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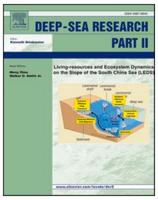

Trophic structure of key taxa in rocky intertidal communities in two contrasting high-latitude environments

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ABSTRACT

Coastal ecosystems in high latitudes are increasingly impacted by glacial melt and river discharge due to climate change. One way to understand ecosystem responses to these stressors is assessing trophic relationships. The goal of this study was to better understand how hydrography influences trophic structure in high-latitude rocky intertidal systems. Our working hypothesis was that food web structure differs based on hydrographic conditions. We compared the trophic structure of key taxa in two rocky intertidal assemblages in the northwestern Gulf of Alaska with a similar regional species pool, but differing hydrological inputs: one glacially influenced and one primarily marine influenced. Common macroalgal and invertebrate taxa, as well as particulate organic matter (POM) were sampled at three rocky intertidal sites in each region in 2017 and 2018. Food web structure was compared using trophic metrics based on the distribution of shared taxa in isotopically-derived (δ^{13}C and δ^{15}N) trophic niche space. The trophic niche space of the select taxa in the glacially-influenced rocky intertidal system was larger, driven by larger ranges in both carbon and nitrogen stable isotope values. Lower δ^{13}C and δ^{15}N values in POM in this system suggest that diverse glacially-influenced allochthonous organic material was incorporated into the food web. Macroalgae were a more important food source than POM in both regions, and even more so in the glacially-influenced region, where macroalgae may be an energetically preferable food source compared to silt-laden glacial inputs. This study suggests that common intertidal taxa have high trophic flexibility enabling them to respond to variable food sources under differing environmental conditions, especially by broadening resource use in more stressful (glacial) conditions. This supported another of our hypotheses, i.e. that taxa in food webs occupying a larger trophic niche space engaged in more heterogeneous trophic pathways and used more diverse resources, which tends to make such systems more stable to perturbations that could affect a single resource. The common taxa of high-latitude rocky intertidal systems studied here seem to be able to respond to the current stress levels of glacial input by using more diverse resources. However, it remains to be seen how well these systems are suited to maintain trophic stability with an expected increase in glacial stress from climate warming.

1. Introduction

Coastal benthic ecosystems are important foraging and nursery habitats for many marine species (Vasconcelos et al., 2011) and are among the most productive areas on earth (Costanza et al., 1997). They are also heavily utilized by humans for harvest and commerce (Halpern et al., 2008). In many high latitudes, these coastal ecosystems are increasingly impacted by glacial melt and river discharge due to climate warming (Dyurgerov and Meier, 2000). Global warming leads to increased glacial ice melt, irregular seasonal precipitation, and abnormal weather patterns, such as extreme storms and marine heat waves (Motyka et al., 2003; Frölicher et al., 2018). These processes influence the input of glacial and terrestrial matter to high-latitude coastal benthic ecosystems and impact key environmental factors, such as salinity, turbidity, and temperature (Hood et al., 2009). The effects of glacial discharge can lead to decreased species richness and abundance (Spurkland and Iken, 2011) and shape food webs (Howe et al., 2017; Whitney et al., 2017) in nearshore systems. In the Gulf of Alaska, the abundance of glaciers at elevations close to sea level exacerbates glacial melt under warming climate conditions (Hood and Scott, 2008),

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presenting the need to understand how communities and food webs respond to these climatic changes. In particular, it is important to distinguish natural variability from future perturbation responses (Underwood, 1991). Investigating food web structure in systems under differing environmental conditions helps establish the current range of food web variations. This study will create a framework for investigating coastal food webs in the region and assess the current range of variation. Future studies can determine if food webs have shifted beyond their historical range after continued climate warming.

One way to understand the response of ecosystems to possible stressors, such as glacial melt, is by assessing trophic relationships. Food web structure reflects energetic processes, driven by top-down (consumer-driven) and bottom-up (resource-driven) interactions within the assemblage (Menge, 2000). From a bottom-up perspective, coastal food webs are linked to local food sources, as well as larger regional oceanographic conditions (Nielsen and Navarrete, 2004; Blanchette et al., 2008). Specifically, in rocky intertidal systems, potential food sources include local, autochthonous sources (e.g. macroalgae) and allochthonous sources (e.g. phytoplankton). In high-latitude systems with glacial melt influences, allochthonous sources also include discharged terrestrial material (Hood and Scott, 2008; Neal et al., 2010). In complex food webs, where multiple food sources support the trophic web, potential food sources are likely to be driven independently by various environmental factors (e.g. seasonal glacial melt, upwelling events, and rainfall). These independent drivers lead to complex food webs that are more stable than simple ones driven by a single food source prone to variability exerted by a limited set of environmental variables (Dunne, 2006; Rooney and McCann, 2012). Trophic pathways based on multiple food sources are more heterogeneous, i.e. pathways that are supported by diverse food sources with differences in size, growth rates, nutritional quality, and biomass turnover, such as macroalgae and phytoplankton. Consumers that can use food sources from multiple pathways also lead to increased diversity, and thus stability, of food webs (Rooney et al., 2006; Godbold et al., 2009; Rooney and McCann, 2012). If the availability of one primary production source is reduced (e.g. low nutrient availability leading to lower phytoplankton biomass), consumers could compensate with other food sources and maintain overall food web structure (Huxel et al., 2002).

Coupling of diverse trophic pathways in a system imparts stability by providing a combination of strong and weak trophic interactions. Strong interactions allow for efficient energy transfer but depend on a stable supply of a specific food source to the consumer. Weak interactions are less efficient, but can dampen oscillations between source availability and consumer demands, balance variability in food sources, and maintain food web structure (McCann et al., 1998). Weak trophic interactions are more associated with 'slow channels', or trophic pathways supported by food sources with slow growth rates, biomass turnover, and larger sizes, such as macroalgae (Rooney and McCann, 2012). Strong trophic interactions are typically associated with 'fast channels', or trophic pathways supported by food sources with faster growth rates, turnover, and smaller sizes, such as phytoplankton (Rooney et al., 2006; Rooney and McCann, 2012). Having both 'fast channels', which allow rapid recovery, and 'slow channels', which help reduce oscillations in populations of producers and consumers, increases overall trophic and ecosystem stability when responding to perturbations. The extent to which these different pathways are used, and how this use varies under different environmental conditions, is typically unknown. Also, the biological and ecological responses of producers and consumers in these pathways to similar physical forcing mechanisms (e.g. upwelling, glacial input) are complex and can be context-dependent (Blanchette et al., 2009).

Trophic metrics based on species distribution in isotopically-derived trophic niche space are often used to quantitatively describe food web structure (Layman et al., 2007; Cucherousset and Villéger, 2015). Stable isotope ratios provide time-integrated information on material assimilated by organisms (Tieszen et al., 1983), reflecting their food sources and trophic relationships (Bearhop et al., 2004; Newsome et al., 2007). Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are most commonly used to assess food web structure and trophic linkages (Peterson and Fry, 1987). The carbon stable isotope ratio changes little from source to consumer (~1‰, DeNiro and Epstein, 1978; McCutchan et al., 2003; Caut et al., 2009), making it a useful tool to trace the flow of a carbon source through the food web. This is particularly important when multiple carbon sources with distinct isotope values enter the food web, allowing their $\delta^{13}C$ values to be used as tracers of these sources through the food web (DeNiro and Epstein, 1978; Boecklen et al., 2011). Nitrogen stable isotope ratios change more between trophic levels (~3‰, Minagawa and Wada, 1984; McCutchan et al., 2003; Vanderklift and Ponsard, 2003) and are useful to distinguish a species' relative trophic position in a food web (Post, 2002a). From these isotope measurements, a series of community-wide trophic metrics can be calculated to compare different food webs (Layman et al., 2007; Cucherousset and Villéger 2015; Rigolet et al., 2015). Food webs occupying a larger trophic niche space indicate that species have more heterogeneous trophic positions (Layman et al., 2007) and typically use both weak and strong trophic pathways (Rooney and McCann, 2012). Large trophic niche space also implies a more trophically diverse system (Layman et al., 2007; Cucherousset and Villéger, 2015), which is thought to be more stable to environmental variability and perturbations (Peterson, 1997). This stability remains as long as these perturbations do not remove heterogeneity in trophic pathways or eliminate the consumers that couple these pathways (Rooney and McCann, 2012).

