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Monograph

Environmental and biotic habitat attributes affect rocky intertidal community variability in glacially influenced estuaries

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ABSTRACT

Climate change is increasing the rate of glacial recession in high latitude coastal environments. The associated increase in cold, sediment-laden freshwater into the nearshore may alter a wide array of water attributes, which will likely have ecosystem-wide impacts. One of these potential impacts is a change in typical patterns of ecological community variability, which can be an indicator of stress in response to an environmental impact. Fluctuation in community composition over multiple temporal scales is natural and can be affected by environmental conditions, as well as by the presence of habitat forming, spatially dominant organisms. The goal of this study was to determine how variation in environmental attributes and spatially dominant species contributes to the seasonal variability of rocky intertidal community assemblages in glacially influenced estuaries. The environmental attributes of interest were both dynamic in nature (water temperature, salinity, dissolved oxygen, turbidity, and $pCO_{2)}$, and static (substrate type, wave exposure, beach slope, and distance to freshwater). Variation in the proportions of three spatially dominant organisms that are common in many intertidal systems, *Mytilus trossulus* (mussels), *Balanus* spp. (barnacles), and *Fucus* spp. (rockweed) were examined as biotic habitat attributes. It was hypothesized that 1) dynamic environmental attributes would be more strongly correlated to community variability patterns than static attributes, and 2) higher proportions of spatially dominant species would correspond to lower levels of community variability. To document seasonal community variability, as well as proportions of spatially dominant species, percent cover and biomass data were collected along with environmental data from 2019 to 2022. Barnacle cover, rockweed cover, and substrate characteristics (cover of gravel and total cover of bare rock) were significantly correlated to community variability levels based on percent cover data. Community variability levels based on biomass data were significantly correlated to mussel cover, rockweed biomass, substrate aspects (cover of gravel and mud), distance to a freshwater source, and variation in dissolved oxygen levels. Almost all relationships between community variability and each of these attributes were negative, where a greater level of an environmental attribute was associated with lower seasonal variability in community composition. Distance to freshwater and dissolved oxygen variation had a positive relationship to community variability, meaning that greater distance to a freshwater source and variation in dissolved oxygen were associated with higher seasonal community variability. As several of these variability drivers may be affected by climate-related changes, the results of this study provide insights into how glacially influenced rocky intertidal communities may in turn be affected by the progression of climate change.

1. Introduction

Variability is a natural aspect of ecological communities, as species composition can change seasonally and interannually due to natural cycles and a multitude of natural or anthropogenic influences (Micheli et al., 1999). Community variability has acquired multiple definitions in ecological literature, but here it will specifically refer to spatial variation in community composition over time (Micheli et al., 1999; Rolls et al., 2023). Influences on community variability can be biotic, living aspects of the community, or related to broader environmental conditions. A biotic attribute known to affect variability in ecological communities is the abundance of spatially dominant species. In rocky intertidal systems, spatially dominant organisms often include sessile invertebrates, like mussels and barnacles, and macroalgae, such as rockweed (Harley,

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2006). Due to their typically large biomasses, they act as ecosystem engineers that structure their associated community through physical and biological mechanisms (Jones et al., 1997). The settlement of these species on bare substrates increases habitat complexity, creating interstitial spaces between individuals, where other species can seek shelter from both hydrodynamic forces and desiccation stress (Seed and Suchanek, 1992; Bertness et al., 1999; Castilla et al., 2004). Filter-feeding activities by mussels and barnacles may also impact the structure of their associated community by ingesting planktonic larvae, exerting top-down control on recruits to the area (Young and Gotelli, 1988; Peharda et al., 2012). In addition, byssal threads, secreted by mussels and used for substrate attachment, bind sediments to reduce erosion in these habitats (Bertness, 1984). Overall, the presence of spatially dominant ecosystem engineers in marine ecosystems tends to increase primary productivity (Bertness, 1985), the abundance of other associated species (Crooks, 2002), and species richness (Castilla et al., 2004). These organisms can also act as a protective presence by gradually exerting a stabilizing force on community structure and functioning (Connell and Slatyer, 1977; Paine and Levin, 1981; Sousa, 1984). Importantly, however, spatially dominant species are also capable of decreasing community diversity and reducing variability in community composition over time, if environmental conditions allow them to form monocultures (Piazzi and Balata, 2008; Rolls et al., 2023). For example, the spread of an invasive macroalga in the Mediterranean Sea caused benthic habitat homogenization, ultimately leading to decreased community diversity and variability (Piazzi and Balata, 2008). This means that impacts from changing environmental conditions on spatially dominant species may result in shifts in variability patterns of their associated community (Miner et al., 2021).

Environmental influences on community variability can be static in nature, unchanging over relatively long periods of time, or dynamic, fluctuating substantially over multiple time scales. Static attributes like substrate type (Sousa, 1979; Gedan et al., 2011), wave exposure (Ricciardi and Bourget, 1999; Harley and Helmuth, 2003; Carrington, 2002; Burrows et al., 2009), beach slope (Ricciardi and Bourget, 1999), and distance to freshwater (Gili and Coma, 1998; Held and Harley, 2009; Gomes-Filho et al., 2010; Law et al., 2013) mediate the effect of broader environmental conditions and impact organism survival. As a result, these attributes have the potential to impact community variability (Rolls et al., 2023). Temporal changes in dynamic environmental attributes are also known to affect community variability. These can be natural or human-caused changes and include disturbance events (Rolls et al., 2023). The effect of a dynamic attribute on community variability depends on the frequency, extent, and intensity of the change and whether it plays a role in homogenizing a community (Richardson et al., 2018) or “resets” a community dominated by a single assemblage type (Rolls et al., 2023). For example, long-term studies at the decadal scale in various systems have linked increasing temperatures to community homogenization and declines in community variability (Gatti et al., 2015; Araujo et al., 2016; Bianchi et al., 2019). In one subtidal rocky reef community in the Mediterranean Sea, an abrupt increase in the surrounding sea’s thermal regime over the 1980s – 90s was followed by community homogenization in the 1990s that persisted for nearly two decades (Bianchi et al., 2019).

Importantly, an understanding of community variability can provide information about community-level responses to stressors. For example, it has been suggested that one sign of an ecosystem approaching an alternative stable state is increasing variability in community structure (Dakos et al., 2012; Carpenter and Brock, 2006; Cline et al., 2014). In essence, if a system is experiencing diminishing resilience due to prolonged stress, it is slower to recover from disturbance events until it reaches a point where it can no longer recover by returning to its original state, instead entering an alternative stable state. The system’s diminishing resilience manifests as increasing variability (Dakos et al., 2012; Menge et al., 2022). Increased community variability could signal an impending shift to an alternative stable state one to ten years in advance (Carpenter and Brock, 2006; Cline et al., 2014). In rocky intertidal communities along the Oregon coast, higher community variability has been associated with ocean warming events and changes in upwelling currents (Menge et al., 2022). The responsiveness of community variability to environmental conditions also highlights its value as a resource management tool (Rolls et al., 2023). Understanding the drivers of community variability can inform predictions of future ecosystem changes and aid resource managers in determining appropriate conservation areas. For example, management efforts can focus on extra protection for systems that appear to be in a state of diminished resilience or those that harbor naturally high community variability and diversity (Socolar et al., 2016; Rolls et al., 2023).

