Feeding ecology of salmon in eastern and central Gulf of Alaska

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ABSTRACT

Diet habits of five Pacific salmon species caught in the marine waters of the eastern and central regions of the Gulf of Alaska (GOA) were analyzed for spatial, interannual, seasonal, and ontogenetic differences. By making comparative analysis of diet variability over several years and marine conditions, between the eastern and central GOA ecosystems, during summer and fall, and between juvenile and adult salmon, we add to the understanding of the role of salmon in the GOA ecosystem. Diet composition differences were significant between all salmon/age-class pairs except for juvenile pink and sockeye salmon (no diet difference). The diets with the strongest separation (difference) were between either piscivorous salmon (Chinook or coho) and any planktivorous salmon (chum, sockeye or pink). Interannual differences in diet were also prevalent (all tested pairs were significant), followed by size-based ontogenetic diet changes between juveniles and adults, seasonal differences, and regional differences (eastern vs. central GOA). Lower and upper trophic level productivity in the GOA varied over the study period which influenced the type and amount of prey available to both piscivorous and planktivorous salmon. The year 2011 was an anomalously low production year in the GOA and this was reflected in poor feeding rate (stomach fullness) and condition factor. In contrast, foraging conditions during 2013 allowed for a positive condition factor for all juvenile salmon across the GOA even with low stomach fullness. Juvenile salmon in 2012 and 2014 had average feeding rates and condition factor. Interannual differences in the type of prey consumed, feeding rate, and condition factor often co-varied across region. These findings suggest that juvenile, immature, and maturing salmon growth and condition can be influenced by bottom-up forces in the ocean which may ultimately affect run timing and survival rate.

Keywords: Pacific salmon; Gulf of Alaska, Diet, Trophic dynamics, Stomach fullness, Condition

1. Introduction

Millions of juvenile salmon (*Oncorhynchus* spp.) out-migrate annually from streams and rivers into the Gulf of Alaska (GOA) where the fish initiate marine feeding and critical early growth (Orsi et al., 2014). Pacific salmon then spend from 1 to 5 years feeding and migrating in coastal and marine waters before returning to spawn in freshwater habitats (Groot and Margolis, 1991), yet it is thought that the first several months of feeding in marine waters is critical for their survival and growth to adults (Pearcy, 1992). As juvenile salmon migrate from freshwater habitats into the GOA and begin marine feeding, adult salmon are feeding while migrating back to freshwater systems to spawn and both life stages co-occur in the GOA. Other salmon stocks, besides those originating from GOA drainages have been shown to migrate into the GOA from hundreds of kilometers away to feed and grow before returning south as adults (Weitkamp, 2010; Fisher et al., 2014). Salmon in the GOA, as reported by Hartt and Dell (1986) tend to migrate through the GOA in a counter-clockwise path along with the Alaska coastal current, as well as offshore. Salmon have been captured in all habitats of the GOA: nearshore, shelf, slope, and basin and have been observed to feed in all these habitats (Kaeriyama et al., 2004; Armstrong et al., 2008; Weitkamp and Sturdevant, 2008). Understanding how marine conditions affect salmon survival, and how global climate change could impact this relationship is key for fisheries management, through the accurate prediction of adult returns required for establishing management quotas that sustain wild populations. Pacific salmon in Alaska waters make up the most valuable commercial fishery managed by the State of Alaska, with more people employed in harvesting and processing salmon than all the other commercial fisheries (Cline et al., 2017).

