Foraging ecology of nearshore fishes in the Gulf of Alaska

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ABSTRACT

The survival of juvenile marine fishes, which support commercial fisheries and provide a prey resource, is often dependent on conditions in protective and nearshore habitats. We examined the trophic interactions of several juvenile fishes in the nearshore Gulf of Alaska (GOA) including Pacific cod (*Gadus microcephalus*), saffron cod (*Eleginus gracillis*), walleye pollock (*Gadus chalcogrammus*), Pacific sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea pallasii*), rockfish (*Sebastes spp.*) and greenlings (*Hexagrammos spp*.). We used fatty acid (FA) and stable isotope (SI) markers to evaluate foraging ecology and the potential for competition among age-0 fish species in broad east (134°W – 136°W) and west (149°W – 153°W) regions of the GOA. Sampling efforts were greater in the west GOA, so many of our findings were focused in that region. In the west GOA, FA and SI markers indicated that Pacific cod and saffron cod usually shared similar diets, potentially leading to competition for resources. Also in the west GOA, we found evidence that Pacific cod and walleye pollock both relied to similar extents on calanoid copepods during summer. Juvenile sand lance and herring were much smaller than the other species and had diets that contrasted with all other species. In both the east and west GOA, rockfish were present in two distinct size classes with the smaller size feeding at a lower trophic level than all other fish species in the study. The smaller rockfish likely consumed mainly calanoid copepods. Throughout the east and west GOA, greenling and rockfish typically consumed prey with a very different lipid source than the other juvenile fish. In addition, we noted few consistencies in FA and SI markers between the east and west, except in rockfish diets. Overall, we found a complex relationship within the nearshore fish communities in the east and west GOA that showed substantial variation across bays, seasons and subareas.

Key words: Gulf of Alaska, Juvenile fish, Biomarkers, Stable isotopes, Fatty acids, Lipids, Competition

1. Introduction

Waters in the nearshore marine environment often provide important habitat for juvenile fishes (Lefcheck et al., 2019). In this study, we define nearshore as a particular zone of the inshore: intertidal and upper subtidal waters ≤ 10 m depth that have the potential for abundant submerged vegetation (Ormseth et al., 2017). These habitats may act as nurseries for juvenile fishes, both minimizing predation risk and offering abundant food resources (Dahlgren et al., 2006; Lefcheck et al., 2019). Juvenile fishes provide an important trophic link between lower trophic levels, such as copepods, and upper trophic levels such as adult fishes, birds, and marine mammals (Springer and Speckman, 1997; Mueter and Norcross, 2000; Sturdevant and Fergusson, 2012). Within these nearshore communities, the juveniles of several fish species overlap both spatially and temporally (Johnson et al. 2012), increasing the potential for resource competition.

In the Gulf of Alaska (GOA), nearshore areas are inhabited by juveniles of several fish species that support important commercial fisheries including Pacific cod (*Gadus macrocephalus*), walleye pollock (*Gadus chalcogrammus*) and Pacific herring (*Clupea pallasii*; Johnson et al., 2012). The GOA has two distinct oceanographic regions: the east GOA, defined here as the waters off southeast Alaska, and the central/west GOA (herein referred to as west GOA; Fig. 1). The east GOA has a much narrower shelf than the west GOA. The Alaska Current flows along the continental shelf from south to north along the east GOA and moves offshore as portions of it merge with the Alaska Coastal Current when it enters the central/west GOA regions (Ladd et al., 2005; Weingartner et al., 2005). Within each of the GOA regions, there is substantial variability in the types of habitat available to juvenile fishes (e.g. glacial runoff, exposure to wave action, bottom type, vegetation, etc.; Zimmerman, 2019). Additionally, water temperature in these nearshore environments can range widely, which in turn can affect the growth and survival of juvenile fish by altering the availability of suitable habitat in nearshore environments (Ottersen and Loeng, 2000; Attrill and Power, 2002).

In addition to regional variability in habitats between the east and west GOA, temporal variation in the ways that fish utilize the nearshore also exists, as availability of prey and species behaviors vary seasonally (Laurel et al., 2007; Bailey et al., 2008; Hanselman et al., 2014). Any changes to this forage base may in turn affect the availability of prey to adult groundfish and other upper trophic level predators, causing a cascade of effects such as changes in the timing of reproduction (e.g. Regular et al., 2014). Competition among juvenile fishes can also affect this forage base and may have a direct impact on survival and recruitment to adult life stages (Osenberg et al., 1992).

Link and Auster (2013) describe four conditions that must be met to demonstrate competition between species: opposite population trajectories, spatiotemporal overlap, dietary overlap and resource limitation. Our focus here is on the third condition of dietary overlap in co-occurring juveniles, and the potential for competition should the other conditions be met. Specifically, we infer diets in juvenile Pacific sand lance (*Ammodytes hexapterus*), Pacific herring, Pacific cod, saffron cod (*Eleginus gracilis*) and walleye pollock, as well as common co-occurring species of juvenile rockfish (*Sebastes* spp.) and greenling (*Hexagrammos* spp.). Since studies have shown resource overlap in the diets of age-0 Pacific cod, saffron cod, and pollock in the southeast Bering Sea (Strasburger et al., 2014), we aimed to investigate the potential for competition among those and other co-occurring nearshore juvenile fishes in the GOA.

A variety of techniques exist to evaluate diet in fish; here, we used the chemical markers of stable isotopes (SI) and fatty acids (FA) to investigate diet overlap of juvenile fishes. Stable carbon isotopes vary in a fixed and predictable manner within a food web and can be used to study dietary sources, while nitrogen isotopes are typically used to estimate the trophic position of predators (DeNiro and Epstein, 1978; Gannes et al., 1997). Fatty acids have a variety of structures in marine organisms and, similar to stable carbon isotopes, they can serve as biomarkers of source, indicating the type of prey a predator has consumed (Budge et al., 2006). The structure of marine FA change very little as they travel through the food web because there are biochemical restrictions on the *de novo* synthesis of a number of FA (Dalsgaard et al., 2003); thus, subtle patterns, or profiles, of FA can be compared among predators (e.g. juvenile fishes) to deduce general information about similarity of diets.

In this work, we determined FA profiles and C and N stable isotopes of juvenile and forage fish in the east and west GOA nearshore environments to make inferences about dietary overlap. Based on recent work in the east GOA (Daly et al., 2019), we hypothesize that age-0 Pacific cod and pollock in the GOA regions have similar diets. We also examined the spatial and temporal variability in relationships among all species examined. We anticipated that the different oceanographic regions in the east and west GOA would influence diets. Similarly, we expected that ontogenetic changes in diet would lead to seasonal variation in dietary overlap.

2. Methods

2.1. Sampling locations

The samples used in this study were collected as part of a larger investigation into the ecology of inshore and nearshore areas in the GOA (Ormseth et al., 2017). For the analyses covered in this paper, a subset of the research sites was selected for sampling (Fig. 1). Some sites were further divided into subareas, listed here in parentheses. Three sites were selected in the east GOA: Islas Bay (Fjordselheim, Ilin), Salisbury Sound, and Graves Harbor. Four sites were chosen in the west GOA: Kiliuda Bay (Dungie, Shearwater), Port Dick (Sunday, Swan, Waterfall), Izhut Bay and Aialik Bay. For more extensive descriptions of the sampling sites and subareas, see Ormseth et al. (2017).

Samples were collected in two different years, during the summer (July 14 – August 15, 2011, and August 1-25, 2013) and fall (September 22 – October 26, 2011, and September 23, 2013 and November 3 - 11, 2013). Two gear types, beach and purse seines, were used for all fish collections. Beach seines occurred in waters less than 2 m in depth and purse seines were used in waters less than 6 m in depth. Additional details on sample location and seining methods are given in Ormseth et al. (2017). Fish were identified to the lowest appropriate taxonomic level, wrapped tightly in plastic film, and individually frozen at -40^{o}C. Pacific cod, pollock, Pacific herring, Pacific sand lance and shiner perch *Cymatogaster aggregata* were identified to species. Greenling represented three undifferentiated species (kelp greenling *Hexagrammos decagrammus*, whitespotted greenling *H. stelleri*, masked greenling *H. octogrammus*); rockfish consisted of up to three species (quillback *Sebastes maliger*, copper *S. caurinus*, black *S. melanops*); and sculpin (Cottidae) represented two unidentified species. Fork length (FL) and mass of individual whole fish were recorded. Fulton's condition factor (K) was calculated as:

$$K = 100\,\frac{M}{L^3}$$

where M is mass in g and L is length in cm (Nash et al., 2006).

2.2. Stable carbon and nitrogen isotopes

The material remaining after lipid extraction was dried and shipped to the Stable Isotope Core Laboratory at Washington State University, Pullman, WA, where it was homogenized and aliquots taken for stable isotope analysis. Between 0.1 – 0.3 mg of each homogenate was weighed into tin capsules and analyzed using continuous-flow stable isotope ratio mass spectrometry with an elemental analyzer (Costech ECS4010) interfaced with a Thermo Finnigan Delta Plus XP isotope ratio mass spectrometry (Thermo Finnigan, Austin, TX, USA). Whole individual $\delta^{13}C$ and $\delta^{15}N$ isotope values were reported relative to international standards (Vienna PeeDee Belemnite for C, atmospheric nitrogen for N) as δ X (‰) = ([$R_{sample}/R_{standard}$] – 1) x 1000, where X is either ^{13}C or ^{15}N and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Analytical precision for both $\delta^{13}C$ and $\delta^{15}N$ was 0.5‰.

2.3. Lipid extraction and FA analysis

Each fish was individually homogenized by mincing and a 1.5 g aliquot was extracted using chloroform and methanol, following a modified Folch et al. (1957) technique (Budge et al., 2006). Lipid proportions were expressed as mass percent wet weight. Isolated lipids were methylated to form FA methyl esters (FAME) using sulphuric acid as a catalyst (Budge et al., 2006). FAME were analyzed by gas chromatography with flame ionization detection, using split injection (1:100 split) and an Agilent DB-23 column ((50%-cyanopropyl)-methylpolysiloxane phase, 30 m, 0.25 mm ID, 0.25 um film thickness). Helium (1 ml min^{-1} flow rate) was used as the carrier gas. The oven temperature began at 150^{o}C and was held for 2 min. It was then ramped at a rate of 2.5^{o}C min^{-1} to 210^{o}C and held for 8 min. FA were identified by comparison of retention times to authentic standards and with GC-mass spectrometry. FA were named following the shorthand notation of A:bn-c where A gives the total number of carbon atoms in the FA, b the number of double bonds and c the position of the double bond closest to the terminal methyl group. FA data were expressed as mass proportion of total FA identified.

2.4. Data Analyses

For each species or group (i.e. greenling and sculpins), stable isotope data were plotted relative to that of Pacific cod (i.e. $\Delta\delta^{13}C = \delta^{13}C_{species} - \delta^{13}C_{pacific\ cod}$, $\Delta\delta^{15}N = \delta^{15}N_{species} - \delta^{15}N_{pacific\ cod}$) to consistently show relationships between Pacific cod and all other species and groups (Figs. 4-6). Thus, Pacific cod are not represented by a symbol but are found at the origin of each plot. Pacific cod were chosen as the focus for comparison here because they were collected at each sampling site, making it a convenient species to use. Analysis of variance (ANOVA), with species, season and year as factors, was used to compare lengths, masses, lipid content and condition factor, using Tukey's test for post-hoc analysis of pairwise differences. The NicheROVER package (Swanson et al., 2015; R Core Team, 2020) was used to estimate the probability of isotopic niche overlap among species. We used an alpha level of 95% to calculate niche overlap areas and then estimated the probability of species A occupying the niche space of species B, as described in Swanson et al., 2015. If the probability of niche overlap was > 50% between two species, we interpreted the overlap to be high for that combination of bay, subarea and season.

To assess consumer diets, FA markers are normally evaluated in fat storage tissues that are rich in triacylglycerols and are thought to best reflect diet (Dalsgaard et al., 2003; Budge et al., 2006); in fish, suitable tissues are muscle in oily fish such as herring, capelin, etc. or liver in leaner fish such as pollock and cods. Here, individual fish were ~10 cm in length and, as reported in other studies with juvenile fish (Copeman et al., 2020), it was impossible to accurately subsample from muscle tissue or liver so entire fish were analyzed. Thus, the FA data does not just reflect dietary FA found in triacylglycerols and is instead also influenced by structural lipids, such as phospholipids. However, while phospholipids and tissues rich in those are often considered refractory in nature, they are not inert and do reflect the FA composition of diet (Bell et al., 1992; Bell et al., 1995). Comparison of FA recovered from whole fish is therefore a valid approach in assessing diet.

