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Monograph

Regional differences in the effects of watershed glacial coverage on the performance of Pacific Blue mussel, *Mytilus trossulus*

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ABSTRACT

Climate change is causing atmospheric warming, leading to increasing global temperatures. Warming is especially evident in high latitude regions, leading to losses in glacial mass and consequences downstream. Pacific Blue mussels are a vital species in such downstream coastal environments where they provide services such as stabilizing substrate, facilitating energy transfer, and supporting the mariculture industry and subsistence communities. As glaciers continue to melt, it is unknown how and to what extent the projected glacial runoff will affect intertidal mussel performance. To determine the effects of glacial melt on mussel performance, mussel morphometrics (weight, length, width), mussel adhesion force, shell breaking force, and growth rates were recorded over five months at nine sites whose watersheds span a gradient of glacial coverage (0–60%) in the Gulf of Alaska (GOA). Five sites were used in Kachemak Bay (Southcentral Alaska) and four sites in Lynn Canal (Southeast Alaska). Overall, adhesion force and shell breaking force decreased with increasing glacial coverage of watersheds. However, oceanic proximity and input appear to buffer against the effects of glacial melt as mussels in the more oceanic Kachemak Bay region had higher adhesion and shell breaking forces relative to the mussels in the less oceanic Lynn Canal region. Within the more oceanic Kachemak Bay region, mussel growth rates decreased with increasing glacial coverage of watersheds. In contrast, mussel growth rates generally increased at sites with increasing glaciation of watersheds in the less oceanic Lynn Canal region. Overall, our results suggest that glacial melt is altering conditions in the nearshore marine environment and reducing mussel performance.

1. Introduction

Pacific blue mussels, *Mytilus trossulus,* are ubiquitous throughout the western coastlines of North America and are dominant competitors along sheltered shorelines. They facilitate energy transfer from primary producers to higher trophic levels and are a predominant food source for nearshore consumers (Bodkin et al., 2018). Mussels serve a foundation species role as they reduce the effects of algal blooms and improve water quality and clarity by removing excess nutrients (Petersen et al., 2014), stabilize substrates by creating complex habitat (Paine, 1974; Blanchette et al., 2007), and link pelagic and benthic systems by filtering the water column (Bodkin et al., 2018). In addition to their ecological role, *M. trossulus* supports the mariculture industry, in which the farm gate value (the market value minus the selling costs) of shellfish in Alaska during 2016 was $1.23 million USD (Raspotnik et al., 2021). Additionally, *M. trossulus* is an important part of traditional and subsistence diets for indigenous communities (Harley et al., 2020).

Climate change and associated atmospheric warming has increased global temperatures; however, high-latitude regions are experiencing warming at twice the global rate (IPCC, 2022). The Gulf of Alaska (GOA) region is losing glacial mass at the highest rate on Earth (O'Neel et al., 2015). As glacial mass declines, the total annual freshwater discharge (glacial runoff) into streams, and subsequently into downstream estuarine environments, increases (Jenckes et al., 2023; Milner et al., 2017; O'Neel et al., 2015; Whitney et al., 2018). Increased specific freshwater discharge from glacial melt is proposed to decrease salinity in the nearshore marine environment and concurrently increase sediment, nutrients, and organic matter (Arimitsu et al., 2018; Hood and Berner,

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2009; Hood and Scott, 2008; Jenckes et al., 2023; Jenckes et al., 2022; O'Neel et al., 2015). Additionally, the freshwater from glacier melt may contribute to ocean acidification as glacial freshwater discharges are low in total alkalinity and have enhanced ability to uptake atmospheric carbon dioxide (Evans et al., 2014; Jenckes et al., 2023; Reisdorph and Mathis, 2014).

Changes in salinity (Arimitsu et al., 2018; Sanders et al., 2018), temperature (Fitzer et al., 2015), food availability (Arimitsu et al., 2018), and accessibility of calcium carbonate, directly affect the development and performance of calcifying organisms such as mussels, making them a model species to obtain direct insight into the health of coastal ecosystems influenced by glacial runoff. The average glacier-to-ocean stream length in the Pacific coastal temperate rainforest area that GOA is a part of, is 10 km (O'Neel et al., 2015). This coupling provides an opportunity to test how changes in the glacierized coverage of coastal watersheds affects nearshore marine ecosystems (O'Neel et al., 2015; Whitney et al., 2017; Milner et al., 2017).

If glacial discharge increases ocean acidification, this may have effects on mussel performance. Manipulative lab experiments addressing ocean acidification have found reductions in mytilid mussel byssal thread strength and shell strength (Zhao et al., 2017), significant reductions in net calcification rates, and reductions in shell strength and thickness in larval *Mytilus californianus* as a result of decreased pH levels (Coleman et al., 2014; Gaylord et al., 2011; Li et al., 2015; O'Donnell et al., 2013). If glacial melt increases specific freshwater discharge and lowers seawater pH in the intertidal, this could be a mechanism affecting mussel attachment strength and shell thickness and strength. However, few studies have looked at the responses of mussels to glacial melt with the exception of how glacial melt alters nutrient conditions in Antarctica (Bascur et al., 2020; Woo et al., 2019). Proximity to glaciers has lead to reductions in lipids, protein, and energy content for the bivalve *Nuculana inaequisculpta*, suggesting that bivalve nutritional condition can decrease with increasing glacial proximity and input (Bascur et al., 2020).

