Monograph

Effects of glacial discharge on thallus condition of northern rockweed (*Fucus distichus*) in the Gulf of Alaska

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ABSTRACT

Glacial melt due to climate warming is expected to accelerate in high-latitude ecosystems, necessitating an understanding of how this may influence foundation species in coastal systems. The goal of this study was to use a gradient of glaciation along five watersheds in a south-central Alaskan fjord to investigate the relationship between downstream effects of glacial cover and the thallus condition of the habitat-building rockweed, *Fucus distichus*. We used compositional and biochemical data from *F. distichus* thallus samples collected across six months from all five watershed sites and related them to nearshore environmental data taken at each month and site. Most thallus condition metrics changed more related to sampling month than watershed glacial cover, with most metrics decreasing over the sampling period. This was possibly related to the build-up of more structural materials such as cell wall and other chemical structural elements during later-season growth. Lipid content was the only metric that differed systematically by watershed glacial cover, with lower lipid content at the sites with higher glacial cover and assumed higher glacial discharge of the watershed. Most thallus condition metrics were related to water temperature, with the increase during the sampling period reflecting a seasonal warming rather than an influence of increased glacial discharge in the summer. Less effects were seen from lower salinity and higher turbidity in the summer related to seasonally increased glacial discharge. These results indicate that *F. distichus* is tolerant to the currently experienced range of environmental conditions in glacial watersheds, at least during the sampling years. Possible effects of increasing glacial discharge conditions on other *F. distichus* life stages (e.g., zygotes) that are vital to maintain genetically diverse populations, or the ability of this species to maintain high primary production and provide habitat and high-quality food for coastal consumers under increasing melt or warming conditions, remain uncertain.

1. Introduction

The Gulf of Alaska drainage basin contains over 10 % of the world's mountain glaciers (Hood et al., 2009; Yang et al., 2020) that are melting at an alarming rate due to climate change, largely driven by anthropogenic carbon emissions (Hill et al., 2015). This melting has led to increased glacial discharge into the downstream, coastal estuaries (Neal et al., 2010; Larsen et al., 2015). About half of the freshwater runoff to the coasts on the Gulf of Alaska comes from glaciers and icefields, and this runoff provides 25–50% of the dissolved organic material (DOM) without much photochemical change (Neal et al., 2010; Hood et al., 2009). Glacial discharge is typically low in important labile dissolved nitrogen although flow through coniferous forest soil can increase the nitrogen content (Hood et al., 2009). Glacial discharge also supplies rare lithogenic minerals like phosphorus, calcium carbonate, silicate, and iron that can be otherwise limiting factors of growth, especially in large-bodied primary producers like kelp and rockweed (Hopwood et al., 2020). Glacial discharge also provides fresh and cold waters, and high turbidity from glacial flour or sediments transported from the glacier into the nearshore environment, influencing the estuarine taxa residing there (Arimitsu et al., 2016; Hopwood et al., 2020).

Fucus distichus, the Northern rockweed*,* is a dominant canopy-forming species in high-latitude intertidal systems along the Pacific coast (Jueterbock et al., 2016). *F. distichus* is a perennial species with a 2 to 5-year lifespan that is well-adapted to grow in environments with cold waters and long dark periods (Jueterbock et al., 2016). *Fucus* spp. are recognized as essential habitat providers, increasing local biodiversity, and thus increasing the complexity and productivity of the overall

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system (Wikström and Kautsky, 2007). Rockweeds such as *Fucus* spp. often occur in high densities in the upper intertidal and ameliorate stressful conditions for associated species from wind and temperature exposure (Bertness et al., 1999; Bulleri et al., 2002). *Fucus* spp. are primary producers that provide essential support to nearshore food webs, either directly for grazers or as particulate organic matter for suspension feeders (Worm et al., 2000; Siegert et al., 2022; Schloemer et al., 2023). Like many other brown algae, *Fucus* spp. can contain chemical defenses, mostly phlorotannins, against grazers, epiphytes, UV radiation effects, etc. (Peckol et al., 1996; Amsler and Fairhead, 2005). These adaptations make *Fucus* spp. a highly adaptive taxon to a range of environmental conditions or biotic pressures. However, differences in the biochemical composition of seaweeds can influence the degradation processes and, therefore, the quality of detrital matter that enters the food web from *Fucus* spp. (Lopes et al., 2011; Gilson et al., 2021).

The ability of *Fucus* spp. to maintain high levels of performance to support natural ecosystem functions depends largely on environmental influences (Wahl et al., 2011). Glacial discharge influences the nearshore environment where *Fucus* occurs in estuaries adjacent to glacierized watersheds. The glacial discharge delivers fresh and cold waters, high turbidity, but also the addition of nutrients (Arimitsu et al., 2016; Hopwood et al., 2020). Low salinity resulting from freshwater discharge can place high osmotic stress on marine macroalgae (Karsten, 2012), although the opposite has also been observed where high salinity negatively correlated with primary producer biomass since it can slow down metabolism (Spurkland and Iken, 2011). In *Fucus* spp., salinity is a recognized stressor (Wahl et al., 2011). For example, low salinity was the main driver to cause decline in thallus size, energy storage compounds, and chemical resistance to grazers in *F. vesiculosus* in the Baltic Sea (Barboza et al., 2019). Glacial discharge can increase nutrients in the nearshore system, which can promote primary production, although this is more pronounced in marine-terminating glaciers than the land-terminating glaciers studied here (Hopwood et al., 2020). Glacial melt in Alaska also releases legacy accumulations of bedrock-derived mercury from coastal watersheds to downstream environments (Nagorski et al., 2021). Heavy metals such as mercury compromised the growth of a number of species within the Fucales in Norway (Strömgren, 1980). Such effects from glacial discharge can strongly influence local population levels in *Fucus* spp. because of limited new recruitment based on the low dispersal ranges of microscopic stages (Coyer et al., 2008). A shift in the nearshore environmental conditions can then influence *Fucus* spp. success both at the recruitment as well as the adult stage (Worm et al., 2000). Such impacts from glacial discharge exposure can, therefore, have repercussions on the wider ecosystem functions of local *Fucus* spp. populations.

There are multiple ways how local *Fucus* spp. populations could respond to pressures from glacial discharge: they could tolerate a certain range of environmental stress based on acclimation and phenotypic plasticity; they could genetically adapt; or they could disappear from sites with unfavorable conditions (Wahl et al., 2011). As an example of phenotypic plasticity, photobiological variables, nutrient content, nitrate uptake, and oxidative stress descriptors of *F. distichus* from Alaska under controlled conditions in the laboratory did not differ among levels of temperature and irradiance (Umanzor et al., 2023). But such phenotypic plasticity is typically limited; for example, under more extreme low-salinity conditions, *F. vesiculosus* in the Baltic Sea became locally extinct (Barboza et al., 2019). These stress levels and reduced growth and survival can also lead to habitat fragmentation, where continuous *Fucus* bands in the intertidal become interrupted with bare substrate (Jonsson et al., 2018). This can pose a serious problem for the population-level persistence for *Fucus* spp. that have low potential for population recovery based on low dispersal ranges (Muhlin et al., 2008). The goal of this work was to evaluate the performance of *Fucus distichus* based on thallus condition metrics using a natural gradient of glacial cover in Alaskan watersheds. Specifically, we hypothesized that various metrics of thallus condition (e.g., elemental composition, lipid and protein content) would overall decrease with presumed increasing effects of glacial discharge, based on glacial cover of the watersheds. We expected glacial discharge to be higher in watersheds with higher glacial cover with more fresh, cold and turbid waters delivered into estuaries connected to watersheds with larger glacial mass. It was also expected that these influences would be larger during times of higher glacial discharge later in the summer. Thallus condition is ecologically important to evaluate the plants in terms of energy storage for growth, reproduction, as well as their quality as a food source for grazers and other feeders. The effort to relate this variation in performance with environmental conditions within the different watersheds will provide new insights into the capacity of *F. distichus* to respond to future environmental changes.

2. Methods

2.1. Study sites and F. distichus collections

This study was conducted in Kachemak Bay, south-central Alaska (Fig. 1). Kachemak Bay is located at the eastern side of Cook Inlet and receives water from the Gulf of Alaska; during the counter-clockwise circulation through Kachemak Bay, this water is modified by freshwater input from multiple watersheds, some of them heavily glaciated (Johnson, 2021). Kachemak Bay also experiences a tidal range exceeding 8 m that contributes to mixing processes within the bay (Muench et al., 1978) and that creates extensive intertidal areas. The bay contains numerous land-terminating glaciers and icefields, many of which are part of the Harding Icefield and Grewingk-Yalik Glacier Complex (Adalgeirsdottir et al., 1998; Yang et al., 2020), that discharge into the coastal system. Discharge effects of Alaskan glaciers (e.g., temperature, conductivity, turbidity) have been found to be correlated with the glacial cover of the watersheds (Hood and Berner, 2009). Therefore, the setting of the watersheds, ranging in area covered by glaciers from 0 to 60% (e.g., Jenckes et al., 2023), was used as a natural experiment to investigate the effects of environmental conditions associated with increasing glacial cover on *F. distichus* thallus condition. Specifically, watershed glacial coverage was: Jakolof 0%, Tutka 8%, Halibut 16%, Wosnesenski 27%, and Grewingk 60% (Fig. 1). This study was part of the EPSCoR (Established Program to Stimulate Competitive Research) "Fire & Ice" program at the University of Alaska Fairbanks (UAF), funded by the National Science Foundation, which was built on studying the effects of glacial cover on estuarine ecology.