Fatty acids with mean < 0.1 % were removed from the dataset. The remainder were renormalized and then transformed using a centered log ratio (Filzmoser et al., 2009). Permutational multivariate analysis of variance (PERMANOVA) indicated that, within all subsites, there was a significant main effect of species on FA profile ($p=0.002$). When followed by pair-wise comparisons, every species was found to have statistically different FA profiles ($p<0.05$) within a subsite, with only one exception: in Port Dick in summer 2011, Pacific cod and saffron cod in subsite Sunday did not have different FA profiles (see Tables S1-S3 for main effects and pair-wise results for all subsites). Relatively large sample sizes with little variability within individual species likely led to this result (Anderson et al., 2008). Therefore, we did not rely on traditional statistical comparisons to identify similarities in FA profiles. The FA data were instead used to qualitatively interpret the isotopic data. Principal components analysis (PCA) was carried out on the full FA profiles for samples collected within each bay by season and year to identify FA markers that contributed to the variation within the dataset. For most bays, the same FA were highly correlated with the principal components; these FA included 20:1n-7, 20:4n-6, n-6 FA, DHA, 20:1 isomers, and 16 carbon polyunsaturated FA (PUFA). Several of these were further grouped into markers representing calanoid copepods (Σ20:1n-11, 20:1n-9, 22:1n-11 and 22:1n-9; Lee et al., 2006; Copeman et al., 2020), n-6 FA (Σ18:2n-6, 20:2n-6, 20:3n-6, 20:4n-6, 22:4n-6 and 22:5n-6) and diatom associated material (Σ16:2n-4, 16:3n-4 and 16:4n-1; Dalsgaard et al., 2003). The FA 20:1n-7 is often found in proportions greater than the other 20:1 FA isomers in bivalves (e.g. Birkely et al., 2003; Copeman and Parrish, 2004) and is here used as a mollusk marker. Proportions of n-6 FA and 20:4n-6 were interpreted as more general benthic invertebrate markers (e.g. Graeve et al., 1997; Oxtoby et al., 2016). When patterns in the FA marker data showed obvious qualitative agreement with the stable isotope data, we added descriptors to the biplots of isotope data to make clear the markers that were elevated in specific species. We also reported the margin of error (ME) for each marker at a 95% confidence interval; when ME did not overlap in a given comparison of markers, we conservatively interpreted that to mean that samples were not similar and used descriptors of ‘higher’, ‘greater’, etc., to aid in interpretation of the patterns in the isotope data.

3. Results

3.1. Length, mass, condition factor (K) and lipid content

When fish were sampled in two seasons or years within a bay, we found significant interactions of species and season, species and year or both on all four measurements. Because we were interested in the potential for competition, and the interactions indicated a complex relationship between the factors, we therefore limited each species comparison to within a season and year.

Mass was variable and there were few patterns within and among species (Figs. 2 and 3). In 2013, Islas Bay rockfish formed two distinct groups based on mass (ANOVA: $F_{5,53} = 52.6$, $p<0.001$; Tukey: $p<0.001$), with one group having values more similar to Pacific cod (Fig. 2). Sand lance in Islas Bay 2013 also formed two groups with very different masses (ANOVA: $F_{5,53} = 52.6$, $p<0.001$; Tukey: $p<0.001$); larger individuals had a mass approximately 5 times greater than the smaller (~1 g) fish that dominated most of the samples (Fig. 2). Similarly, lengths of these sand lance individuals in the larger group were also twice that of the smaller, and likely represented a different species or cohort (Fig. 2). Within a subarea in the east GOA, mean FL of Pacific cod was generally quite similar to that of greenling (Fig. 2). Only in Salisbury Sound were Pacific cod significantly larger than greenling in length (ANOVA: $F_{2,32} = 135.4$, $p<0.001$; Tukey: $p<0.001$).

Saffron cod were only collected in the west GOA and were typically in the same size range as Pacific cod and greenling (< 20 mm variation among species; Fig. 3). Kiliuda Bay represented an exception to this, where saffron cod were significantly larger than greenling and Pacific cod (ANOVA: Various F, all with $p<0.001$; all Tukey: $p<0.001$) in all seasons and subareas (Fig. 3). The length difference was particularly noticeable in fall of both 2011 and 2013. Of the other major species, sand lance, pollock, and rockfish were usually in the same size range (i.e.

within 10-15 mm) as Pacific cod and greenling, while herring, except those collected in Aialik Bay, tended to be smaller in FL (Fig. 3). Sand lance were exceptional in being almost twice as large in 2013 as 2011 (ANOVA: $F_{1,76}$= 7.8, p = 0.007).

There was little variation in condition factor within most species (Figs. 2 and 3). For instance, Pacific cod had a condition factor of 1.0 ± 0.1 across the east and west GOA and all sampling sites in both years, while greenling had a condition factor of 1.7 ± 0.2. However, condition factor in rockfish ranged from 1.5 – 3.4 with mean of 2.3 ± 0.5 and varied with δ^{15}N. All rockfish with δ^{15}N < 3 ‰ relative to Pacific cod had condition factors < 2.2. Fish with condition factors > 2.2 had δ^{15}N values more like those of Pacific cod (Figs. 4b, 5c, 6a).

Lipid content varied much more than condition factor within a species and consequently there were few consistent patterns among species (Figs. 2 and 3). One notable trend in the data was that of sand lance and Pacific cod; when they co-occurred, sand lance generally had higher lipid proportions.

3.4. Stable carbon and nitrogen isotopes

Except for rockfish with low condition factors and a single group of sculpins in Islas Bay 2011, the δ^{15}N values of all species at all sampling sites were within ± 1 ‰ of that of Pacific cod (Figs. 4-6). Relative differences in δ^{13}C were much greater, ranging from a mean of -4 ‰ for rockfish in Islas Bay in 2013 (Fig. 4b) to +3 ‰ greater for greenling in Kiliuda Bay in summer of 2011 (Fig. 5a). Greenling showed little consistency across sampling sites or subareas, with relative δ^{13}C ranging from -3 ‰ in Graves Harbour to ~ + 1 ‰ greater in Salisbury Sound (Fig. 4c-d). In the east, greenling showed a high probability of overlap with Pacific cod (~50-90%) at four of the five sites evaluated (Supplemental Table S4). In contrast, in the west, greenling at most sites had a very different isotopic signature than Pacific cod, and showed much lower probability of overlap (<50%). Only in Kiliuda Bay, summer 2013, and Port Dick, fall 2013, was there significant niche overlap of Pacific cod and greenling (probabilities of 87 and 89%, respectively; Supplemental Table S5 and S6).

Saffron cod only occurred in the west GOA, and at 10 of the 13 sites where they co-occurred with Pacific cod, there was substantial niche overlap (>50% probability). Herring had consistently lower $\delta^{13}C$ than Pacific cod, and showed little evidence of niche overlap with that species (< 36% probability). Sand lance in the west showed substantial niche overlap with Pacific cod (> 50% probability) at three of four sites. The exception was in Port Dick, summer 2011, where sand lance showed greater similarity to herring in isotopic composition (Fig. 6c). In the east, the isotopic composition of the sand lance in the two size classes was very consistent so there was little niche overlap (< 36% probability) of the two but both sizes of sand lance were likely to feed within the same niche as rockfish (>72% probability). There was little evidence of niche overlap with Pacific cod for either size class of sand lance (<1% probability). Pollock only occurred at four subsites and at two of those (Fig. 5a, 6c), it had a very similar isotopic composition as Pacific cod; however, because the within-species data was very consistent, in all cases, we found little evidence to support niche overlap (probabilities < 30% for all).

For rockfish species, smaller fish with condition factors ≤ 2.2 had both $\delta^{15}N$ and $\delta^{13}C$ values that were 3 ‰ lower than Pacific cod (Fig. 4b, 5c, 6a). For sites where sample size was sufficient to assess niche metrics (Izhut and Kiliuda), the smaller rockfish showed near zero probability of overlap with any other species in the area. In most cases, larger rockfish in both the east and west were similar to Pacific cod and greenling, showing ~30-70 % probability of overlap in niche space (Supplemental Tables 1-3). Sculpins in the east in Isla Bay (Fig. 4a) showed moderate (25-30%) probability of overlap with only rockfish, being quite distinct from co-occurring greenling and Pacific cod. This contrasts with sculpins in Izhut Bay in the west that showed much higher probability of overlap (~50%) with greenling, Pacific cod and saffron cod.

3.4. Fatty acid profiles

3.4.1. East GOA

<u>Islas Bay</u>: In summer 2011, greenling at both subareas had the highest abundance of calanus markers of all co-occurring species (Table 1). Greenling also had less DHA than Pacific cod. Proportions of 20:4n-6 and Σn-6 FA in greenling were more like those of Pacific cod relative

to other east GOA sampling sites. Isotopic results in this bay were anomalous, with it being the only location where greenling had both lower $\delta^{13}C$ and $\delta^{15}N$ values than Pacific cod (Fig. 4a-d). Rockfish were in the large size class and had 20:4n-6 and Σn-6 FA levels similar to those of greenling, and distinct from Pacific cod. Sculpin had the highest values of those two markers and lowest DHA levels. Despite having a very high probability (99.7 %) of occurring within greenling's niche space in Fjordselheim, sand lance had a different FA profile on all markers considered, except DHA (Table 1).

In Islas Bay in summer 2013, the influence of size class on FA profile was evident in rockfish; those in the smaller size class had elevated calanus markers and DHA proportions compared to the larger rockfish (Table 1). Despite having very similar isotopic composition, sand lance in the two different size classes had distinct FA profiles, with the larger sand lance having higher calanus markers and the highest diatom markers of all species in this study, but containing relatively less 20:4n-6, Σn-6 FA and DHA. In contrast to 2011, the FA profiles of Pacific cod were most similar to that of large rockfish, with very similar values for all FA markers (Table 1). Herring had higher DHA levels and lower calanus and diatom markers and less 20:4n-6 and Σn-6 FA than Pacific cod (Table 1).

<u>Salisbury Sound</u>: The FA patterns here agreed well with those observed in fall samples in the west GOA (see below) with, for instance, greenling having higher proportions of 20:4n-6 and Σn-6 FA than Pacific cod, and similar levels of calanus markers in both (Table 2). However, levels of DHA in greenling and Pacific cod were very similar; at most other locations in the east and west GOA, DHA was lower in greenling. Perch were only collected in Salisbury Sound and were quite like Pacific cod in all markers except for diatom markers that were much higher in perch (Table 2).

<u>Graves Harbor</u>: Greenling here had the highest calanus markers measured at any site in the study with levels much larger than those in co-occurring Pacific cod and pollock. Greenling also had lower levels of 20:4n-6 and Σn-6 FA than Pacific cod, the opposite of the pattern observed at most other sites in both the east and west GOA. As in Salisbury Sound, greenling's DHA proportion was also unusual in its similarity to Pacific cod. Pollock had the highest DHA proportions, and its calanus and diatom markers were similar to Pacific cod (Table 3).

3.4.2. West GOA

Kiliuda Bay: Within subareas at Kiliuda Bay during summer 2011, Pacific cod and saffron cod had similar levels of diatom markers, DHA, and 20:4n-6 (Table 4), supporting their similar positions in the isotope biplot (Fig. 5a). Greenling were distinguished by higher levels of 20:1n-7, 20:4n-6 and Σn-6 FA, relative to Pacific cod. Greenling in Dungie also had the highest DHA proportion of all species considered at that subarea. Both pollock in Dungie and sand lance in Shearwater showed lower levels of 20:4n-6 and DHA relative to Pacific cod.

In Kiliuda Bay in fall 2011, the FA relationships were similar to those observed in the summer; Pacific cod and saffron cod in Dungie had similar proportions of calanus markers, 20:4n-6 and DHA, and greenling showed the highest levels of 20:1n-7 and diatom markers, and low DHA (Table 4). An inverse relationship between DHA content and the abundance of diatom markers was observed in most of the species sampled in this study. Saffron cod from Shearwater tended to have higher δ^{13}C values relative to Pacific cod (Fig. 5b) and this was reflected in their FA signatures, with levels of 20:1n-7, 20:4n-6 and Σn-6 FA more like those of greenling than Pacific cod (Table 4). Pollock were very distinct, with calanus markers at ~7%, while larger-sized rockfish had the lowest calanus markers and DHA levels.