The overall goal of this project was to better understand how hydrographic conditions influence trophic structure and linkages in high-latitude rocky intertidal ecosystems. Specifically, we characterized and compared the trophic structure of rocky intertidal systems in two regions in the northwest Gulf of Alaska with a similar species pool and differing inputs, one more glacial and the other more oceanic. We suggest that these systems can serve as a model to increase our understanding of how food webs respond to increased glacial melt in high latitudes. We propose that patterns in trophic linkages of key taxa would differ between the two regions based on these hydrographic influences. Specifically, we hypothesized that intertidal trophic linkages in the more glacially-influenced region should be more complex, because of the temporal variability and more diverse array of food sources. We also hypothesized that 'slow channel' autochthonous sources (macroalgae) should play a large role in carbon sourcing in both regions, but more so in the glacially-influenced region due to the higher variability in allochthonous sources (e.g. phytoplankton, terrestrial matter) in that region.

2. Methods

2.1. Site description

The Lower Cook Inlet (LCI) study area is located in the northwestern Gulf of Alaska. It can be separated into two distinct regions based on oceanography: Kamishak Bay on the western side of the inlet, and Kachemak Bay on the eastern side (Fig. 1). Kamishak Bay represents a system where intertidal assemblages are exposed to glacial melt influences, while the outer region of Kachemak Bay is a marine-influenced system largely unaffected by glacial melt (Muench et al., 1978; Okkonen et al., 2009). They have a similar regional species pool (Foster et al., 2010), and intertidal communities are organized in similar ways. Representative taxa for these communities across the northern Gulf of Alaska include *Fucus distichus*, mussels (*Mytilus trossulus*) and barnacles (*Balanus* sp.) as space dominants in upper to mid-intertidal levels; lower intertidal regions are occupied by a variety of fleshy macroalgae (Konar et al., 2009, 2016; Jones et al., 2019; Weitzman et al., 2021). Important grazers in both systems include limpets and periwinkles, and typical predators are whelks and anemones, especially after declines in sea stars due to sea star wasting syndrome in recent years (Konar et al., 2019).

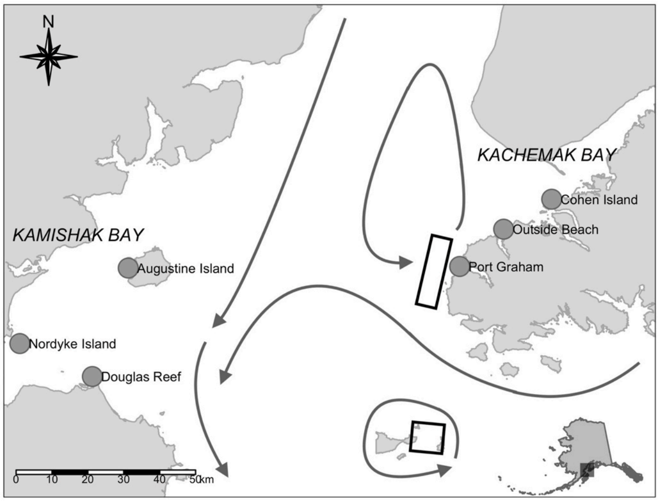

Fig. 1. Map of lower Cook Inlet, Alaska indicating sites sampled (grey points with site names labelled) in the two regions (Kamishak Bay and Kachemak Bay). Surface circulation in lower Cook Inlet indicated by grey arrows; boxes indicate areas with persistent upwelling or strong mixing. Modified from Okkonen et al. (2009).

These regions are characterized by different beach slopes, substrate types, and hydrography. Sites in Kamishak Bay typically have a shallower slope and more uniform substrate, while sites in Kachemak Bay generally have a steeper slope and more heterogeneous substrate, with a higher percentage of boulders and cobble (Muench et al., 1978). Seasonally, Kamishak Bay rocky intertidal habitats experience ice scour, while this rarely occurs in Kachemak Bay (NOAA, 1977). Both regions are impacted by the substantial tidal range present in Cook Inlet (~8 m, Danielson et al., 2016, tidesandcurrents.noaa.gov/tide_predictions.html).

Kamishak and Kachemak bays also differ in their hydrological conditions (Fig. 1). The Alaska Coastal Current (ACC) brings nutrient-rich marine water from the Gulf of Alaska to LCI, primarily entering LCI on the eastern side near Kachemak Bay. Deep, upwelled waters from just outside Cook Inlet join water from the ACC near the mouth of Kachemak Bay (Okkonen et al., 2009) and hydrographically characterize the Kachemak Bay region. Persistent, tidally-driven mixing in this region supplies nutrients to the surface, leading to high primary production from spring through mid-to-late summer (NOAA, 1977). Marine waters flow up the eastern side to Upper Cook Inlet (UCI), where they are modified by seasonally variable riverine and glacial outflow (Muench et al., 1978). A large volume of freshwater enters UCI from snowmelt in early summer, and high amounts of precipitation typically bring freshwater runoff to the region in late summer (Royer, 1982; Okkonen et al., 2009; Weingartner et al., 2005). Throughout summer, glacial melt contributes to the freshwater entering UCI, with large interannual variability (Ashford et al., 2013). These sources of freshwater are well-mixed with marine waters in UCI due to shallow depths and large tidal currents (Muench et al., 1978). This mixing alters the chemistry of surface waters in UCI and leads to increased suspended sediments (including substantial glacial material) and increased terrestrial material in waters flowing out of UCI (Feely and Massoth 1982; Neal et al., 2010). These discharge-influenced waters return southward along the western side of Cook Inlet, passing through Kamishak Bay before re-entering the ACC in the greater Gulf of Alaska (Burbank, 1977).

Glacial inputs may also affect the distribution of coastal wetlands, further contributing to regional differences in allochthonous inputs. For example, salt marsh and peatland inputs contribute more to Kamishak Bay than Kachemak Bay. Salt marsh habitat dominates for long stretches of the shoreline in the upper and middle Inlet along the west side (Hupp et al., 2001; Cusick and Bennett, 2005), with marshes relying on substrate comprised of alternating layers of silt and peat (Karlstrom, 1964). Sections of western Cook Inlet show considerable erosion of peat into the Inlet (authors, personal communication), contributing to a more diverse pool of allochthonous particulate organic matter (POM) in Kamishak Bay.

Three intertidal study sites were sampled in each region: Douglas Reef, Nordyke Island/Reef, and Augustine Island in Kamishak Bay, and Port Graham, Outside Beach, and Cohen Island in Kachemak Bay (Fig. 1, Table 1). Nordyke Island (2017) and Nordyke Reef (2018) were approximately 5 km apart, separated by a shallow channel, and were similar in beach structure (i.e substrate and profile); the site change between years was necessary because of inclement weather conditions in 2018. Regional hydrographic conditions cause sites in Kamishak Bay to be exposed to the freshwater-influenced waters exiting Cook Inlet and sites in Kachemak Bay to be exposed to mostly marine-influenced waters.