Juvenile and adult salmon are found in high numbers across the nearshore, shelf, slope, and basin habitats within the GOA and overlap with numerous other commercially and ecologically valuable groundfish species in the GOA (Orsi et al., 2007). In the GOA, salmon at different phases of their life history feed along with many other competitors. Planktivorous juvenile and adult salmon such as chum (*O. keta*), sockeye (*O. nerka*), and pink (*O. gorbuscha*) salmon spend their summer and fall in the GOA eating small zooplankton such as copepods, euphausiids, amphipods, small squid, and eggs and larval fish (Kaeriyama et al., 2004; Armstrong et al., 2005, 2008; Brodeur et al., 2007a). These prey are also consumed by forage fish such as capelin (*Mallotus villosus*) and Pacific herring (*Clupea pallasii*), as well as commercially important groundfish such as young of the year walleye Pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus microcephalus* (Norcross et al., 2001; Wilson et al., 2006; Moss et al., 2016a). Coho (*O. kisutch)* and Chinook (*O. tshawytscha)* salmon in the GOA are highly piscivorous and feed at a higher trophic level than the planktivorous salmon with more juvenile fish and squid than small zooplankton (Brodeur et al., 2007a; Weitkamp and Sturdevant, 2008; Johnson and Schindler, 2009; Hertz et al., 2015). Salmon diet studies within the GOA have included geographic, interannual, and seasonal differences (Brodeur et al., 2007a; Boldt and Haldorson, 2003). Changes in temperature, food conditions, and growth can have an impact of juvenile salmon during their early ocean period and so understanding salmon trophic ecology across the GOA, could be important in the understanding of salmon survival (Orsi et al., 2004; Weitkamp and Sturdevant, 2008; Moss et al., 2009) which is of interest for the ecosystem management of a complex, rich body of water.

Goals of the Gulf of Alaska Integrated Ecosystem Research Program (GOAIERP) were primarily to understand the GOA marine ecosystem and its response to environmental variability. The GOAIERP study was established to compare ecosystem processes in two large study areas on either side of the GOA, which represent the leading edge and the downstream area of the dominant current in the GOA. With juvenile and adult salmon comprising the majority of the fish biomass in the epipelagic zone during summer and fall in the GOA (Orsi et al., 2007), it is important to understand their role in the trophic structuring of the GOA. Salmon in the GOA consume the same zooplankton prey as other GOA species, as well as directly consume larval and juvenile fish. Understanding the role of salmon as top down predators on zooplankton in competition with other planktivores, as well as their top down effects on important fishes such as young-of-the-year groundfish, can provide valuable additions to our understanding of how salmon influence other GOA species. Moreover, it is important to understand the interannual fluctuations in the lower trophic level production of the GOA and how this production can support higher trophic levels. To add to the understanding of the role of salmon in the GOA ecosystem, we constructed a comparative analysis of diet variability over five years and marine conditions between the eastern and central ecosystems of the GOA in summer and fall and between juvenile and adult salmon. We tested numerous hypotheses, such as, the planktivorous or piscivorous salmon consume similar prey taxa across the GOA, have similar stomach fullness and condition factor, and that these characteristics would not change between years.

2. Methods

2.1. Sample collection and laboratory processing

The National Oceanographic and Atmospheric Administration surveyed the eastern and central coastal regions of the Gulf of Alaska (GOA) during summer and fall using a pelagic surface trawl net (Fig. 1). In the eastern Gulf of Alaska (EGOA) region, there were surveys in summer of 2010-2014, and fall of 2011. In the central Gulf of Alaska (CGOA) region surveys were completed in summers of 2011-2013, and fall of 2011 (Table 1). The 198-m rope trawl net with a 1.2 mm mesh codend liner was towed at stations along transects for 30 minutes at approximately 3.3- 7.0 km h^{-1}. Juvenile salmon collected in the trawl were identified, counted, weighted and measured (up to 50 per station per species). A maximum of 10 juvenile salmon of each species at a sampling station were frozen whole at sea. All juvenile Chinook salmon were retained. At sea, the adult salmon stomachs were removed and the contents pooled together and preserved (a maximum of 10 adult salmon per station per species). In the lab, juvenile salmon stomachs were extracted for diet analysis and individually weighed with prey and then again when empty to obtain stomach content weight for the calculation of stomach fullness. The juvenile salmon stomach contents were then pooled together and preserved from each station for each juvenile salmon species. Pooled and preserved stomach contents for each station/age-class/salmon species were identified to the lowest possible taxonomic category and weighted to the nearest 0.001 g.

2.2. Statistical analysis of diets

To observe general diet patterns, the prey were grouped into broad prey groupings of fish, euphausiids, cephalopods, amphipods, decapods, pteropods and “other” which were invertebrates not eaten in large amounts such as chaetognaths and barnacle larvae. For the statistical analysis, we identified 27 important prey categories by which a prey was at least 5% by weight eaten in any given survey. If prey were < 5.0% in any salmon/region/year/season, they were grouped within the nearest taxonomic category. At each station, the proportion of the known fish prey for each salmon/age-class was utilized to re-proportion the unidentified fish. Stations with only unidentified fish were re-proportioned to the survey proportion of known fish prey for each salmon/age-class. Non-food items (plant material etc.) were not included.