In Kiliuda Bay during summer 2013, in contrast to summer of 2011, the calanus markers in saffron cod Pacific cod were very similar; the levels of all other markers, except diatom FA, were different in the two species. Greenling again had the highest levels of 20:1n-7, 20:4n-6 and Σn-6 FA, but DHA levels were the lowest of the four species evaluated, in contrast to summer 2011 where they were highest (Table 4). The FA patterns in rockfish in the small size class contrasted with that of large rockfish in fall of 2011 in Kiliuda Bay, showing the highest calanoid markers coupled with relatively high DHA proportions and low diatom markers. Levels of 20:4n-6 and Σn-6 FA in rockfish were intermediate between that of Pacific cod and saffron cod.

In the fall of 2013 in the same area, rockfish continued to have the highest calanoid markers but the proportions of the diatom markers were much greater in fall than summer (~1.4 vs 0.2 %; Table 4). Levels of 20:4n-6 and Σn-6 FA in rockfish were lower than Pacific cod and saffron cod (Table 4), also contrasting with results in summer of 2013. In Pacific cod and saffron cod, most FA markers were very similar, following the pattern found in fall of 2011 in Dungie. Pacific cod and saffron cod consistently had similar levels of DHA in all seasons and years.

Izhut Bay: Fish in Izhut Bay in summer of 2013 showed similar FA profiles to those of Kiliuda Bay at the same sampling time. Rockfish in the small size class had much higher calanus markers than all other species but their levels of 20:4n-6 and Σn-6 FA were like Pacific cod (Table 5). Greenling and saffron cod, with higher δ^{13}C values, had higher levels of 20:1n-7, 20:4n-6 and Σn-6 FA relative to Pacific cod and were consistent with Kiliuda Bay during the same season. Sculpin also showed elevated levels of 20:4n-6 and Σn-6 FA relative to Pacific cod. Sand lance had lower levels of calanus markers and 20:4n-6 relative to Pacific cod, but had similar DHA proportions and diatom marker levels.

Aialik Bay: Species in Aialik Bay were collected within 500 m of the glacier at the head of the bay and had FA profiles that contrasted with those sampled at all other sites in the GOA. For instance, Pacific cod had higher levels of calanoid markers, 20:4n-6 and Σn-6 FA than saffron cod, while herring had highest calanoid and diatom markers and lowest DHA, 20:4n-6 and Σn-6 FA (Table 6).

Port Dick: In Port Dick during summer 2011, Pacific cod and saffron cod at all subareas had very similar FA profiles (Table 7), consistent with their similar positions in the biplot (Fig. 6c). Pollock FA from subarea Swan also showed great similarity to those of Pacific cod and saffron cod. Greenling and rockfish had high levels of 20:4n-6 and Σn-6 FA, consistent with their high δ^{13}C values. Herring and sand lance from the Sunday subarea, and pollock from Waterfall had the lowest δ^{13}C values and correspondingly low levels of 20:4n-6 and Σn-6 FA. For all subareas, DHA proportions were highest in herring (~43%) and lowest in greenling and rockfish.

Proportions of 20:4n-6 and Σn-6 FA in Port Dick in summer of 2013 were lowest in herring and sand lance (Table 7), similar to those of summer 2011. However, the strong similarity in FA profile of Pacific cod and saffron cod in 2011 was not evident, with clear differences in DHA levels, 20:4n-6 and calanus markers. In the fall of the same year, the three species present showed very similar calanus markers, and 20:4n-6 and Σn-6 FA levels (Table 7), supporting their similar position in the biplot (Fig. 6e). As observed in other locations, DHA was lowest and diatom markers highest in greenling.

4. Discussion

4.1. Species interactions

Juvenile Pacific cod and saffron cod appear to share diets and habitats, which may increase the potential for competition. The isotope results and FA markers suggested similar diets of age-0 Pacific cod and saffron cod at most locations evaluated. Calanoid copepods are thought to make up a substantial portion of juvenile Pacific cod diets (Abookire et al., 2007; Strasburger et al., 2014) and proportions of calanoid markers were similar in Pacific cod and saffron cod when they co-occurred (representing *Calanus* sp. and *Neocalanus* sp. but excluding *Pseudocalanus* sp.; Fraser et al., 1989; Dalsgaard et al., 2003; Lischka and Hagen, 2007; Yamada et al., 2016). Similarly, age-1 juveniles of these species displayed substantial dietary overlap when they co-occurred at Kodiak Island in the west GOA (Laurel et al., 2009; Brian Knoth, National Marine Fisheries Service, unpublished data). Johnson et al. (2009) reported saffron cod, particularly age-0 fish, as the dominant species in nearshore habitats of west Prince William Sound in 2006-2007 and noted that juvenile Pacific cod rarely co-occurred with these age-0 saffron cod. While the authors did not examine diets of the Pacific cod, they suggested that their low abundance might point to competition with saffron cod. Consistent differences in species abundance were not observed in this study nor was any evidence of resource limitation (Ormseth et al., 2017), but our study was not designed to provide definitive evidence of competition.

Occasional divergence in Pacific and saffron cod diets may be related to differences in habitat use and availability. During summer 2013 in Aialik Bay and Port Dick (west GOA), the FA data indicated that Pacific cod consumed calanoid copepods at a higher level that saffron cod. The reduced dietary overlap corresponded to a lesser degree of spatial overlap between the species (Ormseth et al., 2017). In Aialik Bay, saffron cod were much more abundant and ubiquitous than Pacific cod; in Port Dick abundances were similar but the two species were spatially segregated. These observations are consistent with a difference in habitat preferences; saffron cod appear to have a strong affinity for eelgrass, while Pacific cod are found in a variety of vegetated habitats (Laurel et al., 2007; Ormseth in review, this issue). The spatial distribution of the species in Port Dick, which has a complex geography with a variety of habitats, corresponded to these habitat preferences. The anomalous observations in Aialik Bay may be related in part to unique physical features of that site, which is very large and deep and is heavily influenced by a tidewater glacier at its head where the majority of juvenile fish habitat exists (Zimmerman et al., 2016; Zimmerman, 2019).

Because of the commercial fisheries for Pacific cod and walleye pollock, there has been much interest in interactions and potential competition of these two species (e.g. Laurel et al., 2007; Strasburger et al., 2014). Strasburger et al. (2014) found that both species consumed *Pseudocalanus* sp., *Neocalanus* sp. and *Calanus* sp. but relative amounts varied, thereby avoiding the potential for direct competition. In our study, we found diets of the two to vary markedly with season. For instance, we saw nearly identical FA profiles with very low levels of the calanus marker and similar isotopic compositions in Pacific cod and pollock in Kiliuda Bay (summer, 2011), indicating very similar diets. However, in the fall of 2011 in that location, we found the opposite result with greater consumption of calanoid copepods by pollock. Strasburger et al. (2014) reported a comparable finding in fall and suggested that Pacific cod become more demersal than pollock at that time and likely relied on other foods. Our study, as well as nearshore work on Kodiak island, similarly showed lower relative abundance of age-0 pollock in the fall, likely because of a move out of nearshore areas (Laurel et al., 2007; Ormseth et al., 2017).

In Port Dick, the interaction between cod and pollock seemed to have a greater spatial component. At subarea Swan in summer of 2011, we found similar isotopic values and FA markers; in contrast, at subarea Waterfall, carbon isotopic signatures were very different and FA signatures showed more variability than in Swan, pointing to greater variation in diets in the two species in this subarea. We note that in the west GOA in 2011, *Calanus* sp. markers were relatively low (~2% or less) in all species examined. This is consistent with surveys conducted on the adjacent west GOA shelf during summer and fall of both years that indicated a substantial reduction in the abundance of mesozooplankton in 2011, including calanoid copepods (Hopcroft et al., 2016). Nonetheless, the similar diets point to the possibility of competition between the two species in summer in the west GOA. In contrast, in Graves Harbor, the only site in the east GOA where we collected both species, we found Pacific cod relying on *Calanus* sp. far more than pollock.

Very little is known about the foraging ecology of greenling but our data suggested that at most sites in the west GOA, greenling were foraging on different prey than Pacific cod, saffron cod, sand lance and herring. Only in Port Dick 2013 in fall, where isotopic markers suggested similarity in diets of Pacific cod, saffron cod, and greenling, did we find FA profiles also indicating that the three species had similar reliance on benthic prey and calanoid copepods. Taken together, this suggests that greenling occupy a very different trophic position than the juvenile gadoids in the west GOA. Greenling have a very different mouth shape and gape size than gadoids which may promote consumption of different prey types (Mecklenburg et al., 2002).

In the east GOA, the isotopic data suggested that greenling were much more likely to feed in a similar niche as Pacific cod and other juveniles, with the FA data indicating similar levels of benthic markers in greenling and Pacific cod in summer. The only exception to this was in Graves Harbor (Fig. 4d) where there was no niche overlap of the three species evaluated (greenling, Pacific cod and pollock). This disparity could be due to a size-dependent effect; for instance, Pacific cod in Graves Harbor (east GOA; Fig. 2) at ~ 120 mm mean length were much larger than co-occurring greenling, as well as Pacific cod and greenling collected at all other sites (~60 mm). Within a genus, species are known to have different diets (e.g. rockfish; Bosley et al., 2014). Because we were unable to identify greenling to species, the seemingly different relationships between greenling and Pacific cod in the east and west GOA may be due to different proportions of the three greenling species in the samples from the two regions.

Rockfish undergo a dramatic change in diet during their first year of life, corresponding to a change in size (Love et al., 1991). Our marker data supported this, showing that rockfish of the smaller size class were feeding at a lower trophic level than all other species collected, and having much higher calanoid copepods. Love et al. (1991) suggested that this diet shift might be driven by a change in habitat, as rockfish progress from reliance on prey within the water column to those associated more with bottom substrates. Because the myriad rockfish species in the GOA spawn at different times of the year, it is likely that the size classes we observed in our study correspond to differences in age as well as species. Since rockfish in this study were not identified to species, we face the same issue as with greenling in that we are unable to eliminate the potential effect of species-specific foraging. However, the primary findings here hold regardless of actual species collected: individuals of *Sebastes* spp. in the GOA separated into at least two size classes that had different foraging patterns. Rockfish in the larger size class, presumably foraging in a more demersal environment than the smaller size class, had very different diets than Pacific cod, saffron cod, herring, pollock or sand lance. The selection of available prey would vary with pelagic and demersal environments, leading to the differences in diet markers found here. Large rockfish in Islas Bay in the east GOA represented the only exception, where they had $\delta^{13}C$ values quite similar to Pacific cod, particularly in 2013, and likely shared similar diets as Pacific cod.

There is scant literature on interactions of greenling and rockfish but here we found them often co-occurring (Ormseth et al., 2017; Ormseth in review, this issue) and showing evidence of similar reliance on benthic invertebrates and mollusks, and diatom and dinoflagellate derived material. The dietary overlap was only partial, as contributions of calanoid copepods were different in the two species at all locations. While occurring more rarely, we found very similar dietary patterns among sculpin, shiner perch, and greenling with similar reliance on benthic invertebrates, dinoflagellates and diatoms but varying in calanoid material. The differing reliance on calanoid copepods suggests that, should benthic invertebrates or mollusks become limiting, these co-occurring species may have the ability to diversify their diets and avoid direct competition.

Herring and sand lance, when collected simultaneously, had very similar diets and were both distinct from Pacific cod. Herring and sand lance were often the smallest individuals captured at a sampling site, offering a likely explanation for the similar diets and suggesting a limited selection of smaller prey. When sand lance did not co-occur with herring (e.g. Kiliuda

Bay 2011, Izhut Bay 2013), the isotopic data suggested they might have diets similar to Pacific cod and saffron cod. However, the FA markers did not convey a consistent message. For instance, in west GOA in Kiliuda Bay, summer, 2011 (Fig. 5a; Table 4), sand lance seemed to have a diet more closely associated with diatoms than Pacific cod but the species were similar in terms of calanoid markers. In summer 2013 in Izhut Bay, Pacific cod and sand lance seemed to share similar prey in terms of diatom sources, but markers for calanoid copepods were higher for Pacific cod (Table 5). The mean mass of sand lance in 2013 was almost twice that of 2011, while Pacific cod remained very similar in both years, suggesting again that trophic interactions among species may depend on subtle differences in size distribution within the water column. Size-dependent foraging is underscored by the sand lance data from Islas Bay in 2013 that is likely due to ontogenetic shifts in foraging and/or habitat preferences.