2.2. *Isotope sample collection*

Macroalgal, epifaunal invertebrate, and suspended POM samples were collected for stable isotope analysis at each site. Macroalgae and invertebrates that were common to both regions in both years were collected across the intertidal range at all sites to comprise a representative and regionally comparable assemblage for trophic analysis. These taxa included four macroalgae (the green alga *Acrosiphonia* sp., the brown algae *Fucus distichus* and *Saccharina* spp., and the red alga *Palmaria hecatensis*), two filter feeders (the barnacle *Balanus* sp. and the mussel *Mytilus trossulus*), two grazers (the periwinkle *Littorina sitkana* and the limpet *Lottia* sp.), and two predators (the whelk *Nucella* sp. and the anemone *Urticina crassicornis*). This assemblage was selected to include common consumers and food sources that would allow for a comparative bottom-up trophic niche assessment, tracking how basal resource use may lead to trophic diversification in common, representative taxa. Whenever possible, taxa were sampled in triplicate per site. In the rare cases where a taxon was unavailable at a site in a given year, specimens from shallow subtidal samples (~5 m depth) or a mean value of that taxon from the other sites in that region per year was used to represent the taxon. Samples were identified to the lowest possible taxonomic level in the field and frozen at −20 °C on the day of collection. For macroalgae, non-reproductive blade tissue was collected. For invertebrates, muscle tissue was sampled when possible (i.e. for *M. trossulus, Lottia* sp., and *Nucella* sp.). For barnacles and *L. sitkana*, non-reproductive soft tissue was used, and tentacles were sampled for *U. crassicornis*. Water samples for POM were collected both nearshore (1–2 m from shore) and offshore (approximately 100 m from shore) at each site. These water samples were filtered onto Whatman GF/F filters (~0.7 μm pore size); approximately 50 mL water were filtered from nearshore and 100 mL offshore in 2017, and the amount was increased to around 100 mL nearshore and 200 mL offshore in 2018 to ensure sufficient material for analysis. In addition, three offshore POM samples were taken opportunistically over a two-week period in May/June 2017 in Kasitsna Bay (a site in Kachemak Bay located between Cohen Island and Outside Beach) to assess short-term variability in isotope values of POM at a fixed location.

Table 1
Site locations in each region (Kamishak Bay and Kachemak Bay) by year where samples were collected for stable isotope analysis.

Site	Year(s)	Region	Latitude	Longitude
Port Graham	2017, 2018	Kachemak	59.3733	−151.8941
Outside Beach	2017, 2018	Kachemak	59.4645	−151.7094
Cohen Island	2017, 2018	Kachemak	59.5391	−151.4769
Douglas Reef	2017, 2018	Kamishak	59.1052	−153.716
Nordyke Island	2017	Kamishak	59.1814	−154.082
Nordyke Reef	2018	Kamishak	59.2236	−154.121
Augustine Island	2017, 2018	Kamishak	59.4064	−153.455

2.3. Laboratory analysis

Macroalgal and invertebrate samples were dried at 50 °C for approximately 24 h until a constant weight was reached, then stored dry at room temperature until later analysis. Samples that could still contain some carbonate structures (i.e. barnacles) were carefully acidified using a method of drop-by-drop 1N HCl addition until carbonates were dissolved (Jacob et al., 2005). Samples were then rinsed in deionized water and dried as described above. POM filters were exposed to saturated HCl fumes for at least 4 h to dissolve any carbonates present (Lorrain et al., 2003). Dried macroalgal, invertebrate, and POM samples were analyzed for bulk δ^{13}C and δ^{15}N values. The ^{13}C:^{12}C and ^{15}N:^{14}N ratios of the samples were measured using continuous-flow isotope ratio mass spectrometry (IRMS) at the Alaska Stable Isotope Facility, UAF. These values were expressed in the common delta notation in parts per thousand (‰) following:

$$\delta\,(‰) = \left(\left[R_{sample} : R_{standard}\right] - 1\right) \times 1000$$

where R is the determined ratio of ^{13}C:^{12}C or ^{15}N:^{14}N with standards of Vienna Pee Dee Belemnite for δ^{13}C and atmospheric N_2 for δ^{15}N. Instrument error was 0.09‰ for δ^{13}C and 0.07‰ for δ^{15}N.

Lipids tend to be isotopically lighter than other compounds in their δ^{13}C values (DeNiro and Epstein, 1977), so samples need to be corrected for variable lipid content (e.g. due to reproductive status) to maximize comparability of samples. However, chemical extraction of lipids can have an unwanted effect on δ^{15}N values. To assess the effect of lipid extraction (LE) on the sample isotope values and to determine the most appropriate approach to correct for lipid content, a subset of samples (three of each taxon) was split, with half of a sample analyzed undergoing LE and the second half without LE. Lipids were chemically extracted from the LE sample set three times (until solvent no longer contained color) using a mixture of chloroform:methanol (2:1 v:v) (Folch et al., 1957). Samples were then dried as described above and prepared for stable isotope analysis. Non-LE samples were not further treated. LE did affect the δ^{15}N values in some taxa (*Nucella* sp. and *Urticina crassicornis*); therefore, samples were not exposed to chemical LE. Comparison of LE and non-LE stable isotope values showed that the lipid effect on the δ^{13}C values of those two taxa could be corrected mathematically (δ^{13}C'), using the C:N ratio of the bulk tissue sample to calculate the proportion of lipid (*L*) with the following equations (after McConnaughey, 1978 and Alexander et al., 1996):

$$\delta^{13}C' = \delta^{13}C + 6 \times \left(\frac{L}{100}\right)$$

where

$$L = \frac{93}{1 + (0.246 \times C:N\,Ratio - 0.775)^{-1}}$$

The proportion of lipid *L* is calculated based on stoichiometric body composition (93% as the combined lipid and protein component) and established regression constants (McConnaughey, 1978; McConnaughey and McRoy, 1979) and related to the C:N ratio of the bulk tissue being analyzed. To then estimate a corrected δ^{13}C value (δ^{13}C'), 6‰ as the difference in lipid and protein δ^{13}C values is multiplied by the proportion lipid present and added to measured δ^{13}C values.

2.4. Trophic metrics

Several trophic metrics (δ^{13}C range, δ^{15}N range, convex hull area, corrected standard ellipse area, and isotopic evenness) were calculated for each site from δ^{13}C and δ^{15}N stable isotope values to characterize and compare trophic structure between Kamishak and Kachemak bays. The range of δ^{13}C values is a representation of diversification at the base of the food web (i.e. horizontal food web structure); it includes all endmembers and consumers and is the distance between the two samples with the lowest and highest δ^{13}C values (Layman et al., 2007). The δ^{15}N range represents the overall food chain length, or diversification in vertical food web structure, and is the maximum range of δ^{15}N values among all endmembers and consumers (Layman et al., 2007; Perkins et al., 2014).