Diet variability of salmon (Chinook, coho, sockeye, chum and pink salmon) were examined for interspecific, interannual (2010-2014), regional (EGOA/CGOA), ontogenetic (juvenile/adult), and seasonal (summer/fall) differences to more fully understand how salmon utilize the GOA ecosystem trophically. In our preliminary analysis, we used survey-averaged diets for each salmon/age-class to identify areas where diets were not different and could then be grouped to reduce analysis. There were not any tested factors where diets were not different, and as such, all further tests were performed independently and only the results from the diet differences between species are listed. For the detailed diet analysis, average station diet composition (by mass of prey eaten) were tested for differences by using Analysis of Similarity (ANOSIM), which is a multivariate test equivalent to an ANOVA. A minimum of four sampling stations of a species/age-class/year/season/region was necessary to be included in the analysis. The ANOSIM is based on the matrix of pairwise Bray-Curtis similarity coefficients and the ANOSIM statistical significance is determined by permutations with the output also including an R-statistic (Clarke, 1993). The range of the Global R-statistic was between 0 and 1, where 0 indicates no separation between tested groups and 1 indicates complete separation. When significant ANOSIM values ($P < 0.05$) occurred, we used the SIMPER (similarity percentages) test to determine which prey taxa were responsible for the significant diet differences. The software PRIMER was used for all the diet composition analyses (Clarke and Warwick, 2001).

2.3. *Stomach fullness of juvenile salmon*

To examine differences in juvenile salmon stomach fullness as a percentage of the salmon's weight (% BW) in the GOA between years and regions by season, we calculated stomach fullness (% BW), where:

$$\% BW = \frac{stomach\ content\ weight}{total\ fish\ weight - stomach\ content\ weight} \times 100.$$

Fish with less than 0.05% stomach content to body weight were considered to have empty stomachs. Interannual changes in stomach fullness for each salmon species were compared using the non-parametric Kruskal-Wallis test. When the overall results were significant, we used the overlap in the median notch from box-and whisker plots to identify which years were statistically different (Chambers et al., 1983). For the pairwise regional differences we used the Mann-Whitney test. The significance level was $P < 0.05$ for both tests. Adult salmon were not included in the analysis due to differences in the way adults were processed on-board the ship.

2.4. Length-weight condition factor of juvenile salmon

The length-weight condition factor (up to 50 per station per species) was calculated for each juvenile salmon species. The condition factor was calculated for individual fish based on ln(weight) to ln(length) residuals from linear regression analysis, and a positive condition factor would indicate that the juvenile salmon were heavier than would be expected given their fork length. To test for interannual differences, regressions were fitted for each salmon in a season/region separately, (i.e. coho salmon in summer EGOA 2010-14), and to test for regional differences for each salmon in a season/year (i.e. coho salmon in summer 2011 CGOA-EGOA) regressions were also fitted separately. Interannual changes in condition for each salmon species were compared using the non-parametric Kruskal-Wallis test, and when the overall results were significant, we used the overlap in the median notch from box-and whisker plots to identify which years were statistically different. For the pairwise annual differences in fall EGOA, and to test for pairwise regional differences we used the Mann-Whitney test. For all tests, the significance level was $P < 0.05$. Adult salmon were not included in the analysis.

