Nearshore Food Web Structure on the OCS in Cook Inlet

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Abstract

Rocky intertidal communities in Lower Cook Inlet, Alaska, may be particularly vulnerable from impacts of planned and ongoing oil and gas extraction activities on the OCS in Cook Inlet. Here, food web structure of rocky intertidal communities in Kamishak Bay in lower western Cook Inlet was investigated and compared with food web structure of similar communities in Kachemak Bay, which comprises the same regional species pool but is hydrographically upstream of oil and gas activities. Common macroalgal and invertebrate members of three rocky intertidal communities were sampled in each region in 2017 and 2018. Particulate organic matter (POM) was collected offshore from the rocky intertidal at each site as it is a food source for intertidal invertebrates in addition to macroalgae. Food web structure was assessed using carbon and nitrogen stable isotope analyses. Carbon isotopes inform about the diversity at the base of the food web (endmembers) and the use of different carbon sources (here: POM versus macroalgae) by intertidal consumers. Nitrogen isotopes inform about trophic position of consumers and the length of the food web. Combined, these two metrics allow for the assessment of total trophic niche space for each region. The distribution of taxa within this niche space informs about resource use patterns in the respective regions.

Trophic niche space in Kamishak rocky intertidal systems was larger, driven by larger ranges in both carbon and nitrogen isotope values, than in Kachemak Bay. The larger carbon isotope range in Kamishak Bay was mostly driven by the POM source being more depleted in ^{13}C compared with POM in Kachemak Bay, likely because of the greater influence of freshwater and input of terrestrial matter in Kamishak Bay. A larger δ^{15}N range in Kamishak Bay intertidal pointed towards a longer food web, possibly driven by additional microbial processing steps being needed to render terrestrial matter components of POM labile to marine consumers. In both regions and years, consumers derived the majority of their carbon from macroalgae as opposed to POM. Generally, carbon sourcing from macroalgae was higher in Kamishak Bay compared with Kachemak Bay, possibly because of lower quality of POM in Kamishak Bay due to high levels of inorganic silt in the suspended matter. The results of this study suggest that intertidal organisms in Lower Cook Inlet have high feeding plasticity that can adapt to regionally different conditions as well as potentially different annual conditions. This plasticity, plus the ability to source carbon from multiple sources, increases the overall stability of these food webs against perturbations. However, it is not clear whether these taxa are at their limit of plasticity under current regional conditions, which could increase the potential for future climate-related or human-induced perturbations to exceed this plasticity.

Introduction

Rocky intertidal communities are complex systems strongly influenced by many static and dynamic environmental drivers as well as biological interactions (Menge 2001, Konar et al. 2016). Top-down control of rocky intertidal communities, as from grazing and predation, has been the topic of intense and sometimes seminal studies (e.g., Paine 1966, Menge et al. 1986, Wootton 1995, Hori et al. 2006). Bottom-up factors have also garnered attention in rocky intertidal community studies examining how food supply from primary production can support these systems (e.g., Bustamante et al. 1995, Menge 2000, Wieters 2005). Combined, top-down and bottom-up forces create a network of energy flow through a system that is represented by its food web.

Trophic relationships are an important component of community functioning, particularly as they relate to the use of main carbon sources. Intertidal communities and food webs are linked to both local and regional oceanographic conditions (Nielsen and Navarette 2004, Blanchette et al. 2006, 2008). For example, productive upwelling conditions increase the carbon subsidies to intertidal food webs (Menge and Menge 2013). Estuarine systems provide another example of the impact of strong hydrographic gradients. In these environments, carbon inputs are not only influenced by environmental conditions, but allochthonous sediments contributed by ocean currents may add to the diversity of nearshore food webs. In addition to phytoplankton, primary producers in estuarine rocky intertidal systems include marine macroalgae, terrestrial plants, and benthic microalgae (Guerry et al. 2009). These sources, or carbon subsidies, can contribute variable amounts of carbon to rocky intertidal consumers (Bustamante and Branch 1996, Hill and McQuaid 2008). The availability of multiple food sources can contribute to the stabilization of nearshore food webs (Huxel et al. 2002, McMeans et al. 2013). Different primary producers vary in their vulnerability to environmental stressors; thus, if the availability of one primary production source is reduced, consumers could compensate with other food sources and maintain food web linkages. The number of species contributing to the food web in a specific system, their distribution across trophic levels, the links to different basal food sources, and how species are complementary or independent in their resource use are all important determinants of system resilience (Link 2002, Kondoh 2003, Hillebrand and Shurin 2005).

In addition to influences from climate change or other anthropogenic activities, nearshore marine habitats are particularly vulnerable to the potential impacts of marine oil and gas extraction activities (Crowe et al. 2000). For example, catastrophic effects have been documented on all trophic levels of coastal ecosystems immediately after oil spills (e.g., Estes 1991, Newey and Seed 1995), but effects can also linger for decades (e.g., Thompson et al. 2002, Peterson et al. 2003). These impacts include direct lethal effects of severe incidents such as oil spills and subtle effects, such as the reduction of resilience and health of species and the disruption of the energy flow among the various nearshore ecosystem components (Temara et al. 1999). Therefore, the nearshore food web structure can be a useful metric to assess not just the structure but also the function of coastal ecosystems. To understand possible changes in food web structure,

benchmark understanding has to be created so natural ecosystem functioning and variability can be distinguished from potential impacts (Underwood 1991).

Here, the trophic structure of rocky intertidal communities was evaluated and compared in two regions of Cook Inlet, one of Alaska's outer continental shelf regions of active and planned oil and gas extraction. Based on general hydrography, the western region of Cook Inlet is downstream of resource extraction activities, and the eastern, upstream side is mostly unaffected. These regions also differ hydrographically, with significant influxes from riverine and glacial melt discharges on the western side, which add cold, oligotrophic, and silt-laden waters into coastal habitats (Muench et al. 1978, Feely and Massoth 1982, Arendt et al. 2002, Hood et al. 2009). The eastern side of Cook Inlet is mostly under oceanic influences and can serve as a useful comparative system. The specific questions asked here were (1) Does intertidal food web structure differ between the western and eastern regions of Cook Inlet? (2) Are intertidal food web structure characteristics consistent over two years of study? (3) Do intertidal organisms source carbon more from phytoplankton or macroalgae?

Methods

Site description

Intertidal food webs were analyzed in two regions of Lower Cook Inlet; Kachemak Bay to the east and Kamishak Bay to the west (Figure 1). The northern Outer Continental Shelf Cook Inlet Planning Area reaches into the lower portions of the Inlet (Figure 2). Circulation in Cook Inlet is such that water from the northern Gulf of Alaska enters on the eastern side of the Inlet, where part of this water is diverted to the east into Kachemak Bay (Muench et al. 1978). Within Kachemak Bay, water flows along its southern shore, where riverine and glacial discharge in upper Kachemak Bay modifies the hydrography. Water exits Kachemak Bay on the northern shore and enters back into Lower Cook Inlet at Anchor Point (Burbank 1977). Currents in Cook Inlet then flow along the eastern side, again being modified by significant input of freshwater and sediments from rivers (peak discharge > 5000 m^3 s^{-1}) and glacial discharge (sediment load of up to 2000 mg L^{-1}) in upper Cook Inlet (Sharma and Burell 1970, Muench et al. 1978, Hein et al. 1979, Feeley and Massoth 1982, Neal et al. 2010). Net southward outflow from Cook Inlet is then bathymetrically steered along the western side of the Inlet. Part of this water passes through Kamishak Bay in western lower Cook Inlet before exiting into Shelikof Strait in the Gulf of Alaska. Sites in Kamishak Bay are, thus, downstream from potential oil and gas exploration activities in the BOEM Cook Inlet Planning Area (Figure 2). The large tidal range in Cook Inlet (~ 9 m) causes strong tidal currents upwards of 4 m s^{-1} that relax and enforce this general flow on a twice-daily basis (Muench et al. 1978, Nelson and Whitney 1996).
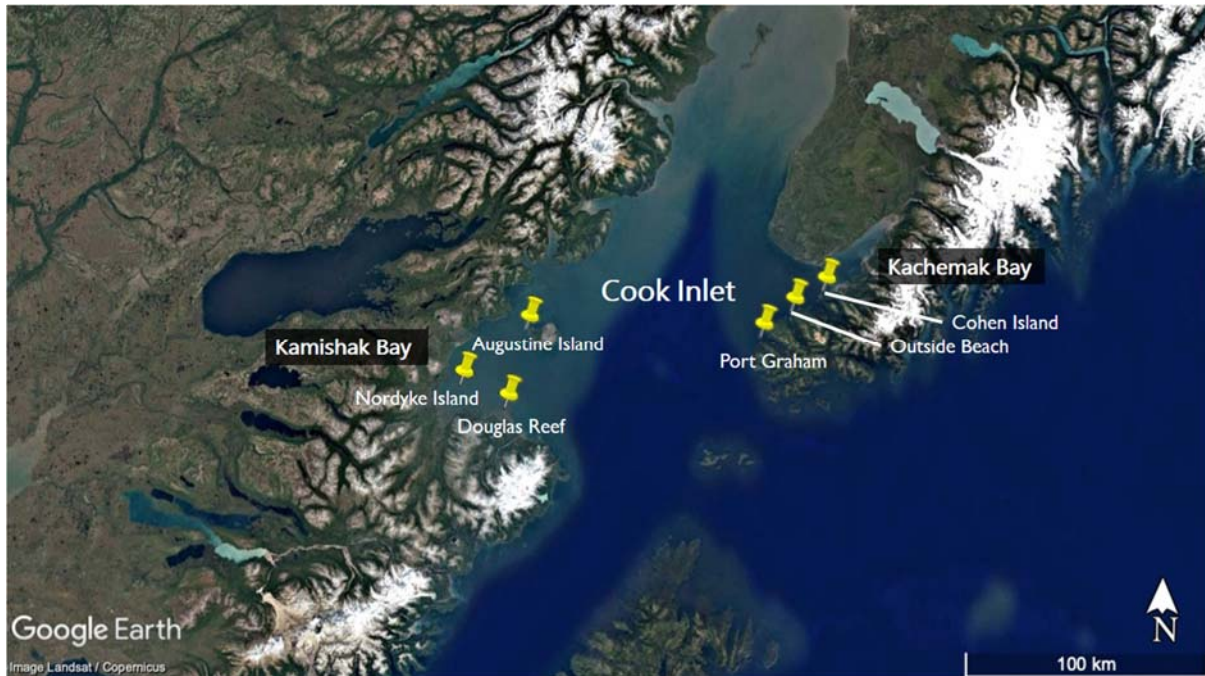
Figure 1: Map of study area of Lower Cook Inlet with Kachemak Bay to the east and Kamishak Bay to the west. The three study sites per region are marked. Glacial and riverine input into the study systems can be seen as green-brown coloration of the water.