Taxa were also assessed in the two-dimensional δ^{13}C - δ^{15}N biplot space (i.e. isospace), which takes into account both horizontal and vertical food web structure. Convex hull area is calculated as the overall area in isospace occupied by an assemblage and is influenced by the most extreme isotope values of the taxa. Convex hull area represents an assemblage's trophic niche space. δ^{13}C range, δ^{15}N range, and convex hull area included all endmembers and consumers and were calculated using the Stable Isotope Analysis in R (SIAR) package (Parnell et al., 2010). The application of the isotope convex hull for niche width is strongly dependent on sample size, or in a community application, by the number of taxa included (Syväranta et al., 2013). The component typically providing the most variability to the convex hull is the source endmembers (Newsome et al., 2012). As we were specifically interested in a bottom-up view of the trophic linkages, we retained endmembers in the convex hull to assess their influence on the trophic niche width. In addition, we addressed the concern of comparability of the convex hull measure by 1) including only the same taxa (including endmembers and consumers) in both regions, 2) calculating the convex hull area excluding endmembers, and 3) by including corrected standard ellipse area (SEA_C) as second measure of isotopic niche width (calculated with endmembers and consumers). SEA_C is a way of assessing the realized trophic niche space and is less influenced by a small sample size and extreme values compared to convex hull area (Jackson et al., 2011; Syväranta et al., 2013). SEA_C is analogous to standard deviation for bivariate data, as it measures isotopic variation. SEA_C is a robust approach that encompasses about 40% of the isotope values of the assemblage and is, thus, less sensitive to extreme values or outliers (Jackson et al., 2011). The size and shape of the ellipse are calculated using the covariance matrix $\Sigma = \begin{bmatrix} \sigma_x^2 & cov(x,y) \\ cov(y,x) & \sigma_y^2 \end{bmatrix}$, where x is δ^{13}C and y is δ^{15}N. The eigenvalues (λ) and eigenvectors (v) of Σ are then used to calculate the lengths of the axes (semi-major axis $a = {\lambda_1}^{-1}$ and semi-minor axis $b = {v_2}^{-1}$) and the angle of the ellipse ($\theta = \sin^{-1}(v_{12})$). The area of the ellipse is calculated as $SEA = \pi ab$. SEA_C is then calculated as $SEA_C = -\ SEA(n-1)(n-2)^{-1}$ (Jackson et al., 2011). Calculations of SEA_C were made using the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al., 2011). In the context of our hypothesis that trophic linkages of key taxa would differ between the two regions, these metrics would all be expected to be larger in a more complex system (i.e. the glacially-influenced region, Kamishak Bay).

Isotopic evenness (IEve) is a proxy for how resources are used within a standardized niche space. While SEA_C describes *how much* niche space is occupied, IEve answers the question of *how* the available niche space is being used (Cucherousset and Villéger, 2015). This is an indicator of whether trophic positions of taxa are distinct within an assemblage (indicated by a high IEve), or if taxa occupy similar trophic positions (indicated by a low IEve). IEve is computed using scaled, unitless values ranging from 0 to 1 within a site. This calculation is based on the minimum spanning tree (MST), or the length of the shortest branching that connects all taxa of an assemblage in isospace. IEve is calculated using

$$IEve = \sum_{l=1}^{N-1} min\left(\frac{EW_l}{\sum_{l=1}^{S-1} EW_l}, \frac{1}{N-1}\right) - \frac{1}{N-1} \Big/ 1 - \frac{1}{N-1}$$

with

$$EW_{l(i,j)} = \frac{\sqrt{\sum_{k=1}^{SI} \left(\delta k_i - \delta k_j\right)^2}}{w_i + w_j}$$

where *l* is a branch of the MST, *i,j* are taxa ranging from 1 to N, $w_{i\ ,j}$ are the weight or abundance of each taxon, k is each stable isotope used ranging from 1 to SI, and $\delta k_i, j$ is the stable isotope value for a given taxon. Taxa used in this calculation included endmembers and consumers. IEve was calculated using commands from the “SI_DIV” script (Cucherousset and Villéger, 2015) in R 3.5.1 (R Core Team, 2018). In the context of our hypothesis, a larger IEve would be expected in a more complex system (i.e. the glaciallyinfluenced region, Kamishak Bay) indicating more diverse resource use.

The δ^{13}C range, δ^{15}N range, convex hull area, and IEve were calculated at the site level based on mean stable isotope values for the selected taxa per site. SEA$_C$ was calculated at the site level based on individual stable isotope values for each taxon to ensure adequate sample size for comparisons (Syväranta et al., 2013). Sites were used as replicates to compare metrics between regions using two-way analysis of variance (ANOVA) assessing the effect of region and year ($\alpha = 0.05$). Assumptions of normality and homoscedasticity were met (tested using Shapiro-Wilk tests and Bartlett tests, respectively). Tukey post-hoc pair-wise tests were carried out where applicable. Differences in nearshore and offshore POM stable isotope values were tested using a one-way paired *t*-test ($\alpha = 0.05$). All statistical analyses were performed using R 3.5.1 (R Core Team, 2018).

To determine the proportional use of macroalgae or POM by consumers, stable isotope mixing models were used to determine relative contributions of endmembers to consumer diets at the regional level. Models were run using MixSIAR in R 3.5.1 (Stock et al., 2018; R Core Team, 2018). MixSIAR incorporates uncertainty in trophic enrichment factors (TEFs) into calculations of these relative proportions using Bayesian methods, which addresses concerns regarding uncertainty in assigning TEFs to consumers. Trophic enrichment factors used in the model were based on literature values, with a given value of 0.75 ± 0.11‰ for δ^{13}C (Caut et al., 2009) and 2.25 ± 0.1‰ for δ^{15}N (Vanderklift and Ponsard, 2003) for each trophic level (Linnebjerg et al., 2016). Models were run in three chains with a length of 100000, burn in of 50000, and 50 samples to thin. Gelman-Rubin convergence statistics were computed to ensure satisfactory runs (i.e. diagnostic values < 1.1). A mixing model was run for each consumer taxon for each combination of region and year (e.g. *Mytilus trossulus* in Kachemak Bay 2017; etc.). The appropriate regional macroalgal isotope values and offshore POM values were used as endmember inputs (e.g. macroalgal species and POM from Kachemak Bay 2017; etc.). Proportional contributions of macroalgal species were aggregated (*a posteriori*) into a single macroalgae source group after running mixing models for easier interpretation. To address concerns that this *a posteriori* combination may increase the relative weighting of macroalgae, models were also run with two