3. Results

3.1. Interannual Diet Composition of salmon in summer and fall

General diet composition of salmon in the GOA (N = 6556) regardless of age class, and temporal or spatial factors indicated that Chinook and coho salmon were primarily piscivorous while, sockeye, chum, and pink salmon had more of a planktivorous diet. Adult Chinook salmon primarily preyed upon fish (~75%) followed by euphausiids and cephalopods (~10% each), while juvenile Chinook preyed upon fish (~50%) cephalopods (~20%) and adult euphausiids (~10%; Fig. 2). Adult coho preyed upon fish (~55%), cephalopods (~20%) and decapod larvae (~10%), while juveniles utilized fish (~60%), decapod larvae and adult euphausiids (~10% each). Juvenile sockeye salmon preyed on early stages of euphausiids (~30%), copepods and larval fish/eggs (~15% each; Fig. 2). Juvenile chum salmon preyed on euphausiids (~30%) copepods and amphipods (~15% each). For adult pink salmon, pteropods were the top prey item (~25%), followed by early stages of euphausiids (~20%) and amphipods (~15%). Juvenile pink salmon preyed on early stages of euphausiids (~30%), pteropods and copepods (~15% each; Fig. 2). Diets between each salmon/age-class were significantly different except for juvenile pink and sockeye salmon (Table 2). Significant diet differences were strongest (higher Global R values) between the planktivorous and piscivorous salmon. Chinook adults and juveniles had the highest Global R values relative to the planktivorous salmon (ANOSIM Global R = 0.348-0.645), followed by adult coho salmon (ANOSIM Global R = 0.341-0.523) and then juvenile coho salmon (ANOSIM Global R = 0.233-0.263; Table 2).

Interannual diet differences were assessed for juvenile and adult salmon during summer in the EGOA (2010-2014; N = 4304) for five juvenile and three adult salmon, and in CGOA (2011-2013; N = 1546) for juvenile coho, sockeye, chum, and pink salmon. There was insufficient interannual diet data for samples collected in the fall in either region for analysis. In the EGOA, all salmon had significant interannual diet differences for all tests (ANOSIM Global R = 0.187-0.546; Table 3). The planktivorous salmon had higher Global R values (more interannual variability) than the more piscivorous salmon, although adult Chinook salmon also had strong interannual differences for the three years when there was data (Global R = 0.403). While the interannual tests were performed between years for each salmon, there were specific prey that were eaten in higher amounts by the majority of the salmon in particular years such as euphausiids in 2010. More pteropods were eaten in 2011, rockfish (*Sebastes* spp.) in 2010 and 2012, Pacific sandlance (*Ammodytes personatus*) in 2012, copepods in 2012, capelin in 2013, and pteropods by the planktivores in 2014. The piscivorous salmon ate cephalopods in all but 2010 (SIMPER; all listed prey contributed to > 15% of significant differences; Fig. 3).

In addition to the prey that were eaten in significantly higher amounts by most of the salmon in EGOA in particular years, there were other prey responsible of interannual diet differences. The adult Chinook salmon consumed more sablefish (*Anoplopoma fimbria*) in 2014 while the juvenile Chinook salmon consumed more flatfish in 2012. The adult coho salmon consumed more amphipods in 2011 and gadid fish in 2012 and 2013, while the juvenile coho salmon consumed more rockfish in 2011 and more gadids in 2013 (SIMPER analysis; all listed prey contributed to > 15% of significant differences; Fig. 3). For the planktivores, juvenile sockeye salmon consumed more hyperiids in 2011 and the juvenile chum salmon consumed more decapods in 2011 and more *Oikoplera* in 2012. The adult pink salmon consumed more pteropods in 2011, more hyperiids in 2012, and more cephalopods in 2014, while the juvenile pink salmon consumed more hyperiids in 2012 (SIMPER analysis; all listed prey contributed to > 15% of significant differences; Fig. 3).

During summer in CGOA between 2011-2013, interannual diet differences for juvenile coho, sockeye, chum, and pink salmon were all highly significant (ANOSIM Global R = 0.405, 0.307, 0.322, and 0.316 respectively; Table 3;). Prey that were consumed in high amounts by the majority of the juvenile salmon in the CGOA in particular years were more euphausiids in 2011 and 2013, amphipods, *Cancer* spp., and decapods in 2011, hyperiids, copepods (all groups), and rockfish in 2012, and capelin in 2013 (SIMPER analysis; all listed prey contributed to > 15% of significant differences; Fig. 4). Juvenile coho salmon consumed significantly more capelin in 2011 and more Pacific sandlance in 2012. Interannual diet differences included an increase in consumption of pteropods in 2012 for juvenile sockeye salmon, an increase in consumption of chaetognaths in 2012 for juvenile chum salmon, and an increase in consumption of *Neocalanus* copepods in 2011 and decapods in 2013 for juvenile pink salmon (SIMPER analysis; all listed prey contributed to > 15% of significant differences; Fig. 4). Of note, prey increases in the diet in both EGOA and CGOA (across the Gulf of Alaska) were more Pacific sandlance, rockfish, and copepods eaten in 2012, and capelin in 2013.