Specific *F. distichus* collection sites were in close vicinity of the freshwater discharge point in each watershed, on cobble to bedrock beaches where *F. distichus* is the dominant macroalgal species in the upper intertidal (Konar et al., 2009; McCabe and Konar, 2021). Five distinct individuals of *F. distichus* per site were haphazardly collected during low tide in the upper intertidal zone along a 50-m transect. Individual samples were separated by several meters (dependent on the continuity of the plants along the transect) and included the growing, non-reproductive tips of the fronds. Samples were collected monthly from March to August 2021, spanning the time approximately before the onset of glacial discharge (March–May) to peak discharge (June/July) to the slowing of seasonal discharge (August) (Jenckes et al., 2023). Samples were kept frozen until later analysis in the home lab.

2.2. Thallus condition analyses

F. distichus samples (five individuals per month and sampling site) were thawed and briefly rinsed with tap water to remove sediment, epiphytic algae, and other contaminants. From each sample, a thallus piece of 0.25–1.5 g not containing reproductive tissue was subsampled for organic content calculations, and a second piece (~ 1 g) of distal, non-reproductive fronds was used of for the protein, lipid, and elemental composition analyses.

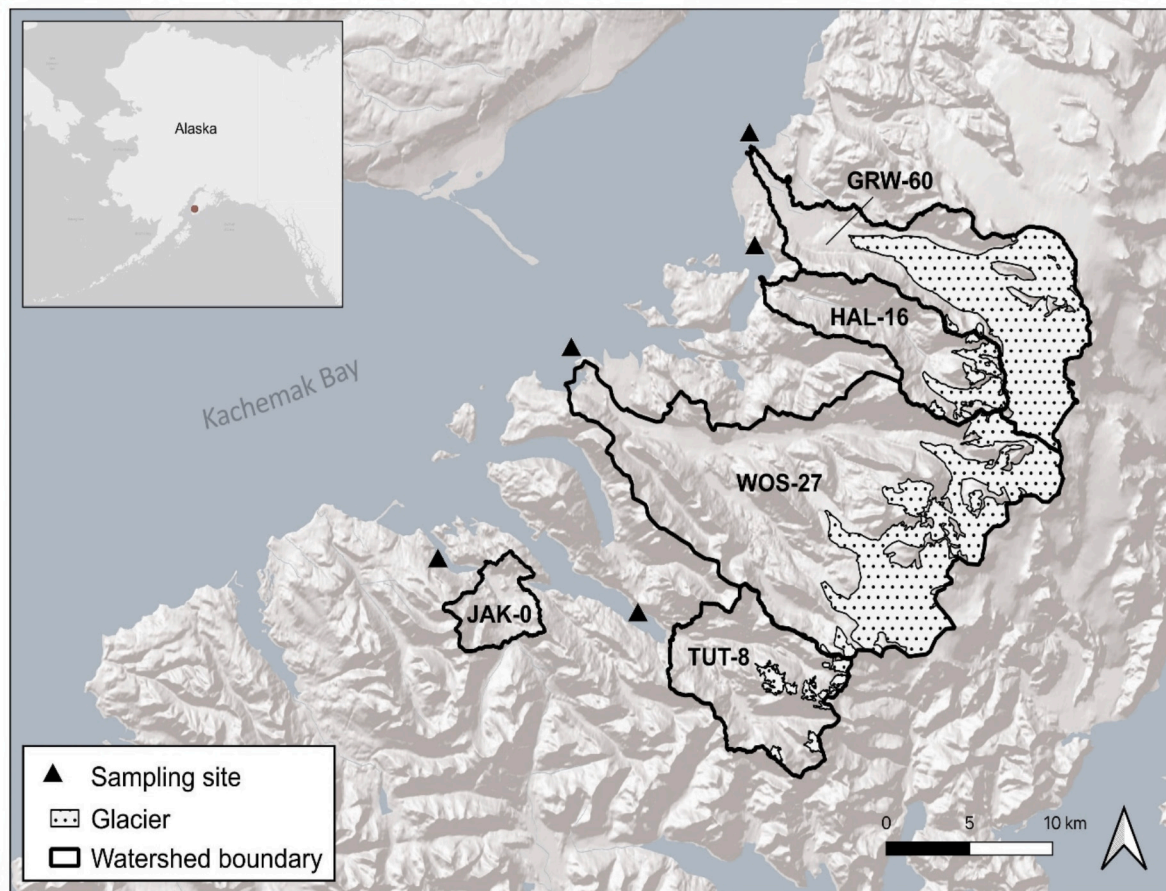The tissue pieces were patted dry of any external water and wet

Fig. 1. Map of the study region in Kachemak Bay, south-central Gulf of Alaska. Watersheds are delineated in black, with the glacier-covered areas in stippled shading. Collection sites for *Fucus distichus* are indicated in black triangles. Numbers after the site name abbreviations indicate the percent glacial cover of the watershed. JAK = Jakolof, TUT = Tutka, WOS = Wosnesenski, HAL – Halibut, GRW = Grewingk. Figure courtesy of J. Schloemer.

weight (WW) was determined. These pieces were then dried at 60 °C for at least 24 h or until constant weight and dry weight (DW) taken to determine dry weight yield:

$$DW\ (\%) = DW/WW \cdot 100 \tag{1}$$

These dried samples were then ashed at 500 °C for 5 h, weight of the remaining ash determined, and ash-free dry weight (AFDW) as a metric of the organic content in the sample calculated as:

$$AFDW\ (\%) = (DW–ash\ weight)/DW \cdot 100 \tag{2}$$

Other distal, non-reproductive branches from each *Fucus* sample were freeze-dried and homogenized to a powder using a pestle and mortar. Approximately 0.8–1.0 mg of thallus powder were weighed into small tin caps at the Alaska Stable Isotope Facility (ASIF) at the Water & Environmental Research Center (WERC) at UAF to determine their carbon and nitrogen composition. Analyzes were conducted on a continuous-flow isotope ratio mass spectrometry (CFIRMS) using a Thermo Scientific Flash 2000 elemental analyzer and Thermo Scientific Conflo IV interfaced with a Thermo Scientific DeltaV^{Plus} Mass Spectrometer. While these analyses are typically done to determine the stable carbon and nitrogen stable isotope composition, we were primarily interested in the output of carbon and nitrogen concentrations (% DW), from which we calculated the C/N ratio.

Protein content of each tissue sample was determined using a Bio-Rad® Standard Protein Assay kit. The assay uses bovine serum albumin (BSA) as the standard and Coomassie Brilliant Blue G-250 as the binding dye. Absorption was measured on a Thermo Spectronic Genesys 5 UV/Visible Spectrophotometer at 595 nm. Processing steps followed the manufacturer descriptions and protein content was expressed as % DW.

Total lipid was determined from a 0.5–1 mg aliquot of dried thallus tissue powder, following slightly modified protocols after Folch et al. (1957). Each sample was weighed into glass vials and soaked in an excess of 2:1 chloroform:methanol solution three times for about 2–4 h at room temperature. The supernatants from each treatment were combined into clean, pre-weighed glass scintillation vials per sample. Then, about 1 ml 0.9% NaCl solution was added, the mixture vortexed, and then let sit for about 15 min at room temperature for phase separation. The upper phase was carefully pipetted and discarded. The lower phase containing the isolated lipids was brought to dryness under a constant air stream (oxidation of lipids was not a concern for total lipid content determination). Total lipid weight was determined gravimetrically and expressed as % DW.

2.3. Environmental monitoring

Environmental data were collected at each study site and month on the shoreline at the same time as *F. distichus* collections. Water sampling was conducted about 5–15 m from shore at 1-m water depth using a handheld YSI Pro2030, which reported dissolved oxygen (DO, mg/l), salinity, and temperature (°C). In addition, a 60 ml water sample was taken at ~0.3 m depth and analyzed for turbidity on the collection day, using a Hach 2100P TurbidityMeter and reported as Nephelometric Turbidity Units (NTU).

2.4. Statistical analysis

The effects of site and month on the various thallus condition metrics were tested using two-way analysis of variance (ANOVA) with site and month as fixed factors, including the interaction effect. Significance level was set at α = 0.05. Prior to analysis, normality of data was tested using Shapiro-Wilk test. Data for DW, nitrogen concentration, and protein content were log-transformed, data for AFDW were log (x/1-x) transformed, data for carbon concentration and C/N ration were rank-transformed, and data for lipid and caloric content did not require transformation to achieve normal distributions.

Environmental variables were first explored for distribution and multi-collinearity. The distribution of the turbidity data was distorted by outliers and these data were log-transformed. Correlations among the environmental variables using Pearson correlations were all <0.65; hence, all predictor variables were retained for the analysis. The explanatory effect of environmental variables on individual *Fucus* thallus condition metrics (using above-mentioned transformations for normality) was explored using multiple linear regression with a backward selection procedure, based on the hypothesized linear effect of glacial cover influences. The significance level was set at α = 0.05.