In the face of climate change, the study of community variability is valuable for assessing community-level responses and can be applied to any ecosystem. High latitude coastal ecosystems are of particular interest, as climate change is exacerbating the effects of seasonal glacial melting in them. This has the potential to alter estuarine dynamics to an extent to which ecological communities are not adapted (Hood and Berner, 2009; O’Neel et al., 2015; Arimitsu et al., 2016; Kroeker et al., 2016, 2019). As such, ecosystems subjected to these changes, including those in the rocky intertidal, are ideal candidates for research that examines drivers of their community variability. Runoff from melting glaciers injects large volumes of cold, fresh, and highly-sedimented water into the nearshore, but this natural process is becoming more extreme as a warming climate causes glaciers to thin and recede at rapid rates (Larsen et al., 2015). Increased glacial melt is expected to alter a host of dynamic environmental attributes in the nearshore, including water temperature, salinity, dissolved oxygen, turbidity, and carbonate chemistry (Hood and Berner, 2009; O’Neel et al., 2015; Arimitsu et al., 2016), with water becoming colder, less saline, more turbid, and having a higher solubility for atmospheric gases that can change dissolved oxygen levels and alter the carbonate system. Changes in these dynamic attributes can significantly influence the food quality, growth, reproduction, recruitment success, and spatial distribution of organisms (Clarke, 1987; Sokolova et al., 2012; Deutch et al., 2015). Further, glacial recession may result in some of these environmental attributes becoming more or less favorable for certain species. One study found that in high latitude regions, filter-feeding organisms like mussels and barnacles appear to be more dominant when living in rocky intertidal habitats that experience more oceanic and less glacial influence. In contrast, primary producers, such as rockweed, seem more dominant in areas with stronger glacial influence. Salinity and turbidity levels were the main driver of this pattern, with lower salinity and higher turbidity being associated with greater glacial coverage and higher primary producer abundance, and the opposite being associated with higher filter feeder abundance (McCabe and Konar, 2021). Nearshore carbonate chemistry can also be impacted by melting glaciers. Injections of cold, low-alkalinity freshwater increases nearshore water’s solubility for atmospheric gases like CO_2. This increase in solubility thereby causes the water’s partial pressure of CO_2 (pCO_2) to increase, and its pH to lower along with decreasing the calcium carbonate saturation states of calcite and aragonite ($\Omega_{calcite}$ and $\Omega_{aragonite}$) (Feely et al., 2004). For mussels and other calcium carbonate shell-bearing species, these conditions decrease calcification ability (Doney et al., 2009; Ries et al., 2009) and corrode internal shells (Bamber, 1990; Michaelidis et al., 2005; Berge et al., 2006). In glacially influenced estuarine environments, it is difficult to predict exactly how alterations in environmental attributes spurred by climate change (e.g., salinity, turbidity, and carbonate chemistry) will impact certain species, their interactions with each other, and the variability of their associated communities.

This study investigated whether variation in environmental attributes and proportion of spatially dominant species corresponds to the seasonal variability of rocky intertidal community assemblages over four years in glacially influenced regions. This study had two objectives: 1) determine the relationship between intertidal community variability and a set of dynamic (water temperature, salinity, dissolved oxygen, turbidity, and pCO_2) and static (percent glaciation, substrate type, beach slope, fetch, and distance to freshwater) environmental attributes. It was hypothesized that dynamic environmental attributes would have a greater contribution to intertidal community variability than differences in static environmental attributes; and 2) determine the relationship between intertidal community variability and abundance (measured as percent cover and biomass) of spatially dominant organisms (*Mytilus trossulus*, *Balanus* spp., *Fucus* spp.). It was hypothesized that higher levels of any of these three spatially dominant organisms would correspond to lower levels of community variability. It is essential to understand the effect and potential interplay of glacially influenced environmental attributes and spatially dominant species on intertidal community variability to predict how this ecosystem may be affected by the process of climate change-driven glacial recession.

2. Methods

2.1. Study sites

This study was conducted in two regions within the model system in the Gulf of Alaska, Kachemak Bay (5 sites) in Southcentral Alaska, and Lynn Canal (4 sites) in Southeast Alaska (Fig. 1, Supplementary Table 1). The sites within these study regions are in watersheds with glacial coverage that spans 0–60%, causing them to have differing amounts of glacial meltwater input that can determine how variability in biological communities or environmental conditions may be affected by glacial influence.

2.2. Environmental data

The dynamic environmental attributes of water temperature, salinity, dissolved oxygen, and turbidity were recorded at each site from April to September, 2019 through 2022. A HOBO Salt Water Conductivity/Salinity logger recorded temperature and salinity measurements, while a PME miniDOT logger recorded dissolved oxygen. All measurements were taken at 15-min intervals. Sensors were deployed in the intertidal zone at the −2–2.5-ft tide level and were occasionally exposed to air during low tides. Sensor arrays also included a ReefNet Sensus Ultra depth logger that recorded when the sensors were out of the water. After the field season, sensors were recovered, and raw data were processed using manufacturer software to compute derived values, which were exported into csv files. To prepare these csv files for quality control, start and end times were trimmed based on deployment times, quality codes were assigned, and individual site and month files were joined together to create comprehensive files for each sensor and year. Sensor data were also trimmed based on depth data from the ReefNet Sensus Ultra depth loggers. Data were plotted to identify anomalies for quality control, and previous steps were repeated as needed. Turbidity data were determined by processing 60 mL surface water samples taken once a month from each site and analyzed on a Hach 2100P TurbidMeter to determine Nephelometric Turbidity Units (NTU).