4.2. Spatial Variation

Within the west GOA, the apparent trophic relationships among species did not differ among sites except for the physically distinct Aialik Bay. In summer 2013 in Kiliuda and Izhut Bays, there was striking similarity in FA markers in the species common to both areas. This similarity existed despite a wide variety of nearshore habitats characterized by kelp, eelgrass or mixtures of the two (Ormseth et al., 2017), as well as sandy or rocky substrate. There were fewer sites and specimens available for comparison in the east GOA, limiting our ability to determine consistencies within the larger east GOA region. However, we did find relationships between Pacific cod and the two size classes of rockfish that were like those in the west GOA, suggesting that the limited overlap among these species is consistent throughout the GOA. In contrast, greenling at two of the three sites where they were collected in the east GOA showed a different foraging relationship with Pacific cod than that found in the west. The east and west GOA differ in multiple and complex ways, including strong zoogeographic patterns in species distributions (Ormseth in review, this issue), and it is unclear what drove this latter result.

4.3. Temporal variation

Kiliuda Bay was sampled in summer and fall in both collection years, allowing a more detailed evaluation of seasonal and annual variation in trophic relationships among the juvenile fishes abundant at that site. We found no evidence to indicate a shift in the diets of Pacific cod, saffron cod or greenling, with the cods having similar diets regardless of season and greenling remaining distinct. Importantly, this suggests that the foraging behavior of age-0 Pacific cod did not change from summer to fall. The FA data did suggest that pollock and Pacific cod diets diverged with season, with pollock displaying higher calanoid sources in fall than summer. Unfortunately, the pollock data were only available for comparison in 2011.

The FA data from Port Dick in 2013 suggested that greenling diets there also remained distinct from Pacific cod and saffron cod in the fall. Survey impacts due to the federal government shutdown in fall 2013 (Ormseth et al., 2017) hampered seasonal comparisons in that year. For example, we were unable to conduct fall sampling in Izhut Bay and very few species were collected in Port Dick and Kiliuda Bay in fall of 2013, losing a critical opportunity for seasonal comparisons with Kiliuda Bay. In east GOA, we did not have sufficient sample collection to make seasonal comparisons within a year.

Although there was limited opportunity to assess interannual differences, where direct comparison was possible, we found similar relationships among species across years. For instance, in the west, saffron and Pacific cod had similar diets in both years that were distinct from greenling. The only exception was in Port Dick in summer in 2013 and, as discussed above, the divergent diets in the cod species were most likely a result of different habitat preferences, rather than a change in foraging ecology. There was an anomalous bloom of salps in 2011 in the GOA (Li et al., 2016) but it would be unlikely to influence the coastal environment where the present study took place. Certainly, the consistency in relationships among these fish species in both years supports the limited impact of offshore conditions on the sheltered inshore environment where these fish were collected.

4.4. Marker interpretation

We were unable to sample discrete fat depots due to the relatively small size of these juvenile fishes. Fish size also prevented us from removing stomach contents. We therefore cannot be certain that both FA and stable isotope data were not influenced by the presence of undigested material. However, we would expect that to be reflected in high variation in the marker data within a single species collected at the same time and place. We instead saw consistent results for most species, particularly for the FA data, and do not believe that the presence of stomach contents has compromised our results.

We used a variety of different FA markers in this work to infer diet composition. Some markers, such as those for calanoid copepods, can represent either direct consumption of the relevant prey item or indirect consumption via an intermediate that itself preyed on the item. Other markers, such the diatom marker, likely indicate only indirect consumption rather than direct feeding on phytoplankton. Similarly, DHA is often cited as a general flagellate marker (Dalsgard et al., 2003; Budge et al., 2014) because it is produced in large amounts by dinoflagellates and prymnesiophytes (Viso and Marty, 1993). However, it is also known to accumulate in secondary producers such as copepods and euphausiids (e.g. Saito et al., 2002; Dalsgard et al., 2003; Stevens et al., 2004), so variation in its levels more likely points to varying reliance on different zooplankton sources. In this study, the consistently low levels of DHA found in greenling relative to Pacific and saffron cod indicate very different diets.

5. Conclusions

To our knowledge, this study represents the broadest spatial and seasonal investigation of trophic relationships among juvenile fishes in the nearshore GOA to date. Perhaps as a result of this broad coverage, we discovered a high degree of spatiotemporal complexity in this environment. The biomarker data supported our hypothesis that Pacific cod, saffron cod and pollock often had similar diets during summer. Dietary overlaps were disrupted by differences in spatial distribution (e.g. Pacific cod and saffron cod segregated by nearshore habitat in Port Dick) and by seasonal differences in behavior (e.g. age-0 pollock moving out of the nearshore in fall). Despite some broad similarities within sites and across regions, trophic relationships among juvenile fishes in the nearshore were highly variable across time and space. Comparisons between the east and west GOA were limited by the reduced sampling in the east. We were also limited in our ability to sample broadly across seasons, but we did obtain evidence of ontogenetic changes in foraging within and among species. We hope that this work provides the foundation for further studies of trophic ecology in the nearshore environment.

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Tables

Table 1. Summary of FA biomarker data for Islas Bay by subarea, species, year and season. Data are shown as mass percent of total FA (mean +/- margin of error (ME) at 95% confidence interval) for the respective biomarker. An “S” indicates the small size class (mass < 3 and 2 g for rockfish and sand lance, respectively) and an “L” indicates the large size class.

Subarea	**n**	**Species**	**Year**	**Season**	**Calanus**	**ME**	**20:1n-7**	**ME**	**20:4n-6**	**ME**	Σn-6	**ME**	**DHA**	**ME**	**Diatoms**	**ME**
Fjordselheim	9	greenling	2011	summer	5.62	2.22	1.55	0.56	2.64	0.64	5.07	0.44	26.03	4.81	0.25	0.11
Fjordselheim	12	Pacific cod	2011	summer	0.95	0.14	0.36	0.12	2.42	0.73	4.52	0.59	37.01	1.80	0.08	0.02
Fjordselheim	12	Rockfish (L)	2011	summer	1.47	0.12	0.87	0.13	3.25	0.52	5.66	0.25	26.01	1.67	0.30	0.08
Fjordselheim	12	sand lance	2011	summer	0.73	0.11	0.20	0.05	1.56	0.22	3.82	0.23	32.23	3.49	0.53	0.28
Ilin	10	greenling	2011	summer	6.86	3.63	0.41	0.19	3.31	2.16	6.06	1.96	32.91	1.31	0.20	0.08
Ilin	10	Pacific cod	2011	summer	0.90	0.09	0.27	0.02	2.82	0.48	5.03	0.26	39.22	1.41	0.08	0.02
Ilin	6	Rockfish (L)	2011	summer	1.07	0.10	0.55	0.05	3.75	0.39	6.19	0.30	28.9	2.79	0.20	0.07
Ilin	7	sculpin	2011	summer	1.57	0.33	0.94	0.39	5.56	0.67	9.31	0.93	22.13	4.09	0.52	0.40
Ilin	12	herring	2013	summer	0.55	0.07	0.24	0.03	1.86	0.19	3.69	0.15	32.43	1.02	0.15	0.03
Ilin	12	Pacific cod	2013	summer	1.10	0.09	0.39	0.05	2.62	0.34	4.68	0.37	26.01	1.54	0.28	0.04
Ilin	9	rockfish (L)	2013	summer	1.28	0.22	0.41	0.07	2.39	0.83	4.80	0.53	24.53	1.80	0.34	0.10
Ilin	2	rockfish (S)	2013	summer	4.90	1.90	0.21	0.07	2.01	0.29	4.37	0.00	30.78	3.01	0.11	0.01
Ilin	12	sand lance (L)	2013	summer	1.32	0.23	0.39	0.05	0.82	0.17	2.64	0.23	13.98	1.06	2.16	0.32
Ilin	12	sand lance (S)	2013	summer	0.85	0.12	0.21	0.04	1.66	0.25	4.35	0.20	29.42	2.07	0.29	0.08

Table 2. Summary of FA biomarker data for Salisbury Sound by species, year and season. Data are shown as mass percent of total FA (mean +/- margin of error (ME) at 95% confidence interval) for the respective biomarker.

Species	n	Year	Season	Calanus	ME	20:1n-7	ME	20:4n-6	ME	Σn-6	ME	DHA	ME	Diatoms	ME
greenling	10	2013	fall	1.71	0.29	1.63	0.42	3.90	0.30	6.45	0.35	20.21	1.96	0.56	0.22
Pacific cod	12	2013	fall	1.84	0.19	0.67	0.28	2.79	0.57	5.22	0.59	19.44	3.07	0.38	0.19
shiner perch	12	2013	fall	2.10	0.38	0.62	0.19	2.06	0.19	4.32	0.27	16.85	1.37	1.61	0.20

Table 3. Summary of FA biomarker data for Graves Harbor by species, year and season. Data are shown as mass percent of total FA (mean +/- margin of error (ME) at 95% confidence interval) for the respective biomarker.

Species	**n**	**Year**	**Season**	**Calanus**	**ME**	**20:1n-7**	**ME**	**20:4n-6**	**ME**	Σn-6	**ME**	**DHA**	**ME**	**Diatoms**	**ME**
greenling	12	2013	summer	9.34	1.96	0.18	0.02	1.60	0.10	3.47	0.08	27.59	1.63	0.53	0.07
Pacific cod	12	2013	summer	1.18	0.09	0.25	0.03	2.55	0.27	4.21	0.38	25.57	1.84	0.38	0.05
pollock	12	2013	summer	1.69	0.66	0.17	0.02	1.96	0.19	3.35	0.18	32.45	0.80	0.34	0.03

Table 4. Summary of FA biomarker data for Kiliuda Bay by subarea, species, year and season. Data are shown as mass percent of total FA (mean +/- margin of error (ME) at 95% confidence interval) for the respective biomarker. An “S” indicates the small size class of rockfish (mass < 3 g) and an “L” indicates the large size class.

Subarea	**Species**	**n**	**Year**	**Season**	**Calanus**	**ME**	**20:1n-7**	**ME**	**20:4n-6**	**ME**	Σn-6	**ME**	**DHA**	**ME**	**Diatoms**	**ME**
Dungie	greenling	11	2011	summer	1.58	0.35	0.27	0.04	4.21	0.35	6.44	0.41	29.72	1.03	0.21	0.05
Dungie	Pacific cod	24	2011	summer	1.20	0.32	0.13	0.02	0.96	0.08	2.84	0.07	26.65	1.32	0.33	0.02
Dungie	pollock	24	2011	summer	1.24	0.30	0.09	0.01	0.76	0.04	2.61	0.07	22.62	1.11	0.49	0.05
Dungie	saffron cod	36	2011	summer	0.70	0.03	0.20	0.02	1.06	0.07	3.30	0.05	25.84	0.55	0.36	0.02
Shearwater	Pacific cod	24	2011	summer	0.99	0.16	0.16	0.02	1.73	0.14	3.55	0.17	30.04	0.91	0.19	0.04
Shearwater	saffron cod	12	2011	summer	0.98	0.08	0.36	0.07	1.67	0.21	3.70	0.21	28.85	1.69	0.32	0.07
Shearwater	sand lance	12	2011	summer	0.89	0.12	0.17	0.02	0.92	0.11	3.09	0.23	22.88	2.99	0.94	0.30
Dungie	greenling	6	2011	fall	1.84	0.53	1.42	0.49	3.68	0.91	6.75	1.48	18.08	4.02	1.14	0.19
Dungie	Pacific cod	12	2011	fall	1.67	0.25	0.47	0.15	3.40	0.39	5.55	0.60	29.01	1.60	0.81	0.12
Dungie	saffron cod	9	2011	fall	1.64	0.12	0.84	0.19	3.16	0.25	5.27	0.25	29.52	0.96	0.49	0.17
Shearwater	greenling	12	2011	fall	1.78	0.29	1.85	0.53	3.79	0.28	6.84	0.57	15.74	1.93	1.54	0.33
Shearwater	Pacific cod	12	2011	fall	2.47	0.38	0.36	0.05	2.70	0.51	4.56	0.58	28.08	1.04	0.79	0.11
Shearwater	pollock	12	2011	fall	7.19	1.88	0.28	0.03	1.36	0.14	3.54	0.14	23.45	0.97	0.92	0.13
Shearwater	rockfish (L)	6	2011	fall	1.13	0.18	0.47	0.10	1.85	0.26	3.61	0.46	12.15	1.04	1.02	0.22
Shearwater	saffron cod	12	2011	fall	2.09	0.24	1.39	0.29	3.44	0.35	5.80	0.41	26.26	2.09	0.60	0.03
Dungie	greenling	10	2013	summer	2.18	1.05	0.84	0.42	3.74	0.53	6.19	0.84	24.96	3.93	0.64	0.17
Dungie	Pacific cod	12	2013	summer	1.06	0.31	0.20	0.03	1.24	0.16	2.67	0.19	38.22	0.94	0.11	0.03
Dungie	rockfish (S)	10	2013	summer	7.03	1.98	0.10	0.01	1.45	0.14	3.59	0.14	34.06	1.99	0.18	0.02
Dungie	saffron cod	11	2013	summer	0.96	0.08	0.42	0.06	1.93	0.24	3.91	0.31	35.50	1.00	0.16	0.02
Dungie	Pacific cod	12	2013	fall	2.03	0.37	0.35	0.04	2.29	0.59	3.85	0.74	28.56	1.48	0.37	0.12
Dungie	rockfish (L)	12	2013	fall	5.25	0.60	0.31	0.04	1.06	0.14	2.99	0.23	22.79	0.68	1.41	0.15
Dungie	saffron cod	12	2013	fall	1.62	0.14	0.58	0.23	2.81	0.44	5.00	0.55	27.94	2.02	0.34	0.22