The goal of this study was to assess the potential effects of glacial melt on Pacific blue mussel performance by utilizing sites that span a gradient in glacial coverage of watersheds and estimating mussel adhesion force, shell breaking force, and growth rates. Estuarine habitats along the GOA may provide sub-optimal conditions for mussels, as increased glacial melting has increased the volume of freshwater released by glaciers, thereby reducing the salinity of the surrounding seawater (Jenckes et al., 2023; O'Neel et al., 2015). It is expected that as glacial melt in the GOA increases, large discharges of glacial runoff will flow into estuarine habitats, potentially exacerbating the already harsh conditions for mussels. It is unknown how glacial runoff in the GOA will affect mussel performance, their role within their ecosystems including the organisms that rely on them, and the growing Alaskan mariculture industry.

With limited studies conducted to determine the effects of glacial runoff on bivalves, there is a need to identify the potential effects on the ecosystem and economy. The influence of glacierized watersheds on seawater characteristics may be greater in inland waters relative to more open-ocean areas. Greater oceanic influence may reduce the impact of changes to seawater's physical and chemical conditions created by glacierized watersheds (McCabe and Konar, 2021). We hypothesized first (1) to observe a regional effect in that mussels from a more oceanic-influenced region would have increased adhesion force, shell breaking force, and growth rates compared to mussels collected from a more inland estuarine region. We next hypothesized (2) to observe an effect of watershed glacial coverage in that increasing glacial coverage would negatively correlate with mussel adhesion force, shell breaking force, and growth rates across regions. Finally, we hypothesized (3) to observe a temporal effect in that we would observe a stronger effect of glacial coverage of watersheds on mussel adhesion force during warmer summer months.

2. Material and methods

2.1. Study site

Kachemak Bay and Lynn Canal are coastal inlets located in South-central and Southeast Alaska, respectively, and differ in amounts of oceanic input (Johnson, 2021). Lynn Canal (LC) receives much less oceanic input as it is located 100 km from the open ocean (Bruce et al., 1977; Johnson, 2021). This region is heavily influenced by freshwater runoff receiving relatively high annual precipitation (~1580 mm/yr, Jenckes et al., 2023) and has rapid salinity fluctuations within estuaries due to tidal and glacial influence (Beaudreau et al., 2022; Jenckes et al., 2023; Lundstrom et al., 2022; McCabe and Konar, 2021). With relatively low tidal current speeds, these inland waters are likley impacted by local freshwater inputs relative to areas closer to oceanic inputs (Royer, 1982; Weingartner et al., 2009). Shorelines characteristic to LC are dominated by soft substrate with infrequent rocky shores, mainly concentrated towards the upper intertidal zones (McCabe and Konar, 2021). Peak streamflow in LC occurs mid-summer when high snow, ice, and glacial melt occur due to warmer summer temperatures (Jenckes et al., 2023; Whitney et al., 2017). Conversely, Kachemak Bay (KB) has greater oceanic influence, less annual precipitation (~900 mm/yr, Jenckes et al., 2023), and higher proportions of rocky substrate (Workman, 1998). The KB region is adjacent to the open ocean, resulting in a strong oceanic influence from the Alaska coastal current (Burbank, 1977; Muench et al., 1978; Johnson, 2021). Broadly, the open ocean influence derives from the counterclockwise circulation of water in KB and upwelling outside the bay (Johnson, 2021). Glacial runoff and freshwater from rivers feed the fjord-type estuary of KB. Peak streamflow in KB occurs in late August to November due to high precipitation and in spring to early summer due to snow melt (Johnson, 2021). Within both regions, study sites were selected to span a gradient of watersheds glacial coverages that are non-glacial (0%) to glacierized (~60%), to consider the effects of glacial influence on downstream estuaries and local mussel performance (Fig. 1, see details in McCabe and Konar, 2021). The glacial coverages of each watershed leading into each site were calculated by Fellman et al. (2014) and shown to influence the timing and flux of freshwater downstream (see full watershed characteristics in Fellman et al., 2014). Generally, specific freshwater discharge is higher in heavily glacierized watersheds than in non-glacierized watersheds (Jenckes et al., 2023). However, specific freshwater discharge increases disproportionately at sites above 20–30% glacial coverage of watersheds, leading to nonlinear relationships between glacial coverage of site watersheds and freshwater discharge downstream (Jenckes et al., 2023). Additionally, there is both within- and among-year variation in specific freshwater discharge at sites, suggesting the potential for nonlinear relationships between glacial coverage of watersheds and specific freshwater discharge (Jenckes et al., 2023). Nine sites with varying glacial coverages of site watersheds were sampled across the two regions, with four sites in LC and five sites in KB (Fig. 1). Locations of mussel collections at sites occurred at downstream estuaries of the watersheds, which were adjacent to river outflow.

