

TROPHIC STRUCTURE OF ROCKY INTERTIDAL COMMUNITIES
IN CONTRASTING HIGH-LATITUDE ENVIRONMENTS

By

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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 hydrographic conditions influence trophic structure in high-latitude rocky intertidal systems. I compared the trophic structure of rocky intertidal assemblages in two regions in the northern Gulf of Alaska that comprise the same regional species pool but are hydrographically distinct, 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 communities 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 ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) trophic niche space. I found that trophic niche space in the glacially-influenced rocky intertidal system was larger, driven by larger ranges in both carbon and nitrogen stable isotope values. In particular, the lower $\delta^{13}\text{C}$ values in Kamishak Bay suggest that an additional food source, most likely terrestrial organic material from glacial discharge, was incorporated into the food web. This supported the hypothesis that patterns in food web structure differed based on hydrographic influences to maintain overall stability. Isotopic evenness, i.e., the distribution of the shared taxa within trophic space, did not differ between the two regions. Macroalgae were overall 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 beneficial food source compared to silt-laden glacial inputs. This study showed that common intertidal taxa have high trophic flexibility enabling them to respond to variable food sources under a variety of environmental conditions. As hypothesized, taxa in food webs occupying a larger trophic niche space engaged in more heterogeneous trophic pathways and used diverse resources depending on local environmental conditions, making these systems more stable to perturbations affecting a single resource. The common taxa of high-latitude rocky intertidal systems studied here are responding to current levels of glacial input with more diverse resource use, but it remains to be seen how well those systems are suited to maintain trophic stability with an expected increase in glacial stress from climate warming.

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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 high latitudes, these coastal ecosystems are increasingly impacted by glacial melt and river discharge due to climate change (Dyrgerov & Meier 2000). Global warming leads to increased glacial ice melt, irregular seasonal precipitation, and abnormal weather patterns, such as extreme storms (Motyka et al. 2003). A warming climate influences the input of glacial and terrestrial matter and nutrients to coastal benthic ecosystems and impacts key environmental factors, such as salinity, turbidity, and temperature (Hood et al. 2009). Glacial discharge can lead to decreased species richness and abundance (Spurkland & Iken 2011) and shape food webs (Howe et al. 2017) in nearshore systems. In the Gulf of Alaska, the abundance of glaciers at elevations close to sea level exacerbates glacial melt (Hood & Scott 2008). Establishing a benchmark understanding of ecosystem function in high latitude nearshore systems potentially impacted by these climatic processes helps distinguish natural variability from perturbation response (Underwood 1991).

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 & 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 & Scott 2008, Neal et al. 2010). Complex food webs, where multiple food sources support the trophic web, provide consumers with potential food sources that are driven by independent environmental factors (e.g., seasonal glacial melt, upwelling events, and rainfall); such complex food webs 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 & 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 are able to 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 & 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 (e.g., 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 food to the consumer. Weak interactions are less efficient, but can dampen oscillations between sources and consumers, balance changes 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 & McCann 2012). Strong trophic interactions are 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 & McCann 2012). Having both a 'fast channel', which allows rapid recovery, and a 'slow channel', which helps reduce oscillations in populations of producers and consumers, increases overall 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).

We used trophic metrics to quantitatively describe high-latitude rocky intertidal food webs based on species distribution in isotopically-derived trophic niche space (Layman et al. 2007, Cucherousset & 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 ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are most commonly used to assess food web structure and trophic linkages (Peterson & Fry 1987). The carbon stable isotope ratio changes little from source to consumer (~ 1 ‰, DeNiro & 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 $\delta^{13}\text{C}$ values to be used as tracers of these sources through the food web (DeNiro & Epstein 1978, Boecklen et al. 2011). Nitrogen stable isotope ratios change more between trophic levels (~ 3 ‰, Minagawa & Wada 1984, McCutchan et al. 2003, Vanderklift & 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 used to compare different food webs (Layman et al. 2007, Cucherousset & 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 both weak and strong trophic pathways (Rooney & McCann 2012). Large niche space also implies a more trophically diverse system (Layman et al. 2007, Cucherousset & 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 & McCann 2012).

In this study, the trophic structure of high-latitude rocky intertidal communities was evaluated and compared in two regions of Lower Cook Inlet (LCI), located along the northern Gulf of Alaska. LCI can be separated into two distinct regions based on oceanography, represented by Kamishak Bay and Kachemak Bay. The regions have the same regional species pool but experience distinct environmental influences. 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). The goal of this project was to characterize and compare the intertidal food webs in these two regions to better understand how hydrographic conditions

may influence trophic structure and linkages in high-latitude rocky intertidal ecosystems. 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 (Neal et al. 2010). We propose that patterns in food web structure would differ between the two regions based on these hydrographic influences. Specifically, we hypothesized that intertidal food web structure in Kamishak Bay should be more complex, because of the higher variability in food sources due to glacial melt influences. We also hypothesized that 'slow channel' autochthonous sources (macroalgae) should play a large role in carbon sourcing in both regions, but more so in Kamishak Bay due to the higher variability in allochthonous sources (phytoplankton, terrestrial matter) in that region.

2. Methods

2.1 Site description

Kamishak Bay and Kachemak Bay are located in the northern Gulf of Alaska, in western and eastern lower Cook Inlet (LCI), respectively (Figure 1). 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 (Figure 2, 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, Figure 2, Danielson et al. 2016, tidesandcurrents.noaa.gov/tide_predictions.html).