Diets were analyzed from one fall survey (2011) and took place in both study regions, with only adult Chinook salmon and juvenile pink salmon diets analyzed across the GOA. Adult Chinook salmon primarily consumed capelin across eastern and central GOA in fall, and adult coho salmon in EGOA primarily consumed capelin, clupeids, and juvenile salmon. The planktivorous salmon consumed euphausiids, pteropods, and capelin in both the CGOA and EGOA, and consumed decapods in the EGOA (Fig. 5). Juvenile pink salmon diets were different diets across the GOA, with more capelin and *Neocalanus* eaten in EGOA and euphausiids eaten in CGOA.

3.2. Size based ontogenetic diet differences

We also tested for ontogenetic diet differences between age-classes of Chinook, coho, and pink salmon in a given year/season/region. There were 12 pairs tested and all but juvenile and adult pink salmon in fall of 2011 in EGOA were significantly different (ANOSIM Global R = 0.092-0.613; Table 3). For Chinook salmon, diets showed a switch from cephalopods for the juveniles to various fish prey for the adults. For coho salmon, diets showed a switch from rockfish and invertebrates like euphausiids and decapods for the juveniles to cephalopods and various fish prey for the adults. For pink salmon, diets showed a switch from copepods for the juveniles to pteropods for the adults (SIMPER analysis).

3.3. Seasonal diet differences between summer and fall 2011

Seasonal diet differences between summer and fall 2011 were examined for four salmon/age-class in each area of the GOA (EGOA and CGOA; Fig. 3-5). All summer-fall diet pairs were modestly significantly different (ANOSIM Global R = 0.12-0.32) except for juvenile Chinook salmon in the EGOA, and adult Chinook and juvenile sockeye salmon in CGOA (Table 3; Figs. 3-5).

3.4. Regional diet differences across the GOA

We also tested for regional diet differences between EGOA and CGOA in summer 2011-2013 and fall 2011, of the 12 pairs of tests, 7 were significantly different with modest Global R values (ANOSIM Global R = 0.12-0.35); Table 3). In 2011, both juvenile chum and adult coho salmon had similar diets in both regions (ANOSIM; Table 3), while juvenile coho, sockeye, and pink salmon and adult pink salmon diets were significantly different (Global R ANOSIM = 0.252, 0.351, 0.238 and 0.256, respectively; Table 3). In 2012, both juvenile pink and coho salmon had similar diets in both regions (ANOSIM; Table 3), while juvenile sockeye and chum salmon both had diets that were significantly different between regions (ANOSIM Global R = 0.137, and 0.176 respectively; Table 3). In 2013, juvenile pink salmon diets were uniform across the GOA (ANOSIM; Table 3). The only salmon in the fall with sufficient sample size for statistical analysis were juvenile pink salmon, and the diets were significantly different across the GOA sampling stations (ANOSIM Global R = 0.029).

3.5. Stomach fullness of the juvenile salmon

Overall, the pattern was one of more food consumed by the juvenile salmon in the even years of the study period in EGOA, and little differences in fullness in CGOA. A second pattern was that the juvenile salmon in EGOA had similar stomach fullness within a year, with high variability between years. Almost without exception, all five of the juvenile salmon stomachs had significantly fuller stomachs in 2010 and 2012 than the other years (Kruskal-Wallis test; ($P < 0.0001$); Fig. 6a). In the odd years of the study period (2011 and 2013), salmon had lower amount of food in their stomachs than in the even years, particularly 2011 (Kruskal-Wallis test; ($P < 0.0001$); Fig. 6a). In CGOA, stomach fullness was not significantly different interannually for juvenile Chinook, coho, chum or pink salmon, while sockeye salmon had significantly less stomach fullness each year. (Kruskal-Wallis test; ($P < 0.0001$; Fig. 6b).