2.2. Sample collection

We estimated the impact of glacial melt on mussel performance by examining the correlation between glacial coverage of watersheds and mussel adhesion force, shell breaking force, and growth rates. *Mytilus trossulus* individuals were collected monthly from the intertidal zones at each site during the lowest low tides from March to August 2021 (Fig. 1). Ten mussels representing the range of sizes at a site (overall range, 18.9–70.0 mm) were haphazardly selected and detached from the substrate using a string lasso attached to a portable handheld force gauge (VTSYIQI VTS-100). Mussels were pulled from the substrate, and the maximum force needed to break the adhesion (herein referred to as

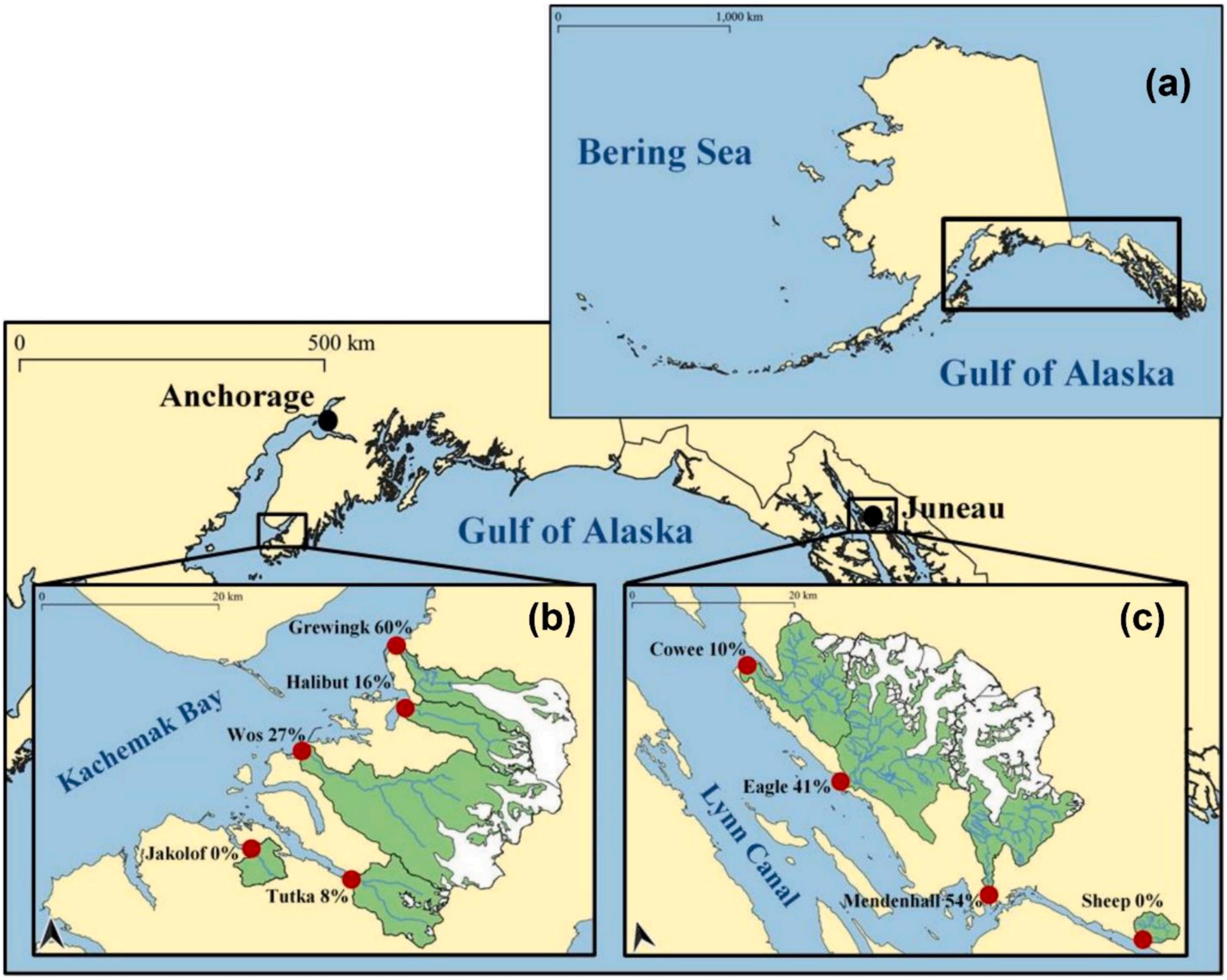

Fig. 1. Map of Alaska (a) with inset of the two study regions (b, c) and intertidal sites (red circles) with percent glacial coverage of watersheds. Watersheds are outlined in black with the white area representing the glacial area and the green area representing the vegetated area. Note that the intertidal site Eagle is located downstream of the convergence of the Eagle and Herbert Rivers and thus is influenced by both the Eagle and Herbert watersheds. Map from McCabe and Konar, 2021, used with permission. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