Table 5. Summary of FA biomarker data for Izhut Bay by species, year and season. Data are shown as mass percent of total FA (mean +/- margin of error (ME) at 95% confidence interval) for the respective biomarker. An “S” indicates the small size class of rockfish (mass < 3 g).

Species	**n**	**Year**	**Season**	**Calanus**	**ME**	**20:1n-7**	**ME**	**20:4n-6**	**ME**	Σn-6	**ME**	**DHA**	**ME**	**Diatoms**	**ME**
greenling	12	2013	summer	3.5	1.50	2.08	0.49	3.63	0.50	6.72	0.72	22.8	2.60	0.26	0.10
Pacific cod	9	2013	summer	1.59	0.42	0.24	0.10	1.75	0.24	3.19	0.34	34.14	1.20	0.15	0.04
rockfish (S)	12	2013	summer	7.18	1.94	0.12	0.01	1.59	0.11	3.74	0.16	30.59	1.48	0.23	0.07
saffron cod	9	2013	summer	1.86	0.42	1.15	0.36	2.48	0.21	4.68	0.41	31.85	2.22	0.16	0.01
sand lance	6	2013	summer	0.54	0.08	0.15	0.02	1.23	0.07	2.98	0.12	36.33	1.16	0.18	0.04
sculpin	12	2013	summer	1.19	0.19	0.35	0.03	4.33	0.29	7.21	0.36	20.84	1.49	0.24	0.05

Table 6. Summary of FA biomarker data for Aialik Bay by species, year and season. Data are shown as mass percent of total FA (mean +/- margin of error (ME) at 95% confidence interval) for the respective biomarker.

Species	**n**	**Year**	**Season**	**Calanus**	**ME**	**20:1n-7**	**ME**	**20:4n-6**	**ME**	Σn-6	**ME**	**DHA**	**ME**	**Diatoms**	**ME**
herring	12	2013	summer	5.51	1.78	0.2	0.02	0.81	0.12	2.5	0.16	25.95	3.42	0.5	0.18
Pacific cod	12	2013	summer	4.81	0.77	0.2	0.03	2.94	0.33	5.21	0.38	31.58	0.49	0.09	0.01
saffron cod	12	2013	summer	1.43	0.20	0.26	0.05	1.69	0.25	3.49	0.45	36.94	1.79	0.09	0.02

Table 7. Summary of FA biomarker data for Port Dick by subarea, species, year and season. Data are shown as mass percent of total FA (mean +/- margin of error (ME) at 95% confidence interval) for the respective biomarker. An “L” indicates the large size class of rockfish (mass > 3 g).

Subarea	**Species**	**n**	**Year**	**Season**	**Calanus**	**ME**	**20:1n-7**	**ME**	**20:4n-6**	**ME**	**Σn-6**	**ME**	**DHA**	**ME**	**Diatoms**	**ME**
Sunday	greenling	7	2011	summer	2.37	0.61	0.29	0.03	3.78	0.13	5.17	0.24	29.32	1.28	0.4	0.04
Sunday	herring	12	2011	summer	0.92	0.27	0.15	0.02	0.88	0.05	2.67	0.11	43.13	2.36	0.09	0.03
Sunday	Pacific cod	12	2011	summer	1.1	0.11	0.24	0.05	2.39	0.17	4.53	0.32	39.56	1.84	0.09	0.03
Sunday	rockfish (L)	9	2011	summer	1.06	0.12	0.4	0.07	3.43	0.20	6.15	0.35	27.23	3.97	0.29	0.08
Sunday	saffron cod	13	2011	summer	1.23	0.10	0.46	0.10	2.66	0.36	4.96	0.42	37.12	1.57	0.15	0.02
Sunday	sand lance	12	2011	summer	0.84	0.09	0.19	0.04	1.11	0.12	3.54	0.19	37.81	2.09	0.14	0.03
Swan	Pacific cod	6	2011	summer	1.11	0.34	0.06	0.02	1.05	0.26	2.68	0.33	33.05	1.93	0.33	0.10
Swan	pollock	8	2011	summer	1.82	0.85	0.06	0.01	0.7	0.11	2.3	0.13	28.02	2.27	0.35	0.06
Swan	saffron cod	3	2011	summer	0.75	0.03	0.06	0.01	1.04	0.25	2.69	0.18	30.18	1.61	0.29	0.12
Waterfall	greenling	12	2011	summer	2.24	1.19	0.8	0.20	3.41	0.37	5.68	0.51	23.36	2.59	0.78	0.20
Waterfall	Pacific cod	5	2011	summer	1.11	0.24	0.12	0.02	2.07	0.50	3.64	0.67	36.47	2.50	0.21	0.18
Waterfall	pollock	4	2011	summer	0.8	0.10	0.06	0.01	0.94	0.13	2.53	0.16	33	1.14	0.34	0.15
Waterfall	saffron cod	5	2011	summer	0.98	0.16	0.25	0.14	1.77	0.59	3.57	0.65	30.45	2.45	0.35	0.11
Sunday	herring	12	2013	summer	1.2	0.11	0.15	0.01	1.36	0.10	3.61	0.09	32.44	1.14	0.13	0.02
Sunday	Pacific cod	12	2013	summer	1.42	0.19	0.32	0.09	3.23	0.37	5.48	0.55	32.11	1.92	0.1	0.02
Sunday	saffron cod	12	2013	summer	3.05	0.48	0.29	0.11	1.87	0.21	4.37	0.35	20.4	0.79	0.25	0.03
Sunday	sand lance	12	2013	summer	2.42	1.69	0.15	0.02	1.03	0.13	3.24	0.11	26.3	3.24	0.44	0.11
Sunday	greenling	12	2013	fall	2.14	0.41	1.64	0.49	5.61	0.57	9.61	0.76	15.41	1.87	0.84	0.23
Sunday	Pacific cod	8	2013	fall	1.83	0.17	0.38	0.06	5.12	1.30	8.08	1.83	24.11	2.36	0.12	0.05
Sunday	saffron cod	11	2013	fall	2.09	0.38	0.88	0.39	4.92	0.40	8.48	0.47	21.85	1.25	0.18	0.05

Figures

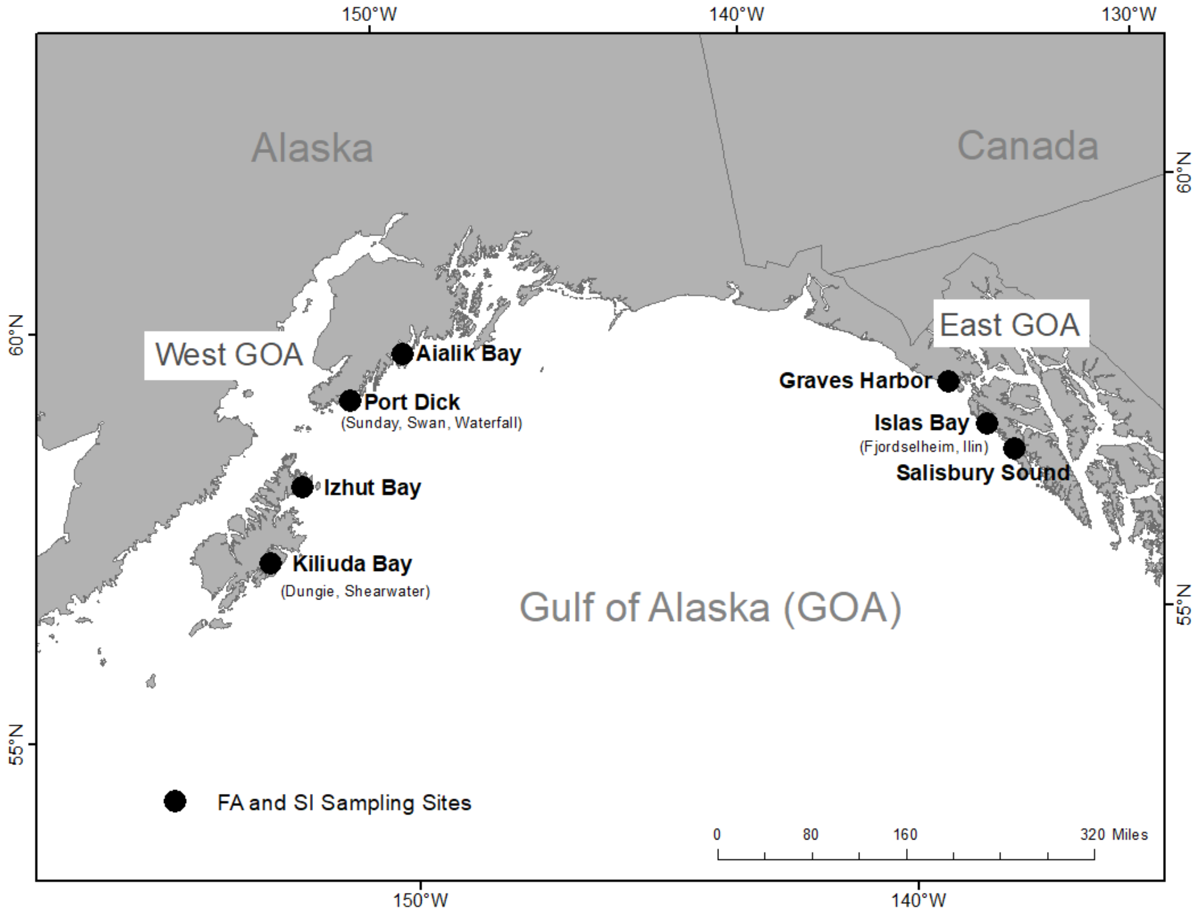

Fig. 1. Map of the study area in the Gulf of Alaska. Black circles indicate the selected sampling sites in 2011 and 2013; subareas within each sampling site are shown in parenthesis below the sampling site name.