Six sites were chosen to represent regional food webs; Port Graham, Outside Beach, and Cohen Island in Kachemak Bay, and Douglas Reef, Augustine, and Nordyke Island in Kamishak Bay (Figure 1, Table 1). The Nordyke site was slightly different between the two years because of accessibility problems in 2018 due to rough weather, but the locations were in close vicinity (~ 2 km apart) on Nordyke Island. Sites in Kachemak Bay were in the outer regions of the bay (i.e., outside of Homer Spit) and mostly influenced by oceanic water properties, while sites in Kamishak Bay were located in the outflow of waters modified from upper Cook Inlet glacial and river discharge (Figure 1). Sites in Kachemak Bay typically had a steeper slope and more heterogeneous substrate of cobble and boulder than sites in Kamishak Bay, which typically had a lower slope and more uniform substrate, often bedrock or uniform grain size. Collections for intertidal food web structure occurred in late April/early May (Kachemak Bay) and June (Kamishak Bay) in both years.
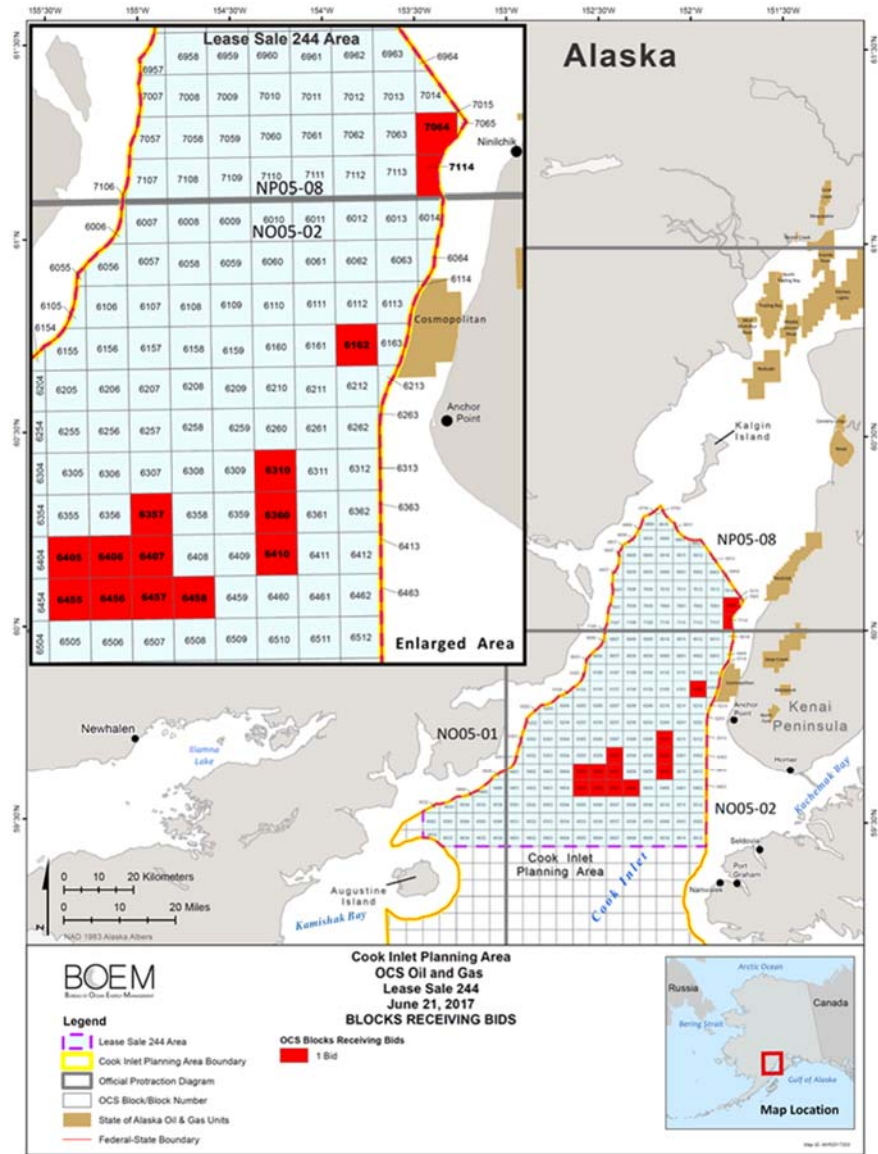
Figure 2: Map of the Outer Continental Shelf (OCS) Cook Inlet Planning Area with lease sale areas in relation to the Kachemak Bay and Kamishak Bay study areas. Map from https://www.boem.gov/Map-of-Blocks-Receiving-Bids/.

Table 1: Site locations in each region and year.

Site	Year	Region	Latitude	Longitude
Port Graham	2017, 2018	KACH	59.37333	-151.8941
Outside Beach	2017, 2018	KACH	59.46458	-151.7094
Cohen Island	2017, 2018	KACH	59.53913	-151.4769
Douglas Reef	2017, 2018	KAMI	59.1052	-153.716
Nordyke Island	2017	KAMI	59.1814	-154.082
Nordyke Reef	2018	KAMI	59.2236	-154.121
Augustine Island	2017, 2018	KAMI	59.4064	-153.455

Sample collection

Common macroalgal, invertebrate, and suspended particulate organic matter (POM) samples were collected at all sites. Surface water samples for POM stable isotope analysis were collected by hand offshore (at least 100 m from shore) at each site. These water samples were filtered onto Whatman GF/F filters (0.7 µm pore size); approximately 100 mL were filtered in 2017, and 200 mL were filtered in 2018 to ensure sufficient material for analysis. Understanding that POM is an extremely heterogeneous source (consisting of various heterotrophic protists, phytoplankton taxa, and detritus) and that stable isotope composition can change based on composition, POM was collected several times over a 6-week period in Kachemak Bay. This was not logistically possible in Kamishak Bay. Macroalgal endmembers collected by hand at each site and year included the green alga *Acrosiphonia* sp., the brown algae *Fucus distichus* and *Saccharina* spp., and the red alga *Palmaria hecatensis*. Intertidal consumers were suspension-feeding mussels (*Mytilus trossulus*) and barnacles (*Balanus* spp.), grazing limpets (*Lottia scutum*), periwinkles (*Littorina* spp.) and chitons (*Katharina tunicata* and *Tonicella* sp.), as well as predatory whelks (*Nucella* spp.) and sea anemones (*Urticina crassicornis*). These taxa were chosen because they were typical and abundant members of the rocky intertidal communities and occurred in both regions, facilitating comparisons. Samples were identified to the lowest possible taxonomic level in the field and frozen (dissected or whole, depending on the organism) on the day of collection. Macroalgae were collected whole, and muscle tissue, body wall, or whole organisms were used for invertebrates, depending on organism size.

Laboratory analyses

Invertebrate samples of sufficient size were dissected to remove soft tissue, avoiding hard parts such as shells and lipid-rich material such as reproductive tissue. When animals were too small to dissect, they were kept whole. Macroalgal and invertebrate tissue samples were dried at 60°C for approximately 24 hours (or until stable weight was achieved). Samples with carbonate structures, such as barnacles and echinoderms, were acidified using 1N HCl until carbonates had dissolved, indicated by the ceasing of bubbling. Samples were then rinsed in deionized water and dried as described above. POM filters were exposed to saturated HCl fumes for at least four hours to dissolve any carbonates present. Dried macroalgal, invertebrate, and POM samples were analyzed for bulk $\delta^{13}C$ and $\delta^{15}N$ values. Carbon stable isotopes are indicative of basal resource uses, and nitrogen stable isotopes are a good indicator of trophic level because of the stepwise enrichment in this isotope between trophic levels (Peterson and Fry 1987). Stable isotope ratios of individual bulk tissue samples were measured using continuous-flow isotope ratio mass spectrometry (IRMS) at the Alaska Stable Isotope Facility. Stable isotope ratios will be reported in conventional δ notation as ‰ deviation from the international standards PDB (carbon) and air (nitrogen) according to the following equation:

$\delta X = [(R_{sample}/R_{standard}) - 1] \cdot 1000$

where *X* is ^{13}C or ^{15}N of the sample, and R is the corresponding ratio ^{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.

