 ± 77.0	11.64	84.40
Littorina spp.	3.0 ± 3.0	7.90	92.30
High Glacial Discharge			
Mytilus trossulus	118.6 ± 114.9	49.94	49.94
Fucus distichus	21.5 ± 45.6	16.97	66.92
Odonthalia floccosa	18.7 ± 30.7	16.85	83.77
Littorina spp.	2.4 ± 2.9	6.31	90.08

Table S7. Average percent coverage (± 1 SD) and percent contribution (Contrib.) of discriminating (or individual) taxa for percent coverage community structure by site over the entire sampling season in each region using SIMPER analysis.

	Average percent % ± 1 SD	Contrib. (%)	Cum. (%)
Kachemak Bay			
Jakolof (0%) Low			
Bare Rock	39.3 ± 18.6	34.58	34.58
Barnacles	43.1 ± 18.2	33.85	68.43
Fucus distichus	13.7 ± 11.4	18.02	86.45
Tutka (8%) Mid			
Bare Rock	59.6 ± 16.4	44.75	44.75
Barnacles	23.6 ± 13.6	23.67	68.42
Fucus distichus	10.1 ± 10.8	17.76	86.18
Halibut (16%) Mid			
Bare Rock	53.7 ± 21.5	45.90	45.90
Barnacles	18.5 ± 19.1	23.46	69.35
Mytilus trossulus	8.5 ± 8.4	15.42	84.77
Fucus distichus	9.2 ± 12.8	15.23	100.00
Wos (27%) High			
Bare Rock	37.9 ± 21.8	33.26	33.26
Fucus distichus	29.9 ± 28.4	30.58	63.84
Barnacles	26.1 ± 20.5	24.25	88.09
Grewingk (60%) High			
Fucus distichus	34.4 ± 34.4	32.01	32.01
Bare Rock	37.5 ± 24.4	30.50	62.51
Barnacles	17.6 ± 15.5	21.18	83.68
Lynn Canal			
Sheep (0%) Low			
Fucus distichus	50.9 ± 30.4	40.11	40.11
Bare Rock	20.6 ± 20.5	25.58	65.69
Barnacles	16.7 ± 14.6	20.94	86.63
Cowee (10%) Mid			
Mytilus trossulus	35.6 ± 25.2	33.13	33.13
Bare Rock	31.3 ± 20.3	29.97	63.10
Odonthalia floccosa	14.2 ± 25.7	13.46	76.56
Barnacles	9.9 ± 13.9	12.64	89.21
Eagle (41%) High			
Barnacles	32.9 ± 15.4	27.46	27.46
Mytilus trossulus	25.3 ± 14.1	23.19	50.65
Bare Rock	16.1 ± 9.1	19.78	70.44
Fucus distichus	13.4 ± 14.6	16.87	87.30
Mendenhall (54%) High			
Bare Rock	28.7 ± 14.2	25.59	25.59
Odonthalia floccosa	26.5 ± 22.8	23.98	49.58
Barnacles	16.8 ± 15.0	19.51	86.25

Table S8. Average percent coverage (± 1 SD) and percent contribution (Contrib.) of discriminating (or individual) taxa for percent coverage community structure by glacial discharge level over the entire sampling season in each region using SIMPER analysis.

	Average % cover ± 1 SD	Contrib. (%)	Cum. (%)
Kachemak Bay			
Low Glacial Discharge			
Bare Rock	41.4 ± 18.9	34.58	34.58
Barnacles	40.7 ± 18.3	33.85	68.43
Fucus distichus	11.7 ± 14.3	18.02	86.45
Mytilus trossulus	5.9 ± 4.7	13.55	100.00
Mid Glacial Discharge			
Bare Rock	56.8 ± 20.2	45.56	45.56
Barnacles	20.7 ± 17.6	23.67	69.22
Fucus distichus	9.5 ± 12.1	16.33	85.55
Mytilus trossulus	7.2 ± 7.2	14.45	100.00
High Glacial Discharge			
Bare Rock	36.4 ± 23.4	32.33	32.33
Fucus distichus	33.5 ± 32.5	31.36	63.58
Barnacles	21.5 ± 18.9	22.65	86.23
Mytilus trossulus	8.5 ± 9.2	13.77	100.00
Lynn Canal			
Low Glacial Discharge			
Fucus distichus	50.9 ± 30.4	40.11	40.11
Bare Rock	20.6 ± 20.5	25.58	65.69
Barnacles	16.7 ± 14.6	20.94	86.63
Mytilus trossulus	6.4 ± 6.2	13.37	100.00
Mid Glacial Discharge			
Mytilus trossulus	35.6 ± 25.2	33.13	33.13
Bare Rock	31.3 ± 20.3	29.97	63.10
Odonthalia floccosa	14.2 ± 25.7	13.46	76.56
Barnacles	9.9 ± 13.9	12.64	89.21
Fucus distichus	5.5 ± 16.0	10.79	100.00
High Glacial Discharge			
Barnacles	24.8 ± 17.2	23.52	23.52
Bare Rock	22.4 ± 13.5	22.90	46.42
Mytilus trossulus	18.7 ± 12.8	20.15	66.57
Odonthalia floccosa	17.3 ± 20.0	17.16	83.73
Fucus distichus	12.8 ± 14.9	16.27	100.00