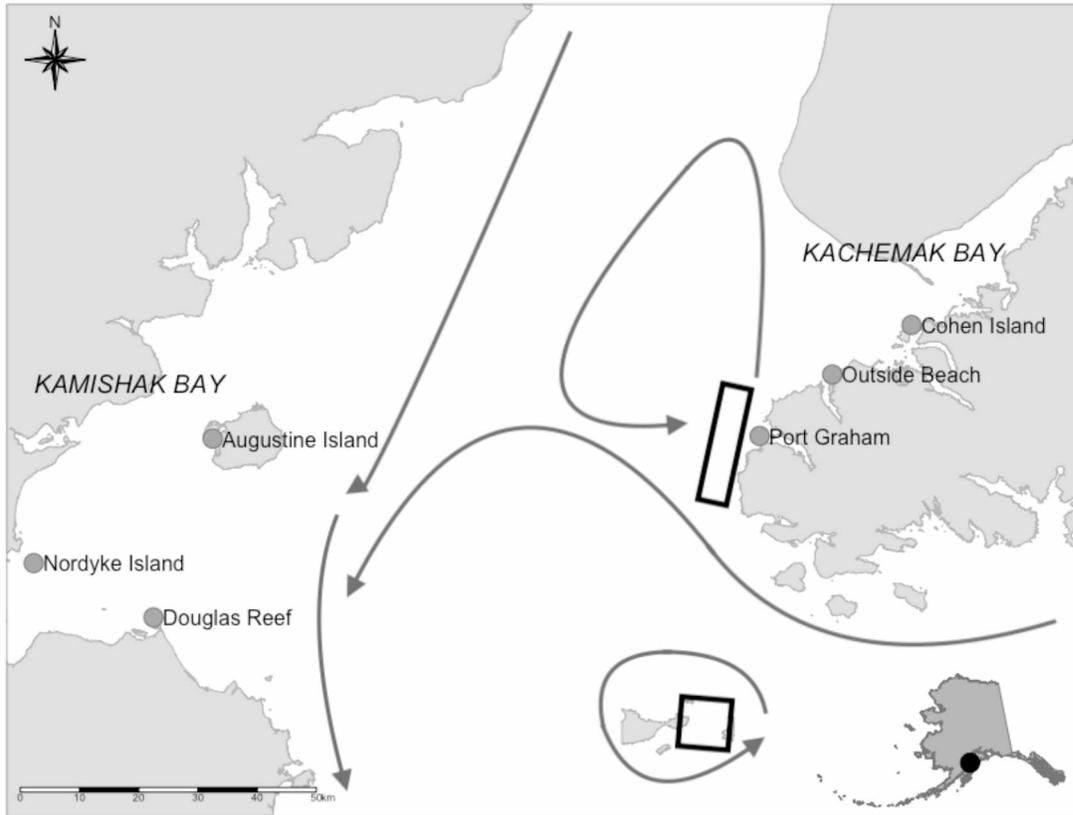


Figure 1. Map of lower Cook Inlet, AK indicating sites sampled in the two regions (Kamishak Bay and Kachemak Bay). Surface circulation in lower Cook Inlet indicated by gray arrows; boxes indicate areas with persistent upwelling or strong mixing. Modified from Okkonen et al. 2009.

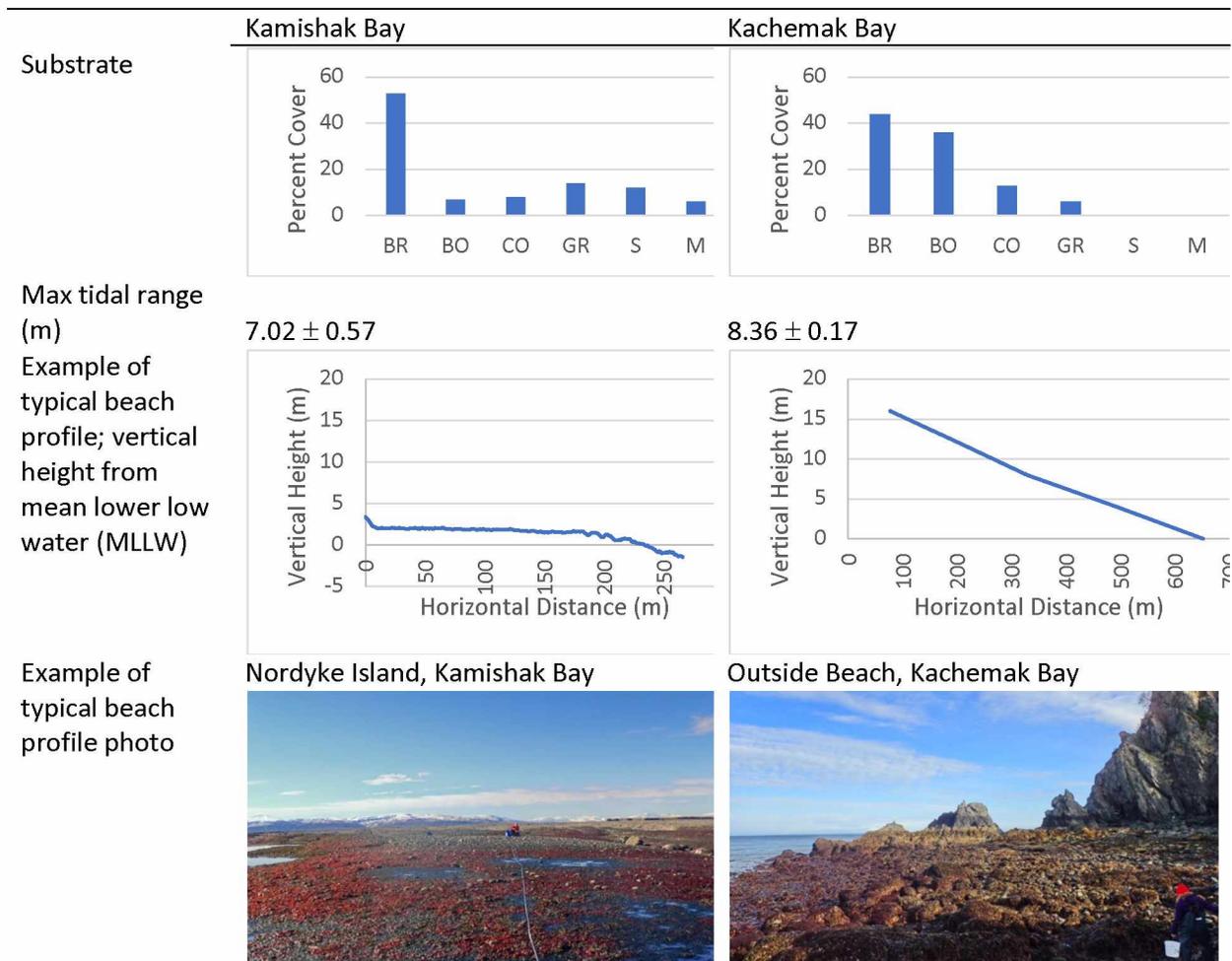


Figure 2. Regional intertidal information for Kamishak and Kachemak bays. Substrate is given as percent cover of bedrock, boulder, cobble, gravel, sand, and mud (BR, BO, C, GR, S, and M, respectively) as a mean across sites per region. Examples of typical beach profiles shown for Kamishak Bay at Nordyke Reef (profile) and Island (photo) and Kachemak Bay at Outside Beach. Substrate and beach profile data were taken as part of collaborative projects (Cook Inlet Characterization Study (Bureau of Ocean Energy Management) in Kamishak Bay and the Gulf Watch Alaska program (Exxon Valdez Oil Spill Trustee Council) in Kachemak Bay). Tidal range data were calculated using a mean of tidal ranges at the three Kamishak Bay sites (Oil Bay, Iliamna Bay, and Nordyke Island) and three Kachemak Bay sites (Seldovia, Port Graham, and Kasitsna Bay) located closest to study sites using data from <https://tidesandcurrents.noaa.gov/>.

Kamishak and Kachemak bays also differ in their hydrological conditions (Figure 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, where they are modified by seasonally variable riverine and glacial outflow (Muench et al. 1978). A large volume of freshwater enters upper Cook Inlet from snowmelt in early summer, while high amounts of precipitation typically bring freshwater runoff to the region in late summer (Royer 1982, Okkonen et al. 2009). Throughout summer, glacial melt contributes to the freshwater entering upper Cook Inlet. These sources of freshwater are well-mixed with marine waters in upper Cook Inlet due to shallow depths and large tidal currents (Muench et al. 1978). This mixing reduces the salinity of waters in upper Cook Inlet and leads to increased suspended sediments (including substantial glacial material) and increased terrestrial material in waters flowing out of upper Cook Inlet (Feely & Massoth 1982, Neal et al. 2010). These low salinity 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).