Lipids tend to be isotopically lighter than other compounds in their δ^{13}C values (DeNiro and Epstein 1977), so samples were corrected for variable lipid content to maximize comparability of samples. However, chemical extraction of lipids can have an unwanted effect on δ^{15}N values, which needed to be accounted for (Mintenbeck et al. 2008). To assess the effect of lipid extraction (LE) on invertebrate samples and to determine the most appropriate approach of correcting for these lipids, a subset of samples from a variety of common species were analyzed in duplicate, one with LE and a second set without LE. Lipids were chemically extracted three times per sample (or more if the solvent still contained color) using 2:1 chloroform:methanol (after Folch et al. 1957). Samples were then dried and prepared as described above for stable isotope analysis. LE did affect the δ^{15}N values in invertebrate samples; therefore, the non-LE δ^{13}C values (denoted as δ^{13}C') for invertebrate consumers were mathematically corrected based on the C:N ratio of the bulk tissue sample using the following equation (after Post et al. 2007):

$$\delta^{13}C = \delta^{13}C' - 3.44 + 0.99 \times C{:}N_{bulk}$$

Where 3.44 is the assumed trophic enrichment step between trophic levels and C:N$_{bulk}$ refers to the carbon:nitrogen (both by volume) of the invertebrate tissue.

Data analyses

A number of community-wide trophic metrics were calculated from the stable isotope data to characterize and compare community trophic structure between the regions and assess species interactions (Parnell et al. 2010, Layman et al. 2007, Cucherousset and Villeger 2015). The range of δ^{13}C values is a representation of trophic niche diversification at the base of the food web; it includes all endmembers and consumers and is the distance between the two species with the lowest and highest δ^{13}C values. The δ^{15}N range represents the overall food chain length, or vertical food web structure, and is the maximum range of δ^{15}N values of all endmembers and consumers. Isotope values (δ^{13}C and δ^{15}N) were averaged among sites within each region and year for overall region descriptions. Differences in δ^{13}C and δ^{15}N ranges between regions and years were determined by two-way ANOVA with region and year as independent factors, using the range in δ^{13}C or δ^{15}N values at each of the three sites within each region as replicates for each of the years. Significance for this and all following comparisons was set at $\alpha = 0.05$.

Total trophic niche area, or trophic richness, is the area in trophic space occupied by a community, measured as the convex hull of all species with δ^{13}C and δ^{15}N as coordinates (Layman et al. 2007, Cucherousset and Villeger 2015, Rigolet et al. 2015). As such, the trophic niche area is closely linked to the δ^{13}C and δ^{15}N ranges at each site. Convex hull area was calculated from the δ^{13}C–δ^{15}N values of macroalgae, POM, and invertebrates for the same taxa at each site in Kachemak and Kamishak Bays; regional convex hull areas were calculated from averaged δ^{13}C and δ^{15}N values across the three sites per region for each taxon. The same taxa were analyzed at all sites in both regions. However, in rare cases where a taxon was not available

at all sites, data for that taxon and site were substituted with an average of the values of the same taxon from the other two sites in that region so that an overall balanced data design could be preserved. Again, differences in convex hull areas between regions and years were determined from convex hull areas determined for each site and region in both years using two-way ANOVA.

Trophic niche area measures only one facet of the trophic diversity, trophic richness (the total amount of trophic space filled by the community, independent of how taxa are distributed within this space). Therefore, measures are needed that detail how organisms utilize trophic space. Isotopic divergence (I_{Div}) measures how species diverge in their distances from the center of gravity in trophic space (i.e., the convex hull) (Cucherousset and Villeger 2015). I_{Div} ranges from 0 to 1, where low values reflect that most species are close to the center of gravity, while higher values reflect more taxa at more extreme (boundary) areas of total trophic niche space. Isotopic dispersion (I_{Dis}) is similar to I_{Div}, but the latter measures the mean distance of individual species within trophic space (convex hull) to the centroid of all species, not the center of gravity of the convex hull (Laliberté and Legendre 2010, Cucherousset and Villeger 2015). I_{Dis} also ranges from 0 to 1, where 0 means all organisms have the same stable isotope values, and larger values mean that most of the taxa's isotope values are far from the centroid of all points. Therefore, while I_{Div} relates taxa to the overall niche space and resources used, I_{Dis} is a better representation of taxa to each other.

Isotopic evenness (I_{Eve}) and isotopic uniqueness (I_{Uni}) are metrics that describe the regularity of species distribution within isotopic space (Cucherousset and Villéger 2015). I_{Eve} is calculated as the sum of branch lengths of the minimum spanning tree linking organisms in isotopic space. I_{Uni} is the average of the nearest distance neighbor distances divided by the maximal distance between the two nearest neighbors. Both metrics range from 0 to 1, where small values indicate the close position of organisms in isotopic space, reflecting a high level of redundancy in trophic resource niche use. In contrast, large values indicate communities that are dominated by more specialist species that exhibit high niche diversification. All trophic isotope metrics were calculated in Matlab after equations given in Cucherousset and Villeger (2015). Differences in all metrics between regions and years were tested with two-way ANOVA.

To characterize carbon sourcing of intertidal organisms in both regions, a stable isotope mixing model (Stable Isotope Mixing Models in R, simmr) was used to determine the relative contributions of different endmembers to consumer diets in each region. Endmembers used were the average values of POM and average combined macroalgae per region and year. A species must have at least four replicates to undergo analysis in simmr, so mixing models were only calculated at the regional level (Parnell et al. 2013). Trophic enrichment factors used in the model were based on literature values, with enrichment of 1.63 ± 0.63 ‰ for $\delta^{13}C$ and 3.54 ± 0.63 ‰ for $\delta^{15}N$ per trophic level (Caut et al. 2009).

Results

In 2017, the range in δ^{13}C values as a representation of trophic niche diversification at the base of the food web was smaller in Kachemak Bay (5.4 ‰) than in Kamishak Bay (9.9 ‰). In 2018, the food web base was more similar between the two regions with 6.7 ‰ in Kachemak Bay and 8.7 ‰ in Kamishak Bay, but the range in Kachemak Bay was still smaller (Figure 3). These differences in δ^{13}C range were significant for the factor region (two-way ANOVA, p=0.002) but not for the factor year or the interaction term (Table 2). In both regions and years, the lowest δ^{13}C values were always associated with POM. The highest δ^{13}C values in 2017 were associated with the periwinkle *Littorina* spp. in both regions. In 2018, the highest δ^{13}C values were from the red alga *Palmaria hecatensis* (Kachemak Bay) and the whelk *Nucella* spp. (Kamishak Bay).

Ranges in δ^{15}N values representing overall food chain length were smaller in Kachemak Bay than in Kamishak Bay in both years; 7.9 ‰ in Kachemak Bay and 9.7 ‰ in Kamishak Bay in 2017, and 8.0 ‰ in Kachemak Bay and 10.2 ‰ in Kamishak Bay in 2018 (Figure 3). The differences in δ^{15}N range were significant by region (two-way ANOVA, p<0.0001) but not by factor year. The interaction effect was marginal (p=0.052), indicating some influence of year on regional patterns (Table 2). The lowest δ^{15}N values were associated with POM in both regions and years, except for Kamishak Bay in 2018, where the lowest δ^{15}N value was obtained for the kelp, *Saccharina* spp. The highest δ^{15}N values in both regions and years were consistently associated with the anemone, *Urticina crassicornis*.

Figure 3: Trophic niche space, represented by the convex hull area in $\delta^{13}C - \delta^{15}N$ biplot space. Each point represents the carbon and nitrogen stable isotope value for a species, averaged from values across the three replicate sites per region. Convex hull area values are given in the legend for both regions and years. The range in $\delta^{13}C$ and $\delta^{15}N$ values is given for each region and year as arrows outside the axes, color-coded by region. Starred data points represent the particulate organic matter samples, data points with a black outline represent macroalgal samples.