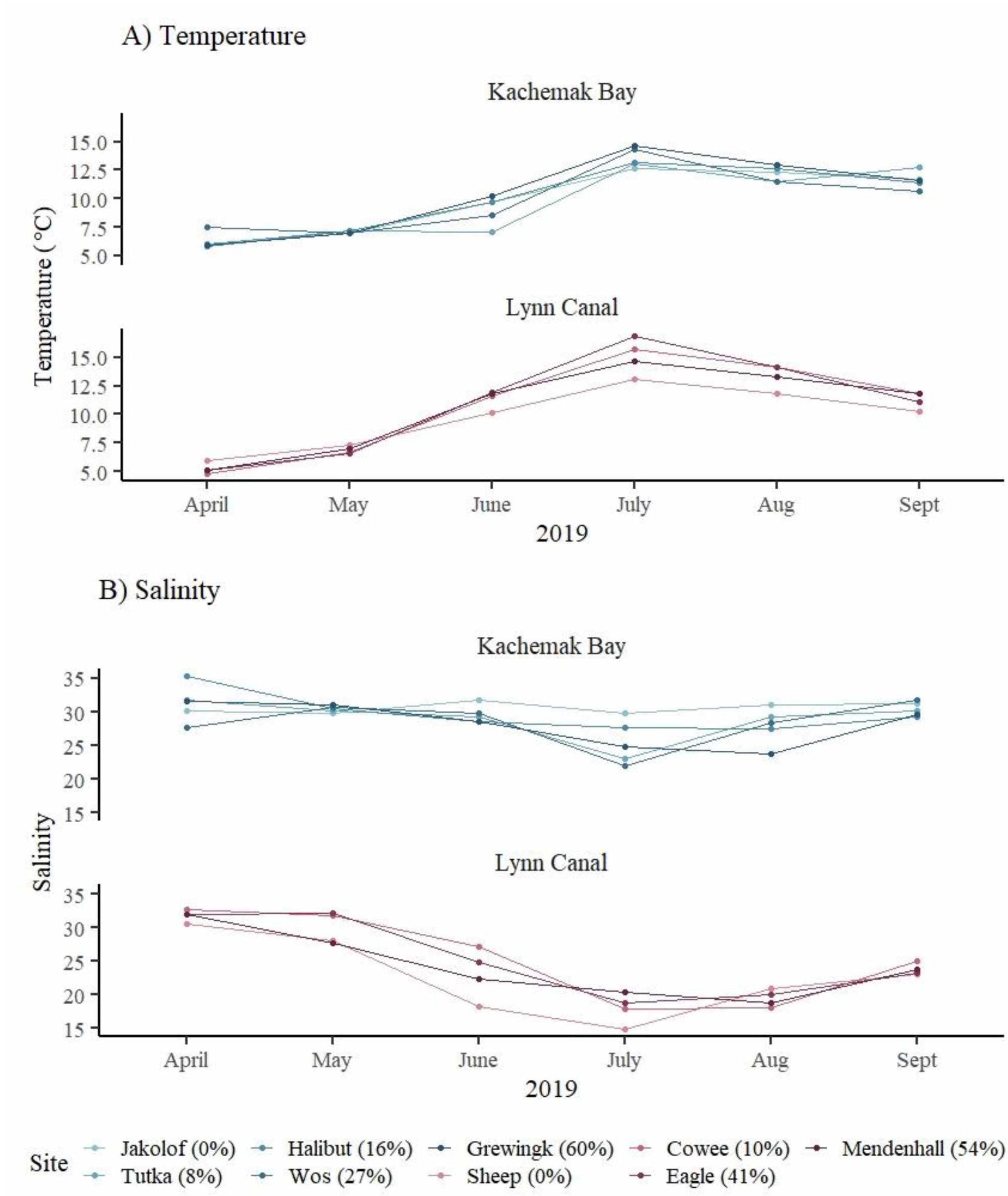
Table S9. Results of a two-way PERMANOVA comparing dynamic environmental variables among glacial discharge levels and (bi-monthly) seasonal time periods. Significant *p*-values (α = 0.05) are in boldface. High values of *Pseudo-F* indicate the magnitude of variance explained by that factor.