The effects of environmental conditions on all *F. distichus* thallus condition metrics combined (multivariate) were also assessed with a distance-based redundancy analysis (dbRDA) (McArdle and Anderson, 2001). dbRDA applies multivariate multiple regression of principal co-ordinate axes on predictor variables and is constrained to linear relationships of the predictor variables that explain the greatest variability in a response dataset (Legendre and Anderson, 1999; McArdle and Anderson, 2001). For the dbRDA, both thallus condition data and environmental data, respectively, were normalized onto a common dimensionless scale by subtracting the mean (across all samples) from each variable value and dividing by the standard deviation of each variable (Clarke and Gorley, 2015). Both the fitted as well as the overall variation explained by axes are reported as well as axis loadings of the environmental variables on the first four dbRDA axes.

All univariate analyses (two-way ANOVA and multiple regressions) were conducted in R version 4.2.3 (R Core Team, 2023). All multivariate statistics were conducted with the Primer-e software V7. The *F. distichus* thallus condition data used in this study are available at: doi:10.24431/rw1k7dx

3. Results

3.1. Environmental conditions at F. distichus collection sites

Temperatures were relatively similar across sites for each month, despite some variation, but increased all sites increased over the study period (Fig. 2a). The greatest diversion from this increasing trend over time trend could be seen at Grewingk, where temperatures for April, May and July were similar. Salinity was highly variable at each site across months, except for similar salinities across all sites in August (Fig. 2b). Salinities tended to be particularly low at Tutka in most
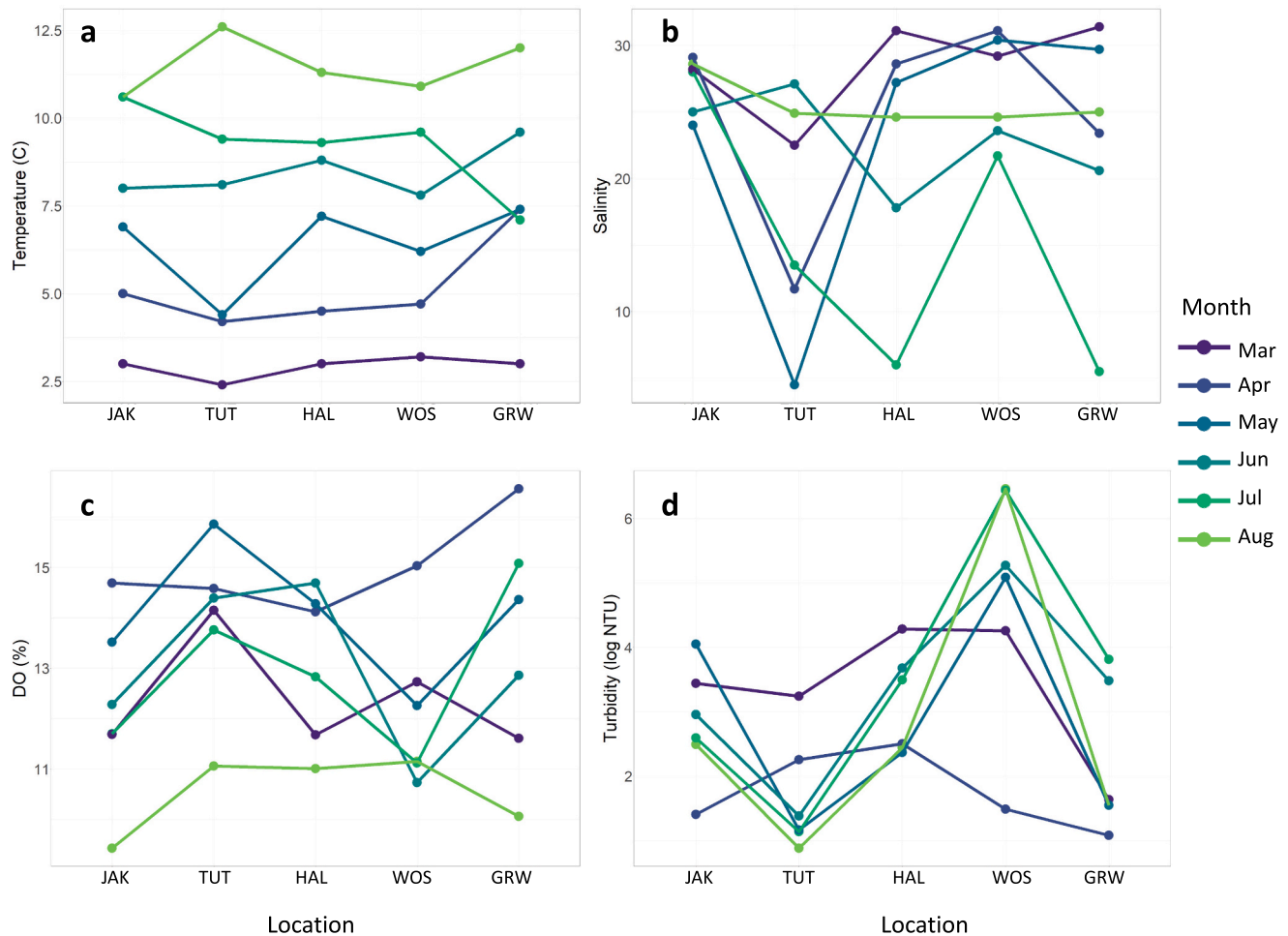

Fig. 2. Progression of environmental variables across the five study sites for six collection months. Environmental measurements were taken from the nearshore environment at the time of *Fucus distichus* sampling: a. temperature (°C); b. salinity; c. dissolved oxygen (DO; %); d. turbidity (log-transformed, Nephelometric Turbidity Units (NTU)).

months, and salinities in July at all sites dropped dramatically except the non-glacierized Jakolof site, where salinity did not change much over the sampling period. Dissolved oxygen levels differed much among sites and with no distinct trends over time, although there was a tendency of lowest oxygen levels in August (Fig. 2c). Turbidity tended to be high at Wosnesenski, especially during the later sampling months, while turbidity was relatively low during most months at Tutka (Fig. 2d).

3.2. Spatial and temporal patterns in F. distichus thallus condition metrics

All thallus condition metrics had strong, significant relationships with both site and month (two-way ANOVA, Table 1), although it differed by condition metric which factor had a greater influence. Briefly, metrics associated with weight and elemental composition were most influenced by the time component (month; indicated by higher F-statistics), while biochemical constituents (protein and lipids) were most influenced by the spatial component (site). The interaction effect also was significant in all cases, except for protein content (Table 1). DW yield was highly variable across sites and month (Fig. 3a) while AFDW and carbon content were more similar across sites and months (Fig. 3b, c). AFDW tended to be lower at Wosnesenski than other sites and increased at all sites over time, but with unusually low values at Halibut in March (Fig. 3b). C/N ratios increased over time, which matched both the increases in carbon concentration and decreases in nitrogen concentrations over time (Fig. 3c-e). Among the variables more influenced

Table 1

Results of two-way ANOVA on effect of site and sampling month on various thallus condition metrics. Significant *p*-values are in bold, and the stronger effect is shaded in grey.

Metric	Source	DF	SS	MS	F-value	P-value
DW	Site	4	0.55	0.14	8.39	**0.0001**
	Month	5	1.62	0.32	19.81	**<0.0001**
	SitexMonth	20	2.54	0.13	7.79	**<0.0001**
	Error	120	1.96	0.02		
	Total	149	6.66	0.05		
AFDW	Site	4	0.01	0.00	9.05	**<0.0001**
	Month	5	0.03	0.01	19.72	**<0.0001**
	SitexMonth	20	0.04	0.00	7.74	**<0.0001**
	Error	120	0.03	0.00		
	Total	149	0.12	0.00		
C conc.	Site	4	32302.87	8075.72	7.41	**<0.0001**
	Month	5	68289.23	13657.85	12.52	**0.0000**
	SitexMonth	20	49387.13	2469.36	2.26	**0.0035**
	Error	120	130863.60	1090.53		
	Total	149	280842.83	1884.85		
N conc.	Site	4	1.22	0.30	21.63	**<0.0001**
	Month	5	6.47	1.29	91.93	**0.0000**
	SitexMonth	20	2.11	0.11	7.48	**<0.0001**
	Error	120	1.69	0.01		
	Total	149	11.48	0.08		
C/N	Site	4	34212.43	8553.11	30.91	**0.0000**
	Month	5	176422.13	35284.43	127.52	**0.0000**
	SitexMonth	20	37397.73	1869.89	6.76	**<0.0001**
	Error	120	33203.20	276.69		
	Total	149	281235.49	1887.49		
Protein	Site	4	2.35	0.59	6.18	**0.0001**
	Month	5	1.15	0.23	2.42	**0.0393**
	SitexMonth	20	2.64	0.13	1.39	0.1412
	Error	120	11.39	0.09		
	Total	149	17.53	0.12		
Lipid	Site	4	1523.53	380.88	67.69	**0.0000**
	Month	5	305.18	61.04	10.85	**<0.0001**
	SitexMonth	20	444.11	22.21	3.95	**<0.0001**
	Error	120	675.26	5.63		
	Total	149	2948.08	19.79		

by site (Table 1), protein content tended to be highest at Grewingk but with otherwise little linear relationships to sites according to the percent glaciation of the watershed (Fig. 3f). Lipid content followed a generally decreasing trend with increasing watershed glacial cover, with highest lipid concentrations at Jakolof, intermediate at Tutka and Halibut, and lowest values at Wosnesenski and Grewingk (Fig. 3g).