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 (Figure 1, Table 1). Nordyke Island (2017) and Nordyke Reef (2018) are approximately 5 km apart, separated by a shallow channel, and are similar in beach structure (i.e., substrate and profile); the site change was necessary because of inclement weather conditions in 2018. Regional hydrographic conditions ensured sites in Kamishak Bay were exposed to the freshwater-influenced waters exiting Cook Inlet and sites in Kachemak Bay were exposed to mostly marine-influenced waters.

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

2.2 Isotope sample collection

Macroalgal, epifaunal invertebrate, and suspended particulate organic matter (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 (barnacles 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*). Whenever possible, taxa were sampled in triplicate per site; when necessary, shallow subtidal samples (~ 5 m depth) or an annual regional mean were used to represent a taxon in the few cases where it could not be collected at an intertidal site in a given year. 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.

2.3 Laboratory analysis

Macroalgal and invertebrate samples were dried at 50 °C for approximately 24 hours 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 acidified using

1N HCl until carbonates were dissolved. Samples were then rinsed in deionized water and dried as described above. POM filters were exposed to saturated HCl fumes for at least 4 hours to dissolve any carbonates present. Dried macroalgal, invertebrate, and POM samples were analyzed for bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$ 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:

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

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

Lipids tend to be isotopically lighter than other compounds in their $\delta^{13}\text{C}$ values (DeNiro & Epstein 1977), so samples needed 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 $\delta^{15}\text{N}$ values. To assess the effect of lipid extraction (LE) on the sample isotope values and to determine the most appropriate approach, 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 $\delta^{15}\text{N}$ values in some samples; therefore, samples were not exposed to chemical LE. To account for the lipid effect on the $\delta^{13}\text{C}$ values of two taxa (*Nucella sp.* and *Urticina crassicornis*), the non-LE $\delta^{13}\text{C}$ values for those taxa were mathematically corrected ($\delta^{13}\text{C}'$) 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):

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

where

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

Where 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) based on the C:N ratio of the bulk tissue being analyzed. To then estimate a corrected $\delta^{13}\text{C}$ value ($\delta^{13}\text{C}'$), 6 ‰ (the difference in lipid and protein $\delta^{13}\text{C}$ values) is multiplied by the proportion lipid present and added to measured $\delta^{13}\text{C}$ values.

2.4 Trophic metrics

Several trophic metrics ($\delta^{13}\text{C}$ range, $\delta^{15}\text{N}$ range, convex hull area, corrected standard ellipse area, and isotopic evenness) were calculated for each site from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values to characterize and compare trophic structure between Kamishak and Kachemak bays. The range of $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ values (Layman et al. 2007). The $\delta^{15}\text{N}$ range represents the overall food chain length, or diversification in vertical food web structure, and is the maximum range of $\delta^{15}\text{N}$ values among all endmembers and consumers (Layman et al. 2007). For an assessment of food chain length based on $\delta^{15}\text{N}$ values, trophic enrichment factors (TEF) were estimated for each region as the difference in $\delta^{15}\text{N}$ values for taxa assumed to represent a distinct feeding type or trophic level, assuming the species sampled here are representative of their respective feeding type/trophic level's $\delta^{15}\text{N}$ value and only fed on the two endmembers. The difference in $\delta^{15}\text{N}$ was calculated between the mean $\delta^{15}\text{N}$ of all macroalgae and the mean $\delta^{15}\text{N}$ of all grazers (*Littorina sitkana* and *Lottia* sp.); the mean $\delta^{15}\text{N}$ of both POM samples and the mean $\delta^{15}\text{N}$ of all filter feeders (barnacles and *Mytilus trossulus*); the mean $\delta^{15}\text{N}$ of all primary consumers (i.e., filter feeders and grazers) and the mean $\delta^{15}\text{N}$ of the specialized predator *Nucella* sp.; and the mean $\delta^{15}\text{N}$ of *Nucella* sp. and the mean $\delta^{15}\text{N}$ of the omnivorous predator *Urticina crassicornis*.

Taxa were also assessed in the two-dimensional $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot space (i.e., isospace), which takes into account both horizontal and vertical food web structure. Convex hull area represents the overall area in isospace occupied by an assemblage. Convex hull area represents

the absolute trophic niche space and is based on the trophic positions of the isotopically extreme taxa within an assemblage. $\delta^{13}\text{C}$ range, $\delta^{15}\text{N}$ range, and convex hull area were calculated using the Stable Isotope Analysis in R (SIAR) package (Parnell et al. 2010). Corrected standard ellipse area (SEA_C) is a way of assessing the realized trophic niche space that is less influenced by a small sample size 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. Calculations of SEA_C were made using the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al. 2011).

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 effectively used, IEve answers the question of *how* the available niche space is being used (Cucherousset & 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 was calculated using commands from the “SI_DIV” script (Cucherousset & Villéger 2015) in R 3.5.1 (R Core Team 2018).

The $\delta^{13}\text{C}$ range, $\delta^{15}\text{N}$ range, convex hull area, and IEve were calculated at the site level based on mean stable isotope values for taxa within the defined assemblage. 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 (Stable Isotope Mixing Models in R, *simmr*) were used to determine relative

contributions of these two endmember groups to consumer diets at the site level. A mean value of macroalgal isotope values, and the mean offshore POM values were used as the two endmember inputs for each site. TEFs used in the model were estimated based on literature values, with a fixed value of 0.75 ± 0.11 ‰ for $\delta^{13}\text{C}$ (Caut et al. 2009) and 2.25 ± 0.1 ‰ for $\delta^{15}\text{N}$ (Vanderklift & Ponsard 2003) for each trophic level (Linnebjerg et al. 2016). Sites were used to create regional means of POM use for all consumers in the assemblage.

3. Results

Several trophic metrics were significantly different between Kamishak and Kachemak bays intertidal assemblages (Figure 3, Table 2). $\delta^{13}\text{C}$ range and $\delta^{15}\text{N}$ range were significantly 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 had a significant interaction of region and year (2-way ANOVA, $p=0.002$ and 0.02 , respectively; Table 2). Tukey post-hoc test indicated a significant difference between Kamishak Bay (in both years) and Kachemak Bay in 2017, but no significant difference between Kachemak Bay in 2018 and any other groups (Figure 3). 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.