adhesion force) in newtons was recorded. Mussels were stored in individual bags and transported to laboratories in Kachemak Bay and Lynn Canal to be frozen. Freezing euthanized individuals stopped degradation and standardized the time between collection and when mussel shell breaking strength was measured. Within a week of collection, mussels were thawed for 30 min before being processed. Morphometrics of each mussel included individual weight, shell length, and shell width. Following morphometric measurements, the force required to break the mussel shell (herein referred to as shell breaking force) in newtons was estimated using the handheld force gauge by piercing the mussels on a foam pad in the center of each shell valve. The middle of the shell was sampled to create a consistent way of estimating shell breaking force and likely represents the effects of the environmental conditions at a site over the organism's lifetime. Mussel shell breaking force was the maximum force in newtons recorded by the gauge for each valve of the mussel shell, which was then averaged. The depth of the piercings was standardized by piercing to just after the tip of the conical attachment. If mussel shells were fully crushed, only one side was used or that sample was omitted. Over the entire sampling period, 445 total mussels were used to determine the effects of watershed glacial cover, region, and sampling time on mussel adhesion and shell breaking forces.

Approximately thirty mussels from each study site were tagged in the field to estimate mussel growth rates. Once a mussel was haphazardly chosen in a stratified way (three locations along a permanent transect, different sizes were selected), canned air was used to dry off the individual, and then a tag was epoxied to the shell. For this, a small section of fishing line was adhered at the growing edge, perpendicular to the growth rings (Fig. S1). Mussel individuals (3–15 per site, smaller numbers were due to mussel mortality or tag loss at a site) were collected after approximately 3–4 months of being tagged. Mussel-specific growth rates were estimated using digital calipers to the closest mm. We estimated linear growth from the fishing line end to the current mussel shell edge over the number of days since tagging. Total tagged mussels recovered was 65.

2.3. Statistical analysis

Statistics and plots were generated using RStudio version 2023.09. A principal component analysis (PCA) plot was first used in an exploratory way to visually examine the relationships between adhesion force, shell breaking force, and mussel morphometrics. To control for the potential effects of mussel size, residuals of ANOVA models testing for differences in the relationships of square root of adhesion force, shell breaking force, and specific growth rates, by mussel shell length were used as input dependent variables for subsequent Analysis of covariance (ANCOVA) models. ANCOVA was then used to test for differences in the relationship between the residuals from previous ANOVA models for mussel adhesion force, shell breaking force, and specific growth rates with percent glacial coverage of site watersheds (fixed) and region (fixed). Follow-up tests to determine if non-linearities were present removed the sites with the highest glacial coverage of watersheds within each region, and ANCOVAs were rerun to determine their impact on linear relationships. Finally, to better understand how temporal variation in glacial melt may affect mussel adhesion forces, ANCOVA was used to test for differences in the residuals from previous ANOVA models for mussel adhesion force with percent glacial coverage of site watersheds (fixed) by monthly sampling time (fixed, spanning late April to late August 2021) and by region (fixed).

3. Results

There was variation in mussel morphometrics (weight, length, and width) across sites both within and between regions (Fig. S2, S3). When including all sites within both regions, there was a negative relationship between mussel adhesion force and percent glacial coverage of watersheds (ANCOVA, $F_{1,441} = 104.28$, $p < 0.001$), with higher forces (intercepts) and a steeper slope for mussels from the more oceanic (Kachemak Bay) region (glacial coverage x region: $F_{1,441} = 24.17$, $p < 0.001$, Fig. 2a, Table 1a, S4a). Removing the sites with the highest glacial coverage of watersheds within both regions led to a continued negative linear relationship within Lynn Canal; however, a change in slope between mussel adhesion force and percent glacial coverage of watersheds flipped from negative to positive in Kachemak Bay (Fig. 2a, Table 1b, S4b). These data suggest regional differences with non-linear effects of glacial coverage of watersheds on mussel adhesion force within the more oceanic Kachemak Bay region relative to the more inland Lynn Canal.

There was a negative relationship between mussel shell breaking force and percent glacial coverage of watersheds (ANCOVA, $F_{1,441} = 188.10$, $p < 0.001$), with higher forces (intercepts) detected for mussels in the more oceanic Kachemak Bay region ($F_{1,441} = 32.33$, $p < 0.001$, Fig. 2b, Table 1c, S4c) and similar negative slopes in both regions (region x glacial coverage: $F_{1,441} = 3.57$, $p = 0.059$). Removing the sites with the highest glacial coverage of watersheds within both regions led to a continued linear negative linear relationship within Lynn Canal; however, a change in slope between mussel shell breaking force and percent glacial coverage of watersheds flipped from negative to positive in Kachemak Bay (Fig. 2b, Table 1d, S4d). These data suggest regional differences with non-linear effects of glacial coverage of watersheds on mussel shell breaking force within the more oceanic Kachemak Bay relative to the more inland Lynn Canal.