Comparisons of the juvenile salmon stomach fullness between regions of EGOA and CGOA were made in summer 2011-13 and fall 2011. For the juvenile salmon in the summer of 2011, all had significantly higher fullness in CGOA (Mann-Whitney test; ($P < 0.01$; Fig. 7a). The pattern was different in 2012, when coho and sockeye salmon had significantly more food in their stomachs in EGOA (Mann-Whitney test; ($P < 0.05$; Fig. 7c) and Chinook and pink salmon stomach fullness were higher in the EGOA but not significantly ($P > 0.05$). Sockeye salmon in EGOA in 2013 consumed significantly more food than in CGOA (Mann-Whitney test; ($P < 0.05$; Fig. 7d). There was not any regional difference in stomach fullness in fall 2011 for any of the juvenile salmon (Mann-Whitney test; ($P > 0.05$; Fig. 7d). In summary, the juvenile salmon ate more food in a given year in one region (summer 2011 CGOA and summer 2012 EGOA) or there was little difference between the regions (summer 2013 and fall 2011).

3.6. Length-weight condition of the juvenile salmon

Condition of juvenile salmon in the GOA ($N = 23{,}373$) generally showed the salmon in physical congruence with each other within a year/region/season (i.e. on average the juvenile salmon were uniformly thin or fat). In particular, for EGOA in summer (2010-2014), for the most part, juvenile Chinook, coho, sockeye and chum salmon were in significantly lower condition (thinner) in 2011 than all other years (Kruskal-Wallis test; ($P < 0.05$; Fig. 8a). The few exceptions were that juvenile Chinook salmon in 2010 were not significantly thinner than in 2011, and pink salmon condition in 2011 was not significantly different than in in 2010 or 2014. The condition of juvenile sockeye, chum, and pink salmon were significantly higher in 2013 than in all other years, except for juvenile sockeye from 2010 (Kruskal-Wallis test; ($P < 0.05$); Fig. 8a). Salmon in 2014 were all in positive condition. In the CGOA in summer (2011-2013), juvenile Chinook salmon did not show significant interannual differences in condition. In 2013, juvenile coho, sockeye, chum, and pink salmon were in significantly higher condition than in 2011 or 2012 (Kruskal-Wallis test; ($P < 0.05$; Fig. 8b). Overall, most juvenile salmon were fatter for their length (higher length-weight residual) across the Gulf in 2013, thin for their length across the GOA in 2011, EGOA salmon in 2014 were in above average condition, and were thin in 2012 in CGOA.

Regional differences in condition of the juvenile salmon in summer of 2011-2013, and fall of 2011 were made between EGOA and CGOA. Chum salmon were in significantly better condition in EGOA in summer 2011-2013, pink salmon were in significantly higher condition in EGOA in summer 2011 and 2012, and sockeye were in significantly higher condition in summer and fall 2011, and summer 2013 in CGOA (Mann-Whitney test; ($P < 0.05$; Fig 9a-d). In the fall of 2011, only sockeye salmon showed any difference between regions. Coho and Chinook salmon did not appear to be in better condition in one region or the other.

4. Discussion

The present study on the comparative feeding ecology of salmon in the Gulf of Alaska illustrated that diets were most prominently different interannually, then ontogenetically, between salmon species, seasonally, and the factor with the least robust significant diet differences was between study regions of eastern and central GOA. By utilizing a large diet data set, we provided new information on the interannual, seasonal, and regional, diet differences and to rank which factors contributed to the greatest diet differences of juvenile and adult Pacific salmon in the GOA, which was interannual, interspecific, and size based diet differences. Food resource partitioning between closely related species of salmon has been well studied. Interspecific and ontogenetic differences in physical morphology of gill rakers, and feeding location (depth from surface and/or distance from shore), and differential selection on diverse fields of prey being some of the identified reasons for diet differences between salmon (Beacham, 1985; Schabetsberger et al., 2003; Bollens et al., 2010; Sánchez-Hernández et al., 2017).

4.1. Feeding Composition of salmon

4.1.1. Interannual diet patterns

Interannual differences in salmon diet composition were highly significant, as salmon are opportunistic predators and these changes were due in part to changes in the forage base. Interannual changes in the diets of salmon in the marine environment is another well-studied aspect of salmon trophic ecology (Brodeur and Pearcy, 1990; Kaeriyama et al., 2004; Weitkamp and Sturdevant, 2008; Fergusson et al., 2013; Thayer et al., 2014; Daly and Brodeur, 2015).