A. Kachemak Bay environmental dynamic variables

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Glacial Discharge	2	202.9	101.5	11.74	**0.001**
Season	2	35.9	17.9	3.25	**0.034**
Glacial Discharge x Season	4	21.2	5.3	0.61	0.834
Residual	21	181.5	8.6		
Total	29	449.7			

B. Lynn Canal environmental dynamic variables

Source	*df*	SS	MS	*Pseudo-F*	*p*-value
Glacial Discharge	2	132.2	66.1	12.92	**0.001**
Season	2	57.1	28.6	9.94	**0.018**
Glacial Discharge x Season	4	11.1	2.8	0.54	0.924
Residual	15	76.8	5.1		
Total	23	283.9			


A) Temperature
Kachemak Bay
Lynn Canal
Temperature (°C)
15.0
12.5
10.0
7.5
5.0
April
May
June
July
Aug
Sept
2019
B) Salinity
Kachemak Bay
Lynn Canal
Salinity
35
30
25
20
15
April
May
June
July
Aug
Sept
2019
Site
Jakolof (0%)
Tutka (8%)
Halibut (16%)
Wos (27%)
Grewingk (60%)
Sheep (0%)
Cowee (10%)
Eagle (41%)
Mendenhall (54%)

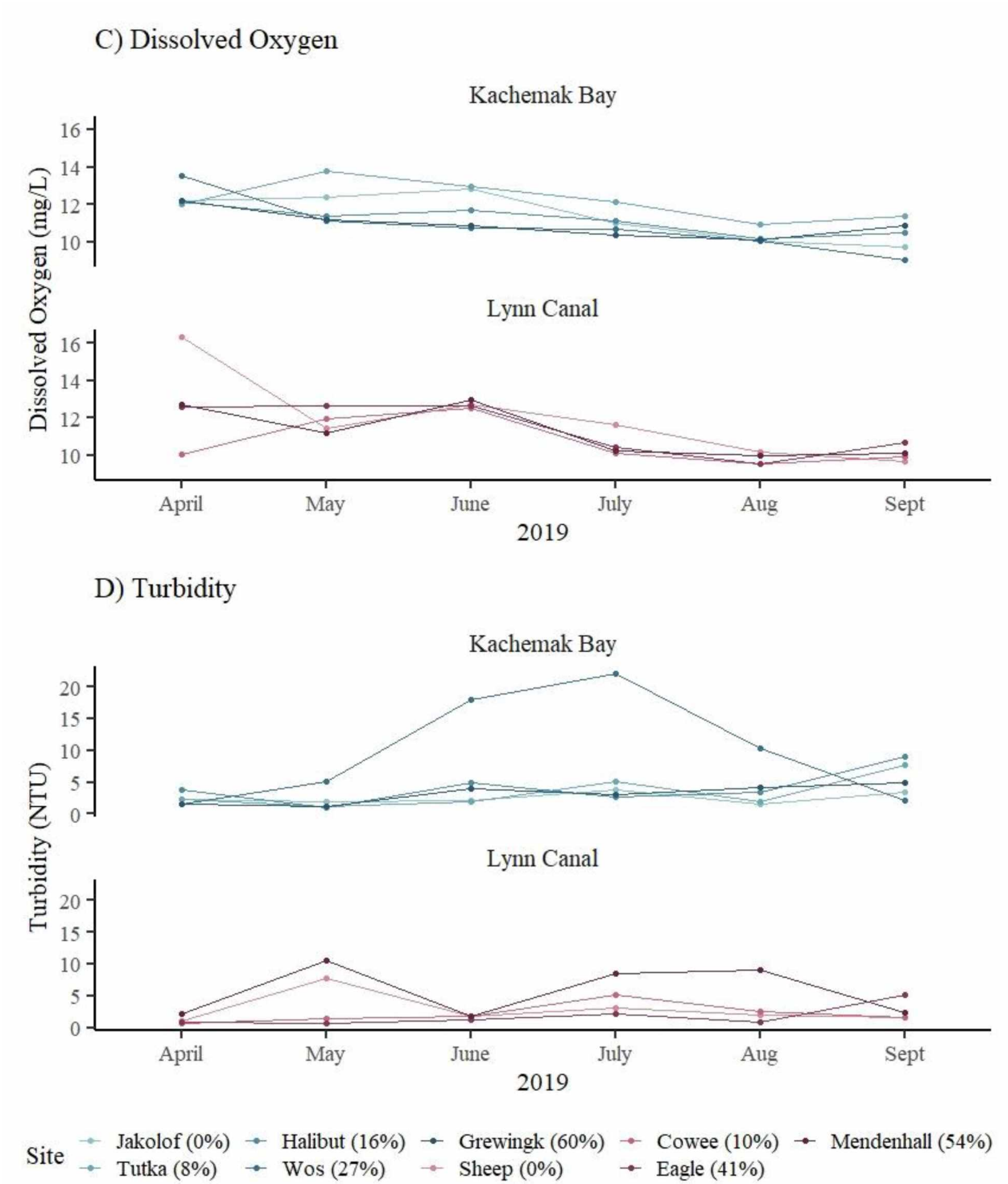


Fig. 1S. Spatiotemporal variability of dynamic environmental variables (water temperature (A), salinity (B), dissolved oxygen (C), and turbidity (D)) among sites and regions from April – September 2019. The blue colors represent the region of Kachemak Bay and red colors represent Lynn Canal. Each region's color gradient represents increasing glacial coverage from light to dark color tones.