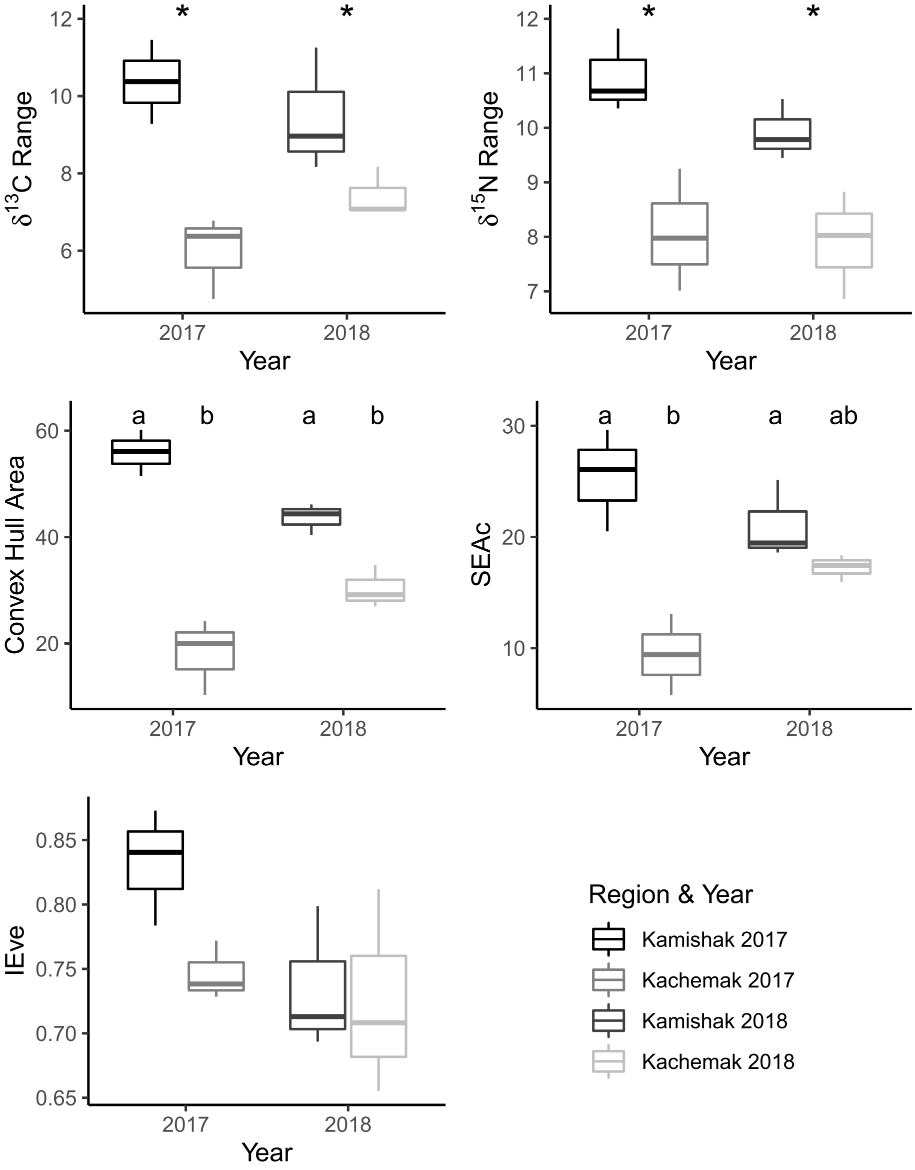

Fig. 2. Boxplots representing trophic metrics (δ^{13}C range, δ^{15}N range, convex hull area, corrected standard ellipse area (SEA$_C$), and isotopic evenness (IEve)) for Kamishak and Kachemak bays in 2017 and 2018. Boxes indicate first and third quartiles, median (horizontal line), and minimum and maximum values (whiskers). Tukey post-hoc test results for metrics with significant interactions effects (convex hull area and SEAc) are represented by different letters above boxes for significant differences. Asterisks indicate a significant difference between regions.

endmembers (one being an *a priori* combination of all macroalgae, the other POM); this only slightly changed the proportional contributions, not the general patterns (data not shown). In the context of our hypothesis, we expected higher macroalgal contribution in the more glacially-influenced region, Kamishak Bay.

3. Results

Several trophic metrics were significantly different between Kamishak and Kachemak bays intertidal assemblages (Fig. 2, Table 2). $\delta^{13}C$ range and $\delta^{15}N$ range were higher in Kamishak Bay compared with Kachemak Bay (2-way ANOVA, $p = 0.001$ and 0.001, respectively), but without a significant effect of year or interaction (Table 2). Convex hull area and SEA_C including all endmembers had a significant interaction effect of region and year (2-way ANOVA, $p = 0.002$ and 0.02, respectively; Table 2). Tukey post-hoc test indicated a difference in these metrics between Kamishak Bay (in both years) and Kachemak Bay in 2017, but no difference between Kachemak Bay in 2018 and any other groups (i.e. Kamishak Bay in both years and Kachemak Bay in 2017; Fig. 2). There were no significant differences between regions or years in IEve (Table 2). High mean values for IEve (~0.75) in both regions indicated an even distribution of taxa's trophic positions within the trophic niche space.

Trophic niche space in Kamishak Bay was larger than in Kachemak Bay in 2017, indicated by a larger convex hull area and SEA_C (Figs. 2–4). These patterns were in part driven by a larger range of $\delta^{13}C$ values in Kamishak Bay compared to Kachemak Bay. However, these regional differences between convex hull areas were maintained even when endmembers were excluded (2-way ANOVA, $p = 0.03$, data not shown), documenting larger trophic diversity in Kamishak Bay at the consumer level. Offshore POM samples consistently had the lowest $\delta^{13}C$ values in both regions and years, while the highest $\delta^{13}C$ values in 2017 in Kamishak Bay and Kachemak Bay were associated with the herbivorous snail, *Littorina sitkana*. The highest $\delta^{13}C$ value in Kamishak Bay in 2018 was associated with the predatory whelk *Nucella* sp., while the highest $\delta^{13}C$ value in Kachemak Bay in 2018 was associated with the red alga *Palmaria hecatensis*. The regional difference in $\delta^{13}C$ range in both years was mostly driven by lower offshore POM values in Kamishak Bay compared with Kachemak Bay, although this pattern was not as pronounced in 2018 (Fig. 3).

The $\delta^{15}N$ range, indicative of food chain length, was significantly larger in Kamishak Bay than Kachemak Bay intertidal assemblages (Fig. 2). The minimum $\delta^{15}N$ values in both regions and years were associated with offshore POM. POM values in Kamishak Bay were lower by up to ~4‰ compared to those in Kachemak Bay, accounting for much of the larger $\delta^{15}N$ range in Kamishak Bay. *Saccharina* spp. also showed notable differences in $\delta^{15}N$ values between the two regions in both years: in Kamishak Bay, $\delta^{15}N$ values were around 5‰ and were at the lower end of the $\delta^{15}N$ range, compared with values around 8‰ in Kachemak Bay (Fig. 3). At the upper end of the $\delta^{15}N$ range, the predatory anemone *Urticina crassicornis* had the maximum $\delta^{15}N$ values in both regions and years. This species contributed to the larger $\delta^{15}N$ range in Kamishak Bay, with slightly higher values in Kamishak Bay (~14‰) than Kachemak Bay (~13‰, Fig. 3). The difference in $\delta^{15}N$ between POM and filter feeders was higher in Kamishak Bay (~4‰) compared to Kachemak Bay (~2.5‰, Fig. 3).

Table 2

Results (p-values) from two-way ANOVA tests of differences in trophic metrics depending on region and year. Regions include Kamishak Bay and Kachemak Bay, years include 2017 and 2018, interaction effects indicated by Region x Year. Trophic metrics include $\delta^{13}C$ range, $\delta^{15}N$ range, convex hull area (CH Area), corrected standard ellipse area (SEA_C), and isotopic evenness (IEve). Significant p-values < 0.05 indicated in bold.

	Region	Year	Region x Year
$\delta^{13}C$ Range	**0.001**	0.686	0.113
$\delta^{15}N$ Range	**0.001**	0.271	0.428
CH Area			**0.002**
SEA_C			**0.016**
IEve	0.168	0.099	0.264

POM was variable between regions and years (Fig. 5A) and over time in the single location of Kasitsna Bay, located in Kachemak Bay (Fig. 5B). Nearshore POM had higher $\delta^{13}C$ values relative to offshore POM in both regions and years (paired *t*-test, $p = 0.005$). There was an increase from 2017 to 2018 in $\delta^{15}N$ of nearshore POM in Kamishak Bay (Fig. 5A). Assessing POM short-term variability independent of spatial constraints, POM measurements in Kasitsna Bay (Kachemak Bay) between 21 May and June 4, 2017 ranged in $\delta^{13}C$ values over about 1‰ and $\delta^{15}N$ values of about 4‰ (Fig. 5B).

The median contribution of macroalgae to consumers based on MixSIAR results with *a posteriori* grouping of macroalgal taxa was mostly >50% in both regions and years, indicating considerable sourcing from macroalgae to all consumers in both regions (Fig. 6). Grazers had the highest macroalgal contributions, with *Littorina sitkana* having the highest contributions of macroalgae in most regions and years (median 89–100%, Fig. 6), but suspension-feeding barnacles having the highest median contribution of macroalgae in Kachemak Bay in 2018 (97%). The filter feeder *Mytilus trossulus* had the lowest macroalgal contributions in Kamishak Bay (medians 65–77%), while in Kachemak Bay *U. crassicornis* had the lowest macroalgal contributions (medians 55–58%). On average, macroalgal contributions to consumer diets were higher in the glacially-influenced Kamishak Bay than the more marine-influenced Kachemak Bay (means of ~90% versus ~76%).