An interaction revealed that there was an opposite relationship between mussel specific growth rate and percent glacial coverage of watersheds by region (glacial coverage x region: ANCOVA, $F_{1,61} = 8.99$, $p = 0.004$, Fig. 2c, Table 1e, S4e), with a negative relationship for mussels in the more oceanic Kachemak Bay region and a positive relationship in the less oceanic and more inland Lynn Canal region. Removing the most glaciated sites for both regions led to similar directionality in relationships, suggesting that the linear relationships observed were not driven by sites with the most glaciated watersheds (Fig. 2c, Table 1f, S4f).

The relationship between mussel adhesion force and glacial coverage of watersheds was generally negative but differed by region and by sampling time (Two-way ANCOVA, Table 2, S5). Follow-up two-way ANCOVAs for each sampling time revealed negative relationships between mussel adhesion force and glacial coverage of watersheds during all sampling times except for Lynn Canal during the first sampling time and for both regions during the third (June) sampling time when relationships appeared non-linear (Fig. 3, Table 3, S6). Higher adhesion forces (intercepts) or steeper slopes for relationships between mussel adhesion force and glacial coverage of watersheds were detected for mussels within the more oceanic Kachemak Bay region during the first (April), second (May), fourth (July), and fifth (August) sampling times relative to Lynn Canal (Fig. 3, Table 3). Generally, intercepts or negative slopes between adhesion force and glacial coverage of site watersheds increased from the first sampling time in April to those in May, July, and August (Fig. 3, Table 3) suggesting stronger effects of glacial coverage of watersheds on mussel adhesion force later in the season.

4. Discussion

We found evidence that downstream conditions associated with relatively high glacial cover of a watershed negatively impacts mussel performance by reducing the force required to remove mussels from the substrate, reducing the strength to break mussel shells, and by altering

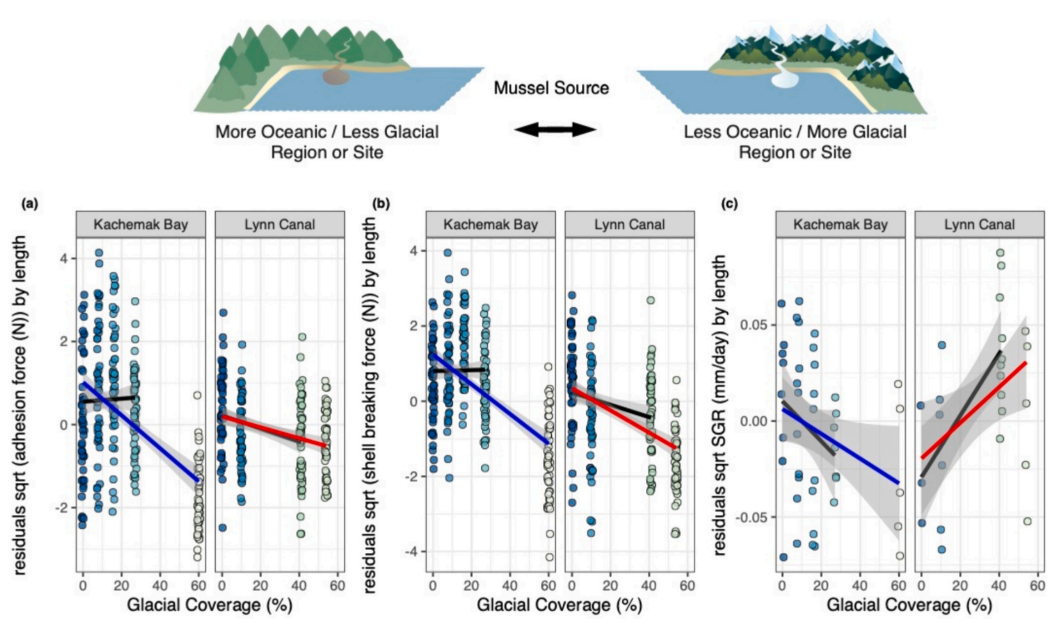

Fig. 2. Relationships for mussel adhesion force (a), mussel shell breaking force (b), and mussel specific growth rate (c) with percent glacial coverage of site watersheds within each region. Dots are individual mussels from five sampling times. Lines are linear relationships, with shading representing standard error. Colored lines represent fits for all sites and black lines are fits with removing sites having the highest glacierized watersheds within each region. See Table 1 for ANCOVA results.

Table 1
Results are testing for differences in residuals of mussel adhesion force (a,b), shell breaking force (c,d), and specific growth rate (e,f), with glacial coverage of site watersheds (fixed) and region (fixed). Two-way ANCOVAs were run testing for differences in mussel performance with all sites (a,c,e) and while removing sites with the highest level of glacial coverage of watersheds within each region (b,d,f).