In 2022, carbonate chemistry data were also obtained at the

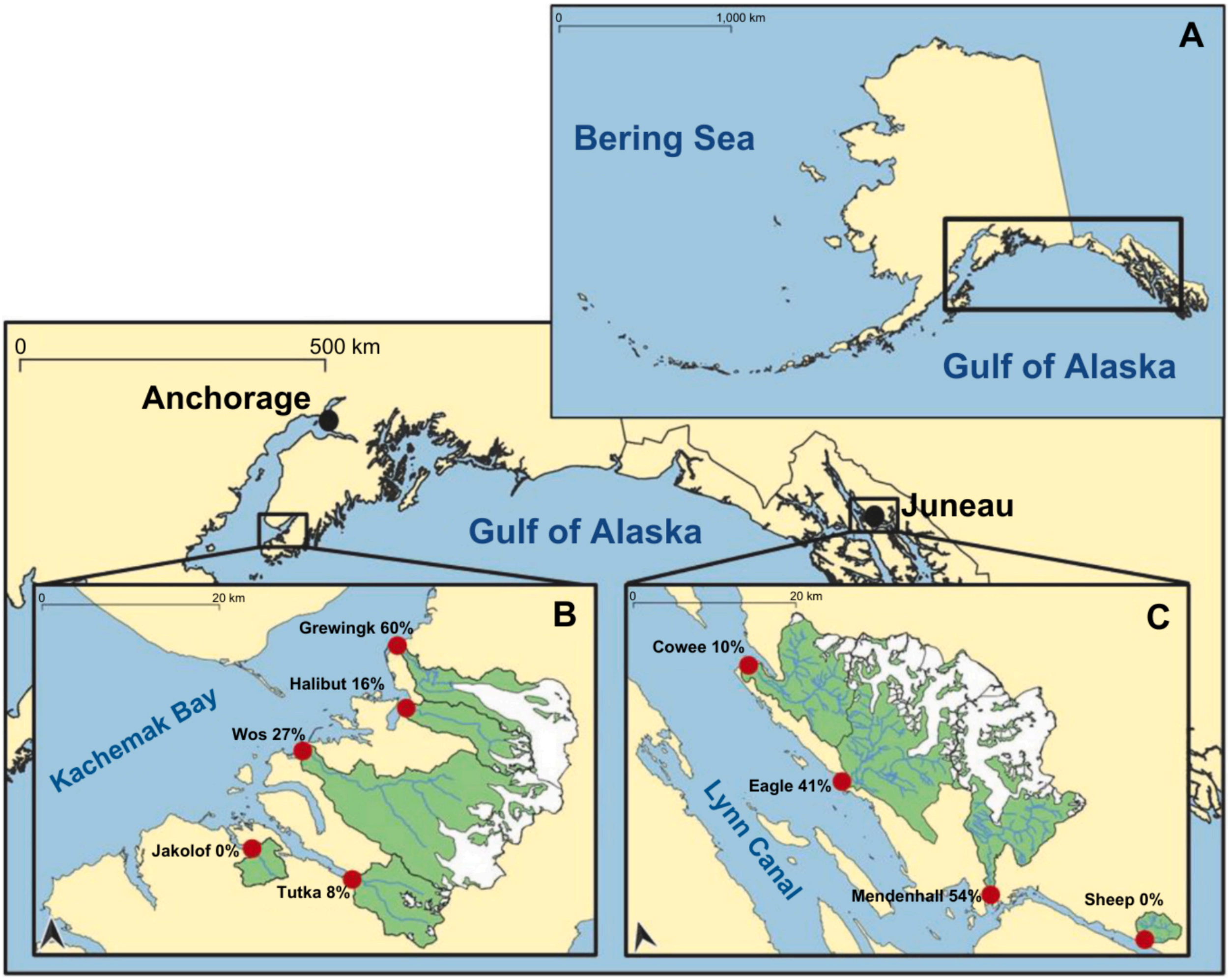

Fig. 1. Map of the Kachemak Bay (B) and Lynn Canal (C) sites and watersheds located within the Gulf of Alaska (A). Percent value after site names indicates the level of glaciation of the respective watershed. Image sourced from McCabe and Konar (2021).

Kachemak Bay sites. For this, seawater samples were collected in triplicate from each site across one tidal cycle (one incoming and one outgoing tide) in May, July, and September, as these months best represent the timeline that glaciers in this region experience pre-peak, peak, and post-peak melting, respectively (McCabe and Konar, 2021). The water samples collected in triplicate were taken at the same time. The two sets of water samples collected during an incoming and outgoing tide, respectively, were taken approximately two hours apart. A Niskin bottle was deployed from a boat to collect water samples approximately two meters below the surface ($n = 90$), adjacent to the intertidal site, regardless of tide level. This water was transferred into 200 mL borosilicate bottles, fixed with 200 μl of a saturated mercuric chloride ($HgCl_2$) solution, and remained sealed until analysis. Water temperature and salinity were also recorded during sampling with a YSI Pro2030 for carbonate chemistry calculations. These water samples were analyzed at the University of Alaska Fairbanks Ocean Acidification Research Center, where total alkalinity (TA) and dissolved inorganic carbon (DIC) of samples were determined using a Versatile Instrument for the Detection of Total Alkalinity (VINTA) and Automated Infra Red Inorganic Carbon Analyzer (AIRICA), respectively. The AIRICA and VINDTA were calibrated using Certified Reference Materials (CRM; batch 190) from the Dickson Laboratory at the Scripps Institute of Oceanography. Then, Ωcalcite and Ωaragonite, pCO_2, and pH values were calculated using TA/DIC input pairs, along with temperature and salinity data in the software program CO2SYS-Excel (Pierrot et al., 2021) with the following constants: carbonic acid dissociation constants K_1 and K_2 from Millero (2010); $KHSO_4$ from Dickson (1990); and B_T from Uppström (1974).

The static environmental attributes included in this study (percent glaciation, substrate type, slope, fetch, and distance to freshwater) have all been determined at these sites in previous studies (Table 1; Konar et al., 2016; LaBarre et al., 2023). Percent glaciation estimates the percentage of glaciated area inside each watershed, where each sampling site is located. In, 2019, abiotic substrate type was visually estimated at each site within ten randomly placed quadrats (0.25 m^2) along alternating sites of a permanent transect. The average substrate type was based on the Wentworth scale that categorizes substrate by percent of bedrock, boulder, cobble, gravel, mud, and sand (McCabe and Konar, 2021). Slope (in degrees) was measured at each site for every one-meter rise in elevation at five equally spaced mid and low-stratum points along a transect. Low (mean low water) and mid (4 m tidal elevation) strata slopes were calculated as a mean of the five slope measurements (LaBarre et al., 2023). Fetch was calculated using a spoke pattern, creating 200 km vertices every 10 degrees for 360 degrees centered on each study site. If a land mass was encountered, vertices were clipped. Potential fetch was estimated by adding the remaining vertices' distances. Distance to freshwater is an estimation of the distance, in meters, each site is from a fresh water source, such as a river or stream (Konar et al., 2016).

2.3. Intertidal community data

Community structure data were collected along the high intertidal zone at each site from April to September 2019 through 2022. In 2020, due to COVID-19 restrictions, sampling only occurred between June and September. These community data include percent cover and biomass estimates using ten quadrats (50 cm^2 and 0.0625 m^2, respectively) placed randomly along alternating sides (high and low) of a single fixed 50 m long horizontal transect at each site once per month. Percent cover quadrats were taken along the permanent transect, while biomass quadrats were taken at least two meters from the transect to avoid the area where the percent cover data were taken. Percent cover data were collected through visual cover estimates of sessile invertebrates, macroalgae, and bare rock. Individual species in each percent cover quadrat were identified to the lowest possible taxonomic level. Biomass quadrats were scraped to collect all individuals, except barnacles, and immediately processed in a laboratory. Samples were sorted and species were identified to the lowest possible taxonomic level, counted, and their wet weight, including shells, was recorded. Barnacles were not included in biomass estimates, because the collection process often destroys their shells to the extent that individuals cannot be quantified. Instead, barnacles were quantified in percent cover estimates.