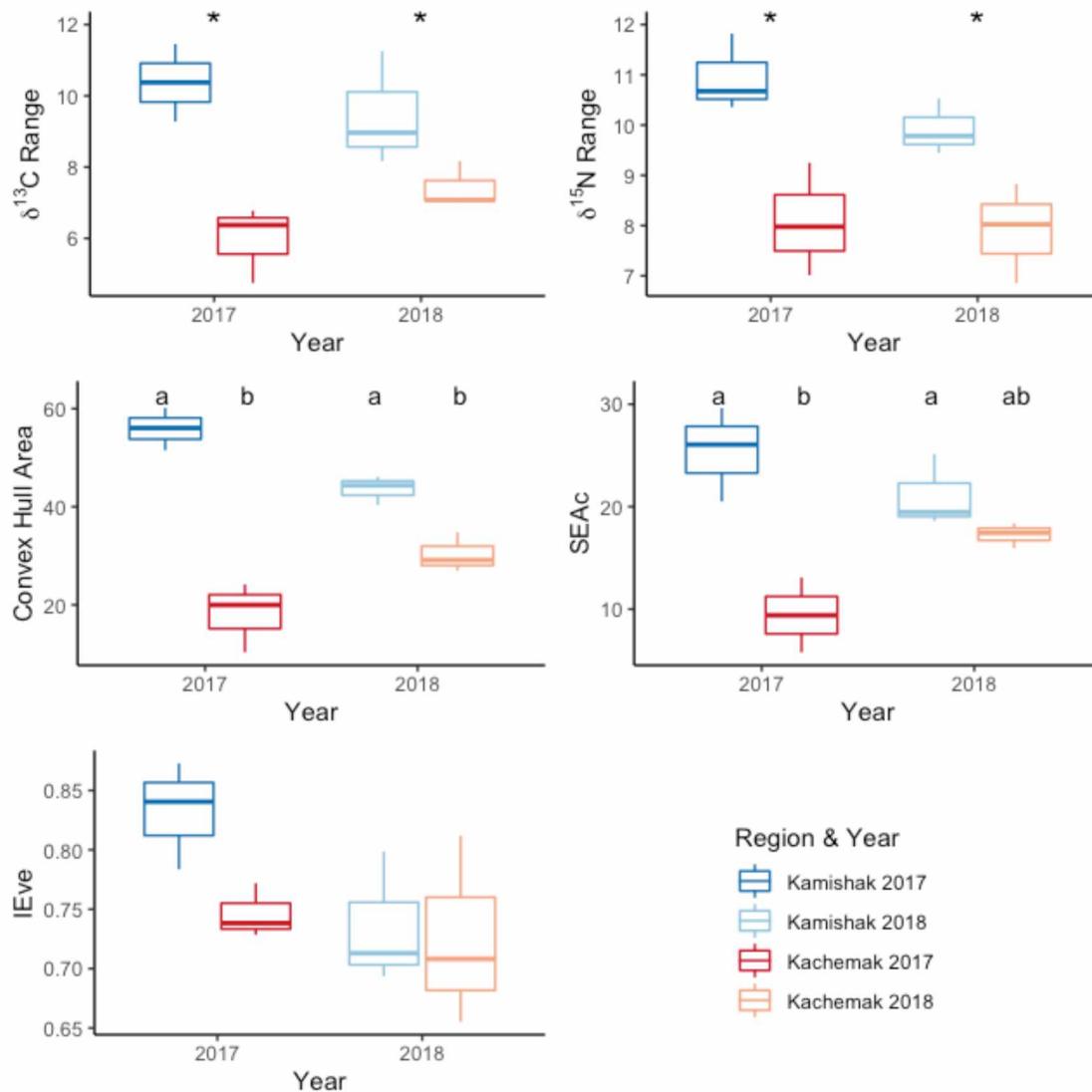


Figure 3. Boxplots representing trophic metrics ($\delta^{13}\text{C}$ range, $\delta^{15}\text{N}$ range, convex hull area, corrected standard ellipse area (SEAc), and isotopic evenness (IEve)) for Kamishak and Kachemak bays in 2017 and 2018. Boxes indicate first and third quartiles, median (horizontal 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.

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 $\delta^{13}\text{C}$ range, $\delta^{15}\text{N}$ 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
$\delta^{13}\text{C}$ Range	0.001	0.686	0.113
$\delta^{15}\text{N}$ Range	0.001	0.271	0.428
CH Area			0.002
SEA_c			0.016
IEve	0.168	0.099	0.264

Trophic niche space in Kamishak Bay was larger than in Kachemak Bay in 2017, as there was a larger convex hull area and SEA_c (Figure 3, Figure 4). These patterns were mostly driven by a larger range of $\delta^{13}C$ values in Kamishak Bay compared to Kachemak Bay. 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 driven by lower offshore POM values in Kamishak Bay compared with Kachemak Bay, although this pattern was not as pronounced in 2018 (Figure 4).

The $\delta^{15}N$ range, indicative of food chain length, was significantly larger in Kamishak Bay than Kachemak Bay intertidal assemblages (Figure 3). 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 (Figure 4). 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 ‰, Figure 4). TEFs between trophic levels were mostly between 2-3 ‰ for all trophic levels, but TEFs were slightly higher in Kamishak than Kachemak Bay (Table 3). The higher TEF in Kamishak Bay was especially pronounced between trophic level 1 and trophic level 2, and the highest TEF (>4 ‰) occurred between POM and filter feeders in Kamishak Bay (Table 3, Figure 4).