(a) adhesion force						(b) adhesion force (without highest glacierized sites)					
Source	df	SS	MS	F	P	Source	df	SS	MS	F	P
Glacial Coverage	1	156.6	156.56	104.2829	**<0.001**	Glacial Coverage	1	11.4	11.42	7.057	**0.008**
Region	1	3.2	3.17	2.1109	0.147	Region	1	30.5	30.51	18.8554	**<0.001**
Glacial Coverage x Region	1	36.3	36.28	24.1657	**<0.001**	Glacial Coverage x Region	1	5.1	5.09	3.1461	0.077
Residual	441	662.1	1.50			Residual	341	551.7	1.62		
(c) shell breaking force						**(d) shell breaking force (without highest glacierized sites)**					
Source	df	SS	MS	F	P	Source	df	SS	MS	F	P
Glacial Coverage	1	268.9	268.95	188.10	**<0.001**	Glacial Coverage	1	15.6	15.63	11.17	**<0.001**
Region	1	46.2	46.22	32.33	**<0.001**	Region	1	55.9	55.91	39.96	**<0.001**
Glacial Coverage x Region	1	5.1	5.11	3.57	0.059	Glacial Coverage x Region	1	4.2	4.22	3.02	0.083
Residual	441	630.5	1.43			Residual	341	477.1	1.40		
(e) Specific Growth Rate						**(f) Specific Growth Rate (without highest glacierized sites)**					
Source	df	SS	MS	F	P	Source	df	SS	MS	F	P
Glacial Coverage	1	0.0003	0.0003	0.2266	0.636	Glacial Coverage	1	0.0061	0.0061	4.4105	**0.041**
Region	1	0.0029	0.0029	1.9154	0.171	Region	1	0.0002	0.0002	0.1284	0.722
Glacial Coverage x Region	1	0.0134	0.0134	8.9855	**0.004**	Glacial Coverage x Region	1	0.0141	0.0141	10.2434	**0.002**
Residual	61	0.0911	0.0015			Residual	51	0.0703	0.0014		

Table 2
Two-way ANCOVA results testing for differences in residuals of mussel adhesion force with glacial coverage of site watersheds (fixed) by region (fixed) and time (fixed).

Source	df	SS	MS	F	P
Glacial Coverage	1	152.0	151.98	111.34	**<0.001**
Region	1	8.3	8.32	6.10	**0.014**
Sample Time	4	19.3	4.82	3.53	**0.008**
GlaCov x Region	1	36.8	36.79	26.95	**<0.001**
Region x SampTime	4	29.7	7.42	5.43	**<0.001**
GlaCov x SampTime	4	28.0	7.01	5.13	**<0.001**
GlaCov x Reg x SampTime	4	3.9	0.97	0.71	0.585
Residual	425	580.1	1.37		

mussel growth rates. While increasing glacial coverage of watersheds reduced mussel adhesion and shell breaking forces in both regions, the more oceanic Kachemak Bay (KB) sites had higher adhesion and shell breaking forces across the gradient in glacial coverage of watersheds compared to Lynn Canal (LC). Within KB, non-linear relationships between mussel adhesion and shell breaking forces were detected by removing the influence of the site with the highest glacial coverage of watersheds and observing different responses. Within KB, without the influence of the site with the highest glacial coverage of watersheds, mussel adhesion and shell breaking forces appeared similar or positive with increasing glacial coverage of site watersheds. These findings suggest that higher oceanic input to the region may increase seawater salinities at sites and dilute the effects of glacial meltwater, and associated changes in seawater chemistry, leading to unchanging adhesion