2.4. Data analysis

The dynamic environmental data (water temperature, salinity, dissolved oxygen, and turbidity) collected from, 2019 to 2022 were compiled and sorted into separate datasheets based on site. A glacial melt season factor based on the timing of peak glacial melt runoff was then added to these data sheets based on the month sampled, where April and May corresponded to the "pre" melt season, June and July the "peak" melt season, and August and September the "post" melt season. Although there is variability among the study sites regarding timing of peak glacial melt runoff, these glacial melt season seasons are commonly used in both the Kachemak Bay and Lynn Canal study regions (Whitney et al., 2017; McCabe and Konar, 2021; Jenckes et al., 2023).

At this point in the analysis, all data were analyzed based on glacial melt season, not month sampled. All dynamic environmental data were normalized to allow for comparison against community variability patterns. For normalization, each observation of water temperature, salinity, dissolved oxygen, and turbidity was subtracted by the overall mean for that attribute and divided by the standard deviation, which removes units and puts all observations on a similar scale. Then, the values in the lowest 25% of the data (first quartile, hereafter Q1), the highest 25% of the data (third quartile, hereafter Q3), mean values, and standard deviation (SD) values were examined separately to determine if extreme values, average values, or the relative variability of these dynamic attribute data are more influential to community variability. This was done for each site and normalized attribute for each season and year (e.g., Jakolof Salinity Pre, 2019). A similar process was conducted

Table 1

Static environmental attributes for each site in Kachemak Bay (KB) and Lynn Canal (LC) in the Gulf of Alaska. Substrate sizes and units are in parentheses next to the substrate types. "Slope 0.5" indicates that slope was measured at each site at the 0.5 m tide level. Adapted from Konar et al. (2016).

Site	Region	% Glaciation	Mud (< 0.25 mm)	Sand (0.26 mm – 2 mm)	Gravel (2.1 mm – 64 mm)	Cobble (65 mm – 256 mm)	Boulder (257 mm – 1 m)	Bedrock (> 1 m)	Slope 0.5	Fetch (200 m)	Dist. to fresh (m)
Jakolof	KB	0	0.00	1.94	19.48	31.90	26.00	17.86	15.03	15.90	563.6
Tutka	KB	8	0.00	0.00	37.00	49.50	13.50	0.00	9.48	33.41	223.6
Halibut	KB	16	2.00	0.20	14.10	48.70	33.50	15.00	12.08	31.65	1035
Wosnesenski	KB	27	0.00	5.30	23.30	28.90	36.00	6.50	7.55	665.7	925.3
Grewingk	KB	60	8.40	1.00	82.90	7.70	0.00	0.00	0.63	412.3	747.5
Sheep Creek	LC	0	46.00	0.00	26.97	20.93	6.34	0.00	3.00	77.36	97.36
Cowee Creek	LC	10	2.50	62.90	2.10	1.30	26.30	16.33	4.33	181.4	204.3
Eagle River	LC	41	13.00	0.00	1.10	26.00	56.00	0.00	6.00	150.4	91.36
Mendenhall River	LC	54	32.00	0.00	27.70	26.20	13.70	0.00	4.00	50.79	99.19

for the carbonate chemistry data (Ωcalcite and Ωaragonite, pCO2, and pH) collected in 2022 at the Kachemak Bay sites; however, only pCO_2 values were used in further analyses and to calculate Q1, Q3, mean, and standard deviation values. These carbonate chemistry parameters are highly correlated, as they are all calculated from total alkalinity and DIC data. Static environmental attributes (percent glaciation, substrate type, beach slope, fetch, and distance to freshwater) and all percent cover and biomass of spatially dominant species (*Mytilus trossulus*, *Balanus* spp., and *Fucus* spp.) were also organized by site and normalized to prepare for analysis. Percent cover and biomass of the spatially dominant species were then averaged by site, glacial melt season, and year.

For the 2019–2022 intertidal community percent cover and biomass data, sampling quadrats were averaged by site, position on the transect taken (high or low), month, and year. This created two community makeup observations per monthly sampling event at each site for both percent cover and biomass, which was necessary for community variability analysis described later in greater detail. These data were square-root transformed and their community structure similarities were calculated via Bray-Curtis similarity matrices (PRIMER-e ltd; Clarke and Gorley, 2015). To quantify community variability over the four-year observation period, PERMDISP analyses were run on the Bray-Curtis similarity matrices for both biomass and percent cover data (PRIMER-e ltd; Anderson et al., 2008). PERMDISPs are used to test the homogeneity of multivariate dispersions using any resemblance measure (e.g., Bray-Curtis, Euclidean Distance) based on distances to centroids or spatial medians, and this can also be used as a test for differences in variability among a factor of interest (e.g., site, year) (Anderson, 2006). PERMDISP analyses also require a minimum of three community composition observations for each factor of interest to calculate an accurate distance to centroid value; therefore, transect position was incorporated into community variability analyses. Sampling months were organized by glacial melt seasons (April – May = “pre”, June – July = “peak”, August – September = “post”) to test seasonal variability for individual study sites. The PERMDISP factor of interest was Site-Melt Season-Year, such that every “season” had four community composition observations for calculation of centroid values. PERMDISP analyses then calculated distance to centroid values for each Site-Melt Season-Year factor, which represented community variability levels. A larger distance to centroid value represents greater dispersion of community composition observations, indicating higher variability levels. These distance to centroid values were visualized in a scatterplot using ggplot2 (Wickham, 2016; R Core Team, 2022). Finally, a one-way SIMPER (similarity percentage) analysis was run on both biomass and percent cover community data to investigate which taxa contribute the most to within-group assemblage similarities based on Site-Melt Season-Year groupings (PRIMER-e ltd; Clarke and Gorley, 2015).

The relationship between dynamic and static environmental attributes and spatially dominant species against community variability patterns were determined using multiple linear regression models with the “lm” function in base R (R Core Team, 2022). To begin, all environmental and biotic attributes taken throughout 2019–2022 were included as potential explanatory variables in a Best Subset Regression using the “regsubsets” function in the leaps package (Lumley, 2022; R Core Team, 2022) against community variability data from the percent cover surveys. The explanatory variables included were the Q1, Q3, mean, and standard deviation values for normalized dynamic attribute data (water temperature, salinity, dissolved oxygen, and turbidity), normalized static attribute data (percent glaciation, substrate type, slope, fetch, and distance to freshwater), and average normalized percent cover and biomass of spatially dominant species (*Mytilus trossulus*, *Balanus* spp., and *Fucus* spp.). The Best Subset Regression analysis considered all possible combinations of explanatory variables and used Bayesian Information Criteria to determine which subset of them best-predicted community variability patterns. This analysis also detected if collinearity was present in any explanatory variables. If collinearity was detected, those attributes were removed from further analysis. Another Best Subset Regression was run on all explanatory variables and community biomass variability data. Two multiple linear regression models were constructed for percent cover and biomass data based on the explanatory variables identified by the Best Subset Regressions. To check for model accuracy, these multiple linear regression models were assessed for the presence of heteroscedasticity. If heteroscedasticity was detected via a Breusch-Pagan test ($p < 0.05$) using the “bptest” function in the lmtest package (Zeileis, 2022; R Core Team, 2022), the model was rerun with fitted values to correct it using the following code:

$$``\text{fitted value} = 1\Big/\text{lm}\Big(\text{abs(original\_model\$residuals)} \sim \text{original\_model\$fitted.values}\Big)\ \text{\$fitted.values\^{}2}''.$$

Then, Lindeman, Merenda, and Gold (LMG) indices were calculated for both regression models using the “calc.relimp” function in the relaimpo package (Groemping, 2021; R Core Team, 2022). LMG indices allocate a share of the R^2 value to each explanatory variable to assess their relative contribution and importance to the model.