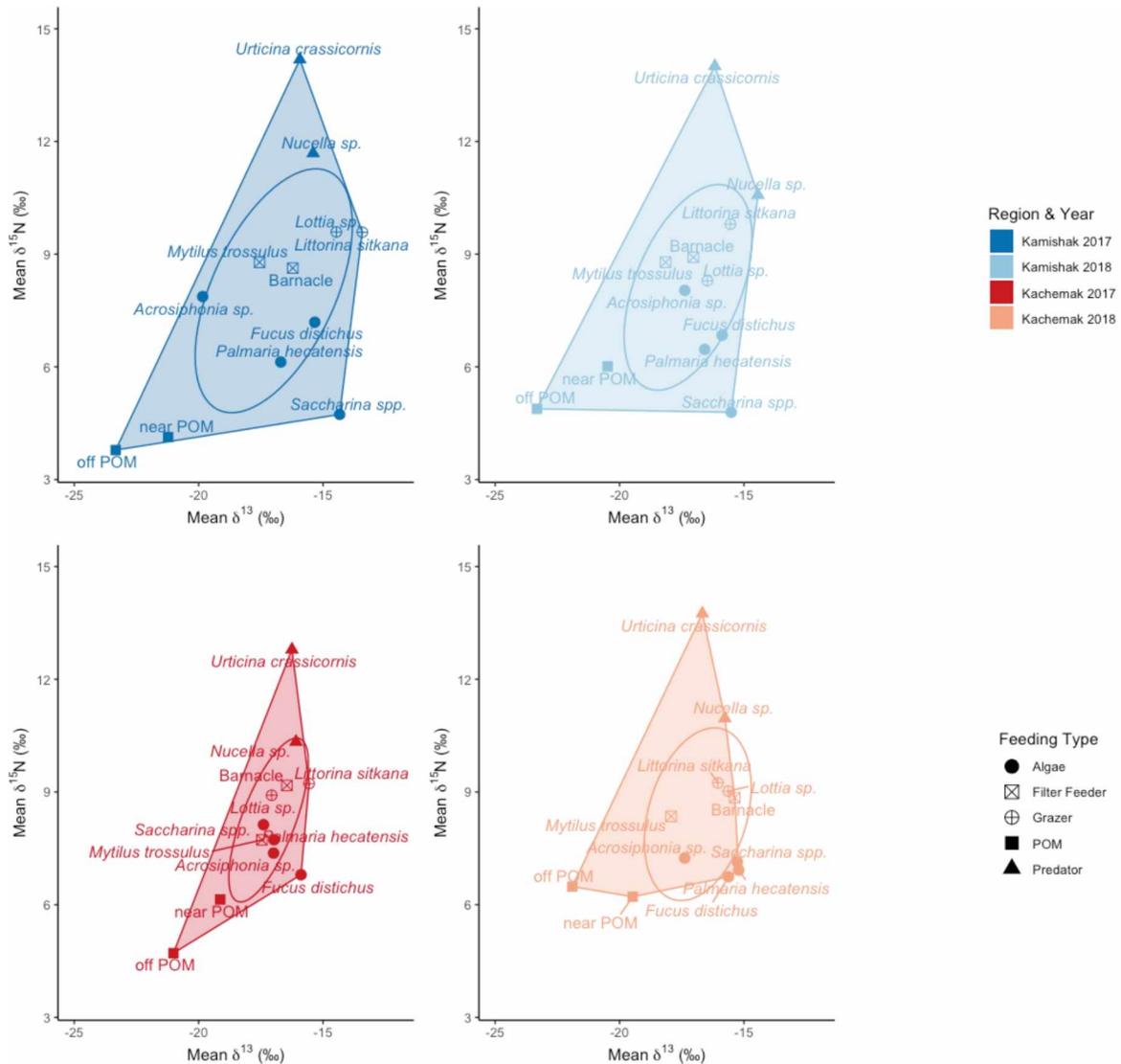


Figure 4. Total convex hull area and corrected standard ellipse area (SEAc) in isospace based on carbon and nitrogen stable isotope values in Kamishak (blue) and Kachemak (red) bays in 2017 (dark colors) and 2018 (light colors). Taxa are represented by points in isospace; endmember or feeding types are indicated by symbols.

Table 3. Means of trophic enrichment factors (TEFs, in %) between feeding types/taxa (trophic levels, TL) for Kamishak and Kachemak bays, AK in 2017 and 2018 (years combined).

	Kamishak Bay	Kachemak Bay
Macroalgae → Grazers (TL1→TL2)	2.81	1.84
POM → Filter Feeders (TL1→TL2)	4.08	2.64
Primary Consumers → <i>Nucella sp.</i> (TL2→TL3)	2.08	1.84
<i>Nucella sp.</i> → <i>Urticina crassicornis</i> (TL3→TL4)	2.96	2.62

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

Mean contribution of POM to consumers based on *simmr* results was mostly <50 % in both regions and years, indicating considerable sourcing from macroalgae by all consumers in both regions (Figure 6). The filter feeder *Mytilus trossulus* had the highest POM contributions in both regions and years (31-47 %), except for Kachemak Bay in 2018, where *U. crassicornis* had the highest POM contribution (52 %). Grazers had the lowest POM contributions, with *Littorina sitkana* having the lowest contribution of POM in most regions and years (13-16 %, Figure 6), but suspension-feeding barnacles having the lowest contribution of POM in Kachemak Bay in 2018 (16 %). On average, contribution of macroalgae to consumer diets was higher in Kamishak Bay than Kachemak Bay (~78 % versus ~70 %).

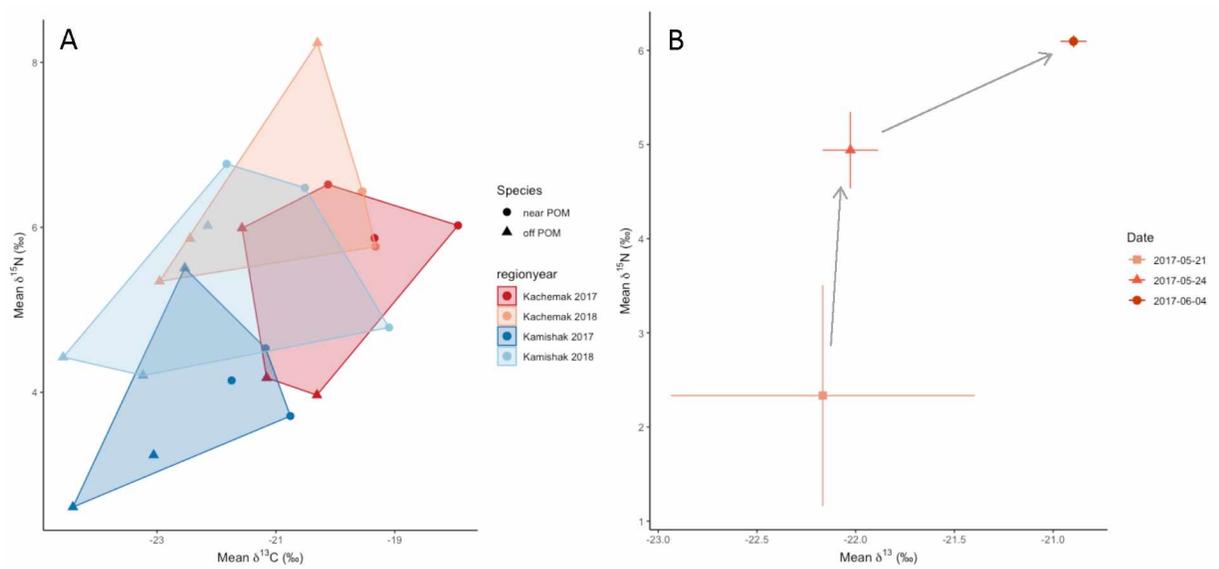


Figure 5. Mean carbon and nitrogen stable isotope values of particulate organic matter (POM) for Kamishak and Kachemak bays, AK in 2017 and 2018 (A). Mean and standard deviations of carbon and nitrogen stable isotope values of POM in Kasitsna Bay, AK over time (indicated by arrows; B).