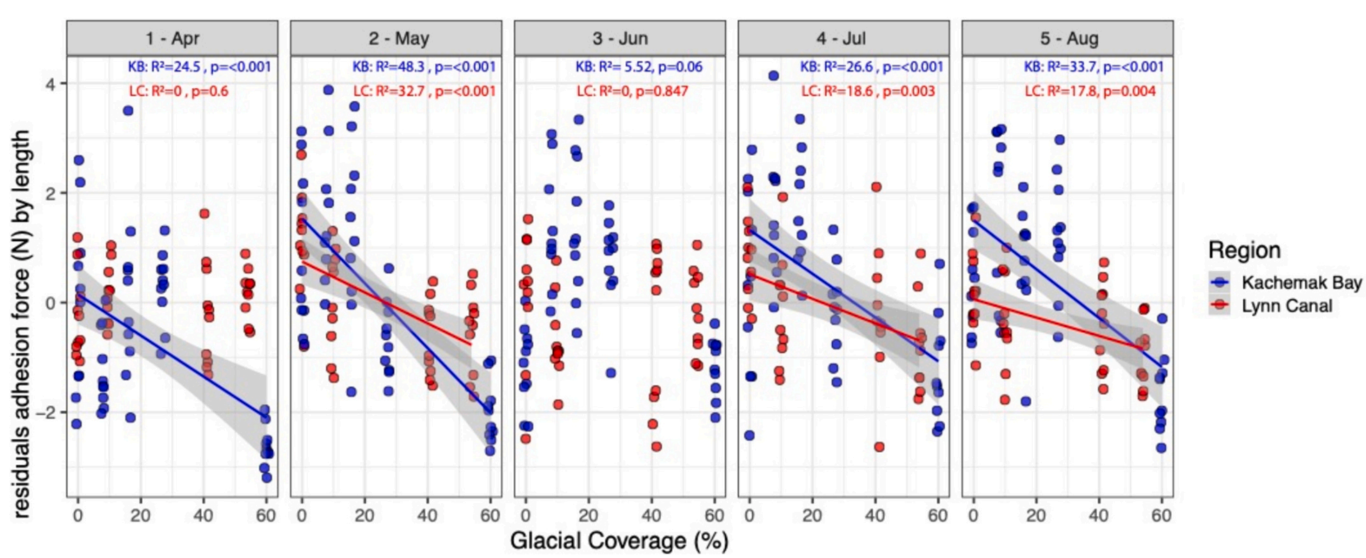

Fig. 3. Relationships for mussel adhesion force with percent glacial coverage of site watersheds by region for each sampling time (April 2021 through August 2021). Dots are mussels from each sampling time. Lines are linear relationships, with shading representing standard error. See Table 2 for ANCOVA results including sample time as a factor and Table 3 for ANCOVA results within each sampling time. Adjusted R^2 and *p*-values are values for each region within a sampling time.

Table 3
Two-way ANCOVA results testing for differences in residuals of mussel adhesion force with glacial coverage of site watersheds (fixed) by region (fixed) during each sampling time.

Time 1, April–May					
Source	df	SS	MS	F	P
Glacial Coverage	1	11.7	11.73	9.50	**0.003**
Region	1	11.8	11.78	9.53	**0.003**
Glacial Coverage x Region	1	16.8	16.80	13.59	**<0.001**
Residual	86	106.3	1.24		
Time 2, May					
Source	df	SS	MS	F	P
Glacial Coverage	1	81.9	81.88	65.27	**<0.001**
Region	1	0.0	0.02	0.01	0.910
Glacial Coverage x Region	1	9.8	9.76	7.78	**0.007**
Residual	85	106.6	1.25		
Time 3, June					
Source	df	SS	MS	F	P
Glacial Coverage	1	5.6	5.58	3.33	0.071
Region	1	4.4	4.41	2.63	0.108
Glacial Coverage x Region	1	3.1	3.10	1.85	0.177
Residual	85	142.2	1.67		
Time 4, July					
Source	df	SS	MS	F	P
Glacial Coverage	1	43.1	43.14	29.00	**<0.001**
Region	1	3.1	3.07	2.06	0.155
Glacial Coverage x Region	1	3.1	3.13	2.10	0.151
Residual	84	124.9	1.49		
Time 5, August					
Source	df	SS	MS	F	P
Glacial Coverage	1	43.9	43.95	37.34	**<0.001**
Region	1	12.5	12.46	10.58	**0.002**
Glacial Coverage x Region	1	7.9	7.88	6.69	**0.011**
Residual	85	100.0	1.18		

force and shell breaking force with increasing glacial coverage of watersheds until relatively high levels of glacial coverage. The influence of more saline open ocean water due to current patterns (Johnson, 2021) along with homogenization of among-site differences during tidal flux may act as a buffer against freshwater input from glacial melt within KB, leading to the elevated and more similar adhesion and shell breaking forces of mussels at sites with glacial coverages 27% or lower. The strong influence of open ocean water in KB contrasts the more inland and less oceanic conditions of LC, where consistent linear trends between mussel adhesion and shell breaking forces with glacial coverage were observed. The lower tidal current speeds may contribute to higher retention times of freshwater inputs in Lynn Canal (Weingartner et al., 2009), homogenizing seawater at the sites, and leading to the more general declines observed in adhesion and shell breaking forces. Additionally, our study showed evidence for adhesion forces varying throughout time, where the greatest difference in adhesion forces across sites occurred during the warmer summer months when freshwater discharge downstream of sites with relatively high glacial cover tends to be highest (Jenckes et al., 2023).

Overall, the growth rate of mussels was inversely related to the glacial coverage of site watersheds within the more oceanic KB region. With increasing glacial coverage of site watersheds, we predicted that specific growth rates would decrease (as observed in KB) due to a decline in salinity, causing reduced calcification and potentiality growth (Sanders et al., 2018). However, since ecological energy costs of mussel calcification is not thoroughly understood, other environmental factors like food availability could explain the trend (Sanders et al., 2018). In the Antarctic, there is evidence that lipid and protein concentrations in available food were lower near glacier edges (Bascur et al., 2020). With no indication of mussel diets shifting with increasing glacial coverage of watersheds in KB (Schloemer et al., 2023), future work could consider how glacial input affects the quality of food resources downstream and mussel growth rates.