The carbonate chemistry data (pCO_2) that were only collected in 2022 at the Kachemak Bay sites were included in separate multiple linear regression models against 2022 Kachemak Bay community variability data for percent cover and biomass, respectively. As previously described, the pCO_2 data included in this model were the normalized Q1, Q3, mean, and standard deviation values for each glacial melt season (pre, peak, post).

3. Results

3.1. Drivers of percent cover community variability

Among all study sites, percent cover surveys were mainly characterized by bare rock, the filter feeders *Mytilus trossulus* (mussels) and *Balanus* spp. (barnacles), the brown alga *Fucus* spp. (rockweed), the green alga *Ulva* spp. (sea lettuce), the red alga *Odonthalia* spp. (sea brush), and filamentous diatoms (SIMPER; Supplementary Table 2). Among the sites, community variability levels (PERMDISP; Supplementary Table 3) were significantly different from each other (ANOVA; $p < 0.05$; Fig. 2).

Gravel substrate, bare rock cover, barnacle cover, and rockweed cover were the most influential attributes explaining community variability patterns from the percent cover surveys (Best Subset Regression and BIC; Supplementary Fig. 1). During the process of explanatory variable selection, collinearity was detected in two aspects of substrate type, boulder cover and bedrock cover. These attributes were removed from further analysis (Best Subset Regression). In the initial multiple linear regression model constructed, heteroscedasticity was detected (Breusch-Pagan = 15.09; $p = 0.005$). The model was re-run as a weighted regression, where less weight is placed on data areas with high variance to correct the heteroscedasticity. The resulting weighted multiple linear regression model was significant ($p < 0.05$) and found that differences in gravel substrate, bare rock cover, barnacle cover, and rockweed cover explained approximately 42% of the variance found in intertidal community percent cover variability (Multiple $R^2 = 0.4192$) (Table 2). The individual contributions of each explanatory variable to predicting community variability were 26.2% for barnacle cover, 6.3% for gravel substrate, 5.9% for rockweed cover, and 3.6% for bare rock cover (LMG; Table 1). The relationships between gravel substrate, bare rock cover, barnacle cover, and rockweed cover with community variability were negative, where higher levels of any of these explanatory variables were associated with lower community variability. These results identified key attributes associated with percent cover community variability and highlighted a strong relationship between barnacle cover and community variability.

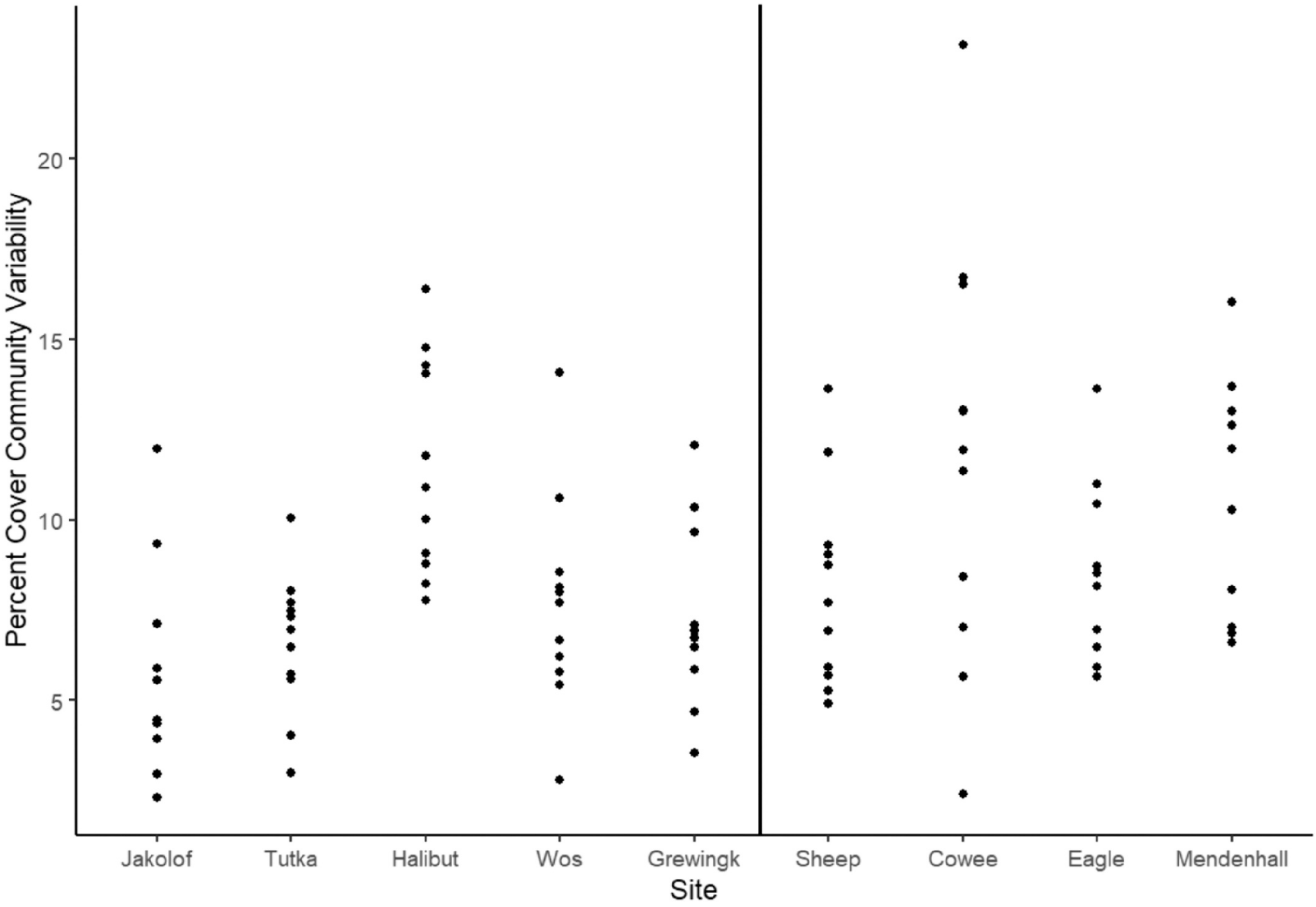

Fig. 2. Scatter plot for seasonal variability/dispersion values in intertidal community percent cover in the Gulf of Alaska study sites calculated via PERMDISP analyses. To test seasonal variability, sampling months were organized by glacial melt seasons (April – May = "pre", June – July = "Peak", August – September = "post") for any sampling year (2019-2022). Each point in the figure represents a sampling season and year (e.g., Peak 2020) for any site. The vertical line | separates the Kachemak Bay sites (Jakolof, Tutka, Halibut, Wos, Grewingk) from the Lynn Canal sites (Sheep, Cowee, Eagle, Mendenhall).