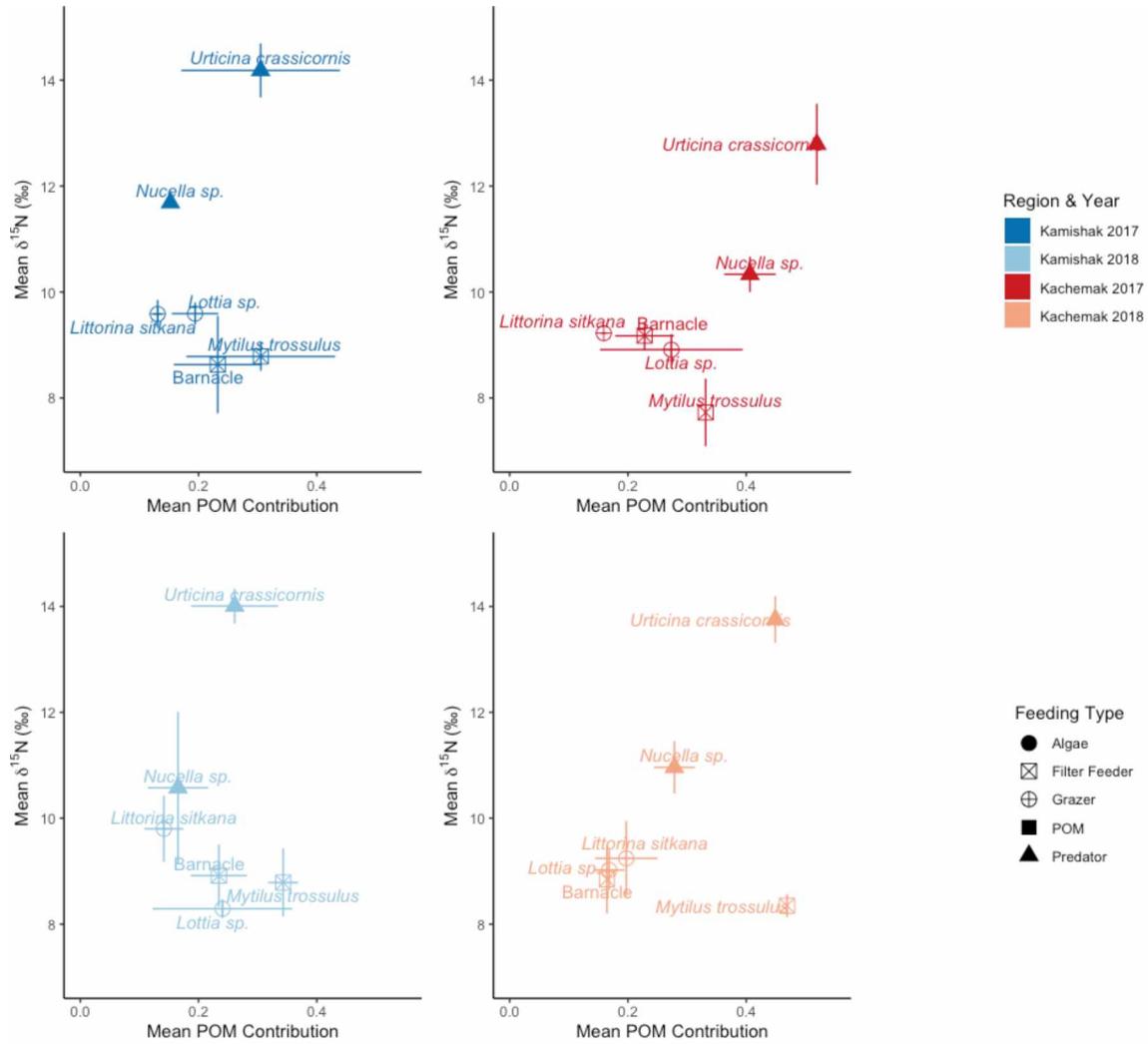


Figure 6. Mean contribution of particulate organic matter (POM) to consumers based on *simmr* results, arranged by their mean $\delta^{15}\text{N}$ values, in Kamishak and Kachemak bays, AK in 2017 and 2018. Feeding type is indicated by symbol; error bars indicate standard deviation.

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 $\delta^{13}\text{C}$ values of the POM source, which may be linked to the hydrographic conditions bringing more terrestrial matter into Kamishak Bay. Kamishak Bay was also characterized by slightly longer food chains, also resulting from POM characteristics and higher trophic position of top-level consumers. Intertidal consumers in both regions derived the majority of their carbon from macroalgal rather than POM sources, even more so in Kamishak Bay. This could indicate reliance on macroalgae as a temporally more stable food source or weaker trophic linkages (higher trophic flexibility) in Kamishak Bay consumers.

4.1 Regional influences on carbon sources

The combination of allochthonous (phytoplankton, terrestrial matter) and autochthonous (macroalgae) inputs to both systems were reflected by a wide, isotopically diverse food web base, especially in Kamishak Bay. Isotopic diversification at the base of the food web is represented by the $\delta^{13}\text{C}$ range (Layman et al. 2007). As the same taxa were analyzed in both regions, the higher diversity (larger $\delta^{13}\text{C}$ range) at the base of the food web in Kamishak Bay mostly originated from differences in the carbon isotope values of some of the same primary producers. Most of the increased $\delta^{13}\text{C}$ range in Kamishak Bay was driven by lower POM $\delta^{13}\text{C}$ values, indicating the endmembers assessed here (POM and macroalgae) were more isotopically distinct in Kamishak Bay compared to Kachemak Bay.

The heterogeneous composition of POM contributes to differences in $\delta^{13}\text{C}$ values of POM samples. POM is a mixture that includes phytoplankton, terrestrial organic matter, macroalgal detritus, fecal pellets, bacteria, and aggregates or remineralized forms of these components (Lee et al. 2004). These components have a range of stable isotope and nutritional values (Rau et al. 1990, Grémare et al. 1997, Grey et al. 2001). When the relative proportions of these components change, the overall $\delta^{13}\text{C}$ value of POM changes as well. For example, increased proportions of macroalgal detritus relative to phytoplankton in POM lead to increases in the $\delta^{13}\text{C}$ values, as was likely seen in this study by the higher $\delta^{13}\text{C}$ values of nearshore

compared to offshore POM. This is a pattern also reported from other regions worldwide (Heip et al. 1995, Duggins & Eckman 1997). Macroalgae have higher $\delta^{13}\text{C}$ values than phytoplankton due to the thicker boundary layer surrounding macroalgal blades, which causes higher concentration gradients and less diffusion of dissolved CO_2 or HCO_3^- across the boundary layer during photosynthesis (France 1995, Raven et al. 2002). The slow replenishment of the photosynthetic carbon source leads to a deficit of the typically metabolically preferred ^{12}C atom and an increased use of the ^{13}C atom, resulting in higher $\delta^{13}\text{C}$ values in macroalgae (France 1995). This difference in nearshore versus offshore POM composition, as indicated by stable carbon isotope values, can have important trophic implications. Macroalgal detritus that is more prevalent in nearshore POM can be less labile than phytoplankton (Duarte & Cebrián 1996), but it also presents a consistent, less seasonally variable autochthonous carbon source available to nearshore consumers than phytoplankton.

POM composition was also likely a main reason for the regionally lower $\delta^{13}\text{C}$ POM values in Kamishak Bay compared with Kachemak Bay. This regional difference may be due to a higher input of terrestrial and glacial material to Kamishak Bay, and/or differences in the $\delta^{13}\text{C}$ value of the photosynthetic carbon source for phytoplankton. Terrestrial material is typically characterized by lower $\delta^{13}\text{C}$ values than marine production (Prah et al. 1994), which would influence Kamishak Bay POM, given the strong terrestrial inputs from glacial melt and river discharge in upper Cook Inlet (Muench et al. 1978, Okkonen et al. 2009). In addition, lower salinity and pH in Kamishak Bay in early summer (Muench et al. 1978, Okkonen et al. 2009) would lead to increased CO_2 relative to HCO_3^- availability, and, therefore, increased use of CO_2 by primary producers (Prins & Elzenga 1989). Dissolved CO_2 has a $\delta^{13}\text{C}$ value of around -6 ‰, compared to 1 ‰ in HCO_3^- , resulting in low $\delta^{13}\text{C}$ values in primary producers using dissolved CO_2 (Laws et al. 1995). These mechanisms alone or in concert could explain the lower POM $\delta^{13}\text{C}$ values in Kamishak Bay. However, the consequences for the trophic system differ based on which mechanism drives POM $\delta^{13}\text{C}$ values. A higher amount of terrestrial matter in Kamishak Bay POM would have trophic implications for consumers based on typically low quality and lability of the terrestrial POM component (Ittekkot 1988). In contrast, different photosynthetic

carbon sources do not change food quality but are an indicator of differences in ecosystem processes in the two regions.