The opposite relationship between glacial coverage of site watersheds and mussel growth rates was observed in LC (Fig. 3c) and is not fully understood. Heavily glaciated watersheds can be associated with influxes of limiting nutrients (McCabe and Konar, 2021) that may increase food and, subsequently, growth rates of downstream fauna (Whitney et al., 2017). Differences in beach morphology and resulting surf zone hydrodynamics can affect seawater retention and food availability for mussels (Salant et al., 2021). With mussels being able to utilize both phytoplankton and macroalgal detritus (Duggins et al., 1989; Duggins and Eckman, 1997; Schloemer et al., 2023) they may be benefitting from limiting nutrients from glacial melt that may increase the quality of phytoplankton or macroalgal detritus within inland LC waters. It should be mentioned that the mortality of tagged mussels was high, complicating our interpretation. Future work could consider making comparisons between areas with differing amounts of oceanic inputs on how freshwater discharge created by glacial melt affects primary producer food quality and mussel growth.

Glacial melt may lead to downstream changes in seawater chemistry in addition to reducing seawater salinities. Limited preliminary evidence revealed positive relationships between salinity and Total Alkalinity (TA), pH, carbonate saturation state, and aragonite saturation state, and a negative relationship between salinity and pCO_2 (unpublished data). Decreased pH due to ocean acidification has reduced the number and strength of mussel byssal threads (Zhao et al., 2017) and a reduction in shell thickness (Fitzer et al., 2015; Fitzer et al., 2014). Studies show significant reductions in shell strength with low pH but noticed that mussels still maintained linear growth when pH was lowered (O'Donnell et al., 2013; Fitzer et al., 2015). Reductions of TA, pH, carbonate saturation state, and aragonite saturation state at lower salinities would help to explain the observed patterns in mussel adhesion and shell breaking forces as lower values may lead to dissolution and weakening of byssal thread number and strength and shell thickness and strength. These impacts may lead to an increased risk for dislodgement and increased vulnerability to predation due to thinner shells in natural environments and in suspended line aquaculture. Glacial melt is predicted to increase in high latitude areas such as Alaska (IPCC, 2022). The impacts of meltwater and lowering of seawater pH may inhibit the expansion of mussel aquaculture in some regions where freshwater inputs and retention is relatively high. Understanding the similarities or differences between the effects of freshwater discharge from glacial melt and ocean acidification can help us better understand the impacts of glacial influence on other invertebrates that calcify.

Mussels are a foundation species in the intertidal (Gaylord et al., 2011), an important cultural and subsistence harvest species (Harley et al., 2020), and a species with expanding mariculture interest. Reductions in mussel adhesion and shell breaking forces may have unique implications for the ecosystems they bolster. Mussels play an inherent role in the marine environment where they form structurally complex beds that provide habitats for diverse communities of marine invertebrates. For example, the total biomass of marine invertebrate communities associated with mussels was three times higher at sites where mussels were abundant (Singh et al., 2013). With an increased risk of dislodgement due to weakened byssal threads or mortality due to shell damage, mussel communities may be dramatically altered. Loss of this competitive dominant foundation species may increase variability in intertidal community composition, biomass, richness, and diversity (Paine, 1974; Pfister et al., 2016; Singh et al., 2013). The demand for mussels from subsistence harvesting and for mussel farms can lead to increased pressure on *M. trossulus* in more oceanic-influenced regions.

Reduced adhesion strength for farmed mussels may lead to increased mortality rates during seasonal storms (Dayton and Tegner, 1984), heatwaves (Raymond et al., 2022), periods of increased wave action (Fitzhenry et al., 2004), and during periods of reduced byssal thread production (Carrington, 2002). Broadly, heatwave events can negatively impact mussel survival through thermal stress (Raymond et al., 2022); however, less is known about how freshwater discharge may contribute. For example, a mass mortality event in Pacific blue mussels occurred during the summer of 2021 in Skagway, Southeast Alaska. It is suggested that this mortality was triggered by significant temperature increases and freshwater discharge during summer (personal communication Reuban Cash). The effects of glacial melt on mussel performance may interact with other climate driven changes (warming and acidification) and potentially lead to antagonistic impacts on this species, altering the role they play ecologically and economically. With global warming leading to increasing glacial and snow melt worldwide, this study has provided insight into the effects of glacial melt on mussels, which may increase in severity in the coming decades (Jenckes et al., 2023; Sergeant et al., 2020; Young et al., 2021). Reductions in mussel abundance have the potential to disrupt the function of ecosystems as well as reduce aquaculture production and subsistence harvest.

CRediT authorship contribution statement

Gracelyn Ham: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Scott Gabara:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Preslee Chase:** Project administration, Methodology, Investigation, Data curation. **Brenda Konar:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Schery Umanzor:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Brenda Konar reports financial support was provided by National Science Foundation. Gracelyn Ham reports financial support was provided by National Institutes of Health. Gracelyn Ham reports a relationship with University of Alaska Southeast that includes: funding grants. Scott Gabara, Schery Umanzor, Brenda Konar, Preslee Chase reports a relationship with University of Alaska Fairbanks that includes: employment and funding grants. Gracelyn Ham reports a relationship with University of Alaska Fairbanks that includes: employment.

Data availability

Data is attached as supplemental files

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Appendix A. Supplementary data

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