Table 2
Results of the weighted multiple linear regression assessing explanatory variables for intertidal community variability patterns (percent cover) by glacial melt season. Est. = estimate, S.E. = standard error of the estimate, t val. = t value, p = p-value, LMG = Lindeman, Merenda, and Gold index, Contribution = contribution of explanatory variable to overall model as a percentage. Significant p-values ($p < 0.05$) are in bold text.

	Est.	S.E.	t val.	p	LMG	Contribution
(Intercept)	8.74	0.30	29.03	$\mathbf{< 2 \times 10^{-16}}$		
Barnacle Cover	−3.69	0.50	−7.36	$\mathbf{1.22 \times 10^{-10}}$	0.262	26.2%
Gravel Substrate	−0.86	0.30	−2.92	**0.005**	0.063	6.3%
Rockweed Cover	−2.74	0.65	−4.25	$\mathbf{5.67 \times 10^{-5}}$	0.059	5.9%
Bare Rock Cover	−2.3	0.66	−3.58	**0.0006**	0.036	3.6%

Residual Standard Error: 1.232 on 83 degrees of freedom
Multiple R^2: 0.4192
Adjusted R^2: 0.3912
F-statistic: 14.97 on 4 and 83 degrees of freedom
p-value: $\mathbf{2.971 \times 10^{-9}}$

3.2. Drivers of biomass community variability

For biomass surveys, intertidal communities among all study sites primarily consisted of the filter feeders *Mytilus trossulus* and *Balanus* spp., the grazers *Lottia* spp. (limpets) and *Littorina* spp. (periwinkles), the brown algae *Fucus* spp. and *Pylaiella* spp. (sea felt), the green algae *Ulva* spp. and *Acrosiphonia* spp. (arctic sea moss), the red alga *Odonthalia* spp., and filamentous diatoms (SIMPER; Supplementary Table 4). There were significant differences (ANOVA; $p < 0.05$) in community variability (PERMDISP; Supplementary Table 3) among the sites (Fig. 3).

Dissolved oxygen standard deviation values (SD), gravel substrate, mud substrate, distance to freshwater, mussel cover, and rockweed biomass were chosen as the best predictor variables to explain intertidal community biomass variability patterns (Best Subset Regression and BIC; Supplementary Fig. 2). The initial multiple linear regression model constructed with these six explanatory variables was not free of heteroscedasticity (Breusch-Pagan = 13.89; $p = 0.03$) and was rerun as a weighted regression. The resulting model was significant ($p < 0.05$) and showed that approximately 64% of the variance in intertidal community biomass variability patterns could be explained by dissolved oxygen (SD), gravel substrate, mud substrate, distance to freshwater, mussel cover, and rockweed biomass (Table 3). Individually, gravel substrate contributed 19.6%, while mussel cover, mud substrate, dissolved oxygen (SD), rockweed biomass, and distance to freshwater contributed 11.7%, 10.6%, 9.3%, 7.8%, and 4.8%, respectively (LMG; Table 3). Each of these attributes had a negative relationship with community variability levels except dissolved oxygen (SD) and distance to freshwater. These results showed a unique set of attributes that contribute to biomass community variability and revealed a strong relationship between gravel substrate and community variability. Moderate relationships

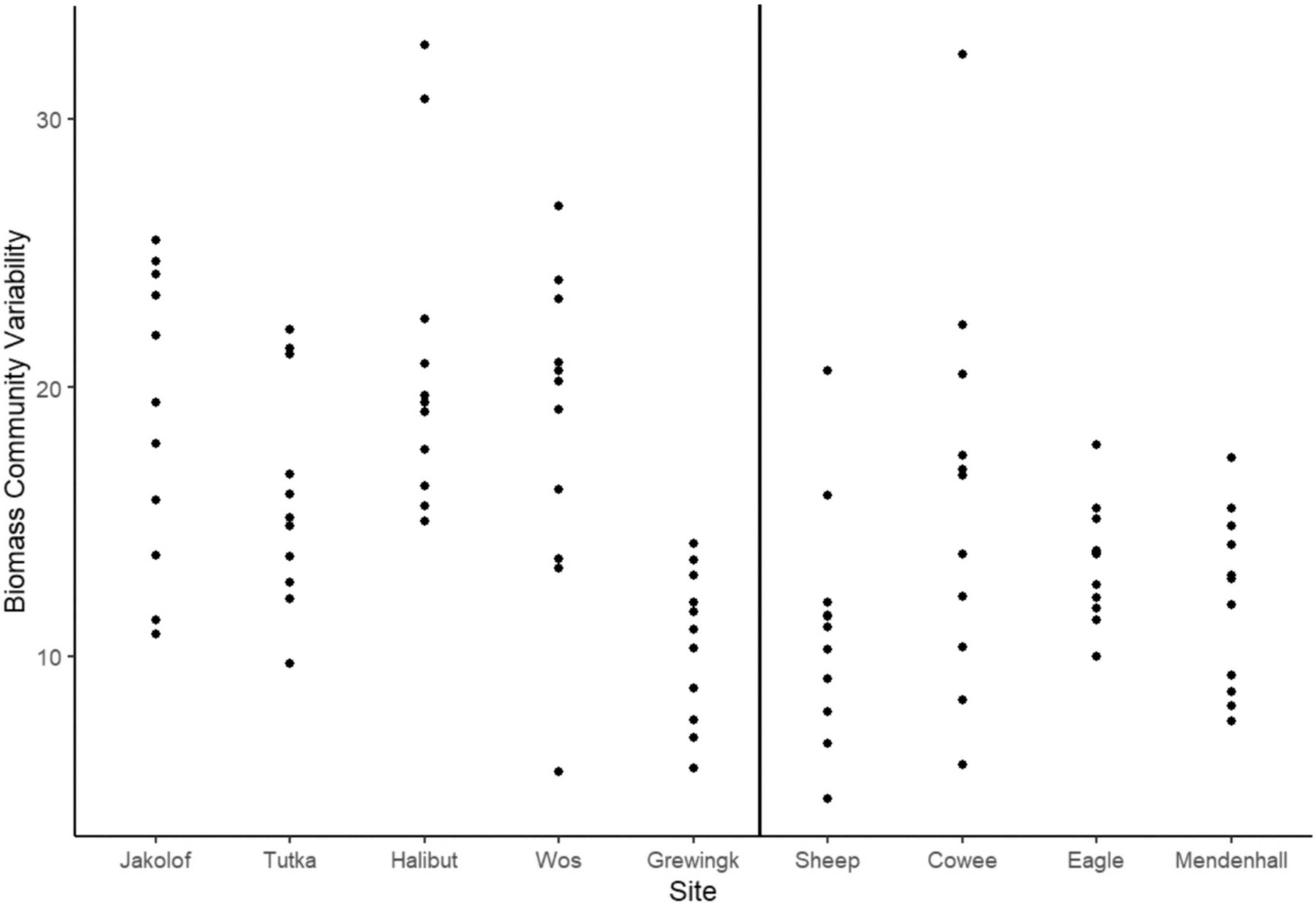

Fig. 3. Scatter plot for seasonal variability/dispersion values in intertidal community biomass calculated via PERMDISP analyses. To test seasonal variability, sampling months were organized by glacial melt seasons (April – May = "pre", June – July = "Peak", August – September = "post") for any sampling year (2019-2022). Each point in the figure represents a sampling season and year (e.g., Peak 2020) for any site. The vertical line | separates the Kachemak Bay sites (Jakolof, Tutka, Halibut, Wos, Grewingk) from the Lynn Canal sites (Sheep, Cowee, Eagle, Mendenhall).