3.3. Environmental correlates with Fucus thallus condition metrics

None of the environmental variables were significant predictors of either DW or AFDW (Table 2). Carbon concentration and C/N ratio were negatively related with turbidity and salinity and positively with temperature, and the reverse relationships existed for nitrogen concentration. In contrast, protein content was significantly negatively predicted by salinity, albeit with an extremely low coefficient of determination that is unlikely to be biologically relevant (Table 2). Lipid content was significantly negatively related to turbidity and temperature (Table 2).

In the dbRDA of all condition metrics with all environmental drivers, the first two axes combined explained a cumulative 97.2% of the fitted and 47.9% of the total variation (Fig. 4). Of these axes, the first explained by far the most variation (84.6% of fitted and 41.8% of total), with the second adding only 12.7% of fitted and 6.2% of total variation explanation (Table 3). The strongest predictor loadings of the first axis were a positive relationship with salinity (0.483) and negative with temperature (−0.834). The second axis was mostly positively related to the effect of turbidity (0.925) and a lesser, negative effect of DO (−0.323) (Table 3). The ordination of the combined thallus condition metrics by month and location were mostly arranged in a line along axis 1, in an arrangement of samples from April and May from high salinity at the positive end of axis 1 to samples from July and August associated with high temperatures at the negative end of axis 1 (Fig. 4). This arrangement included samples from all sites, confirming that overall thallus condition of *Fucus* was mostly driven by a seasonal transition of environmental variables. Only samples from July and August from Wosnesenski were clearly separated along axis 2, characterized by high turbidity.

4. Discussion

The critical ecological roles that rockweeds play globally as a key foundation species in intertidal systems and as a food source to coastal food webs may be threatened by changes occurring in marine systems due to climate warming, marine heatwaves, and increasing human impacts. We investigated the effects that environmental conditions of watersheds with variable glacial cover in Alaska may have on the thallus condition of *F. distichus*. Overall, instead of glacial cover of a watershed as a driver of *F. distichus* thallus condition, we found specific environmental drivers in each watershed to be related to various condition metrics, indicating more complex environmental controls than glacial cover of a watershed alone. Understanding these controls of *F. distichus* thallus conditions is important to gage their performance in providing ecosystem services and their quality as a food source in coastal food webs.

4.1. Patterns in F. distichus thallus condition metrics

We hypothesized that *F. distichus* thallus condition would, overall, linearly decrease with increasing higher glacial cover of the watersheds. Contrary to our expectation, trends in most thallus condition metrics, especially metrics related to weight and elemental composition, were associated more with the month of sampling rather than watershed. We had also hypothesized that thallus condition metrics that are indicative of nutritional value would be lower during times of greater glacial discharge, i.e., during the later collection months (Jenckes et al., 2023). For example, we saw an increase in AFDW over sampling months, similar to findings of higher AFDW later in the summer in other
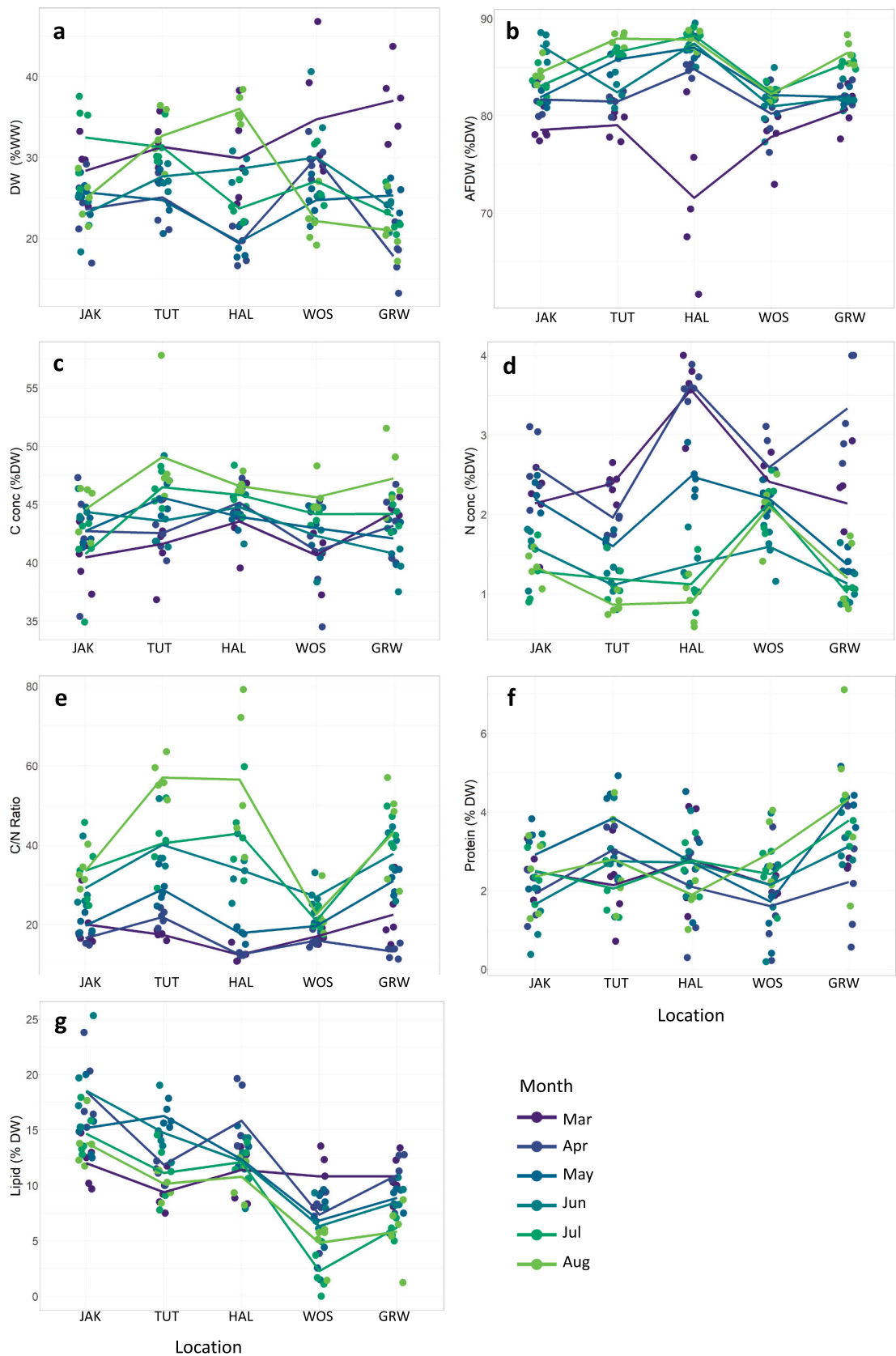
Fig. 3. Thallus condition metrics across five study sites and for six sampling months, indicated by colors: a. dry weight, b. ash-free dry weight, c. carbon concentration, d. nitrogen concentration, e. C/N ratio, f. protein content, and g. lipid content. Individual samples per site are indicated by dots and the line connects site means for each month.

Table 2

Multiple linear regression results, testing the influence of all environmental variables on each *Fucus distichus* thallus condition metric. Given are the overall regression equation, statistics of the overall regression, R^2 and adjusted R^2 values, as well as the specific predictor coefficients for each of the significant environmental variables. Significant p-values of the overall regressions are in bold.

DW	Regression equation	$\hat{Y} = 3.2605 + 0.0058\ Temp$	
	Overall statistics	$F_{1,\ 148} = 0.97, p = 0.325$	
	R^2	0.01	
	Adjut. R^2	0.00	
AFDW	Regression equation	$\hat{Y} = 0.5122 + 0.0008\ Temp$	
	Overall statistics	$F_{1,\ 148} = 1060, p = 0.305$	
	R^2	0.01	
	Adjut. R^2	0.00	
C conc.	Regression equation	$\hat{Y} = 74.7892\text{–}9.7871\ Log\ Turb - 1.1603\ Sal + 5.4354\ Temp$	
	Overall statistics	$F_{3,\ 146} = = 14.01,$ **p < 0.001**	
	R^2	0.22	
	Adjut. R^2	0.21	
	Predictor coefficients	*Log Turb*	$t = -2.218, p = 0.028$
		Sal	$t = -2.773, p = 0.006$
		Temp	$t = 5.025, p < 0.0001$
N conc.	Regression equation	$\hat{Y} = 1.0978 + 0.0671\ Log\ Turb + 0.0123\ Sal - 0.0611\ Temp$	
	Overall statistics	$F_{3,\ 146} = = 80.25,$ **p < 0.001**	
	R^2	0.62	
	Adjut. R^2	0.61	
	Predictor coefficients	*Log Turb*	$t = 3.411, p < 0.001$
		Sal	$t = 6.607, p < 0.001$
		Temp	$t = -12.681, p < 0.001$
C/N	Regression equation	$\hat{Y} = 62.7801\text{–}11.0675\ Log\ Turb - 2.0579\ Sal + 10.1822\ Temp$	
	Overall statistics	$F_{3,\ 146} = 116.19,$ **p < 0.001**	
	R^2	0.70	
	Adjut. R^2	0.69	
	Predictor coefficients	*Log Turb*	$t = -4.064, p < 0\ 0.001$
		Sal	$t = -7.971, p < 0.001$
		Temp	$t = 15.256, p < 0.001$
Protein	Regression equation	$\hat{Y} = 1.5074\text{–}0.0115\ Sal$	
	Overall statistics	$F_{1,\ 148} = 10.42, \mathbf{\mathit{p} = 0.002}$	
	R^2	0.007	
	Adjut. R^2	0.006	
	Predictor coefficients	*Sal*	$t = -3.216, p = 0.002$
Lipid	Regression equation	$\hat{Y} = 16.327763\text{–}2.5347\ Log\ Turb - 0.3068\ Temp$	
	Overall statistics	$F_{2,\ 147} = 19.32,$ **p < 0.001**	
	R^2	0.21	
	Adjut. R^2	0.20	
	Predictor coefficients	*Log Turb*	$t = -5.570, p < 0.001$
		Temp	$t = -2.771, p = 0.006$

macroalgae (e.g., Himmelman and Carefoot, 1975). AFDW is a measure of the organic, non-structural components in macroalgae (Kaehler and Kennish, 1996), where higher AFDW is typically thought to be associated with a higher nutritional quality in seaweeds, such as higher caloric content (Lamare and Wing, 2001; Weil et al., 2019). Much of our observed temporal increase in AFDW, however, occurred over the first two months of sampling (from April to May), coinciding with the start of the *Fucus* growing season (Lehvo et al., 2001) rather than the onset of glacial discharge (Jenckes et al., 2023).