While some studies found low interannual variability in diets (Weitkamp and Sturdevant, 2008; Brodeur et al., 2007b) other long term data sets found significant interannual variability in diets that were also related to environmental conditions and/or survival (Kaeriyama et al., 2004; Armstrong et al., 2008; Fergusson et al., 2013; Daly and Brodeur, 2015; Hertz et al., 2016). In our study, interannual changes in diets were significant for all species, in both study areas in the GOA, and for all years tested. As the diets were distinct between the salmon species, except for the highly numerous juvenile pink salmon and juvenile sockeye salmon, the significant changes in prey that were consumed in each year were typically different for each salmon species. For example, juvenile coho salmon ate more capelin in 2010 in EGOA, which was not significantly reflected in the diets of the other salmon. While this was the case for the interannual differences for most tested pairs, there were prey types that were increasingly eaten by most of the salmon in a given year reflecting higher reliance, and conceivably, the abundance of specific prey during that year.

4.1.2. Interannual patterns in the prey community

Higher than usual amounts of juvenile rockfish were eaten by most of the adult and juvenile salmon in 2010 and 2012 EGOA and 2011 and 2012 CGOA. This increase of rockfish in the diets was aligned with higher catches of juvenile rockfish in surveys as observed (Rhea-Fournier, personal communication). Exceptions to this were in CGOA in 2011 when rockfish were captured in higher abundance in the environment (yet were eaten in low amounts), and there were high numbers of juvenile rockfish caught in EGOA 2013, which were also not reflected in the diets. Pacific sandlance were eaten in higher amounts by the piscivorous adult and juvenile salmon in EGOA in 2012, as well as by sea birds as observed by Sydeman et al. (2017) suggesting that Pacific sandlance were widely available to piscivores in EGOA 2012.

Cephalopods (mostly squid) were one of the top prey for the piscivorous salmon in EGOA for all years except 2010, when an El Niño influenced ocean conditions. Of note, squid were also highly reduced in the diets of salmon in the GOA during the1997-98 El Niño, possibly linking how environmental conditions can dramatically affect the availability of important prey type for salmon (Kaeriyama et al., 2004). With squid being an important prey during most years of the study, they may act as an important prey resource in years, like 2011, when there were fewer juvenile fish available for the piscivorous salmon (Moss et al., 2016b). Overall, there were salmon prey types that were increasingly eaten by most of the salmon in a year with some evidence that this was due to the prey being increasingly available in the GOA and salmon, as well as other predators, taking advantage of this increase. To understand and predict how a changing environment will affect salmon, it is important to identify the environmental drivers of the important prey resources of salmon within the GOA.

Commercially and ecologically important groundfish have larval and juvenile stages that overlap temporally and spatially with the highly numerous piscivorous salmon in the GOA. The groundfish that appeared most significantly in the diets of the salmon (including the planktivorous salmon) in central and eastern GOA were larval and juvenile rockfish, which are a dominant proportion of the larval fish assemblage across the GOA (Goldstein et al., this issue). Other groundfish modestly eaten by salmon, particularly in EGOA, were gadids (walleye Pollock (*Theragra chalcogramma*) and Pacific cod), juvenile sablefish which were also caught in high numbers during the survey (Moss, personal communication), and flatfish (Pleuronectidae) which may have included arrowtooth flounder (*Atheresthes stomias*). While planktivorous salmon are not highly piscivorous, they consume similar prey types as the young groundfish, and may compete for plankton resources if they are limited (Moss et al., 2016a). For the ecosystem management of the GOA, it would be important to identify the spatial and trophic overlap between the numerous salmon populations in the GOA along with young groundfish, and if there are any trophic bottlenecks.

4.2. Size based ontogenetic, seasonal and regional diet patterns

Diets were different ontogenetically and seasonally for most salmon, which has been shown in previous diet studies (Myers et al., 2004; Armstrong et al., 2008; Weitkamp and Sturdevant, 2008; Daly et al., 2009). The low differences in diets of the salmon across the GOA (between EGOA and CGOA) in the majority of the comparisons was noteworthy due to the large and physically complex conditions across the GOA that potentially alter plankton transport across the GOA creating prey resource differences (Ladd et al., 2016; Goldstein et al., this issue). Environmental conditions that drive salmon food production may be similar in a year throughout the GOA, as the composition of prey in the diets did not differ for most salmon across the GOA. This is an interesting finding because we know the currents in the EGOA operate differently from the CGOA (Stabeno et al., 2016) and primary production in each region operates on different scales and production regimes (Waite and Mueter, 2013).