Table 3
Results of the weighted multiple linear regression assessing explanatory variables for intertidal community variability patterns (biomass) by glacial melt season. Est. = estimate, S.E. = standard error of the estimate, t val. = t value, p = p-value, LMG = Lindeman, Merenda, and Gold index, Contribution = contribution of explanatory variable to overall model as a percentage. Significant p-values ($p < 0.05$) are in bold text.

	Est.	S.E.	t val.	p	LMG	Contribution
(Intercept)	12.05	0.82	14.77	$\mathbf{< 2 \times 10^{-16}}$		
Gravel Substrate	−2.45	0.42	−5.91	$\mathbf{7.82 \times 10^{-8}}$	0.196	19.6%
Mussel Cover	−3.37	0.63	−5.34	$\mathbf{8.38 \times 10^{-7}}$	0.117	11.7%
Mud Substrate	−1.18	0.48	−2.46	**0.016**	0.106	10.6%
Dissolved Oxygen (SD)	4.78	1.05	4.57	$\mathbf{1.70 \times 10^{-5}}$	0.093	9.3%
Rockweed Biomass	−3.23	0.95	−3.40	**0.001**	0.078	7.8%
Dist. to Freshwater	1.63	0.70	2.33	**0.023**	0.048	4.8%

Residual Standard Error: 1.387 on 81 degrees of freedom
Multiple R^2: 0.6382
Adjusted R^2: 0.6114
F-statistic: 23.81 on 6 and 81 degrees of freedom
p-value: $\mathbf{4.85 \times 10^{-16}}$

between mussel cover and mud substrate to community variability were also revealed.

3.3. *Effect of pCO_2 on community variability*

The multiple linear regression model run with pCO_2 data (Q1, Q3, mean, standard deviation) collected in 2022 as explainers of community variability patterns revealed no significant relationships. For the percent cover and biomass models, neither the individual correlates nor the overall model had statistical significance ($p > 0.05$; Supplementary Tables 5 and 6).

4. Discussion

In high latitude coastal ecosystems, climate warming and associated glacial recession are driving rapid and significant changes in environmental attributes (Arendt et al., 2002; Bliss et al., 2014; IPCC et al., 2019). These changes provide a key research opportunity to study how ecological communities in these regions, including their variability levels, are impacted. The goal of this study was to determine how seasonal variability patterns of rocky intertidal communities in glacially influenced estuaries correlate with environmental and biotic attributes. Examining glacially influenced intertidal sites with unique environmental conditions was expected to allow us to correlate environmental and biotic attributes with different levels of community variability. For instance, there were significant negative correlations between percent cover variability and barnacle cover, gravel, rockweed cover, and bare rock. A different set of correlates corresponded to variability levels acquired from biomass community surveys, with variability in dissolved oxygen values (SD values), and distance to freshwater having significant positive relationships to community variability levels, in contrast to gravel and mud substrate, mussel cover, and rockweed biomass having significant negative relationships. The strongest correlate was gravel, then mussel cover, mud, dissolved oxygen, rockweed biomass, and distance to freshwater. The unique results obtained by analyzing community variability through the lens of both percent cover and biomass highlight the value of using multiple survey types to document patterns in ecological communities.

4.1. Hypothesis 1

It was hypothesized that stronger relationships would be found between community variability and dynamic environmental attributes rather than static ones. Between both percent cover and biomass community surveys, static attributes relating to substrate were revealed as significant correlates (gravel substrate, bare rock cover, mud substrate), in addition to a site's distance to a freshwater source. One dynamic attribute, dissolved oxygen, was also significant to community variability patterns. Although the multiple linear regression models showed that static attributes had a stronger relationship to community variability than dynamic attributes, the overall small number of environmental attributes found to be significant correlates to community variability indicate that there was not enough information to support or reject this hypothesis. More research is needed to determine whether dynamic or static attributes have a greater impact on community variability patterns in this system.

Previous research has found that low substrate heterogeneity, or low spatial variation in substrate size, can be associated with greater homogeneity of community assemblages and lower community variability levels (Balata et al., 2007; Rolls et al., 2023). The findings of this study support these previous works, as we found negative relationships between community variability and higher coverage of gravel and mud, where higher coverage of these smaller substrate types also indicates low substrate heterogeneity. There are multiple reasons why these relationships may exist. Smaller substrates are more prone to temperature change (Gedan et al., 2011), offer less protection from physical disturbances like wave action, and are less stable structures than larger substrates (Sousa, 1979; Gedan et al., 2011), leading to habitats that are generally more difficult for macro epibenthic organisms to survive. Further, lower heterogeneity in substrate structure has reduced buffering capacity from disturbance impacts (Caley and StJohn, 1996; Herrnkind et al., 1997; Lewis and Eby, 2002) and harbors less diverse communities (Pianka, 1966; Horner-Devine et al., 2004). Here, study sites with small substrate types and low substrate heterogeneity may also have lower species richness and abundance. Species interactions like predation, competition, herbivory, or habitat modification are known to affect community variability by influencing the occurrence and abundance of organisms in the community (Rolls et al., 2023). A community with lower species richness and abundance may have fewer species interactions taking place than a community with higher richness and abundance (Bairey et al., 2016). Lower species richness, abundance, and fewer species interactions could also manifest as the lower community variability levels that were measured in this study. In addition to the importance of substrate size and substrate heterogeneity, a weak negative relationship between community variability and overall bare rock was also detected, further illustrating the importance of substrate characteristics on community variability levels.

The last significant static correlate to community variability was distance to a freshwater source. Study sites located further from a freshwater source seem to experience greater community variability. Typically, when a rocky intertidal site is located near a riverine freshwater source, it experiences lower salinity and greater turbidity (Held and Harley, 2009; Law et al., 2013). These conditions can cause lower species richness, as the ability of a species to live at a site can be limited by its salinity and sedimentation tolerances. In this study, it is possible that sites located further from a freshwater source are more oceanic and less turbid, leading to habitats that are generally easier for intertidal species to live in and thereby resulting in greater species richness. Again, community variability may be higher when species richness is higher due to a greater number of species interactions (Bairey et al., 2016; Rolls et al., 2023). These findings may also be useful for informing the placement of conservation areas in rocky intertidal habitats. If habitats with greater substrate size and heterogeneity, as well as distance to freshwater, are associated with higher community diversity and variability, these may be key areas to prioritize for conservation (Socolar et al., 2016; Rolls et al., 2023).