The range of $\delta^{13}\text{C}$ values was also larger in Kamishak Bay because some taxa, such as the grazer *Littorina sitkana*, were more enriched in ^{13}C than in Kachemak Bay. High grazer $\delta^{13}\text{C}$ values could indicate that they feed almost exclusively on the most isotopically enriched macroalgae (brown algae), or that the systems have an unacknowledged carbon source important to the rocky intertidal food web. In addition to the carbon sources studied here (POM and macroalgae) influencing the $\delta^{13}\text{C}$ range in both regions, microphytobenthos (MPB) is another possible carbon source. MPB is a film of organic material and microorganisms, such as diatoms, bacteria, and settling macroalgal spores covering the substrate (Hill & Hawkins 1991). Both of the grazers sampled here (*L. sitkana* and *Lottia* sp.) are highly mobile and known to rely strongly on MPB as a food source (Nicotri 1977, Sommer 1999). Both grazers are usually found in the upper intertidal, where MPB is a main source of benthic primary productivity (Norton et al. 1990). Previous studies have reported MPB in Kachemak Bay to have mean $\delta^{13}\text{C}$ values around -16 ‰ (fide McTigue & Dunton 2017), similar to those of the more ^{13}C -enriched macroalgae. This unsampled carbon source may explain the relatively high $\delta^{13}\text{C}$ values of both *L. sitkana* and *Lottia* sp., even compared to the high $\delta^{13}\text{C}$ values of macroalgae sampled here.

4.2 Regional influences on food chain length

The overall larger trophic niche space in Kamishak Bay compared with Kachemak Bay was also driven by larger stable nitrogen isotope ranges in Kamishak Bay. The larger $\delta^{15}\text{N}$ range in Kamishak Bay may indicate greater isotopic fractionation between trophic levels (i.e., a higher TEF) and/or additional trophic levels. $\delta^{15}\text{N}$ of an organism increases with increasing trophic level, so $\delta^{15}\text{N}$ range can be used as a proxy for the food chain length of an assemblage, especially when investigating the same taxa in the assemblages (Layman et al. 2007, Perkins et al. 2014). The smaller $\delta^{15}\text{N}$ range in Kachemak Bay indicated a shorter food chain length and, therefore, a more efficient transfer of energy from lower to higher trophic levels (Elton 1927, Post 2002b). When comparing across the assemblage investigated in both regions, the larger $\delta^{15}\text{N}$ range in Kamishak Bay was due to both lower primary producer (offshore POM) $\delta^{15}\text{N}$

values and higher predator (*U. crassicornis*) $\delta^{15}\text{N}$ values than in Kachemak Bay, as well as generally larger TEF in Kamishak Bay.

Similar to $\delta^{13}\text{C}$, the $\delta^{15}\text{N}$ values of POM samples are also influenced by the $\delta^{15}\text{N}$ values of the various POM components (Owens 1985, Rau et al. 1990). The lower $\delta^{15}\text{N}$ values in Kamishak Bay offshore POM compared to Kachemak Bay were likely a result of terrestrial material present in the region and/or local phytoplankton composition. Terrestrial material has lower $\delta^{15}\text{N}$ 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 & Casciotti 2001). Therefore, overall lower POM $\delta^{15}\text{N}$ values in Kamishak Bay could be a consequence of allochthonous terrestrial inputs from upper Cook Inlet, as also discussed for POM $\delta^{13}\text{C}$ values. POM $\delta^{15}\text{N}$ values can also be influenced by phytoplankton bloom events and inorganic nitrogen availability. For example, nitrate and ammonium are the most common inorganic nitrogen forms used during phytoplankton production. Production based on regenerated ammonium tends to have lighter $\delta^{15}\text{N}$ values compared with nitrate-based production (Sigman & Casciotti 2001). Ammonium is generally more prevalent in low-salinity, estuarine systems (Sigman & Casciotti 2001), which could explain the lower POM $\delta^{15}\text{N}$ values in Kamishak compared with Kachemak Bay.

The overall $\delta^{15}\text{N}$ range in a region is also dependent on the number of consumer levels and the TEF between trophic levels, where consumer $\delta^{15}\text{N}$ values are driven by the TEF and the trophic level of their prey. The TEFs were slightly higher in Kamishak compared to Kachemak Bay, especially the higher TEF between POM and filter feeders in Kamishak Bay. 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). This breakdown adds a trophic step, increasing the TEF between terrestrial organic matter and consumers. If POM in Kamishak Bay indeed contained a large proportion of terrestrially derived organic matter, as discussed above, this additional trophic step via microbial degradation would explain this larger TEF between POM and filter feeders in Kamishak Bay (Macko & Estep 1984). Stepwise trophic enrichment is also dependent on the

ontogenetic status and body size of consumers (Polis 1984, Scharf et al. 2000), and some of the differences in $\delta^{15}\text{N}$ positions of the same top consumer taxa in the two regions may have been due to different ages or sizes of the predators. Lastly, the anemone, *U. crassicornis*, at the upper end of the food chain, is a large-bodied, long-lived anemone that is a non-selective, opportunistic feeder, preying on a wide variety of organisms even larger than their own body size (Den Hartog 1986). While *U. crassicornis* had the highest $\delta^{15}\text{N}$ values of the assemblage in both regions and years, slight regional differences could indicate that they were likely feeding on prey outside of the assemblage studied here. This could include prey at higher trophic levels, explaining their high $\delta^{15}\text{N}$ value relative to other more specialized top consumers, such as whelks (Burrows & Hughes 1991).

4.3 Regional influences on trophic niche space

The larger $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges in the glacially influenced Kamishak Bay, especially in 2017, resulted in larger overall trophic niche space as represented by larger convex hull and standard ellipse areas than the more marine-influenced Kachemak Bay. In contrast, a recent study conducted in a glacial fjord system concluded that glacial input reduced trophic diversity and increased trophic redundancy (Cari et al. 2020). High trophic diversity is generally associated with a larger niche space (i.e., a larger SEAc), while trophic redundancy is often higher when there is a smaller niche space (i.e., a smaller SEAc), especially when considering the same number of taxa (Layman et al. 2007, Jackson et al. 2011). However, non-glacial estuarine systems that receive terrestrial inputs typically exhibit larger niche space (i.e., higher $\delta^{13}\text{C}$ range and SEAc), similar to our results (Abrantes et al. 2014). In one non-glacial estuarine system, a 'transition zone' between riverine-estuarine and coastal-marine zones exhibited higher trophic diversity ($\delta^{13}\text{C}$ range) than other zones (Kim et al. 2019). It is possible that Kamishak Bay may be positioned at a similar mixing/transition zone between the highly glacially influenced upper Cook Inlet and the marine Gulf of Alaska, represented by Kachemak Bay. While data were not collected from upper Cook Inlet (i.e., a region with strong glacial influence), the higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges and a higher SEAc in 2017 in Kamishak Bay compared to the marine-influenced Kachemak Bay agree with the characteristics of a transition zone (Kim et al. 2019).