An increase over sampling months was also seen in C/N ratios, mirrored by a temporal increase in carbon content and decrease in nitrogen content, where higher C/N ratios are considered to be of lower nutritional quality (Weykam et al., 1996; Peters et al., 2005). The C/N ratio in samples also reflects the availability of carbon and nitrogen in

the environment, with high C/N ratios indicating conditions that are more stressful and less conducive to growth (Xu et al., 2021). A typical baseline C/N ratio for marine macroalgae is around 18, with significantly higher ratios generally indicating lower tissue quality and more stressful environments (Atkinson and Smith, 1982). The C/N ratios in our samples were relatively high compared to that baseline, ranging from ~16 across all sites in April to ~42 in August. The increase in C/N ratio in *F. distichus* over the sampling period indicated decreasing nutritional quality, driven by the increase in carbon content and strong decrease in nitrogen content in our samples over the summer. High-latitude *F. vesiculosus* is known to mobilize internal nitrogen stores at the beginning of their growing season into the summer, with limited replenishment due to decreased ambient nitrogen stores due to summer nutrient draw-down (Lehvo et al., 2001).

The observed increase in C/N ratio could also result in a decrease in nitrogen-containing components like proteins and in an increase in carbon-based compounds, such as cell wall components or lipids. Contrary to that, protein content did not change noticeably or consistently over the course of the sampling period and lipid content decreased. If the increase in carbon content and decrease in C/N ratio over time is not related to lipids, these patterns could be associated with an increase in phlorotannins. Phlorotannins are a common brown algal constituent composed of phloroglucinol polymers that strengthen cell walls and also exhibit a range of secondary functions such as herbivore defense, anti-fouling agents, and UV protection, among others (Amsler and Fairhead, 2005). *Fucus* spp. are known for high levels of phlorotannins (Pavia and Toth, 2000; Jormalainen and Honkanen, 2004; Koivikko et al., 2005), including *F. distichus* from Alaska (Kellogg et al., 2014). Phlorotannin levels in *Fucus* spp. in other temperate and high-latitude systems increased seasonally with longer daylight hours and warmer temperatures, and higher phlorotannins were correlated with lower tissue nitrogen levels (Pavia and Toth, 2000; Dethier and Williams, 2009; Bogolitsyn et al., 2023). Therefore, it is possible that the patterns in C/N and increase in tissue carbon we saw in our study could be related to seasonally higher phlorotannin production. It would be useful in future studies to confirm spatial and temporal patterns of phlorotannin content in *F. distichus* in our study system.

The only thallus condition metrics more influenced by location than time were related to the biochemical content, i.e., protein and lipid contents. Of these, protein content tended to be higher at Grewingk, especially during later sampling months, and also Tutka, while it was lowest at Wosnesenski. Thus, protein content did not follow the hypothesized linear trend with glacial coverage of the watershed and may rather be related to other site-specific environmental factors. The overall range of protein in *F. distichus* in our samples was relatively low compared to that found in many other *Fucus* species (e.g., 10–17% DW in various other *Fucus* species versus 0.2–7.1% in our samples; Lorenzo et al., 2017; Catarino et al., 2018), although our values were similar to those found in *F. vesiculosus* from the Arctic White Sea (Bogolitsyn et al., 2023). High protein content in *Fucus* spp. is considered to be an important component of nutritional quality of this seaweed genus in human food supplement applications (Catarino et al., 2018). Hence, the slightly higher protein content at the site with the highest glacial cover indicates an opposite trend, if any, to our hypothesized inverse relationship between glacial cover and thallus condition.

Lipid content was the only thallus condition metric that reflected the hypothesized spatial trend, with higher values at the non-glacierized Jakolof watershed, and lowest values at the watershed sites with the highest glacial cover, Wosnesenski and Grewingk. This would suggest lower energy content of *F. distichus* at the sites with higher glacial cover, based on the high energy content of lipids (D'Armas et al., 2019). However, the range of total lipid content across all our samples was much higher than reported for many other *Fucus* or other rockweed species (Lorenzo et al., 2017; Catarino et al., 2018), although *Fucus* is known to be lipid rich compared to many other brown algae (Bogolitsyn et al., 2023). The overall high lipid content would suggest generally high
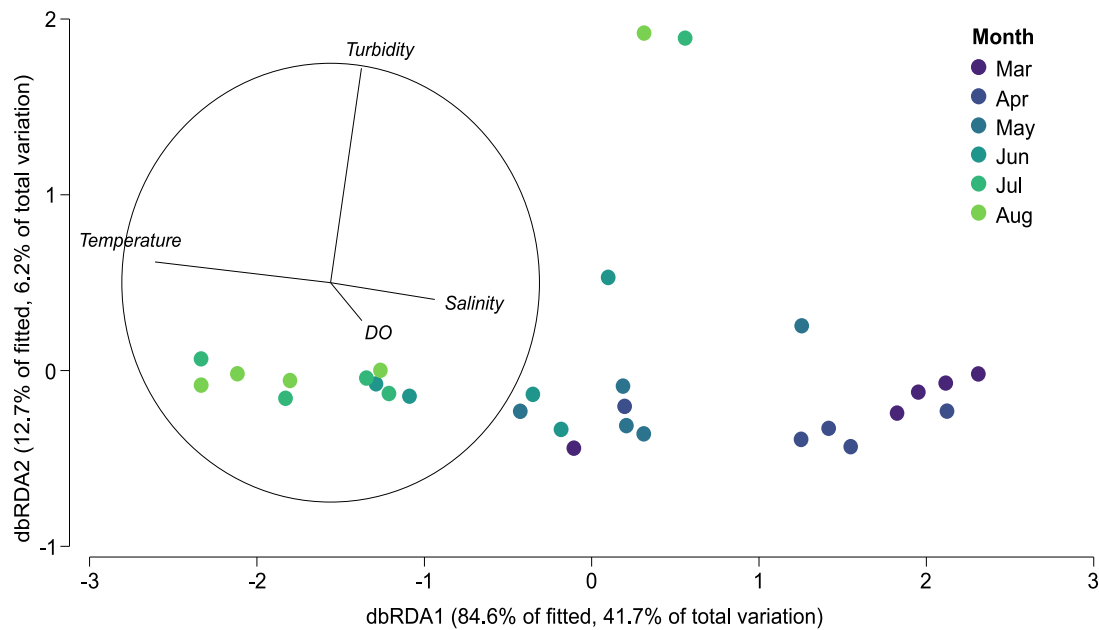
Fig. 4. Distance-based redundancy analysis (dbRDA) ordination of combined *F. distichus* thallus condition metrics. Each point is the mean of all thallus condition metrics at a site (mean of $n = 5$ replicates) and color represents sampling month. Axis values in parentheses show fitted and total explained variance. Predictor variables are represented as vectors, with length relative to maximum predictor strength (circle).

Table 3
Results of distance-based redundancy analysis (dbRDA) for the first four axes, with the specific axis loadings for each of the environmental variables. DO = dissolved oxygen.

dbRDA	% explained variation fitted	% explained variation total
Axis 1	84.57	41.66
Axis 2	12.65	6.23
Axis 3	1.98	0.98
Axis 4	0.79	0.39

Predictor	Axis 1	Axis 2	Axis 3	Axis 4
Turbidity	0.246	0.925	0.232	−0.174
DO	0.103	−0.323	0.742	−0.578
Salinity	0.483	−0.096	−0.600	−0.631
Temperature	−0.834	0.177	−0.188	−0.487

energy content across all sites and seasons in our samples. Macroalgal lipids, and of rockweeds in particular, are known to contain many essential fatty acids (e.g., omega-3 polyunsaturated fatty acids) that are an important source for consumers (Garcia-Vaquero et al., 2021; Bogolitsyn et al., 2023). Future studies investigating the fatty acid profiles of *F. distichus* in the study region would be particularly useful. This could indicate that *F. distichus* from Kachemak Bay could generally contribute high-quality nutrition to consumers in the coastal food web (Schloemer et al., 2023), particularly early in the season and at locations with less glacial influence. The decline in lipid content over sampling months can also be related to the onset of the reproductive cycle of *F. distichus* (Ang Jr, 1991), as macroalgal gamete release is known to expend lipid stores (Renaud and Luong-Van, 2006).