Total convex hull area from the distribution of species in isotopic space (in $\delta^{13}C - \delta^{15}N$ biplots) represents the total trophic niche space of the system and was larger in Kamishak Bay compared with Kachemak Bay in both years (Figure 3). These differences were again significant for the factor region (two-way ANOVA, $p<0.0001$) but not for the factor region or the interaction term (Table 2). The larger trophic niche space in Kamishak Bay was also reflected in the site-specific niche space measures in both study years (Figures 4 and 5). The particularly small overall trophic niche space in Kachemak Bay in 2017 was mostly driven by a very small niche space at Cohen Island that year (Figure 4). While Cohen Island's niche space was larger in 2018, it was still smaller than other sites in Kachemak Bay (Figure 5). Trophic niche space in Port Graham and Outside Beach in Kachemak Bay were more similar to each other, and there was no consistent trend in niche space area between the two years (Figure 5). Trophic niche space at the three sites in Kamishak Bay was overall more similar without any trend among sites in the two years (Figures 4 and 5). In an annual comparison within each region, the average niche space in Kachemak Bay was smaller in 2017 than in 2018, but the overall area and patterns of distribution of taxa within that niche space were still relatively similar (Figure 6). The average niche space and distribution of taxa in Kamishak Bay were also similar across the two years (Figure 6).
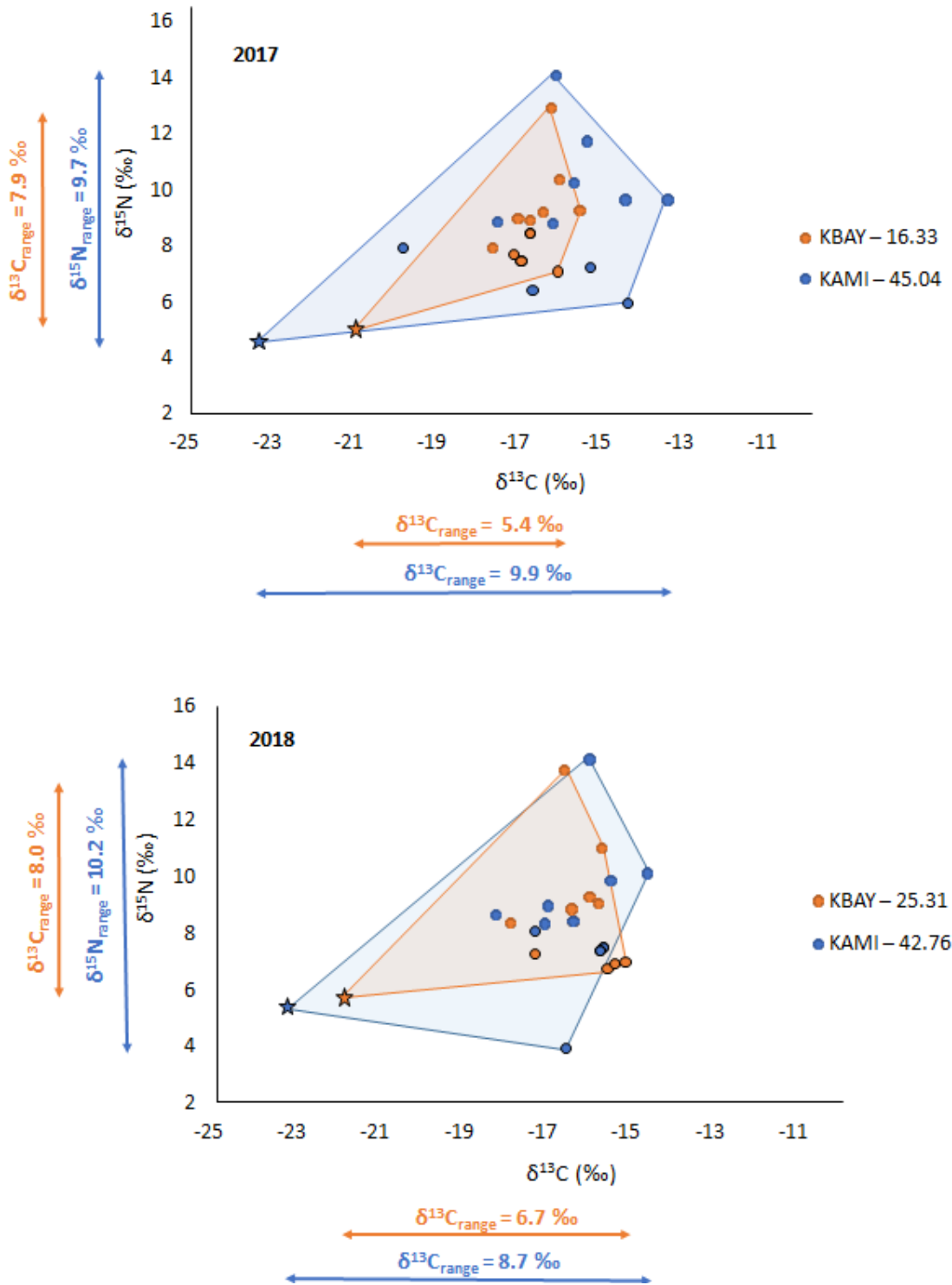
Figure 4: Trophic niche space, represented by the convex hull area in $\delta^{13}C - \delta^{15}N$ biplot space, for sites in Kachemak Bay (top panel) and Kamishak Bay (bottom panel) in 2017. Each point represents the carbon and nitrogen stable isotope value for a species, averaged from three replicate samples per taxon and site. Convex hull area values are given in the legend for sites in both regions. Crossed data points represent the particulate organic matter samples.

Figure 5: Trophic niche space, represented by the convex hull area in $\delta^{13}C - \delta^{15}N$ biplot space, for sites in Kachemak Bay (top panel) and Kamishak Bay (bottom panel) in 2018. Each point represents the carbon and nitrogen stable isotope value for a species, averaged from three replicate samples per taxon and site. Convex hull area values are given in the legend for sites in both regions. Crossed data points represent the particulate organic matter samples.
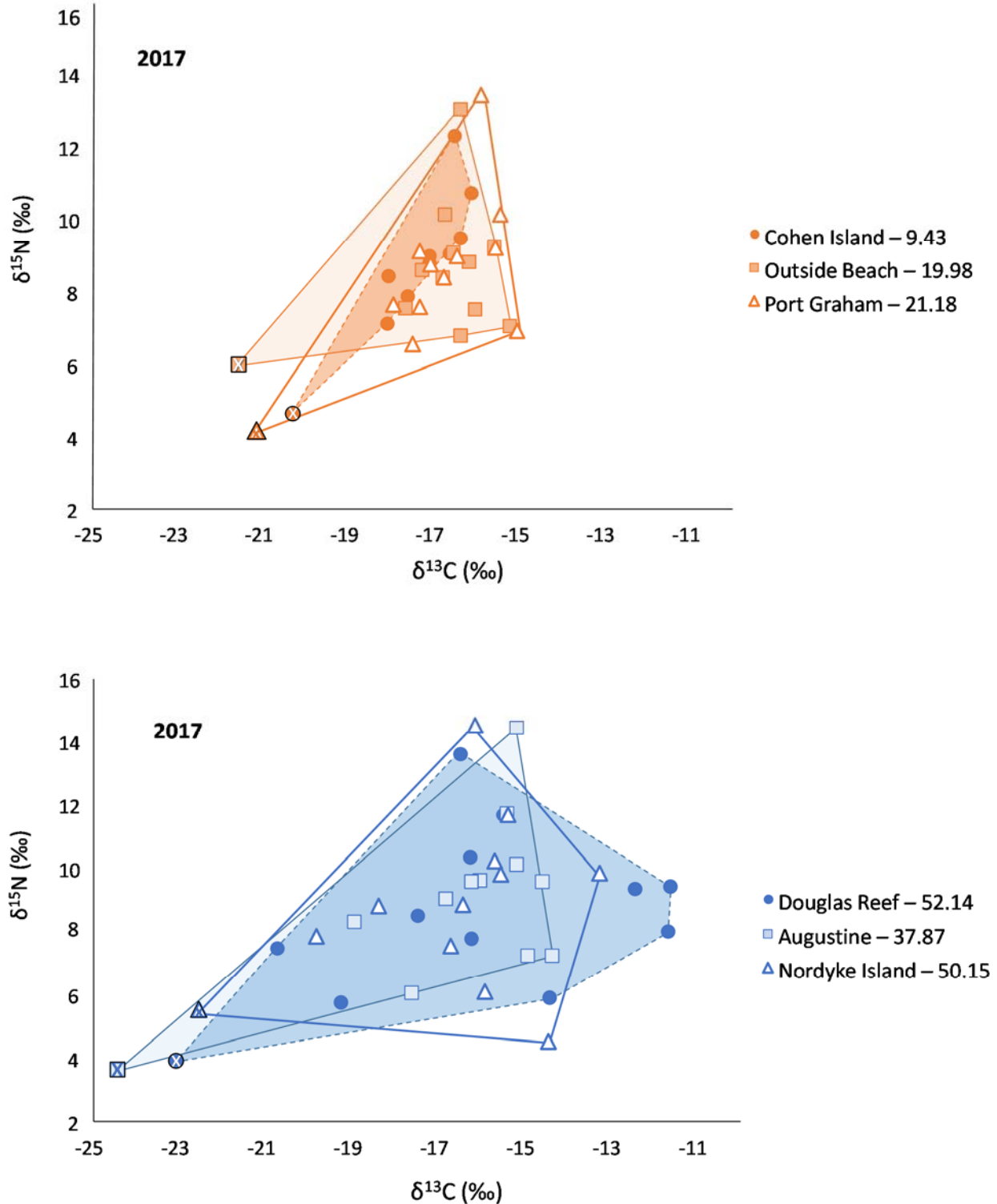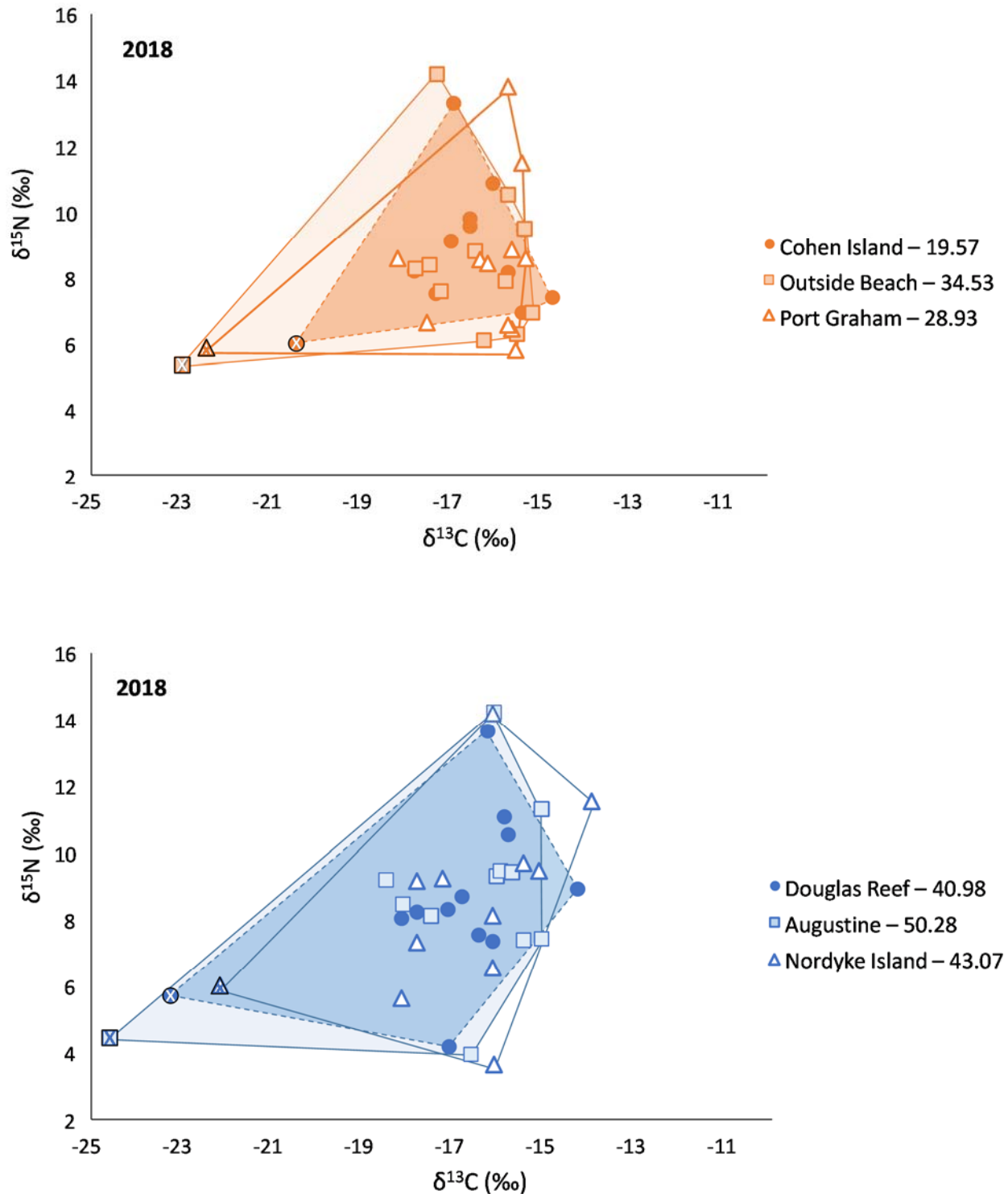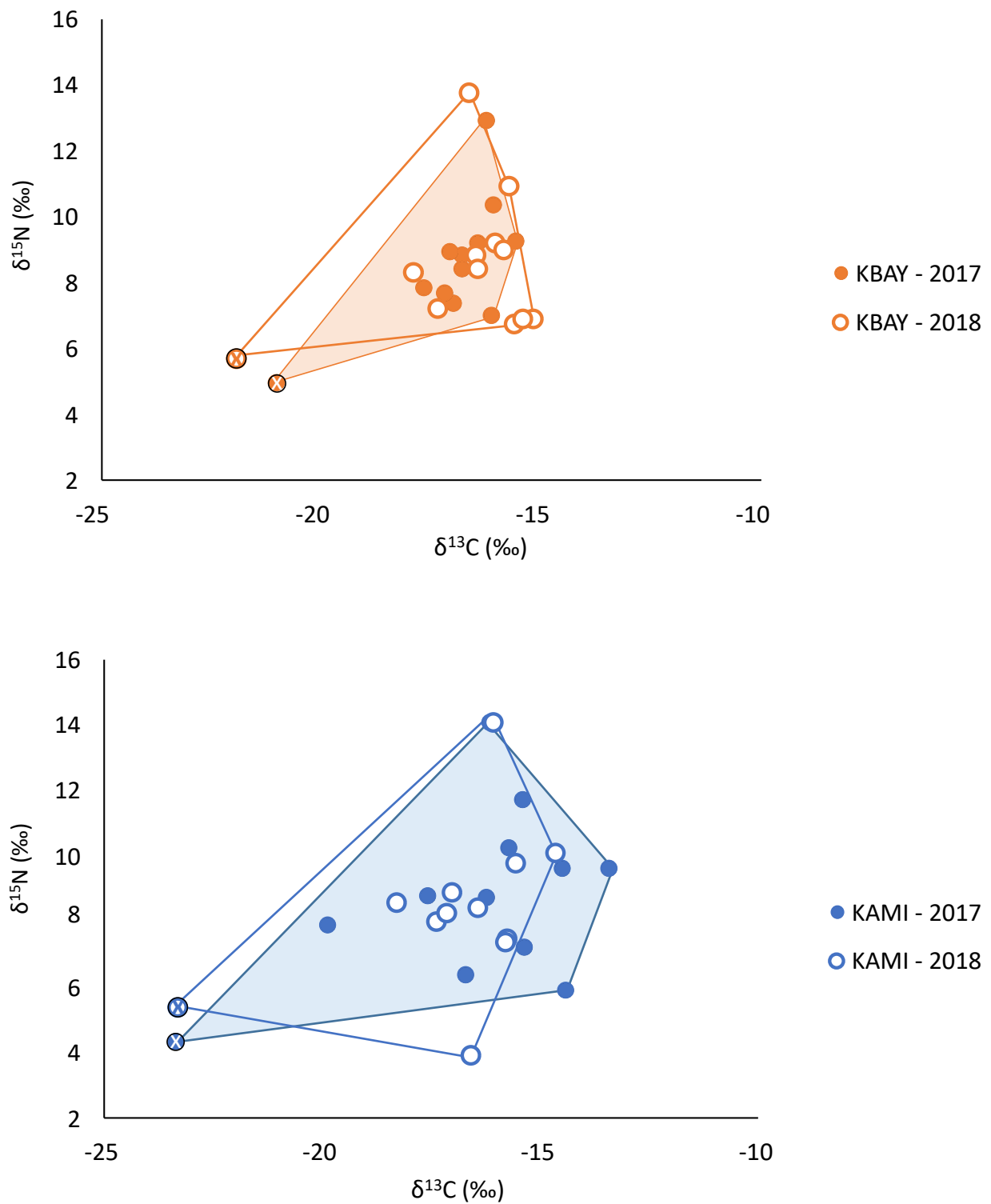
Figure 6: Trophic niche space, represented by the convex hull area in $\delta^{13}C – \delta^{15}N$ biplot space, for Kachemak Bay (top panel) and Kamishak Bay (bottom panel) compared between the two study years. Crossed data points represent the particulate organic matter samples.