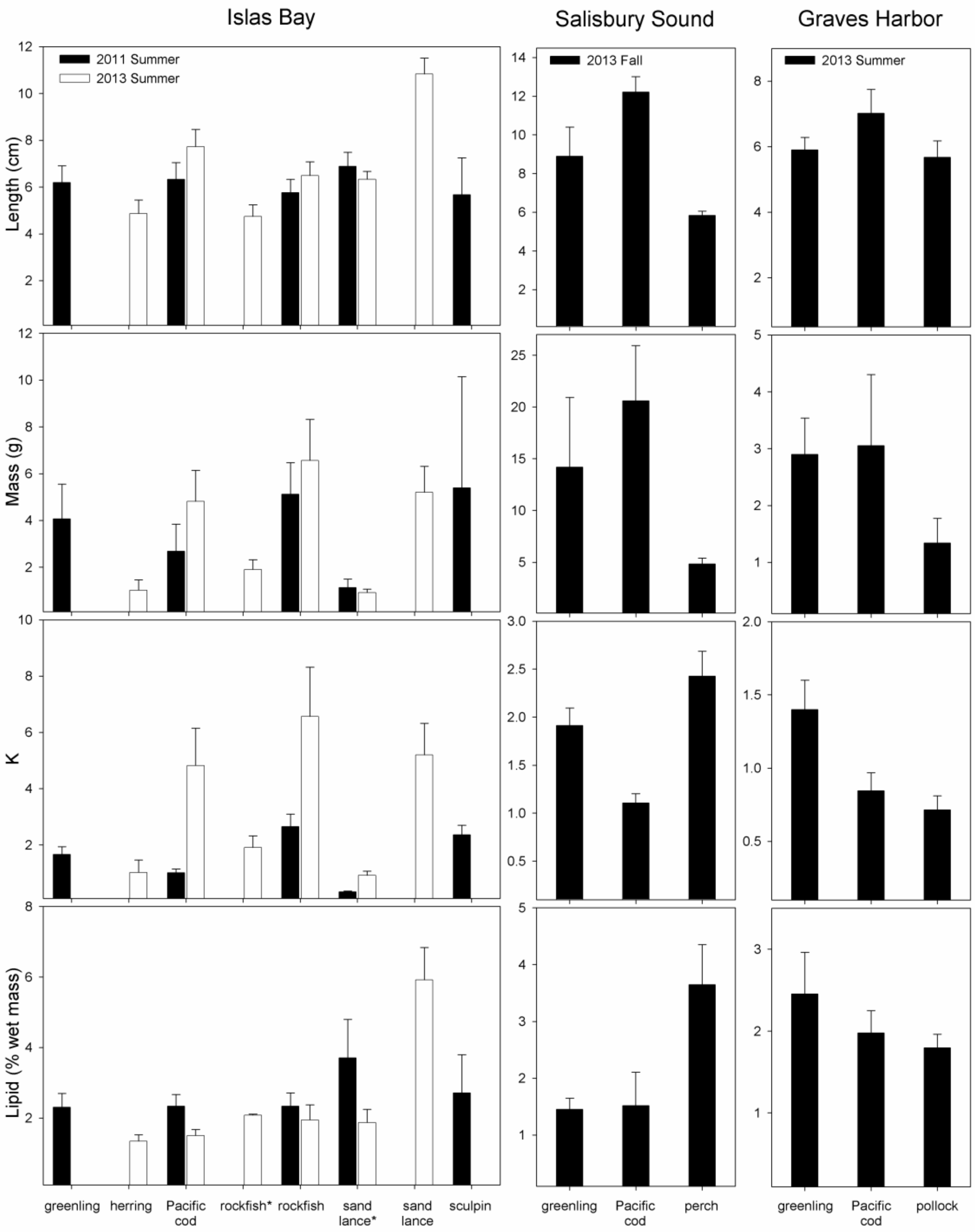

Fig. 2. Mean length, mass, condition factor (K), and percent lipid for fish species analyzed in the east GOA. Error bars indicate standard deviation. Differential shading of columns indicates season and/or year. Asterisks indicate the smaller size class for that species.

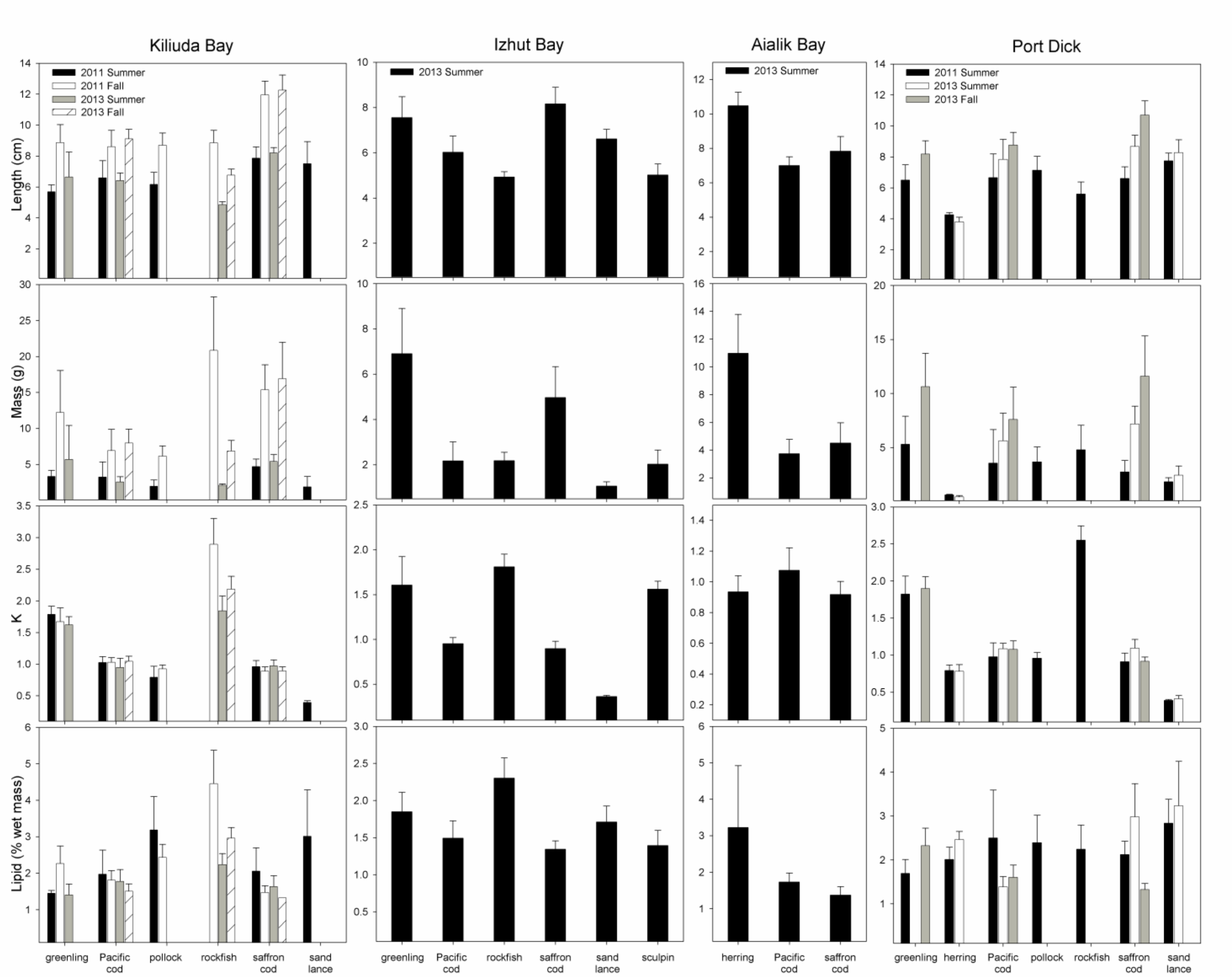

Fig. 3. Mean length, mass, condition factor (K), and percent lipid for fish species analyzed in the west GOA. Error bars indicate standard deviation. Differential shading of columns indicates season and/or year.

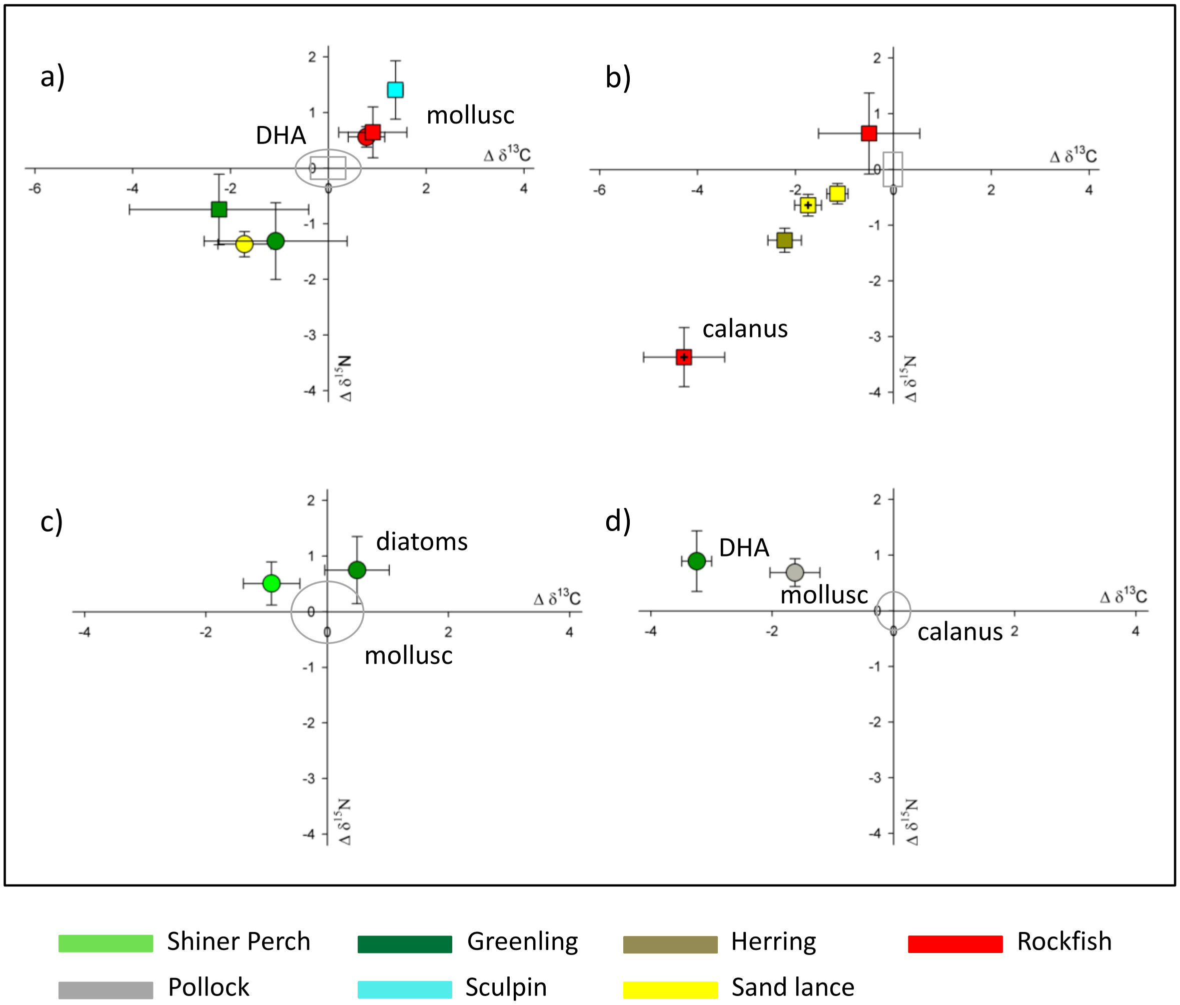

Fig. 4. Stable isotope biplots for whole fish tissues of species collected in the east GOA. Data are shown relative to values for Pacific cod, as explained in the text. (a) Islas Bay, 2011 summer; (b) Islas Bay, 2013 summer; (c) Salisbury Sound, 2013 fall; (d) Graves Harbor, 2013 summer. Fish were collected from a single sampling area in Salisbury Sound and Graves Harbor. In Islas Bay, subareas where samples were collected (see Fig. 1) are indicated by circles (Fjordselheim) or squares (Ilin). Error bars indicate standard deviation. Symbols with crosses denote individuals in smaller size classes (mass < 3 and 2 g for rockfish and sandlance, respectively). Hollow shapes at origin show standard deviation of Pacific cod in corresponding sampling areas. Text within the plot indicates FA biomarkers that were present at consistently higher proportions in species with the corresponding stable isotopic composition.