4.2. Environmental drivers in F. distichus thallus condition

Contrary to the expectation of our hypothesis, patterns in thallus conditions mostly did not correlate to glacial cover in a linear fashion, although glacial discharge effects have been suggested to correlate with glacial cover (Hood and Berner, 2009). For example, *F. distichus* AFDW or C/N ratio in most month was lower at Wosnesenski (27% glaciation)

than at Halibut (16% glaciation) and Grewingk (60% glaciation). In other metrics, we did not find any distinctive site trends across all watersheds (e.g., dry weight). This suggests that the glacial cover of a watershed alone is not a useful proxy for the environmental conditions *F. distichus* experiences in these watersheds. Instead, most thallus condition metrics were related to individual environmental variables occurring in the watersheds that varied independently from glacial cover among watersheds. We tested the effects of multiple environmental variables that are often associated with glacial discharge on the thallus condition of *F. distichus*. Discharge from land-terminating glaciers in Alaska provide cold, fresh and turbid waters to the coastal environment (Fellman et al., 2015), with specific patterns strongly influenced by the seasonal progression of glacial melt and discharge (Jenckes et al., 2023). The only thallus condition metrics not associated with any of the environmental variables tested in this study were DW and AFDW. Conversely, the environmental variable not associated with any of the thallus condition metrics was DO, likely because the mixing associated with strong tidal exchange in the region prevents oxygen depletion (Muench et al., 1978). Salinity and temperature were major drivers of several thallus condition metrics, typically in opposite directions when both variables had an effect. That was especially the case with the C/N ratio and the associated carbon and nitrogen contents, where the negative relationship with salinity (higher C/N ratios at lower salinities) and positive relationship with temperature (higher C/N ratios at higher temperatures) are reflective of the seasonal progression. The least effect was from turbidity, but influenced thallus conditions similarly as salinity. The two biochemical metrics (protein and lipids) were not driven by the same variables, where protein associated with salinity, although the low explanatory power of this relationship is unlikely to be biologically relevant. In contrast, lipid content was related to turbidity and temperature, where turbidity had a larger effect than temperature.

Waters from glacial discharge are characterized by low temperature, low salinity and high turbidity. However, despite the increase in discharge over our sampling period (Jenckes et al., 2023), nearshore water temperatures actually increased (by about 10 °C from March to August) rather than decreased. Likely, seasonal warming of coastal waters superseded any cooling effects from discharge. The steep seasonal temperature increases likely directly facilitated some of the

composition changes that we propose to be associated with the onset of growth and the reproductive season of *F. distichus* (Lehvo et al., 2001; Keser et al., 2005; Graiff et al., 2015). Of course, phenological cues for reproduction from longer summertime day length, rather than temperature increase, could also be responsible for some of the changes in carbon and nitrogen concentrations (Pearson and Brawley, 1996). The observed lower lipid content later in the season may also, in part, be due to the coincident reproductive cycle of *F. distichus*, which releases gametes during the summer months and may expend its lipid stores during its proliferation (Renaud and Luong-Van, 2006). If some of the changes in carbon and nitrogen content were indeed associated with phlorotannin production, as suggested above, these could also be related to more light exposure as this is a known driver of increased phlorotannin levels in *Fucus* (Pavia and Toth, 2000). While turbidity may interfere with any light clues, *F. distichus'* high intertidal niche allows it to live in shallower waters where light regimes are likely not limiting for growth, contrary to limitations for subtidal species (Dethier and Williams, 2009; Wahl et al., 2011). This may explain the relatively small effect of turbidity on these metrics, except for lipid content. High turbidity was particularly prominent at the more glacierized sites (Wosnesenski and Grewingk) later in the sampling season and the increased shading from turbid waters may have contributed to either limited build-up of large lipid stores or increased mobilization of lipids to maintain other metabolic functions.

In contrast to temperature, the variability and overall decrease in salinity over the sampling season were likely associated with the seasonally increasing discharge of glacial freshwater. Salinity has been identified as the largest stressor of *Fucus* spp. across many geographical regions, affecting distribution, morphology, photosynthesis, growth, and reproduction, among others (e.g., Ruuskanen and Bäck, 1999; Wahl et al., 2011; Barboza et al., 2019; Cotas et al., 2019; Romoth et al., 2019). In our study, salinity was a driver of carbon and nitrogen tissue concentrations as well as protein concentrations, although the effect on protein was small despite its statistical significance. Higher protein content at lower salinities, like in our study, was also detected in *F. vesiculosus* and considered a stress response (Munda and Hudnik, 1988).

5. Conclusions

We investigated thallus condition of *F. distichus* in relation to glacial influences in a high-latitude system; while thallus conditions were related to environmental variables that are modulated by both seasonal changes and glacial discharge, these variables did not relate linearly to the gradient in glacial cover of the watersheds. Overall, however, thallus condition was more influenced by collection time than by the specific location, reflecting seasonal changes related to growth and reproduction. These findings are similar to responses of the same species in photophysiological characteristics to similar gradients in high-latitude glacial watershed cover in Southeast Alaska (Umanzor et al., 2023). This indicates that *F. distichus* is overall relatively tolerant to the environmental conditions they currently experience along a range of glacial discharge conditions in Alaskan watersheds. As an intertidal species, resilience to a large range of environmental conditions is common but there are limits to that resilience (e.g., Rugiu et al., 2018; Raymond et al., 2022), and sublethal effects on population genetics, or effects on different life stages (e.g., zygotes), can erode the resilience of a species to continued environmental pressures from a changing climate (Pearson and Brawley, 1996; Coyer et al., 2008; Jormalainen et al., 2017; Barboza et al., 2019). We tested a limited array of environmental variables and extending those to include others, such as variables related to ocean acidification, would be particularly valuable (Gutow et al., 2014; Graiff et al., 2017), especially given that glacial discharge is low in alkalinity (Reisdorph and Mathis, 2014). Heat waves are another environmental perturbation that is known to affect *F. distichus* abundance (Weitzman et al., 2021). In summary, thallus condition metrics are important to assess *Fucus* spp.'

ability to invest resources into vital functions (growth, reproduction, defense) so that critical ecological functions as a habitat provider and a food resource for the coastal food web can be maintained (Wahl et al., 2011; Bahamonde et al., 2022; Schloemer et al., 2023).

CRediT authorship contribution statement

Michael A. Kim: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Katrin Iken:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, 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 are availabke as Iken, K. (2023). Fucus distichus body condition, Kachemak Bay 2021. Dataset. doi: 10.24431/rw1k7dx

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References

Adalgeirsdottir, G., Echelmeyer, K.A., Harrison, W.D., 1998. Elevation and volume changes on the Harding icefield, Alaska. J. Glaciol. 44 (148), 570–582. https://doi.org/10.3189/S0022143000002082.

Amsler, C.D., Fairhead, V.A., 2005. Defensive and sensory chemical ecology of brown algae. Adv. Bot. Res. 43, 1–91. https://doi.org/10.1016/S0065-2296(05)43001-3.

Ang Jr., P.O., 1991. Natural dynamics of a *Fucus distichus* (Phaeophyceae, Fucales) population: reproduction and recruitment. Mar. Ecol. Prog. Ser. 78 (1), 71–85. https://www.jstor.org/stable/24827008.

Arimitsu, M.L., Piatt, J.F., Mueter, F., 2016. Influence of glacier runoff on ecosystem structure in Gulf of Alaska fjords. Mar. Ecol. Prog. Ser. 560, 19–40. https://doi.org/10.3354/meps11888.

Atkinson, M., Smith, S., 1982. C:N:P ratios of benthic marine plants. Limnol. Oceanogr. 28 (3), 568–574. https://doi.org/10.4319/lo.1983.28.3.0568.

Bahamonde, F., Rodríguez, J.P., Rosenfeld, S., Mendez, F., Lopez, Z., Gerard, K., Mansilla, A., 2022. Variability at multiple spatial scales in intertidal and subtidal macrobenthic communities in a fjord with glaciers, Magellanic Subantarctic ecoregion, Chile. Prog. Oceanogr. 208, 102879 https://doi.org/10.1016/j.pocean.2022.102879.

Barboza, F.R., Kotta, J., Weinberger, F., Jormalainen, V., Kraufvelin, P., Molis, M., Schubert, H., Pavia, H., Nylund, G.M., Kautsky, L., Schagerström, E., 2019. Geographic variation in fitness-related traits of the bladderwrack *Fucus vesiculosus* along the Baltic Sea-North Sea salinity gradient. Ecol. Evol. 9 (16), 9225–9238. https://doi.org/10.1002/ece3.5470.

Bertness, M.D., Leonard, G.H., Levine, J.M., Schmidt, P.R., Ingraham, A.O., 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology 80 (8), 2711–2726. https://doi.org/10.1890/0012-9658(1999)080[2711:TTRCOP]2.0.CO;2.

Bogolitsyn, K., Parshina, A., Ivanchenko, N., Polomarchuk, D., 2023. Seasonal variations in the chemical composition of Arctic brown macroalgae. Algal Res. 72, 103112 https://doi.org/10.1016/j.algal.2023.103112.

Bulleri, F., Benedetti-Cecchi, L., Acunto, S., Cinelli, F., Hawkins, S.J., 2002. The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the Northwest Mediterranean. J. Exp. Mar. Biol. Ecol. 267 (1), 89–106. https://doi.org/10.1016/S0022-0981(01)00361-6.

Catarino, M.D., Silva, A.M., Cardoso, S.M., 2018. Phycochemical constituents and biological activities of *Fucus* spp. Mar. Drugs 16 (8), 249. https://doi.org/10.3390/md16080249.