There was a significant relationship between community variability and the relative variability, or standard deviation, in dissolved oxygen values in this study. It is known that low or hypoxic dissolved oxygen levels can drive structural differences in ecological communities (Spietz et al., 2015; Hernandez and Tapia, 2021) indicating that these extreme conditions may also affect community variability (Rolls et al., 2023). Here, it appears that community variability is also greater when there is greater variability in dissolved oxygen levels. There is increasing recognition of, and research interest in, the effect of environmental variability on organisms. Fluctuating conditions can provoke different physiological responses in organisms than stable conditions, and natural environmental conditions typically expose organisms to more variability than stability (Pansch et al., 2022). The correlation we found between community variability and the standard deviation of dissolved oxygen levels further illustrates the importance of continued research into the effects of environmental variability on organsisms, communities, and ecosystems. Although only one dynamic attribute was identified as significant in this study, temporal changes in other dynamic habitat attributes have been associated with community variability (Rolls et al., 2023). A community-level response to a drastic change in an environmental attribute was not observed in this study, and we only found one significant dynamic environmental correlate while temperature, salinity, turbidity and pCO_2 appeared to have no relationship to community variability. This low number of correlates may be partly due to the relatively short-term nature of this study (only 4 four years), which did not have the scope to capture community changes over the course of environmental changes, nor did it include multiple stressor events. Additionally, the sample sizes for attributes like turbidity (collected once a month) and pCO_2 (collected once a month only in 2022) may have been insufficient for investigating relationships between them and community variability. It is possible that longer-term studies (10+ years) are better equipped to observe relationships between environmental change and community variability than studies taking place over a shorter time (Gatti et al., 2015; Araujo et al., 2016; Bianchi et al., 2019). Future studies examining drivers of community variability would benefit from utilizing long-term monitoring data that could potentially observe increases or decreases in community variability levels and link them to environmental change (Rolls et al., 2023).

4.2. Hypothesis 2

This study's second hypothesis was that there would be a negative relationship between community variability and the abundance of spatially dominant species. Or, that higher levels of barnacles, mussels, or rockweed would correspond to lower levels of community variability. There is support for this hypothesis, as we found significant negative relationships between both barnacle and rockweed cover and percent cover community variability, with 26.2% of the variance in variability levels being explained by barnacles and 5.9% being explained by rockweed. For the biomass community variability model, mussel cover contributed 11.7% and rockweed biomass contributed 7.8%. Spatially dominant species enhance community stability (Grman et al., 2010;

Miner et al., 2021) by influencing community structure and species abundance in their associated communities, typically through the mechanism of habitat modification (Seed and Suchanek, 1992; Bertness et al., 1999; Castilla et al., 2004; Rolls et al., 2023). Habitat complexity is often thought to be increased by the presence of spatially dominant species, as they provide additional habitat opportunities for organisms to seek shelter or feed (Seed and Suchanek, 1992; Bertness et al., 1999; Castilla et al., 2004). These species, however, can have the opposite effect in situations where they achieve widespread dominance, reducing habitat heterogeneity and causing significant declines in community variability (Piazzi and Balata, 2008; Rolls et al., 2023). In this study, we observed lower levels of variability when there was a greater coverage of barnacles, mussels, or rockweed. These findings align with previous research that associate spatially dominant species to higher community stability and lower variability (Grman et al., 2010; Miner et al., 2021; Rolls et al., 2023). The results of this study also indicate that changes in the abundance of these species could significantly affect community variability. In recent years, rocky intertidal communities in the northern Gulf of Alaska have experienced significant macroalgal declines, barnacle and mussel cover increases, and greater homogenization of intertidal communities overall (Weitzman et al., 2021). These patterns were possibly driven by the Pacific Marine Heatwave (PMH), which occurred from 2015 to 2019 in the Gulf of Alaska (Weitzman et al., 2021), and by the effects of sea star wasting, which occurred over approximately the same time period as the PMH and saw significant declines in multiple sea star species that are major mussel predators (Traiger et al., 2022; Konar et al., 2019). Globally, marine heatwaves are occuring at a higher freqency and intensity (Frölicher et al., 2018; Oliver et al., 2018; Holbrook et al., 2020) indicating that these intertidal community trends of macroalgae loss, filter feeder expansion, and as this study suggests, decreased community variability via homogenization may continue.

4.3. *Implications for glacially influenced rocky intertidal communities*

The relative proportions of spatially dominant species in high latitudes may be experiencing climate-related changes. One study found that filter feeder cover was higher at sites with less glacial influence, while macroalgal cover was higher at sites with higher glacial influence (McCabe and Konar, 2021). It is expected that as glaciers recede in high latitudes, glacial influence in the nearshore will decline and perhaps create more favorable conditions for filter feeding organisms (McCabe and Konar, 2021). This may mean that glacially influenced intertidal communities could experience homogenization with filter feeders, like barnacles and mussels, colonizing habitats and outcompeting macroalgae. Declines in macroalgae could coincide with declines in associated grazers and predators (Tejada-Martinez et al., 2016; Guerry and Menge, 2017) and an overall decrease in species diversity (Paine, 1966, 1974; Menge et al., 1994). Further, these homogenized, low-diversity communities may also experience reduced resilience to disturbance as a result of having a narrowed range of species responses (Olden and Poff, 2003; Cassey et al., 2008; Baiser and Lockwood, 2011). As supported by this study and others, the process of community homogenization by filter feeding species could be observable through declines in community variability (Miner et al., 2021; Rolls et al., 2023). Long term monitoring efforts in high latitude coastal ecosystems and others can use this information to pay particular attention to to filter feeder populations and patterns of community variability and homogenization, as these could be used to detect when a community's resilience is in decline (Carpenter and Brock, 2006; Cline et al., 2014; Menge et al., 2022).

5. Conclusion

Temporal variation in community composition is a useful metric for evaluating the impact of disturbances or environmental change on ecological systems. This study identified environmental and biological attributes that correlate to rocky intertidal community variability levels in glacially influenced estuaries. Aspects of substrate (gravel cover, mud cover, total bare rock cover), distance to freshwater, coverage of spatially dominant species (barnacles, mussels, and rockweed), and one dynamic attribute, dissolved oxygen, were significantly correlated to community variability levels. As climate change progresses globally, understanding which habitat attributes have the greatest influence on community variability can help us predict how changes in those attributes might alter community variability, and in turn how community structure and function may be affected. This study suggests that coverage of spatially dominant species is a key habitat attribute, as they tend to decrease their associated communities' variability levels if present in high proportions. Further, their abundance can be greatly impacted by environmental conditions, including those that climate change may alter.

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CRediT authorship contribution statement

Madeleine McArthur: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Schery Umanzor:** Writing – review & editing, Conceptualization. **Julie Schram:** Writing – review & editing, Conceptualization. **Brenda Konar:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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