Table 2: Two-way ANOVA results for core measures of isotope space with factors region and year. Significant factors in bold.

Metric	Source	SS	df	MS	F	Sig.
$\delta^{13}C$ range	**Region**	13.534	1	13.534	21.032	**0.002**
	Year	0	1	0	0	0.993
	Reg x Year	0.019	1	0.019	0.03	0.867
	Error	5.148	8	0.643		
$\delta^{15}N$ range	Region	32.323	1	32.323	36.534	**<0.0001**
	Year	0.062	1	0.062	0.07	0.799
	Reg x Year	4.594	1	4.594	5.192	**0.052**
	Error	7.078	8	0.885		
Convex hull	Region	1,653.96	1	1,653.96	36.259	**<0.0001**
	Year	58.96	1	58.96	1.293	0.288
	Reg x Year	121.973	1	121.973	2.674	0.141
	Error	364.916	8	45.615		

Inspection of the isotopic data showed that regional isotopic niche space was, in part, driven by differences in the POM values. POM $\delta^{13}C$ values in Kachemak Bay were, on average, 2–3 ‰ higher than in Kamishak Bay, while $\delta^{15}N$ values were similar between the two regions (Figure 7). For carbon stable isotope POM values, there was a significant effect of the factor region but not of the factor year and no interaction effect; no significant effect was detected for either factor or the interaction for nitrogen stable isotope POM values (Table 3). Temporal variation in POM $\delta^{13}C$ values over a 6-week period in Kachemak Bay varied by 1.3 ‰ and by 2.6 ‰ for $\delta^{15}N$ values (comparisons for both isotopes significant at p=0.01, t-test) (Figure 8).
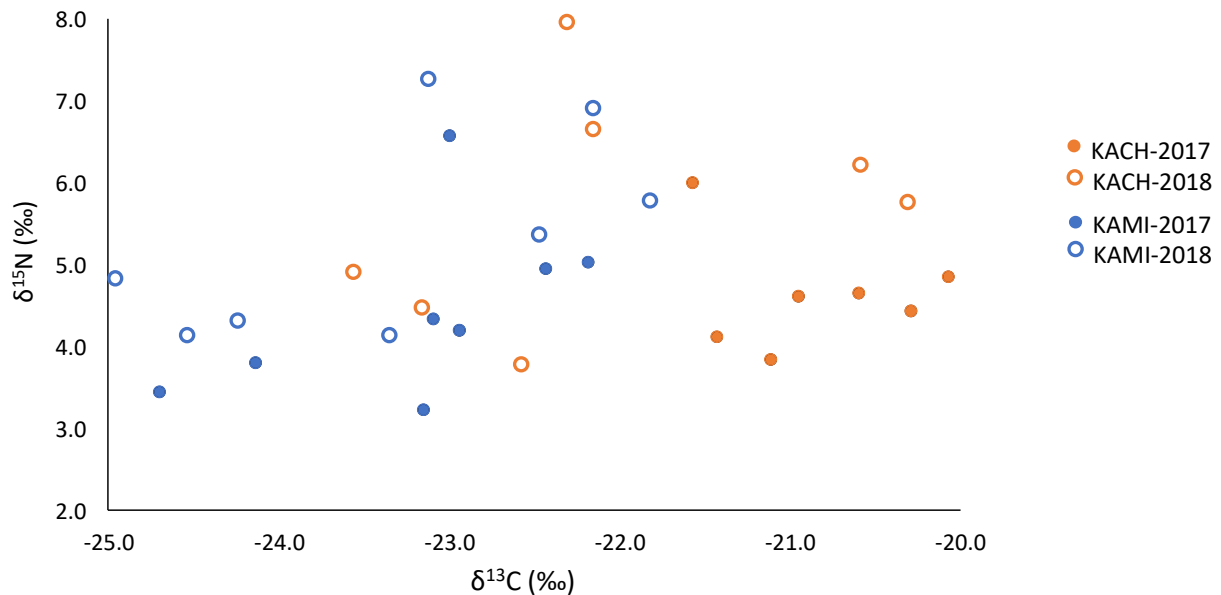
Figure 7: POM values from all locations in Kachemak Bay and Kamishak Bay in 2017 (closed symbols) and 2018 (open symbols). Higher $\delta^{13}C$ values occurred in Kachemak Bay.
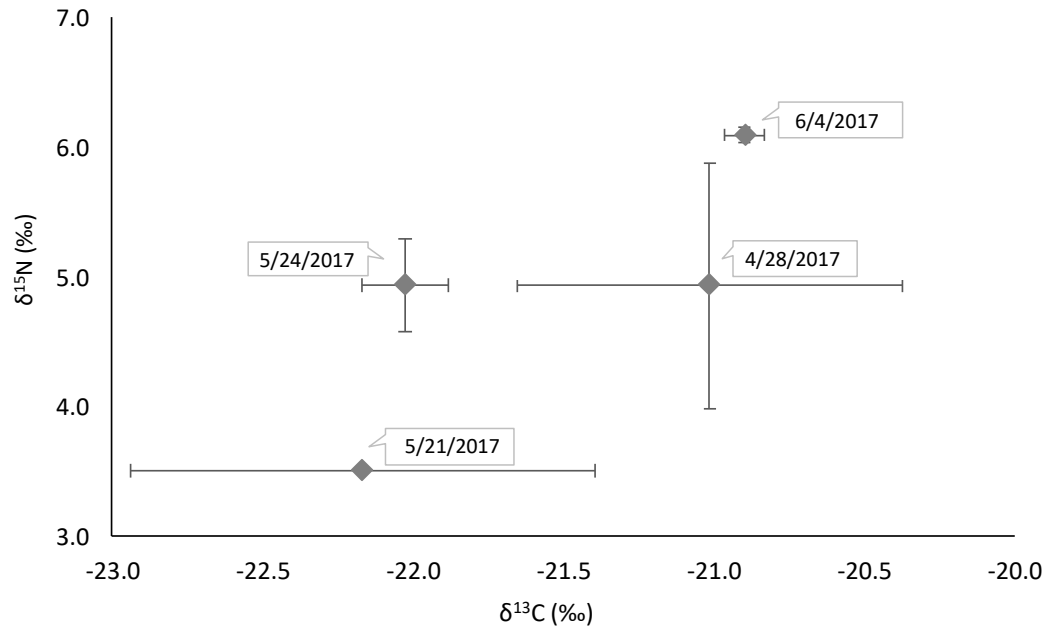
Figure 8: POM isotope values taken in Kachemak Bay (close to Cohen Island site) over several weeks in 2017 to assess short-term variability in POM isotope values. Dates of collection are given as M/DD/YYYY.