Clarke, K.R., Gorley, R.N., 2015. PRIMER v7: User Manual/Tutorial PRIMER-E: Plymouth.

Cotas, J., Figueirinha, A., Pereira, L., Batista, T., 2019. The effect of salinity on *Fucus ceranoides* (Ochrophyta, Phaeophyceae) in the Mondego River (Portugal). J. Oceanol. Limnol. 37, 881–891. https://doi.org/10.1007/s00343-019-8111-3.

Coyer, J.A., Hoarau, G., Sjøtun, K., Olsen, J.L., 2008. Being abundant is not enough: a decrease in effective population size over eight generations in a Norwegian population of the seaweed, *Fucus serratus*. Biol. Lett. 4 (6), 755–757. https://doi.org/10.1098/rsbl.2008.0403.

D'Armas, H., Jaramillo, C., D'Armas, M., Echavarría, A., Valverde, P., 2019. Proximate composition of several macroalgae from the coast of Salinas Bay, Ecuador. Rev. Biol. Trop. 67 (1), 61–68. https://doi.org/10.15517/rbt.v67i1.33380.

Dethier, M.N., Williams, S.L., 2009. Seasonal stresses shift optimal intertidal algal habitats. Mar. Biol. 156, 555–567. https://doi.org/10.1007/s00227-008-1107-8.

Fellman, J.B., Hood, E., Dryer, W., Pyare, S., 2015. Stream physical characteristics impact habitat quality for Pacific salmon in two temperate coastal watersheds. PLoS One 10 (7), e0132652. https://doi.org/10.1371/journal.pone.0132652.

Folch, J., Lees, M., Sloane Stanley, G.H., 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226 (1), 497–509.

Garcia-Vaquero, M., Rajauria, G., Miranda, M., Sweeney, T., Lopez-Alonso, M., O'Doherty, J., 2021. Seasonal variation of the proximate composition, mineral content, fatty acid profiles and other phytochemical constituents of selected brown macroalgae. Mar. Drugs 19 (4), 204. https://doi.org/10.3390/md19040204.

Gilson, A.R., Smale, D.A., Burrows, M.T., O'Connor, N.E., 2021. Spatio-temporal variability in the deposition of beach-cast kelp (wrack) and inter-specific differences in degradation rates. Mar. Ecol. Prog. Ser. 674, 89–102. https://doi.org/10.3354/meps13825.

Graiff, A., Bartsch, I., Ruth, W., Wahl, M., Karsten, U., 2015. Season exerts differential effects of ocean acidification and warming on growth and carbon metabolism of the seaweed *Fucus vesiculosus* in the western Baltic Sea. Front. Mar. Sci. 2, 112. https://doi.org/10.3389/fmars.2015.00112.

Graiff, A., Dankworth, M., Wahl, M., Karsten, U., Bartsch, I., 2017. Seasonal variations of *Fucus vesiculosus* fertility under ocean acidification and warming in the western Baltic Sea. Bot. Mar. 60 (3), 239–255. https://doi.org/10.1515/bot-2016-0081.

Gutow, L., Rahman, M.M., Bartl, K., Saborowski, R., Bartsch, I., Wiencke, C., 2014. Ocean acidification affects growth but not nutritional quality of the seaweed *Fucus vesiculosus* (Phaeophyceae, Fucales). J. Exp. Mar. Biol. Ecol. 453, 84–90. https://doi.org/10.1016/j.jembe.2014.01.005.

Hill, D.F., Bruhis, N., Calos, S.E., Arendt, A., Beamer, J., 2015. Spatial and temporal variability of freshwater discharge into the Gulf of Alaska. J. Geophys. Res.-Oceans 120 (2), 634–646. https://doi.org/10.1002/2014JC010395.

Himmelman, J.H., Carefoot, T.H., 1975. Seasonal changes in calorific value of three Pacific coast seaweeds, and their significance to some marine invertebrate herbivores. J. Exp. Mar. Biol. Ecol. 18 (2), 139–151. https://doi.org/10.1016/0022-0981(75)90070-2.

Hood, E., Berner, L., 2009. Effects of changing glacial coverage on the physical and biogeochemical properties of coastal streams in southeastern Alaska. J. Geophys. Res.-Biogeo. 114, G03001. https://doi.org/10.1029/2009JG000971.

Hood, E., Fellman, J., Spencer, R.G., Hernes, P.J., Edwards, R., D'Amore, D., Scott, D., 2009. Glaciers as a source of ancient and labile organic matter to the marine environment. Nature 462 (7276), 1044–1047. https://doi.org/10.1038/nature08580.

Hopwood, M.J., Carroll, D., Dunse, T., Hodson, A., Holding, J.M., Iriarte, J.L., Ribeiro, S., Achterberg, E.P., Cantoni, C., Carlson, D.F., Chierici, M., 2020. How does glacier discharge affect marine biogeochemistry and primary production in the Arctic? Cryosphere 14 (4), 1347–1383. https://doi.org/10.5194/tc-14-1347-2020.

Jenckes, J., Munk, L.A., Ibarra, D.E., Boutt, D.F., Fellman, J., Hood, E., 2022. Hydroclimate drives seasonal riverine export across a gradient of glacierized high-latitude coastal catchments. Water Resour. Res. https://doi.org/10.1029/2022WR033305 e2022WR033305.

Johnson, M.A., 2021. Subtidal surface circulation in lower cook inlet and Kachemak Bay, Alaska. Reg. Stud. Mar. Sci. 41, 101609 https://doi.org/10.1016/j.rsma.2021.101609.

Jonsson, P.R., Kotta, J., Andersson, H.C., Herkül, K., Virtanen, E., Sandman, A.N., Johannesson, K., 2018. High climate velocity and population fragmentation may constrain climate-driven range shift of the key habitat former *Fucus vesiculosus*. Divers. Distrib. 24 (7), 892–905. https://doi.org/10.1111/ddi.12733.

Jormalainen, V., Honkanen, T., 2004. Variation in natural selection for growth and phlorotannins in the brown alga *Fucus vesiculosus*. J. Evol. Biol. 17 (4), 807–820. https://doi.org/10.1111/j.1420-9101.2004.00715.x.

Jormalainen, V., Danelli, M., Gagnon, K., Hillebrand, H., Rothäusler, E., Salminen, J.P., Sjöroos, J., 2017. Genetic variation of a foundation rockweed species affects associated communities. Ecology 98 (11), 2940–2951. https://doi.org/10.1002/ecy.2002.

Jueterbock, A., Smolina, I., Coyer, J.A., Hoarau, G., 2016. The fate of the Arctic seaweed *Fucus distichus* under climate change: an ecological niche modeling approach. Ecol. Evol. 6 (6), 1712–1724. https://doi.org/10.1002/ece3.2001.

Kaehler, S., Kennish, R., 1996. Summer and winter comparisons in the nutritional value of marine macroalgae from Hong Kong. Bot. Mar. 39, 11–17. https://doi.org/10.1515/botm.1996.39.1-6.11.

Karsten, U., 2012. Seaweed acclimation to salinity and desiccation stress. In: Wiencke, C., Bischof, K. (Eds.), Seaweed Biology: Novel Insights into Ecophysiology, Ecology and Utilization. Springer Berlin Heidelberg, Berlin, pp. 87–107.

Kellogg, J., Grace, M.H., Lila, M.A., 2014. Phlorotannins from Alaskan seaweed inhibit carbolytic enzyme activity. Mar. Drugs 12 (10), 5277–5294. https://doi.org/10.3390/md12105277.

Keser, M., Swenarton, J.T., Foertch, J.F., 2005. Effects of thermal input and climate change on growth of *Ascophyllum nodosum* (Fucales, Phaeophyceae) in eastern Long Island sound (USA). J. Sea Res. 54, 211–220. https://doi.org/10.1016/j.seares.2005.05.001.

Koivikko, R., Loponen, J., Honkanen, T., Jormalainen, V., 2005. Contents of soluble, cell-wall-bound and exuded phlorotannins in the brown alga *Fucus vesiculosus*, with implications on their ecological functions. J. Chem. Ecol. 31, 195–212. https://doi.org/10.1007/s10886-005-0984-2.

Konar, B., Iken, K., Edwards, M., 2009. Depth-stratified community zonation patterns on Gulf of Alaska rocky shores. Mar. Ecol. 30 (1), 63–73. https://doi.org/10.1111/j.1439-0485.2008.00259.x.

Lamare, M.D., Wing, S.R., 2001. Calorific content of New Zealand marine macrophytes. New Zeal. J. Mar. Fresh. Res. 35 (2), 335–341. https://doi.org/10.1080/00288330.2001.9517004.

Larsen, C.F., Burgess, E., Arendt, A.A., O'Neel, S., Johnson, A.J., Kienholz, C., 2015. Surface melt dominates Alaska glacier mass balance. Geophys. Res. Lett. 42 (14), 5902–5908. https://doi.org/10.1002/2015GL064349.

Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecol. Monogr. 69 (1), 1–24. https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2.

Lehvo, A., Bäck, S., Kiirikki, M., 2001. Growth of *Fucus vesiculosus* L. (Phaeophyta) in the northern Baltic proper: energy and nitrogen storage in seasonal environment. Bot. Mar. 44, 345–350. https://doi.org/10.1515/BOT.2001.044.