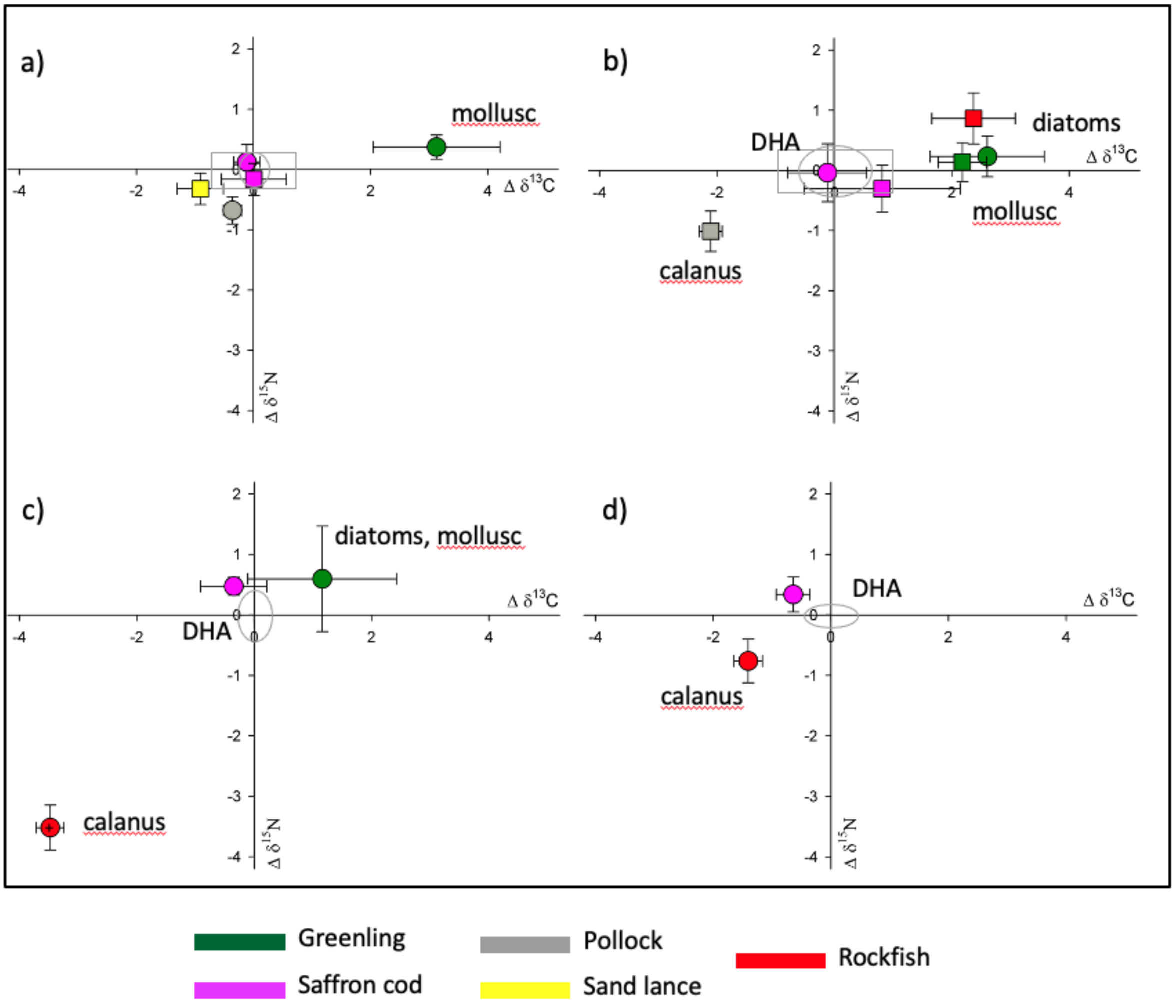

Fig. 5. Stable isotope biplots for whole fish tissues of species collected at the Kiliuda Bay site in the west GOA. Data are shown relative to values for Pacific cod, as explained in the text. (a) 2011 summer; (b) 2011 fall; (c) 2013 summer; (d) 2013 fall. Subareas where samples were collected (see Fig. 1) are indicated by circles (Dungie) or squares (Shearwater). Error bars indicate standard deviation. Hollow shapes at origin show standard deviation of Pacific cod in corresponding sampling areas. Symbols with crosses denote individuals in the smaller size class (mass < 3 for rockfish). Text within the plot indicates FA biomarkers that were present at consistently higher proportions in species with the corresponding stable isotopic composition.

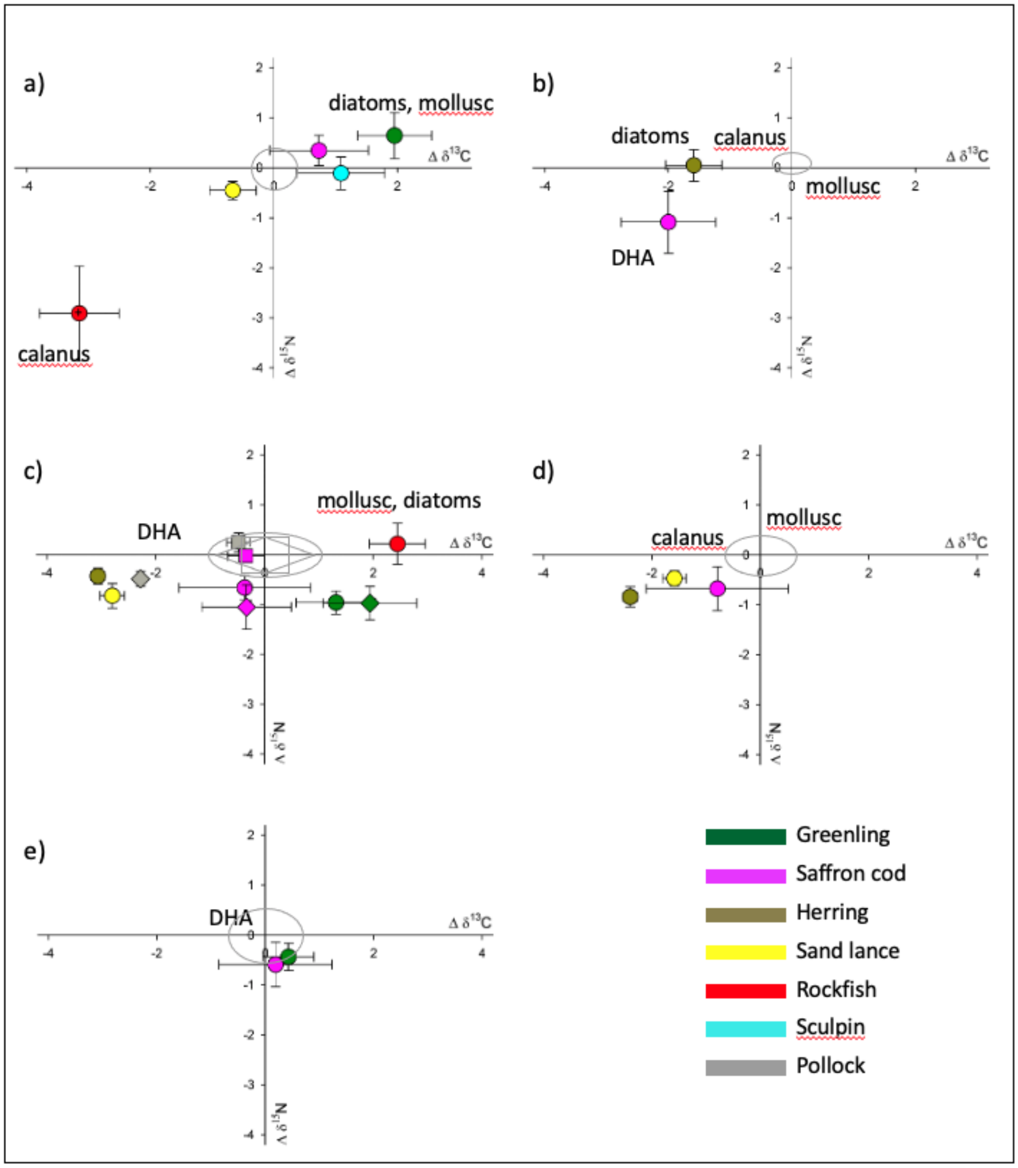

Fig. 6. Stable isotope biplots for whole fish tissues of species collected at multiple sites in the west GOA. Data are shown relative to values for Pacific cod, as explained in the text. (a) Izhut Bay, 2013 summer; (b) Aialik Bay, 2013 summer; (c) Port Dick, 2011 summer; (d) Port Dick, 2013 summer; (e) Port Dick, 2013 fall. Fish were collected from a single sampling area in Izhut and Aialik Bays. In Port Dick, subareas are indicated by circles (Sunday); squares (Swan); diamonds (Waterfall). Error bars indicate standard deviation. Hollow shapes at origin show standard deviation of Pacific cod in corresponding sampling areas. Symbols with crosses denote individuals in the smaller size class (mass < 3 for rockfish). Text within the plot indicates FA biomarkers that were present at consistently higher proportions in species with the

corresponding stable isotopic composition.

Supplementary Tables

Table S1. PERMANOVA results (t statistic, p value) of species comparison within subsites in the East GOA. Resemblance matrices were based on Euclidean distances calculated using the log transformed data.

Islas Bay – 2011 – Summer – Subsite: Fjordselheim
Main effect: Pseudo-F = 21.2, P=0.001

SPECIES	Greenling	Pacific cod	Rockfish (L)	Sand lance
Greenling	----	----	----	----
Pacific cod	4.7, 0.001	----	----	----
Rockfish (L)	4.0, 0.001	5.3, 0.001	----	----
Sand lance	4.6, 0.001	4.1, 0.001	5.2, 0.001	----

Islas Bay – 2011 – Summer – Subsite: Ilin
Main effect: Pseudo-F = 9.1, P=0.001

SPECIES	Greenling	Pacific cod	Rockfish (L)	Sculpin (unid)
Greenling	----	----	----	----
Pacific cod	3.4, 0.001	----	----	----
Rockfish (L)	2.5, 0.005	5.1, 0.001	----	----
Sculpin (unid)	2.8, 0.008	5.4, 0.001	2.1, 0.003	----

Islas Bay – 2013 – Summer – Subsite: Ilin (note: 2 samples of rockfish in the small size class were removed from the analysis)
Main effect: Pseudo-F = 52.0, P=0.001

SPECIES	Pacific herring	Pacific cod	Rockfish	Sand lance (S)	Sand lance (L)
Pacific herring	----	----	----	----	----
Pacific cod	5.7, 0.001	----	----	----	----
Rockfish	3.6, 0.001	2.7, 0.001	----	----	----
Sand lance (S)	4.4, 0.001	5.8, 0.001	3.0, 0.001	----	----
Sand lance (L)	14.6, 0.001	13.6, 0.001	7.8, 0.001	8.6, 0.001	----

Graves Harbor – 2013 – Summer
Main effect: Pseudo-F = 61.6, P=0.001

SPECIES	Greenling	Pacific cod	Pollock
Greenling	----	----	----
Pacific cod	9.8, 0.001	----	----
Pollock	7.8, 0.001	3.6, 0.002	----

Salisbury Sound – 2013 – Fall
Main effect: Pseudo-F = 19.2, P=0.001

SPECIES	Greenling	Pacific cod	Shiner perch
Greenling	----	----	----
Pacific cod	2.5, 0.001	----	----
Shiner perch	6.9, 0.001	4.5, 0.001	----

Table S2. PERMANOVA results (t statistic, p value) of species comparison within subsites in the Kiliuda Bay site in the west GOA. Resemblance matrices were based on Euclidean distances calculated using the log transformed data.

Kiliuda Bay – 2011 – Summer – Subsite: Dungie
Main effect: Pseudo-F = 60.0, P=0.001

SPECIES	Greenling	Pacific cod	Pollock	Saffron cod
Greenling	----	----	----	----
Pacific cod	8.3, 0.001	----	----	----
Pollock	11.7, 0.001	3.4, 0.001	----	----
Saffron cod	15.2, 0.001	3.8, 0.001	5.2, 0.001	----

Kiliuda Bay – 2011 – Summer – Subsite: Shearwater
Main effect: Pseudo-F = 30.5, P=0.001

SPECIES	Pacific cod	Saffron cod	Sand lance
Pacific cod	----	----	----
Saffron cod	2.9, 0.001	----	----
Sand lance	7.4, 0.001	4.9, 0.001	----

Kiliuda Bay – 2011 – Fall – Subsite: Dungie
Main effect: Pseudo-F = 11.6, P=0.001

SPECIES	Greenling	Pacific cod	Saffron cod
Greenling	----	----	----
Pacific cod	4.0, 0.001	----	----
Saffron cod	3.6, 0.001	2.2, 0.002	----

Kiliuda Bay – 2011 – Fall – Subsite: Shearwater
Main effect: Pseudo-F = 36.3, P=0.001

SPECIES	Greenling	Pacific cod	Pollock	Rockfish (L)	Saffron cod
Greenling	----	----	----	----	----
Pacific cod	5.5, 0.001	----	----	----	----
Pollock	7.1, 0.001	6.8, 0.001	----	----	----
Rockfish (L)	3.8, 0.001	6.9, 0.001	7.0, 0.001	----	----
Saffron cod	3.7, 0.001	4.6, 0.001	8.1, 0.001	6.3, 0.001	----

Kiliuda Bay – 2013 – Summer – Subsite: Dungie
Main effect: Pseudo-F = 30.2, P=0.001

SPECIES	Greenling	Pacific cod	Rockfish (S)	Saffron cod
Greenling	----	----	----	----
Pacific cod	4.9, 0.001	----	----	----
Rockfish (S)	5.1, 0.001	7.7, 0.001	----	----
Saffron cod	3.7, 0.001	3.4, 0.001	7.7, 0.001	----

Kiliuda Bay – 2013 – Fall – Subsite: Dungie
Main effect: Pseudo-F = 34.8, P=0.001

SPECIES	Pacific cod	Rockfish (L)	Saffron cod
Pacific cod	----	----	----
Rockfish (L)	7.2, 0.001	----	----
Saffron cod	2.2, 0.001	7.5, 0.001	----

Table S3. PERMANOVA results (t statistic, p value) of species comparison within subsites in the west GOA. Resemblance matrices were based on Euclidean distances calculated using the log transformed data.