4. Discussion

Trophic structure of rocky intertidal assemblages in two hydrographically distinct regions in Cook Inlet, Alaska differed in several aspects of the trophic niche space used by shared taxa. An overall larger niche space in the more glacially-influenced Kamishak Bay was mostly driven by lower $\delta^{13}C$ values of the POM source, which seems to be linked to the hydrographic conditions contributing more diverse allochthonous material to the POM in Kamishak Bay. Intertidal consumers in both regions derived most of their carbon from macroalgal rather than POM sources, even more so in Kamishak Bay. This could indicate a greater reliance on macroalgae as a temporally stable food source and represent weaker trophic linkages, indicating trophic flexibility in consumers to changing hydrographic conditions.

4.1. *Regional trophic structure*

The rocky intertidal trophic system in the glacially-influenced Kamishak Bay region was characterized by a wider, isotopically more diverse food web base (represented by a larger $\delta^{13}C$ range, Layman et al., 2007), as well as longer food chain length (represented by $\delta^{15}N$ range) compared with the more marine-influenced Kachemak Bay region. For both patterns, the lower isotope values of POM in Kamishak Bay accounted for much of this difference, suggesting compositional differences in POM in the two regions. POM is a mixture that includes phytoplankton, terrestrial organic matter, macroalgal detritus, fecal pellets, bacteria, and aggregates or degraded forms of these components (Lee et al., 2004). These components have a range of stable isotope and nutritional values, and changes in the relative proportions of these components affect the overall stable isotope values of POM (Rau et al., 1990; Grémare et al., 1997; Grey et al., 2001). For example, increased proportions of macroalgal detritus relative to phytoplankton in POM lead to increases in $\delta^{13}C$ values (France, 1995; Heip et al., 1995; Duggins and Eckman, 1997), which was likely the cause for the higher $\delta^{13}C$ values of nearshore compared to offshore POM. However, the regional difference of lower carbon and nitrogen isotope POM values in Kamishak Bay was likely due to a higher proportion of non-marine allochthonous material in the POM in that region. Terrestrial material

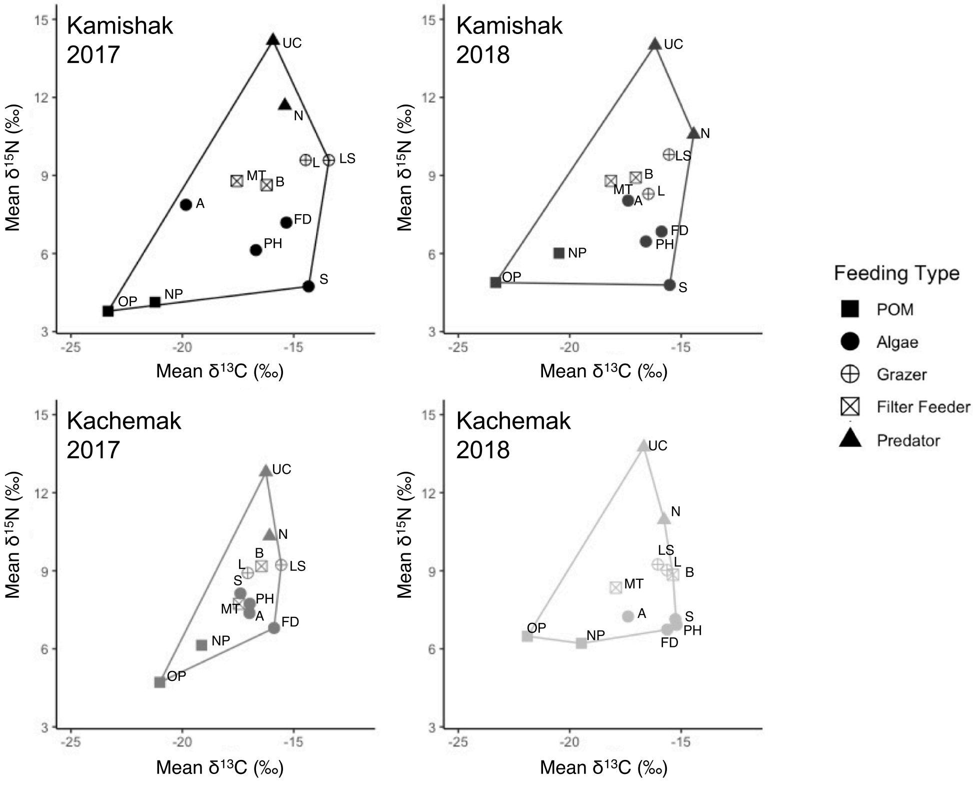

Fig. 3. Total convex hull area in isospace based on carbon and nitrogen stable isotope values in Kamishak and Kachemak bays in 2017 and 2018. Endmember or feeding types of taxa are indicated by symbols, and abbreviations represent species (UC=Urticina crassicornis, N=Nucella sp., LS = Littorina sitkana, L = Lottia sp., B=Barnacle, MT = *Mytilus trossulus*, A = Acrosiphonia sp., FD=Fucus distichus, PH=Palmaria hecatensis, S=Saccharina spp., NP = near POM, and OP = off POM).

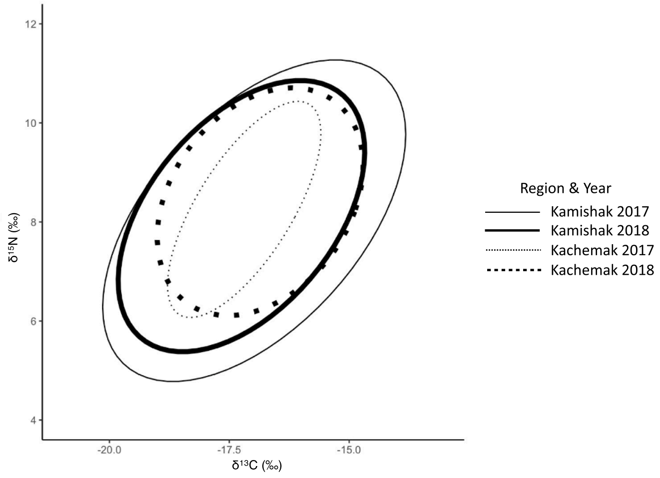

Fig. 4. Regional corrected standard ellipse area (SEA$_C$) in isospace based on carbon and nitrogen stable isotope values for endmembers and consumers in Kamishak and Kachemak bays, Alaska in 2017 and 2018.

is typically characterized by lower δ^{13}C values than marine production (Peterson, 1999; Skrzypek et al., 2008), which would particularly influence the Kamishak Bay POM, given the diverse inputs from glacial melt, river discharge, peatlands, and salt marsh habitat in UCI (Muench et al., 1978; Okkonen et al., 2009; Cusick and Bennett, 2005). Terrestrial material also has lower δ^{15}N values than marine material due to the low level of fractionation associated with atmospheric nitrogen fixation (Owens, 1988) compared to higher levels of fractionation from the more common inorganic nitrogen sources and remineralization processes in the marine system (Sigman and Casciotti, 2001). POM δ^{15}N values can also be influenced by phytoplankton bloom events and inorganic nitrogen availability. Production based on regenerated ammonium prevalent in low-salinity, estuarine systems tends to have lower δ^{15}N values compared with nitrate-based production under more oceanic conditions (Sigman and Casciotti, 2001). It should be noted that, given the high variability and turnover of the POM composition, the perceived regional differences in POM isotope values may simply be a result of temporal variability and the specific time of sampling. Differences in POM δ^{13}C isotope values between Kamishak and Kachemak bays were larger for regional (2–3‰) compared to temporal shifts (~1‰; from the Kasitsna Bay time-series), suggesting that regional differences were not merely reflecting temporal variability. And while temporal and regional variability occurred on similar scales for δ^{15}N values, the consistent pattern of lower POM isotope values in the glacially-influenced system points toward a systematic regional difference rather than solely being a result of variability.