Table 3: Results of a two-way ANOVA for POM stable isotope values with factors region and year. Significant factors in bold.

Metric	Source	SS	df	MS	F	Sig.
POM $\delta^{13}C$	**Region**	10.237	1	10.237	8.895	**0.018**
	Year	0.638	1	0.638	0.554	0.478
	Reg x Year	0.678	1	0.678	0.59	0.465
	Error	9.207	8	1.151		
POM $\delta^{15}N$	Region	0.666	1	0.666	0.965	0.355
	Year	2.548	1	2.548	3.695	0.091
	Reg x Year	0.044	1	0.044	0.064	0.807
	Error	5.518	8	0.69		

Isotopic divergence (I_{div}) was smaller in Kachemak Bay compared with Kamishak Bay in 2017, but the pattern was reversed for 2018 (Table 4). This reflects a significant region x year interaction effect while neither the factor region nor the factor year was significant (Table 5). The smaller I_{Div} values in Kachemak Bay in 2017 are reflective of the more clustered concentration of taxa around the center of gravity in the convex hull, or the center of total trophic niche space (Figure 3). In 2018, I_{Div} values in both regions were intermediate to the values of both regions in 2017, reflecting the more similar clustering of taxa around the respective center of gravity of their convex hulls (Table 4, Figure 3). None of the other isotope trophic diversity measures showed any significant effects (Table 5). Isotopic dispersion (I_{Dis}) was slightly smaller

in Kachemak Bay compared with Kamishak Bay in 2017, while values for 2018 were intermediate to 2017 values in both regions (Table 4). I_{Eve} and I_{Uni} were both slightly larger in Kamishak Bay than Kachemak Bay in 2017, indicating more evenly distributed and more unique consumer species than in Kachemak Bay, where consumers had a higher level of redundancy (Table 4). These trends were not noticeable in 2018.

Table 4: Regional values (for Kachemak and Kamishak Bays) of various isotope trophic diversity measures. I_{Div} = isotopic divergence, I_{Dis} = isotopic dispersion, I_{Eve} = isotopic evenness, I_{Uni} = isotopic uniqueness.

Year	Region	I_{Div}	I_{Dis}	I_{Eve}	I_{Uni}
2017	KACH	0.604	0.310	0.604	0.241
2017	KAMI	0.688	0.377	0.799	0.375
2018	KACH	0.648	0.360	0.612	0.245
2018	KAMI	0.605	0.339	0.558	0.265

Table 5: Two-way ANOVA results for various isotope trophic diversity measures with factors region and year. Significant factors in bold. I_{Div} = isotopic divergence, I_{Dis} = isotopic dispersion, I_{Eve} = isotopic evenness, I_{Uni} = isotopic uniqueness.

Metric	Source	SS	df	MS	F	Sig.
I_{Div}	Region	0.001	1	0.001	2.273	0.17
	Year	0	1	0	0.437	0.527
	Reg x Year	0.01	1	0.01	18.801	**0.002**
	Error	0.004	8	0.001		
I_{Dis}	Region	0.007	1	0.007	1.774	0.22
	Year	0.001	1	0.001	0.318	0.588
	Reg x Year	0.004	1	0.004	1.083	0.328
	Error	0.031	8	0.004		
I_{Eve}	Region	0.006	1	0.006	0.923	0.365
	Year	0.008	1	0.008	1.22	0.301
	Reg x Year	0.008	1	0.008	1.236	0.299
	Error	0.055	8	0.007		
I_{Uni}	Region	0.011	1	0.011	1.212	0.303
	Year	0.007	1	0.007	0.774	0.405
	Reg x Year	0.005	1	0.005	0.517	0.493
	Error	0.07	8	0.009		

Carbon sourcing from POM versus macroalgae was calculated for intertidal taxa in both regions. The average percent sourcing from POM was 40 % in Kachemak Bay and 22 % in Kamishak Bay in 2017 (Figure 9), indicating considerable sourcing from macroalgae in both regions. In 2018, however, POM sourcing in Kachemak Bay (34%) was only marginally larger than the 32% in Kamishak Bay (Figure 9). This sourcing was relatively consistent across trophic levels, from filter feeders to grazers to predators, in both regions and years.
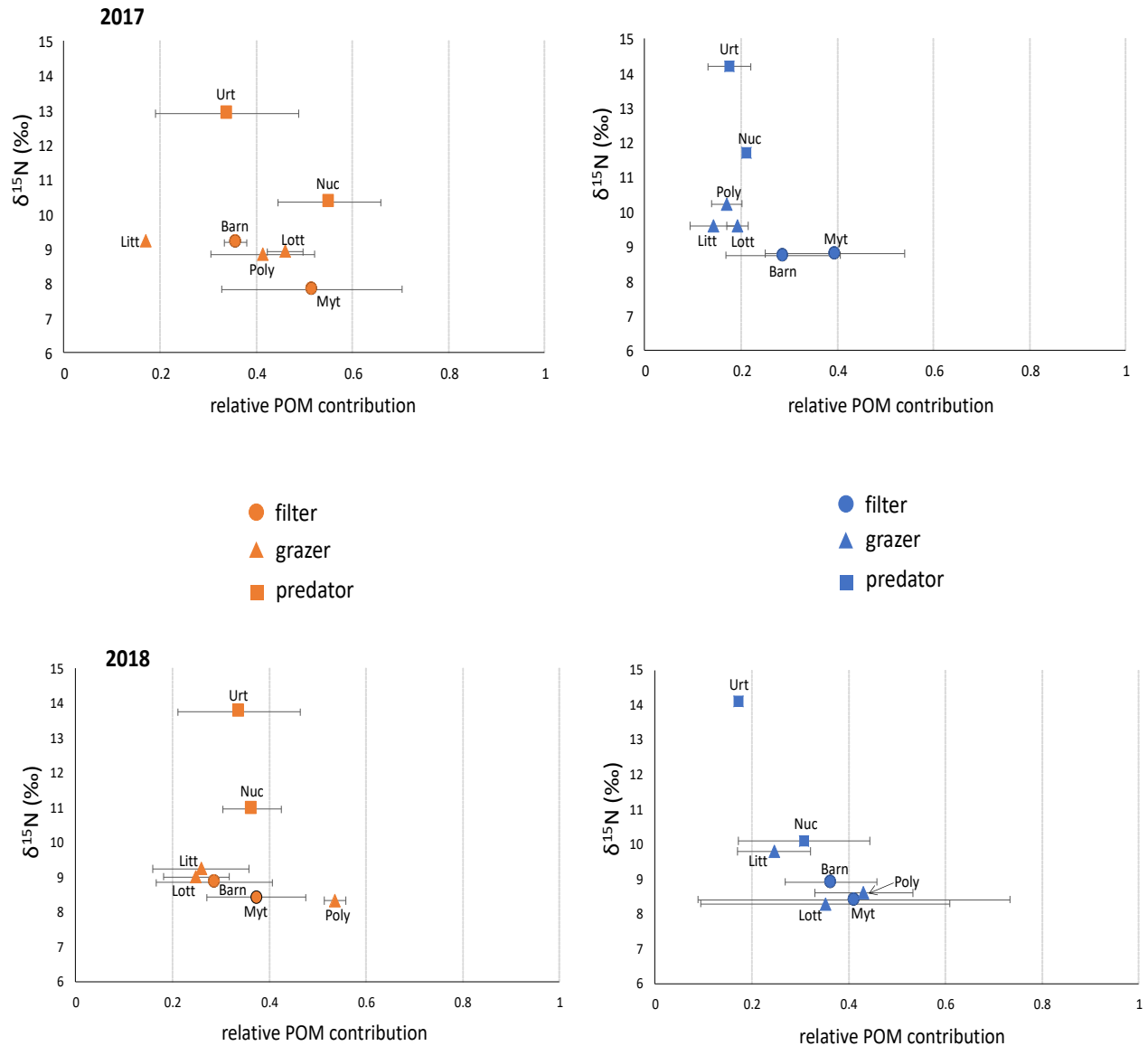
Figure 9: Results of a carbon source mixing for Kachemak Bay (left panels, orange) and Kamishak Bay (right panels, blue) in 2017 (top panels) and 2018 (bottom panels). Carbon source input into the model was POM and macroalgae. Shown here is the percent contribution of POM to consumer diets, with macroalgae providing the remaining percent. Consumers are abbreviated as Myt – Mytilus, Barn – barnacles, Poly – Polyplacophora, Lott – Lottia, Litt – Littorina, Nuc – Nucella, Urt – Urticina.