Isotopic evenness was consistent between regions, despite regional differences in other trophic metrics. In other words, consumers maintained similarly effective use of available resources regardless of environment (Mason et al. 2005). Marine taxa often have inherently flexible feeding habits, resulting in weak trophic links to their food sources (Padilla & Savedo 2013, Portail et al. 2018). Isotopic composition of the same taxa varies depending on the origins of available organic matter food sources (Sarà et al. 2007), as discussed above for POM sources. Even though the absolute isotopic position of taxa may have been slightly different between the two regions, the taxa's relative trophic positions seemed to have remained fairly consistent, which resulted in similar levels of isotopic evenness. It seems that trophic flexibility allowed taxa to use the available resources in the two regions, maintaining trophic evenness even with environmental differences. This analysis suggests that both food webs in LCI can be considered stable, at least for the common intertidal taxa investigated here, supported by taxa with weak trophic links in variable environments (Bordeyne et al. 2017, Portail et al. 2018).

4.4 Temporal variability in trophic metrics

The relative proportions of the components comprising POM in the Gulf of Alaska are seasonally influenced as early summer brings spring blooms, snowmelt, and shifts in hydrology (Weingartner et al. 2005). For example, short-term variability in early summer in POM stable isotope values was seen in Kasitsna Bay, where $\delta^{13}\text{C}$ values shifted by about 1 ‰ and $\delta^{15}\text{N}$ values shifted by about 4 ‰ at the same location in just a few weeks. This may be explained by an increase in diatoms during the sampling period (KBNERR 2018). POM $\delta^{15}\text{N}$ values increase as the ambient nitrate pool is drawn down over the course of a bloom, when the metabolically preferred ^{14}N source (i.e., nitrate or ammonia) is depleted and large isotopic fractionation occurs during the uptake of the ^{15}N source by phytoplankton (Mariotti et al. 1984, Altabet 2001). Besides the increase in $\delta^{15}\text{N}$ values, a bloom could also explain the decrease in variability associated with the POM samples in the Kasitsna Bay time series as phytoplankton dominate over other components of POM, making the POM mixture more homogeneous.

Short-term variability in isotope values of POM on the order of days, resulting from events like phytoplankton blooms, can range over similar scales to the observed regional

differences in POM. Regional differences in POM isotope values between Kamishak and Kachemak bays were larger for $\delta^{13}\text{C}$ values, around 2-3 ‰ compared to temporal shifts (~ 1 ‰). However, our results suggest that there was a systematic regional difference in POM composition separate from temporal variability. Regional differences in $\delta^{13}\text{C}$ were generally larger than temporal variability, indicating a difference in carbon sources to POM between the two regions, and POM values in Kamishak Bay were consistently lower compared with Kachemak Bay. Additionally, the general pattern of larger niche space in Kamishak Bay remained consistent. There was some convergence of niche space values between the two study regions in 2018, probably caused by annual variability in regional drivers (e.g., precipitation, phytoplankton community composition and bloom timing). Macroalgal stable isotope values turnover times are on the order of several weeks to months in meristematic tissues (Viana et al. 2015), contrasting with shorter turnover times in POM. Longer turnover times make macroalgal samples less susceptible to confounding of spatial and temporal variability. Similarly, temperate invertebrate tissue turnover times are on the order of weeks to months (Hawkins 1985, Vermeulen et al. 2011, Weems et al. 2012, Vander Zanden et al. 2015), so they are less temporally variable than POM but could contribute to long-term regional or annual differences in trophic niche space.

4.5 Trophic pathways

Rocky intertidal consumers in both systems derived the majority of their carbon from macroalgal sources as opposed to POM sources. Between the two regions, the Kamishak Bay assemblage relied more on macroalgae and less on POM than the Kachemak Bay assemblage. The presumably higher relative proportion of terrestrial material in Kamishak Bay POM (Okkonen et al. 2009) could decrease POM use due to lowered food quality (Schell 1983, Berglund et al. 2007). Ultimately, even though there were additional sources to POM in Kamishak Bay, this trophic pathway was weaker and a less-used carbon source.

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. Within POM, there can be both new production and recycled

production (e.g., phytoplankton), as well as detritus, which can include phytoplankton detritus, terrestrial organic matter, macroalgal detritus, or fecal pellets. Macroalgal and detrital pathways are both examples of 'slow channels', or trophic pathways supported by food sources with low biomass turnover (Rooney et al. 2006). On the other hand, the phytoplankton pathway is 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 large glacial and other terrestrial inputs, the Kachemak Bay assemblage seems to have a more prominent 'fast channel' reliant on phytoplankton. With a more prominent macroalgal pathway in Kamishak Bay, combined with the presence of the terrestrial detritus pathway (i.e., two weak pathways), we would expect to see increased stability of the food web in Kamishak Bay. Slow channel dynamics support food web stability as they are characterized by weak trophic links, allowing for multiple possible pathways from slow channel sources to top consumer (McCann et al. 1998, Rip et al. 2010). There are other mechanisms that increase 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 & McCann 2012), and sources such as macroalgae provide a structurally complex habitat that can also increase biological diversity (Hooper & 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 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 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). Consumers in Kamishak Bay may rely more on macroalgae as a food source if it is energetically preferable to glacial silt-laden terrestrial POM, which may be energetically costly to process and physically stressful on particle sorting along the feeding apparatus (Bayne et al. 1987, Airoidi 2003). The ability of consumers (including primary consumers like *M. trossulus* and 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 demand a flexible trophic structure. Kamishak Bay has particularly high seasonal variability, including summer freshwater 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 explains the need for additional trophic flexibility in this region, potentially leading to higher stability.

5. Conclusion

The goal of this study was to understand the influence of hydrography on trophic processes in glacially-influenced ecosystems. To address this goal, we compared the trophic structure of rocky intertidal assemblages in two hydrographically distinct regions. We suggest that increased terrestrial and glacial discharge influenced the trophic structure of the assemblages studied here. Carbon and nitrogen stable isotope results supported the existence of additional components of POM (namely, terrestrial organic matter) being used throughout the food web in the glacially-influenced Kamishak Bay. Annual variability in trophic metrics indicated these food webs are flexible, but there was a consistent pattern of higher trophic diversity in Kamishak Bay. This may be due to Kamishak Bay's location in a 'transition zone' between terrestrial and marine influences based on its location in lower Cook Inlet and local hydrological patterns. Macroalgae were an important food source in both regions, even more so in Kamishak Bay where they may be an energetically beneficial food source compared to silt-laden glacial inputs. Consumers were able to use the unique inputs in each region, exhibiting flexible feeding habits and maintaining an even use of resources. In both regions, the combination of multiple trophic pathways potentially contributes to stability in both food webs. Given the larger niche space and more diverse resource use, Kamishak Bay may be well suited to deal with expected increased glacial stress from additional climate warming (Moon et al. 2019). However, the limits of this trophic flexibility are unknown. If the assemblage in Kamishak Bay is near the limits of its trophic flexibility, then it may not be able to maintain its trophic structure with additional environmental stressors. The comparison of the two hydrographically contrasting rocky intertidal systems suggests, however, that the food webs in these systems have the flexibility necessary to thrive and be stable in the "typical" range of conditions experienced in this region.

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