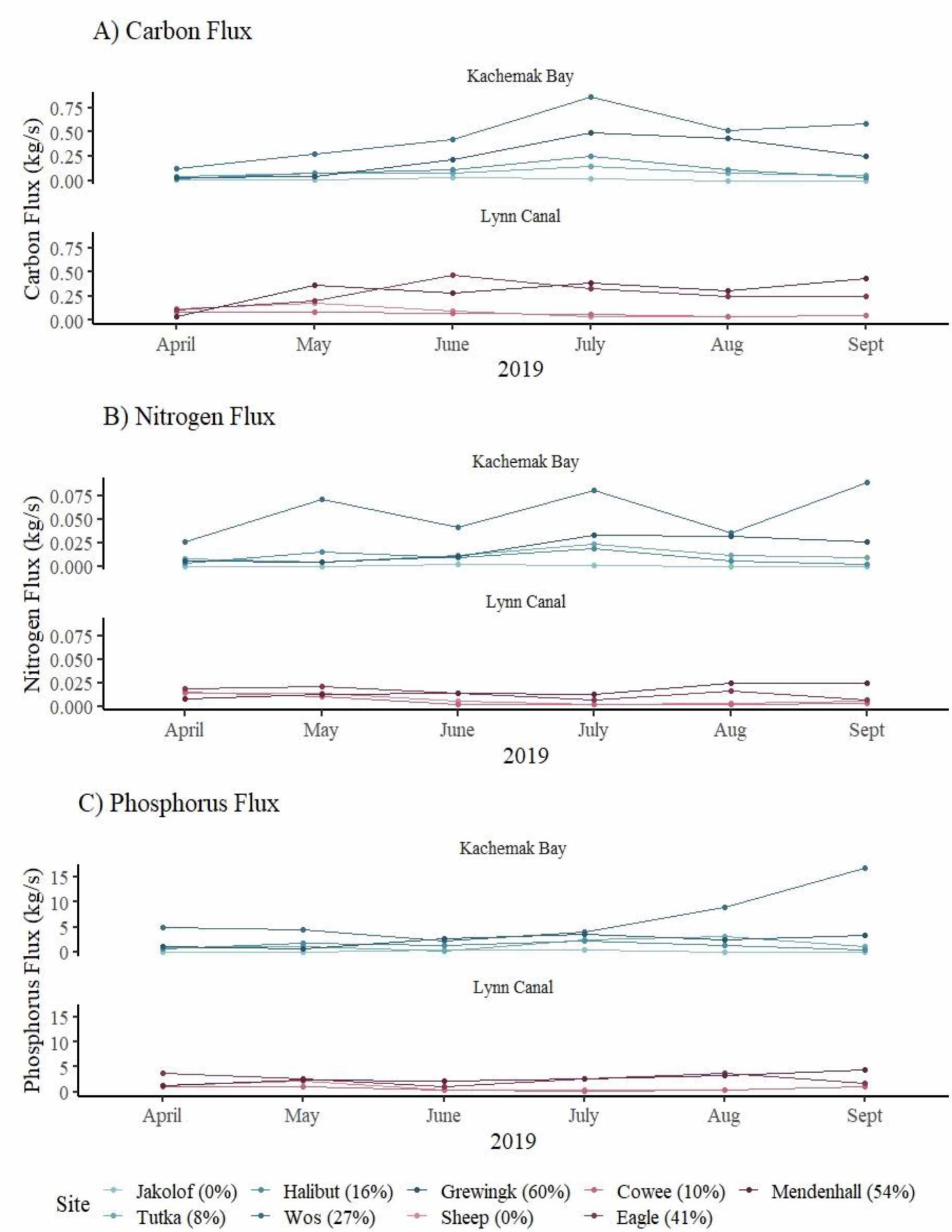


Fig. 2S. Spatiotemporal variability of nutrient fluxes (Carbon (A), Nitrogen (B), and Phosphorus (C)) among sites and regions. The blue colors represent the region of Kachemak Bay and red colors represent Lynn Canal. Each region's color gradient represents increasing glacial coverage from light to dark color tones.