Discussion

Rocky intertidal food web structure in two hydrographically different regions of Cook Inlet was generally similar, although there were some differences in trophic niche space metrics and isotopic divergence; both were larger in the Kamishak Bay intertidal than in Kachemak Bay. Some of these differences were driven by the more depleted carbon isotope signatures of the POM source in Kamishak Bay, which may be linked to the hydrographic conditions in the two regions. There was higher carbon sourcing from POM in Kachemak Bay compared with Kamishak Bay, but consumers in both regions derived the majority of their primary carbon source from macroalgae. The use of several carbon sources in both regions points to an increase in food web stability and plasticity in consumers to capitalize on multiple carbon sources.

The rocky intertidal systems in Kamishak Bay covered larger ranges in δ^{13}C and δ^{15}N, ultimately resulting in a larger trophic niche space (isotope convex hull) utilized by the Kamishak communities compared with Kachemak Bay. The δ^{13}C range, an indication of the diversity of carbon sources, reflected a broader range in carbon sources in Kamishak Bay than in Kachemak Bay. Given that the same taxa were analyzed in both regions, the higher diversity at the base of the food web in Kamishak Bay stems to a large part from differences in the carbon isotope values of some of the primary producers. Specifically, the δ^{13}C values of POM in Kamishak Bay were about 2 ‰ lower than in Kachemak Bay. POM is a heterogeneous source that combines cell components (phytoplankton, bacteria, ciliates) with detrital components as well as different particle sizes (Benner et al. 1997, Lee et al. 2004, Bianchi and Bauer 2011). Phytoplankton δ^{13}C values are driven by a network of biosynthetic reactions from photosynthesis to the production of nucleic acids, proteins, carbohydrates, and lipids that form biomass during growth (Hayes 1993, 2001). For these processes, isotopic fractionation in primary producers depends on the isotopic composition and abundance of dissolved inorganic carbon (DIC) utilized by the cells (Boschker and Middelburg 2002, Vuorio et al. 2006) and nutrient availability (Brutemark et al. 2009). In addition, biological factors, such as identity, size and morphology of the cells (Popp et al. 1998, Sato et al. 2006, Vuorio et al. 2006), carbon fixation pathways (Leboulanger et al. 1995), and growth rates (Burkhardt et al., 1999), and environmental factors, such as light/irradiance (Thompson and Calvert 1994), temperature (Sackett et al. 1965), salinity (Leboulanger et al. 1995), and pH (Hinga et al. 1994; Thompson and Calvert 1994) play a role. Considerable amounts of DIC are discharged into the coastal ocean from rock weathering in high-latitude watersheds (Tank et al. 2012), influencing the DIC availability and, in combination with the drivers noted above, influencing the stable isotope composition of coastal phytoplankton in estuaries such as Cook Inlet. Estuarine phytoplankton in low-salinity regions are typically depleted in ^{13}C, with subsequent strong gradients of increasing POM δ^{13}C values indicative of oceanic conditions at the mouth of estuaries (Middelburg and Nieuwenhuize 1998, Fry 2002). This fits the POM carbon isotope patterns observed in Cook Inlet, where POM δ^{13}C values in the more freshwater-influenced Kamishak Bay region were depleted compared with more enriched values in the more oceanic-influenced Kachemak Bay.

In addition to freshwater effects on DIC, estuaries such as Cook Inlet receive variable, often considerable, amounts of terrestrial detritus from river and glacial discharge (Schlünz and Schneider 2000, Mannino and Harvey 2000, Fellman et al. 2014). This terrestrial material is isotopically lighter than marine primary production because atmospheric CO_2 ($\delta^{13}C$ about $-8‰$) used for photosynthesis by terrestrial vegetation is more depleted in ^{13}C than the dissolved inorganic carbon ($\delta^{13}C$ about $0‰$) used by marine phytoplankton (Farquhar et al. 1989). The addition of terrestrial detritus modifies the isotopic composition of the POM pool that provides a food source to nearshore consumers (Hedges et al. 1997, Raymond and Bauer 2001). Freshwater and terrestrial matter input are larger in Kamishak Bay as it is downstream from the major river and glacier discharges in upper Cook Inlet, while sites in Kachemak Bay are only marginally influenced by discharge and mostly receive input from the Gulf of Alaska (Muench et al. 1978). The Alaska Stream hugging the coastal Gulf of Alaska and turning into lower Cook Inlet, including Kachemak Bay, is also influenced by freshwater sources (Royer 1981), but this freshwater (and related terrestrial matter) loading is much smaller than inputs in upper Cook Inlet. This difference in freshwater and terrestrial matter inputs explains the consistently lower $\delta^{13}C$ values of POM in Kamishak Bay compared with Kachemak Bay.

Characteristics of the POM source, including contributions from terrestrial matter, will influence the POM chemical composition and $\delta^{13}C$ values on seasonal to shorter time scales (Mayzaud et al. 1989, Sato et al. 2006). For example, high variability in POM $\delta^{13}C$ values was visible in POM measurements taken in Kachemak Bay over a 6-week period in 2017, which varied over about 1 ‰ in $\delta^{13}C$. The lower POM $\delta^{13}C$ values in Kamishak Bay may be part of this strong temporal variability; however, their consistency, especially in 2017, points beyond variability towards a more systematic difference. The most likely explanation for this difference is the higher terrestrial component in Kamishak Bay, as discussed above. This pattern in POM $\delta^{13}C$ values was similar but not as pronounced in 2018, which may indicate that greater inputs of freshwater and terrestrial matter influencing the POM in 2017 compared with 2018.

The range of $\delta^{13}C$ values was also larger because some species were more enriched in ^{13}C in Kamishak Bay than Kachemak Bay. Differences on the higher end of the $\delta^{13}C$ range were less pronounced among the primary producers but were driven by some of the grazers. Specifically, the grazer *Littorina* was the most enriched in both regions, with higher values in Kamishak Bay. *Littorina,* a common grazer in rocky intertidal systems, can feed on filamentous green algae but most commonly scrapes off benthic microalgae from the biofilm covering rocks (Sommer 2000, Van Alstyne et al. 2009). The high *Littorina* $\delta^{13}C$ values in both regions could indicate that this species feeds almost exclusively on the most enriched macroalgae (brown algae), which would be consistent with an approximate 1 ‰ enrichment between producer and consumer (Vander Zanden and Rasmussen 2001). Alternatively, the systems can have an unacknowledged carbon source channeling into the food web, specifically benthic microalgae (Takai et al. 2004). Benthic microalgae are much enriched in ^{13}C compared with phytoplankton (here: POM) because of the higher concentration gradients of the CO_2 substrate across the boundary layers for benthic compared with pelagic algae (France 1995). Diffusion of CO_2 or HCO_3^- in water is slow,

especially across stagnant boundary layers surrounding benthic algae. The slow replenishment of the carbon sources for photosynthesis across these boundary layers leads to a deficit of the typically metabolically preferred ^{12}C atom and increased use of the ^{13}C atom (Osmond et al. 1981, Keeley and Sandquist 1992). This applies not only to benthic macroalgae but also benthic microalgae, and their high growth rates (equaling high CO_2 demand) can lead to highly enriched $\delta^{13}C$ values (Fry and Wainright 1991). Benthic microalgae were not included in this study, but high $\delta^{13}C$ values in consumers such as in *Littorina* would be consistent with these assumptions.

The overall larger trophic niche space in Kamishak Bay compared with Kachemak Bay was also driven by larger nitrogen isotope ranges in Kamishak Bay. The POM sources with the lowest $\delta^{15}N$ values were nearly identical in both regions and years. While there was variability in the nitrogen isotope values of the different macroalgal endmembers, these differences were not systematic (i.e., not consistently higher in one over the other region). Therefore, the larger nitrogen isotope range in Kamishak Bay must have been driven by longer trophic transfer pathways to predators. While $\delta^{15}N$ undergoes stepwise enrichments between trophic levels (3–4 ‰ per step, Vander Zanden and Rasmussen 2001), this enrichment is influenced by temporal variation in endmembers (Vander Zanden and Rasmussen 1999), trophic level of the consumers (Buchheister and Latour 2010, Malpica-Cruz et al. 2012, Hussey at al. 2014), ontogenetic status of consumers (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 top consumers may have been driven by differences in the transfer of energy modulated by differences in consumer physiology and biology in the two study regions. For example, consumers of the same species could have been of different ages or sizes in the two regions. In addition, the terrestrial component in POM may require additional microbial degradation before the material becomes labile for marine consumers (Moran and Hodson 1989, Garneau et al. 2009). Energetically and isotopically, these microbial processes present additional trophic steps, increasing the $\delta^{15}N$ values or trophic level of subsequent consumers (Middelburg and Herman 2007, Bell et al. 2016). This additional trophic step could be responsible for the higher $\delta^{15}N$ values of top consumers in Kamishak Bay, where POM presumably contained higher levels of terrestrial materials (see above), resulting in the overall larger trophic niche space in Kamishak Bay.