Izhut Bay – 2013 – Summer **Main effect: Pseudo-F = 32.1, P=0.001**						
SPECIES	Greenling	Pacific cod	Rockfish	Saffron cod	Sand lance	Silver-spotted sculpin
Greenling	----	----	----	----	----	----
Pacific cod	5.3, 0.001	----	----	----	----	----
Rockfish	5.5, 0.001	5.5, 0.001	----	----	----	----
Saffron cod	3.2, 0.001	3.8, 0.001	5.6, 0.001	----	----	----
Sand lance	5.2, 0.001	5.2, 0.001	5.3, 0.001	5.7, 0.001	----	----
Sillver spotted sculpin	5.3, 0.001	7.4, 0.001	8.2, 0.001	6.6, 0.001	9.7, 0.001	----

Aialik Bay – 2013 – Summer **Main effect: Pseudo-F = 24.4, P=0.001**			
SPECIES	Pacific herring	Pacific cod	Saffron cod
Pacific herring	----	----	----
Pacific cod	4.9, 0.001	----	----
Saffron cod	4.8, 0.001	5.6, 0.001	----

Port Dick – 2011 – Summer – Subsite: Sunday **Main effect: Pseudo-F = 29.9, P=0.001**						
SPECIES	Greenling	Pacific herring	Pacific cod	Rockfish (L)	Saffron cod	Sand lance
Greenling	----	----	----	----	----	----
Pacific herring	6.4, 0.001	----	----	----	----	----
Pacific cod	3.8, 0.001	4.7, 0.001	----	----	----	----
Rockfish (L)	2.6, 0.001	7.4, 0.001	4.1, 0.001	----	----	----
Saffron cod	3.8, 0.001	5.8, 0.001	**1.3, 0.144**	4.4, 0.001	----	----
Sand lance	7.0, 0.001	4.8, 0.001	6.6, 0.001	8.2, 0.001	7.5, 0.001	----

Port Dick – 2011 – Summer – Subsite: Swan
Main effect: Pseudo-F = 4.7, P=0.002

SPECIES	Pacific cod	Pollock	Saffron cod
Pacific cod	----	----	----
Pollock	2.5, 0.003	----	----
Saffron cod	2.3, 0.016	1.7, 0.049	----

Port Dick – 2011 – Summer – Subsite: Waterfall
Main effect: Pseudo-F = 11.4, P=0.001

SPECIES	Greenling	Pacific cod	Pollock	Saffron cod
Greenling	----	----	----	----
Pacific cod	3.6, 0.001	----	----	----
Pollock	4.1, 0.001	4.1, 0.006	----	----
Saffron cod	2.8, 0.001	2.2, 0.008	2.6, 0.015	----

Port Dick – 2013 – Summer – Subsite: Sunday
Main effect: Pseudo-F = 49.1, P=0.001

SPECIES	Pacific herring	Pacific cod	Saffron cod	Sand lance
Pacific herring	----	----	----	----
Pacific cod	11.0, 0.001	----	----	----
Saffron cod	10.2, 0.001	8.4, 0.001	----	----
Sand lance	3.3, 0.001	6.5, 0.001	6.0, 0.001	----

Port Dick – 2013 – Fall – Subsite: Sunday
Main effect: Pseudo-F = 14.3, P=0.001

SPECIES	Greenling	Pacific cod	Saffron cod
Greenling	----	----	----
Pacific cod	4.7, 0.001	----	----
Saffron cod	3.8, 0.001	2.1, 0.006	----

Table S4. Mean overlap metrics for each species collected in the East GOA, giving the probability that an individual from SPECIES A (rows) will be found in the niche of SPECIES B (columns) at an alpha level of 95%.

Islas Bay – 2011 – Summer – Subsite: Fjordselheim

Alpha = 95%	**SPECIES B**			
SPECIES A	Greenling	Pacific cod	Rockfish (L)	Sand lance
Greenling	NA	10.3	0.7	24.1
Pacific cod	52.8	NA	9.6	0.1
Rockfish (L)	15.9	24.9	NA	0
Sand lance	99.7	0.3	0	NA

Islas Bay – 2011 – Summer – Subsite: Ilin

Alpha = 95%	**SPECIES B**			
SPECIES A	Greenling	Pacific cod	Rockfish (L)	Sculpin (unid)
Greenling	NA	7.3	7.5	0.9
Pacific cod	90.1	NA	43.4	0
Rockfish (L)	50.5	14.4	NA	25.2
Sculpin (unid)	10.7	0	30.7	NA

Islas Bay – 2013 – Summer – Subsite: Ilin (note: 2 samples of rockfish in the small size class were removed from the analysis)

Alpha = 95%	**SPECIES B**				
SPECIES A	Pacific herring	Pacific cod	Rockfish	Sand lance (S)	Sand lance (L)
Pacific herring	NA	0	22.3	9.7	0.1
Pacific cod	0	NA	64.6	0	0.2
Rockfish	1.6	8.8	NA	5.3	5.7
Sand lance (S)	14.1	0.0	71.9	NA	21.7
Sand lance (L)	0.2	0.3	80.8	35.5	NA

Salisbury Sound – 2013 – Fall

Alpha = 95%	**SPECIES B**		
SPECIES A	Greenling	Pacific cod	Shiner perch
Greenling	NA	64.7	16.2
Pacific cod	56.4	NA	33.0
Shiner perch	27.8	69.6	NA

Graves Harbor – 2013 – Summer			
Alpha = 95%	**SPECIES B**		
SPECIES A	Greenling	Pacific cod	Pollock
Greenling	NA	0	0.9
Pacific cod	0	NA	2.3
Pollock	0.7	3.1	NA

Table S5. Mean overlap metrics for each species collected at the Kiliuda Bay site in the west GOA, giving the probability that an individual from SPECIES A (rows) will be found in the niche of SPECIES B (columns) at an alpha level of 95%.

Kiliuda Bay – 2011 – Summer – Subsite: Dungie				
Alpha = 95%	**SPECIES B**			
SPECIES A	Greenling	Pacific cod	Pollock	Saffron cod
Greenling	NA	1.1	0	0.8
Pacific cod	6.5	NA	9.2	87.1
Pollock	0.1	23.8	NA	16.7
Saffron cod	5.8	87.9	7.2	NA

Kiliuda Bay – 2011 – Summer – Subsite: Shearwater			
Alpha = 95%	**SPECIES B**		
SPECIES A	Pacific cod	Saffron cod	Sand lance
Pacific cod	NA	74.8	40.0
Saffron cod	86.7	NA	38.7
Sand lance	85.1	62.1	NA

Kiliuda Bay – 2011 – Fall – Subsite: Shearwater					
Alpha = 95%	**SPECIES B**				
SPECIES A	Greenling	Pacific cod	Pollock	Rockfish (L)	Saffron cod
Greenling	NA	11.4	0	11.0	80.3
Pacific cod	3.9	NA	3.5	9.0	82.8
Pollock	0	29.8	NA	0	22.2
Rockfish (L)	30.4	39.8	0	NA	24.1
Saffron cod	20.7	36.1	1.3	5.3	NA

Kiliuda Bay – 2011 – Fall – Subsite: Dungie			
Alpha = 95%	**SPECIES B**		
SPECIES A	Greenling	Pacific cod	Saffron cod
Greenling	NA	12.6	11.3
Pacific cod	16.0	NA	86.1
Saffron cod	13.7	85.3	NA

Kiliuda Bay – 2013 – Summer – Subsite: Dungie

Alpha = 95%	**SPECIES B**			
SPECIES A	Greenling	Pacific cod	Rockfish (S)	Saffron cod
Greenling	NA	18.0	0	10.8
Pacific cod	97.4	NA	0	30.0
Rockfish (S)	0.1	0	NA	0
Saffron cod	91.3	58.6	0	NA

Kiliuda Bay – 2013 – Fall – Subsite: Dungie

Alpha = 95%	**SPECIES B**		
SPECIES A	Pacific cod	Rockfish (L)	Saffron cod
Pacific cod	NA	0.1	26.9
Rockfish (L)	0.1	NA	5.0
Saffron cod	22.4	5.8	NA

Table S6. Mean overlap metrics for each species collected at multiple sites in the west GOA, giving the probability that an individual from SPECIES A (rows) will be found in the niche of SPECIES B (columns) at an alpha level of 95%.

Izhut Bay – 2013 – Summer

Alpha = 95%	**SPECIES B**					
SPECIES A	Greenling	Pacific cod	Rockfish	Saffron cod	Sand lance	Silver-spotted sculpin
Greenling	NA	9.2	0	57.8	0.1	45.0
Pacific cod	10.3	NA	0.4	65.4	5.6	49.0
Rockfish	0	0.2	NA	0.1	0.1	0
Saffron cod	42.6	56.2	0.2	NA	0.7	51.5
Sand lance	0.9	66.2	2.3	11.7	NA	30.8
Silver spotted sculpin	53.6	48.8	0.1	59.5	2.2	NA

Aialik Bay – 2013 – Summer

Alpha = 95%	**SPECIES B**		
SPECIES A	Pacific herring	Pacific cod	Saffron cod
Pacific herring	NA	6.7	56.0
Pacific cod	12.6	NA	27.8
Saffron cod	47.0	6.0	NA

Port Dick – 2011 – Summer – Subsite: Sunday

Alpha = 95%	**SPECIES B**					
SPECIES A	Greenling	Pacific herring	Pacific cod	Rockfish (L)	Saffron cod	Sand lance
Greenling	NA	0	36.0	26.8	31.4	0
Pacific herring	0.3	NA	32.8	0	5.0	62.4
Pacific cod	35.1	0.5	NA	11.3	28.3	1.8
Rockfish (L)	65.7	0	53.0	NA	12.6	0
Saffron cod	39.9	0.2	72.7	6.7	NA	4.1
Sand lance	0.3	16.3	37.1	0	41.8	NA

Port Dick – 2011 – Summer – Subsite: Swan			
Alpha = 95%	**SPECIES B**		
SPECIES A	Pacific cod	Pollock	Saffron cod
Pacific cod	NA	4.0	27.2
Pollock	15.9	NA	30.9
Saffron cod	67.4	32.2	NA

Port Dick – 2011 – Summer – Subsite: Waterfall				
Alpha = 95%	**SPECIES B**			
SPECIES A	Greenling	Pacific cod	Pollock	Saffron cod
Greenling	NA	24.6	0	8.8
Pacific cod	17.6	NA	0.2	10.7
Pollock	0	11.5	NA	24.7
Saffron cod	12.9	17.4	0.5	NA

Port Dick – 2013 – Summer – Subsite: Sunday				
Alpha = 95%	**SPECIES B**			
SPECIES A	Pacific herring	Pacific cod	Saffron cod	Sand lance
Pacific herring	NA	5.1	95.8	1.9
Pacific cod	0.2	NA	66.3	3.1
Saffron cod	4.2	46.2	NA	11.3
Sand lance	1.1	56.3	99.9	NA

Port Dick – 2013 – Fall – Subsite: Sunday			
Alpha = 95%	**SPECIES B**		
SPECIES A	Greenling	Pacific cod	Saffron cod
Greenling	NA	88.6	97.6
Pacific cod	33.8	NA	66.8
Saffron cod	42.8	70.5	NA