Ecologically, a higher amount of terrestrial matter in the POM of the glacially-influenced system has trophic implications for consumers. Generally, terrestrial organic matter is less labile than marine organic matter (Ittekkot 1988) and requires microbial breakdown to transform it into a labile food source for primary consumers (Tenore, 1983; Garneau et al., 2009). Additional trophic steps decrease the energy transferred from lower to higher trophic levels in a system (Elton, 1927; Post, 2002b). In the glacially-influenced Kamishak Bay, this would decrease the energy available from POM to consumers such as filter-feeding mussels and barnacles compared with energy transfer to these same consumers based on a more marine phytoplankton-based POM source in Kachemak Bay. This additional trophic step via microbial degradation would also explain the observed larger isotopic difference between POM and filter feeders in Kamishak Bay (Macko and Estep, 1984) and contribute to the slightly longer food chain length (δ^{15}N range) in

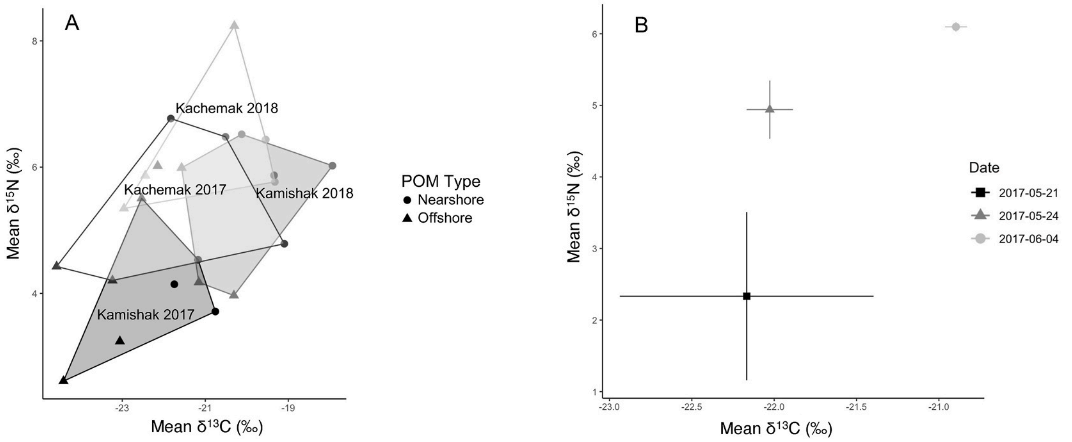

Fig. 5. Mean carbon and nitrogen stable isotope values of particulate organic matter (POM) for Kamishak and Kachemak bays, Alaska in 2017 and 2018 (A). Mean and standard deviations of carbon and nitrogen stable isotope values of POM in Kasitsna Bay, Alaska over time (B).

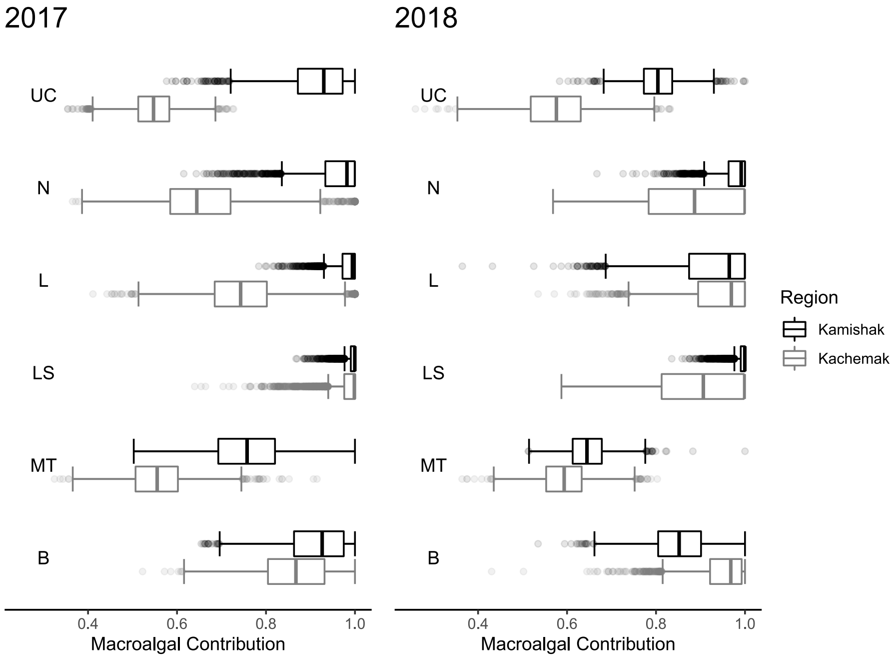

Fig. 6. Contribution of macroalgae to consumers based on MixSIAR results in Kamishak and Kachemak bays, Alaska in 2017 and 2018. Each boxplot represents the contribution to a taxon in a given region and year; abbreviations represent taxa (UC=*Urticina crassicornis*, N=*Nucella* sp., L = *Lottia* sp., LS = *Littorina sitkana*, MT = *Mytilus trossulus*, B=*Balanus* sp.).

Kamishak Bay.

Longer food chain length in the glacially-influenced Kamishak Bay was also observed based on slightly longer trophic transfer pathways to predators. While $\delta^{15}N$ generally undergoes stepwise enrichments between trophic levels (3–4‰ per step, Vander Zanden and Rasmussen, 2001), this enrichment is influenced by the ontogenetic status and body size of consumers (Polis, 1984; Scharf et al., 2000) and the level of omnivory in consumers (Svanbäck et al., 2015). Therefore, some of the differences in $\delta^{15}N$ positions of the same top consumer taxa in the two regions may have been due to different ages, sizes, or feeding preferences of the predators. For example, *U. crassicornis* at the upper end of the intertidal food chain, is a large-bodied, long-lived anemone that is a non-selective, opportunistic feeder, preying on a wide variety of organisms that can be even larger than their own body size (Den Hartog, 1986). While *U. crassicornis* had the highest $\delta^{15}N$ values of the assemblage in both regions and years, slight regional differences could indicate that they may have been feeding on prey outside of the selected taxa included in the present study. This could include prey at higher trophic levels, explaining their high $\delta^{15}N$ value relative to other more specialized top consumers, such as whelks (Burrows and Hughes, 1991).

The larger diversity at the base of the food chain and the longer food chain length ($\delta^{13}C$ and $\delta^{15}N$ ranges, respectively) in the glacially-influenced Kamishak Bay resulted in larger overall trophic niche space (larger convex hull and standard ellipse areas) than the more marine-influenced Kachemak Bay. These results are similar to other, non-glacial estuarine systems where terrestrial inputs increased the trophic niche space (Abrantes et al., 2014). In contrast, a recent study conducted in a glacial fjord system concluded that glacial input reduced trophic diversity (i.e. decreased niche space) and increased trophic redundancy (Cari et al., 2020). In some estuarine systems, a 'transition zone' between estuarine and marine zones can be associated with peaks in trophic diversity (Kim et al., 2019). It is possible that the glacially-influenced Kamishak Bay may be positioned in a similar transition zone where the levels of allochthonous marine, glacial, and various terrestrial material support the observed food web diversification without causing reductions in trophic diversity seen in other glacial systems.