Total trophic niche space, as discussed above, provides a quantitative measure of the extent of resources available to the system (Rigolet et al. 2015). Total trophic niche space does not, however, describe whether and how these resources are being utilized. Measures of the distribution of taxa within this trophic niche space are indicative of trophic functioning and resource use. Those isotopic measures were not significantly different between the two regions, except for isotopic divergence. This index measures how species diverge in their distances from the center of gravity in trophic space, that is, the extent to which species are located towards the center (low I_{Div}) or towards the border (high I_{Div}) of the trophic niche space (Cucherousset and Villeger 2015). Ecologically speaking, high I_{Div} means that most of the resources in trophic space are utilized by the assemblage, indicative of resource use specialization and niche differentiation (Rigolet et al. 2015). In contrast, low I_{Div} indicates that some resources are likely to be

underutilized, pointing to a system of more generalist feeders and less diversified ecosystem functioning.

In this study, there was a significant interaction effect between region and year for I_{Div}, with much larger values in Kamishak than Kachemak Bay in 2017. This larger distribution across trophic space in Kamishak Bay was due to both primary producers and consumers. For primary producers, the larger divergence indicates that a broader array of resources (i.e., carbon substrate and nutrients) is being utilized during photosynthesis in the Kamishak Bay system, which could be due to a difference in available inorganic carbon and nutrients in the two regions. Glacial and riverine runoff influence nearshore dissolved organic matter, inorganic carbon sources, and nutrients in high latitude systems, but the direction and scale of these influences depend on erosional characteristics of the glaciers, vegetation in the watershed, and bacterial mineralization processes (Hodson et al. 2005, Hood and Scott 2008). Barring any carbon and nutrient data in the two regions, it can only be inferred that the strong glacial and riverine discharge upstream from Kamishak Bay heavily influences carbon and nitrogen sources in that region, creating different characteristics than in Kachemak Bay. The significant interaction effect for the I_{Div} metric suggests that these influences are variable across years, possibly due to regional and local weather conditions in any given year, influencing discharge rates from rivers and glaciers, mixing of the water column, etc. In terms of consumers contributing to higher divergence in Kamishak Bay, this could stem from broader utilization of the more diverse primary production base, or include the potentially unacknowledged endmembers (e.g., benthic microalgae) discussed above.

Rocky intertidal consumers in both systems derived the majority of their carbon from macroalgal as opposed to phytoplankton (POM) sources. This utilization of macroalgae occurs not only in the form of direct grazing but also as consumption of the macroalgal detritus formed when algae senesce and thallus tissue is sloughed off and broken into small particles via hydrodynamics and bacterial degradation (Rieper-Kirchner 1989). Consumers of all feeding types can make use of the macroalgal subsidy, which was obvious in this study where grazers and filter feeders had similar proportions of macroalgal contributions to their diets. Predators are unlikely to consume macroalgae directly (although it is a possibility); it is more likely that macroalgal carbon is transferred into these higher trophic levels through their prey items. The dependence of a large number of consumers on macroalgal carbon is not uncommon in many rocky intertidal systems. For example, both mussels and barnacles are known to consume a mixture of organic matter derived from phytoplankton as well as macroalgal production in many rocky intertidal systems worldwide (Bustamante and Branch 1996, Tallis 2009), including Alaska (Duggins et al. 1989). The use of multiple food subsidies (i.e., diversification of the food base) in a system is considered important for overall food web stability (Huxel et al. 2002). This may be particularly important in high-latitude systems where phytoplankton production is extremely seasonal (McMeans et al. 2013, Renaud et al. 2015). While macroalgae have seasonal peak growth cycles, many are perennial and provide a more temporally-stable food supply than phytoplankton (Leclerc et al. 2013). This overall pattern of diversified endmember use applied to both regions

in this study. However, the slightly larger dependence of consumers on POM in Kachemak Bay may indicate that the POM source there is of higher quality and/or more accessible. Due to high glacial discharge upstream, The POM in Kamishak Bay contains a large portion of inorganic, silty glacial flour. Filter feeders can get clogged by this fine and non-nutritious material, and the excessive production of mucus required to capture and shed this inorganic material is energetically costly (Riisgård and Larsen 1995). Hence, a larger reliance on macroalgae could be more energetically beneficial for consumers in Kamishak Bay.

Differences between resource use and utilized trophic niche space were discussed here for the two rocky intertidal systems in Kachemak and Kamishak Bays. It should be noted that the same taxa were considered in both systems, which increased the overall comparability of the two systems but does not describe either system in its entirety. A benefit of the direct comparison is that comparisons could be made at the individual species level and in larger metrics such as niche space. The variability in trophic position of the same species in the two systems suggests high feeding plasticity in these intertidal producers and consumers (Padilla and Savedo 2013).

Plasticity is not a new concept but bears discussing here as it can inform about the resilience of ecosystem functioning against disturbances. For example, in different systems, the mudsnail *Hydrobia* can switch food sources from macroalgae and marine detritus to terrestrial marsh plant detritus, depending on organic matter availability in their estuarine environment (Riera 2010). Similarly, filter-feeding oysters (*Crassostrea gigas*) can change the proportions of various food sources along an estuarine gradient (Marchais et al. 2013). Plasticity in estuarine systems also occurs in biological aspects other than feeding. Macroalgae can show plasticity in photosynthesis and growth over a wide range of estuarine conditions, as documented for the kelp *Saccharina latissima* in locations of differing salinity and nutrients within Kachemak Bay (Spurkland and Iken 2011a, 2011b, 2012). *Fucus* is known to thrive over a large range of temperature and salinity conditions in estuarine settings (Takolander et al. 2017). Barnacles are adaptable in morphology, growth, reproduction, and body condition to a wide range of salinities (Wrange et al. 2014). Hence, plasticity to a broad range of environmental conditions is likely an inherent trait of these intertidal, estuarine taxa, even though adaptation to extreme conditions can be energetically costly (Sanford 2002). This plasticity is a tremendous contributor to the long-term persistence of rocky intertidal communities, but it can also place these communities close to their physiological limits (Dahlhoff et al. 2002). While the taxa included in this study seem to be adaptable to a range of environmental conditions, it is unknown how these conditions relate to their physiological performance (i.e., Are some taxa operating at their limits?). Also, this plasticity may not apply to the overall community and some differences in the taxonomic composition of the rocky intertidal systems (see Konar et al. 2009 and BOEM final report for M15PG00037) may stem from low plasticity of certain taxa to the prevalent conditions in a region.

In summary, trophic niche space was larger in the Kamishak Bay assemblage due to a higher diversity in food sources but also due to longer food chains. In both regions, food webs were

stabilized by the use of multiple carbon sources and greater use of persistently available macroalgae use over more seasonal POM by all consumer taxa. The question remains: Which system is more resilient to changes or disturbances? The larger niche space and more efficient resource use in Kamishak Bay may suggest this system is more resilient; however, the opposite argument can be made. The larger niche space and higher divergence in Kamishak Bay could be a result of a more stressed system (overall lower nutrient availability in the glacially-influenced system), which may stretch species more towards the limits of their physiological and trophic plasticity. In that case, disturbances or changes could be more devastating to the Kamishak than Kachemak rocky intertidal food webs. It is not clear if the current regional conditions push these taxa to the limit of their plasticity, nor whether future climate-related or human-induced perturbations would overextend this plasticity. Regardless, the high plasticity of common rocky intertidal taxa observed in this study suggests that, in general, these systems can thrive in the "typical" range of conditions for lower Cook Inlet.

Study Products

Siegert D, Iken K, Saupe S, Lindeberg M. 2019. Comparing intertidal food web and community structure across two regions of lower Cook Inlet. Alaska Marine Science Symposium, Anchorage, AK. 28–31 January 2019 (poster presentation)

Siegert D, Iken K, Saupe S, Lindeberg M. 2019. Comparing intertidal food web and community structure across two regions of lower Cook Inlet. CMI Annual Review, Anchorage, AK. 1 February 2019 (oral presentation)

Siegert D, Iken K, Konar B, Saupe S, Lindeberg M. 2018. Nearshore food web structure in two contrasting regions of Cook Inlet. Alaska Marine Science Symposium, Anchorage, AK. 22–25 January 2018 (poster presentation)

Siegert D, Iken K, Konar B, Suape S, Lindeberg M. 2018. Nearshore food web structure in two contrasting regions of Cook Inlet. CMI Annual Review, Anchorage, AK. 26 January 2018 (oral presentation)

Siegert D, Iken K, Konar B, Saupe S, Lindeberg M. 2018. Nearshore food web structure in two contrasting regions of Cook Inlet. Kachemak Bay Science Conference, Homer, AK. 8–9 March 2018 (poster presentation)

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The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the sound use of our land and water resources, protecting our fish, wildlife and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island communities.

The Bureau of Ocean Energy Management

The Bureau of Ocean Energy Management (BOEM) works to manage the exploration and development of the nation's offshore resources in a way that appropriately balances economic development, energy independence, and environmental protection through oil and gas leases, renewable energy development and environmental reviews and studies.