Lopes, M.L., Martins, P., Ricardo, F., Rodrigues, A.M., Quintino, V., 2011. *In situ* experimental decomposition studies in estuaries: a comparison of *Phragmites australis* and *Fucus vesiculosus*. Estuar. Coast. Shelf Sci. 92 (4), 573–580. https://doi.org/10.1016/j.ecss.2011.02.014.

Lorenzo, J.M., Agregán, R., Munekata, P.E., Franco, D., Carballo, J., Şahin, S., Lacomba, R., Barba, F.J., 2017. Proximate composition and nutritional value of three macroalgae: *Ascophyllum nodosum*, *Fucus vesiculosus* and *Bifurcaria bifurcata*. Mar. Drugs 15 (11), 360. https://doi.org/10.3390/md15110360.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82 (1), 290–297. https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2.

McCabe, M.K., Konar, B., 2021. Influence of environmental attributes on intertidal community structure in glacial estuaries. Deep-Sea Res. II 194, 104986. https://doi.org/10.1016/j.dsr2.2021.104986.

Muench, R.D., Mofjeld, H.O., Charnell, R.L., 1978. Oceanographic conditions in lower cook inlet: spring and summer 1973. J. Geophys. Res.-Oceans 83 (C10), 5090–5098. https://doi.org/10.1029/JC083iC10p05090.

Muhlin, J.F., Engel, C.R., Stessel, R., Weatherbee, R.A., Brawley, S.H., 2008. The influence of coastal topography, circulation patterns, and rafting in structuring populations of an intertidal alga. Mol. Ecol. 17 (5), 1198–1210. https://doi.org/10.1111/j.1365-294X.2007.03624.x.

Munda, I.M., Hudnik, V., 1988. The effects of Zn, Mn, and co accumulation on growth and chemical composition of *Fucus vesiculosus* L under different temperature and salinity conditions. Mar. Ecol. 9 (3), 213–225. https://doi.org/10.1111/j.1439-0485.1988.tb00329.x.

Nagorski, S.A., Vermilyea, A.W., Lamborg, C.H., 2021. Mercury export from glacierized Alaskan watersheds as influenced by bedrock geology, watershed processes, and atmospheric deposition. Geochim. Cosmochim. Acta 304, 32–49. https://doi.org/10.1016/j.gca.2021.04.003.

Neal, E.G., Hood, E., Smikrud, K., 2010. Contribution of glacier runoff to freshwater discharge into the Gulf of Alaska. Geophys. Res. Lett. 37 (6), L06404. https://doi.org/10.1029/2010GL042385.

Pavia, H., Toth, G.B., 2000. Influence of light and nitrogen on the phlorotannin content of the brown seaweeds *Ascophyllum nodosum* and *Fucus vesiculosus*. Hydrobiol 440 (1–3), 299–305. https://doi.org/10.1023/A:1004152001370.

Pearson, G.A., Brawley, S.H., 1996. Reproductive ecology of *Fucus distichus* (Phaeophyceae): an intertidal alga with successful external fertilization. Mar. Ecol. Prog. Ser. 143, 211–223. https://doi.org/10.3354/meps143211.

Peckol, P., Krane, J.M., Yates, J.L., 1996. Interactive effects of inducible defense and resource availability on phlorotannins in the North Atlantic brown alga *Fucus vesiculosus*. Mar. Ecol. Prog. Ser. 138, 209–217. https://doi.org/10.3354/meps138209.

Peters, K.J., Amsler, C.D., Amsler, M.O., McClintock, J.B., Dunbar, R.B., Baker, B.J., 2005. A comparative analysis of the nutritional and elemental composition of macroalgae from the western Antarctic peninsula. Phycologia 44 (4), 453–463. https://doi.org/10.2216/0031-8884(2005)44[453:ACAOTN]2.0.CO;2.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL. https://www.R-project.org/.

Raymond, W.W., Barber, J.S., Dethier, M.N., Hayford, H.A., Harley, C.D., King, T.L., Paul, B., Speck, C.A., Tobin, E.D., Raymond, A.E., McDonald, P.S., 2022. Assessment of the impacts of an unprecedented heatwave on intertidal shellfish of the Salish Sea. Ecology 103 (10), e3798. https://doi.org/10.1002/ecy.3798.

Reisdorph, S.C., Mathis, J.T., 2014. The dynamic controls on carbonate mineral saturation states and ocean acidification in a glacially dominated estuary. Estuar. Coast. Shelf Sci. 144, 8–18. https://doi.org/10.1016/j.ecss.2014.03.018.

Renaud, S., Luong-Van, J., 2006. Seasonal variation in the chemical composition of tropical Australian marine macroalgae. In: Proc. 18th Int. Seaweed Symp, 1, pp. 155–161. https://doi.org/10.1007/s10811-006-9034-x.

Romoth, K., Nowak, P., Kempke, D., Dietrich, A., Porsche, C., Schubert, H., 2019. Acclimation limits of *Fucus evanescens* along the salinity gradient of the southwestern Baltic Sea. Bot. Mar. 62 (1), 31–42. https://doi.org/10.1515/bot-2018-0098.

Rugiu, L., Manninen, I., Rothäusler, E., Jormalainen, V., 2018. Tolerance and potential for adaptation of a Baltic Sea rockweed under predicted climate change conditions. Mar. Environ. Res. 134, 76–84. https://doi.org/10.1016/j.marenvres.2017.12.016.

Ruuskanen, A., Bäck, S., 1999. Morphological variation of northern Baltic Sea *Fucus vesiculosus* L. Ophelia 50 (1), 43–59. https://doi.org/10.1080/00785326.1999.10409388.

Schloemer, J., Munk, L.A., Iken, K., 2023. Marine and Not Terrestrial Resources Support Nearshore Food Webs across a Gradient of Glacial Watersheds in the Northern Gulf of Alaska. Estuar. Coasts. https://doi.org/10.1007/s12237-023-01277-9.

Siegert, D., Konar, B., Lindeberg, M.R., Saupe, S., Iken, K., 2022. Trophic structure of key taxa in rocky intertidal communities in two contrasting high-latitude environments. Deep-Sea Res. II 198, 105050. https://doi.org/10.1016/j.dsr2.2022.105050.

Spurkland, T., Iken, K., 2011. Salinity and irradiance effects on growth and maximum photosynthetic quantum yield in subarctic *Saccharina latissima* (Laminariales, Laminariaceae). Bot. Mar. 54 (4), 355–365. https://doi.org/10.1515/bot.2011.042.

Strömgren, T., 1980. The effect of lead, cadmium, and mercury on the increase in length of five intertidal Fucales. J. Exp. Mar. Biol. Ecol. 43 (2), 107–119. https://doi.org/10.1016/0022-0981(80)90019-2.

Umanzor, S., Sandoval-Gil, J.M., Conitz, J., 2023. Ecophysiological responses of the intertidal seaweed *Fucus distichus* to temperature changes and reduced light driven by tides and glacial input. Estuar. Coasts 46 (5), 1269–1279. https://doi.org/10.1007/s12237-023-01207-9.

Wahl, M., Jormalainen, V., Eriksson, B.K., Coyer, J.A., Molis, M., Schubert, H., Dethier, M., Karez, R., Kruse, I., Lenz, M., Pearson, G., 2011. Stress ecology in *Fucus*: abiotic, biotic and genetic interactions. Adv. Mar. Biol. 59, 37–105. https://doi.org/10.1016/B978-0-12-385536-7.00002-9.

Weil, J., Trudel, M., Tucker, S., Brodeur, R.D., Juanes, F., 2019. Percent ash-free dry weight as a robust method to estimate energy density across taxa. Ecol. Evol. 9 (23), 13244–13254. https://doi.org/10.1002/ece3.5775.

Weitzman, B., Konar, B., Iken, K., Coletti, H., Monson, D., Suryan, R., Dean, T., Hondolero, D., Lindeberg, M., 2021. Changes in rocky intertidal community structure during a marine heatwave in the northern Gulf of Alaska. Front. Mar. Sci. 8, 115. https://doi.org/10.3389/fmars.2021.556820.

Weykam, G., Gómez, I., Wiencke, C., Iken, K., Klöser, H., 1996. Photosynthetic characteristics and C: N ratios of macroalgae from King George Island (Antarctica). J. Exp. Mar. Biol. Ecol. 204 (1–2), 1–22. https://doi.org/10.1016/0022-0981(96)02576-2.

Wikström, S.A., Kautsky, L., 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. Estuar. Coast. Shelf Sci. 72 (1–2), 168–176. https://doi.org/10.1016/j.ecss.2006.10.009.

Worm, B., Lotze, H.K., Sommer, U., 2000. Coastal food web structure, carbon storage, and nitrogen retention regulated by consumer pressure and nutrient loading. Limnol. Oceanogr. 45 (2), 339–349. https://doi.org/10.4319/lo.2000.45.2.0339.

Xu, N., Wang, W., Xu, Y., Ji, D., Chen, C., Xie, C., Xu, K., 2021. Effects of nutrient availability on the release of dissolved and particulate organic carbon by *Pyropia haitanensis* and its implications. Front. Mar. Sci. 8, 696938 https://doi.org/10.3389/fmars.2021.696938.

Yang, R., Hock, R., Kang, S., Shangguan, D., Guo, W., 2020. Glacier mass and area changes on the Kenai peninsula, Alaska, 1986–2016. J. Glaciol. 66 (258), 603–617. https://doi.org/10.1017/jog.2020.32.