Isotopic evenness did not differ between regions, despite regional differences in other trophic metrics. In other words, consumers maintained a similarly effective use of available resources regardless of the environment (Mason et al., 2005). Even though the absolute isotopic position of taxa may have been slightly different between the two regions, the taxa's relative trophic positions in the food web remained fairly consistent, resulting in similar levels of isotopic evenness. Marine taxa often have inherently flexible feeding habits (Padilla and Savedo, 2013), and isotopic composition of the same taxa can vary depending on the origins of available food sources (Sarà et al., 2007), as discussed above for POM sources in our study. It seems that trophic flexibility allowed taxa in our study to use the specific resources that were available in the two regions, maintaining trophic evenness despite the environmental differences. Trophic flexibility results in weak trophic links to their food sources (Padilla and Savedo, 2013; Portail et al., 2018), which typically enhances food web stability (Rooney and McCann, 2012). Our study suggests that the trophic flexibility of the common intertidal taxa investigated here imparts food web stability to these high-latitude rocky intertidal systems by increasing weak trophic links (Bordeyne et al., 2017; Portail et al., 2018) under more variable environmental conditions.

4.2. *Trophic pathways*

Rocky intertidal consumers in both systems derived most of their carbon from macroalgal sources as opposed to POM sources. Between the two regions, the glacially-influenced Kamishak Bay assemblage relied more on macroalgae and less on POM than the more marine Kachemak Bay assemblage. The presumably higher relative proportion of terrestrial material in glacially-influenced POM could have decreased POM use in Kamishak Bay due to lowered food quality (Schell, 1983; Berglund et al., 2007). Ultimately, even though it seems that there were additional sources to the POM composition, and trophic flexibility allowed the consumers to use these sources, POM was an overall less-used food source in the Kamishak Bay glacial system. One caution in the interpretation of the data is that isotope fractionation between source and consumer can be influenced by environmental conditions (e.g. Gannes et al., 1997; Gillikin et al., 2006; Barnes et al., 2007). In our study system, the most likely environmental variables influencing carbon isotope fractionation would be salinity and temperature. While we do not have readings during the time of sample collection, CTD measurements on August 31, 2016 (peak summer glacial discharge time) showed a surface water temperature difference of ∼2 °C (12.14 °C and 14.15 °C at the entrance of Kachemak and lower Kamishak Bay, respectively) and a <0.2 salinity difference (26.69 and 26.84 in Kachemak and Kamishak Bay, respectively) between the two systems (Holderied, 2016). We contend that these differences likely have a minor influence on isotope fractionation as they are less than daily fluctuations in these variables during a single tidal cycle.

Of the two main trophic pathways addressed here, one supported by autochthonous macroalgal production, the other supported by allochthonous POM, the POM pathway is potentially more complex, depending on POM composition. Highly heterogeneous POM can include fresh biomass (e.g. phytoplankton) as well as detrital components. Detrital pathways, similar to macroalgal pathways, are an example of 'slow channels', or trophic pathways supported by food sources with low biomass turnover (Rooney et al., 2006). In contrast, trophic pathways based on fresh phytoplankton are an example of a 'fast channel', or a trophic pathway supported by food sources with fast growth rates and high biomass turnover (Rooney et al., 2006). In the absence of the glacially-influenced allochthonous inputs found in Kamishak Bay, the Kachemak Bay assemblage seems to be characterized by a more prominent 'fast channel' reliant on phytoplankton. With the presence of a detrital pathway based on diverse allochthonous matter and a prominent macroalgal pathway in the glacially-influenced Kamishak Bay (i.e. two slow channels to consumers using weak pathways), we would expect to see increased stability of the food web in Kamishak Bay. Slow channel dynamics and weak trophic links allow for multiple possible pathways from slow channel sources to top consumer, thus increasing food web stability (McCann et al., 1998; Rip et al., 2010). There are other mechanisms that increase trophic diversity associated with slow channel pathways; microbial processing of terrestrial detritus potentially allows multiple groups of microbes and invertebrates to use this material as it is broken down (Rooney and McCann, 2012), and sources such as macroalgae provide a structurally complex habitat that can also increase biological diversity (Hooper and Davenport, 2006). While this study did not address food web stability directly, there was a general pattern of higher trophic diversity in Kamishak Bay than Kachemak Bay, supporting the idea of greater food web stability in the more glacially-influenced Kamishak Bay.

Macroalgae are an important food source in rocky intertidal systems (Duggins et al., 1989; Riera et al., 2009) and are less temporally variable than phytoplankton or POM (Leclerc et al., 2013). As a temporally consistent source, macroalgae would be expected to be especially important in early spring before phytoplankton and terrestrial organic matter peak in later spring and summer. Macroalgae can contribute directly to rocky intertidal food webs through grazers, or indirectly as detritus to filter feeders such as mussels, *M. trossulus* (Duggins et al., 1989). While macroalgal detritus in POM can be less labile than phytoplankton (Duarte and Cebrián, 1996), it presents a more consistent, less seasonally variable autochthonous carbon source available to nearshore consumers than phytoplankton. Consumers in Kamishak Bay may also rely more on macroalgae as a food source if it is energetically preferable to glacial silt-laden POM, which may be metabolically costly to process and physically stressful for particle sorting along the feeding apparatus (Bayne et al., 1987; Airoldi, 2003). The ability of consumers (from primary consumers like *M. trossulus* to predators like *U. crassicornis*) to link different trophic pathways and to change feeding preferences in response to variability in food sources confers stability to rocky intertidal food webs (Jiang et al., 2009). Rocky intertidal systems, particularly at high latitudes, are inherently dynamic and may experience high levels of disturbance. Kamishak Bay as a strongly glacial system experiences high seasonal variability, including summer freshwater and glacial silt inputs (Muench et al., 1978) and potentially severe winter ice scouring that can rearrange the entire benthic community structure (Scrosati and Heaven, 2008). This seasonal variability likely explains the observed trophic flexibility exhibited by consumers in the Kamishak Bay region, potentially leading to higher stability.

5. Conclusions

In both of the hydrographically distinct regions studied here, rocky intertidal consumers showed flexible use of multiple food sources and trophic pathways, which has been observed to convey system stability. The question remains, how resilient are high-latitude rocky intertidal systems to the impacts of climate change or other disturbances. The larger niche space and more diverse resource use by common intertidal taxa in glacially-influenced Kamishak Bay suggest that these high-latitude organisms are, in principle, well-adapted to the current range of environmental variability. However, the limits of this trophic flexibility, and the level to which these taxa will be able to respond and be resilient to expected increased glacial stress from additional climate warming, are unknown. If rocky intertidal communities in glacially-influenced systems were near the limits of their trophic flexibility, then they may not be able to maintain their trophic structure with additional environmental stressors. The comparison of the two hydrographically contrasting rocky intertidal systems suggests, however, that the food webs in these high-latitude systems have the flexibility necessary to thrive and maintain trophic stability in the "typical" range of glacial melt conditions experienced. The trophic metrics calculated here can be used as a “benchmark” of the currently expressed range of trophic flexibility of common intertidal species in the area. Based on the results of this study it could be hypothesized that with additional glacial melt, rocky intertidal communities will become more reliant on macroalgae for food web support, but that trophic niche space will broaden as glacially derived organic matter becomes more prevalent in the system. To test such a hypothesis in the future, similar calculations to those used here can be used for comparison to the present study. This will help follow shifts in trophic niche space with increased glacial melt - whether niche space increased, conferring additional stability to the food web, or decreased, indicating decreased stability.

Author contributions

DS: Methodology, Analysis, Funding acquisition, Visualization, Writing – Original draft preparation. BK: Conceptualization, Resources, Funding acquisition, Writing - Review & Editing. ML: Resources, Writing – Review & Editing. SS: Resources, Writing – Review & Editing. KI: Conceptualization, Methodology, Resources, Funding acquisition, Writing - Original Draft, Project administration, Supervision.

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.

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