4.3. Stomach fullness of juvenile salmon

The amount of food eaten by the salmon in a region/year showed a pattern of congruency between the salmon with less food in their stomachs in EGOA in 2011, across the Gulf in 2013, and with higher amount of food in their stomachs in 2010 and 2012. Low stomach fullness in 2011 may be linked to anomalously low production as observed from the base of the food web (Strom et al., 2016) and few juvenile marine fish and forage fish were sampled in 2011 (Moss et al., 2016a). Identifying if stomach fullness is related to a fluctuation in prey biomass in the GOA was beyond the scope of this project, however, stomach fullness also has been shown to be related to colder temperatures in northern latitudes. It has been shown that fish inhabiting colder ocean conditions have more food in their stomachs than those in warmer conditions (Fergusson et al., 2013; Bachiller et al., 2016). Summer temperature anomalies in the GOA were the warmest in 2013 and 2014, and coldest in 2012, with average temperatures in 2010 and 2011 (Goldstein et al., this issue). This study observed the highest stomach fullness in 2010 and 2012, followed by less full stomachs in the warmer years of 2013-2014, which is similar to Fergusson et al. (2013) and Bachiller et al. (2016). Higher stomach fullness corresponded to higher survival of pink salmon in a previous study (Armstrong et al., 2008). Years when juvenile pink salmon had the fullest stomachs in EGOA, corresponded to greater year class survival for the adults returning the following year (Orsi et al., 2014).

The observed even-year higher stomach fullness of the juvenile salmon could also be related to how the abundance of adult pink salmon fluctuations between odd and even years. During even years, the abundance of adult pink salmon in the region is typically many times lower than the odd-years, and as such, there may be more food and less competition in the North Pacific during even-years (Ruggerone and Nielsen, 2004). The abundance of large copepods, during a 15-year study in the North Pacific, was significantly higher during even-years when adult pink salmon were less abundant (Batten et al., 2018) and during our study, stomachs were significantly fuller during the even-years, possibly due to fewer adult pink salmon in the region.

4.4. Length-weight condition of the juvenile salmon

Salmon also showed physical congruency in the GOA with salmon in 2013 being in higher condition (fatter) and salmon in 2011 being in lower condition (thin). Years when salmon had the least amount of food in their stomachs were also years when salmon were in highest (2013) and lowest (2011) condition, demonstrating a disconnect between the metrics of fullness and growth in some years. Salmon are constantly migrating from the freshwater to the GOA as summer progresses, and primarily enter the GOA and move west (Rhea-Fournier, personal communication). With a constant influx of recent migrants into the GOA during the summer while the surveys are occurring, salmon catches are a mixture of recent out-migrants with low marine growth. Therefore, the condition factor metric could reflect a mixture of salmon from various periods of their early marine growth, and does not make a good indicator of how salmon may fare overall in the GOA during a given year. However, knowing the amount of time the juvenile salmon had been in the GOA and combining this information with condition factor could prove to be a useful metric of salmon health.

5. Conclusions

Overall, salmon diets varied the least across the GOA, and the most interannually and between the salmon species. Salmon appear to take advantage of highly available prey, and the prey community appears to be highly variable in the GOA based on salmon diet analysis. Understanding trophic characteristics of salmon in the GOA and ultimately how environmental factors affect the production of the several trophic levels of prey can help us understanding the overall trophic structuring in the GOA and how salmon influence other GOA species. Ultimately, salmon body size, condition, and potentially marine survival are influenced by foraging conditions in the ocean. Fisheries oceanographic surveys that provide information on small pelagic fish and plankton abundance may prove useful in providing and index of feeding conditions for juvenile, immature, and maturing salmon (Daly et al., 2017).

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Table 1. Sample size of juvenile and adult salmon with diet analysis by season (summer or fall), region (EGOA or CGOA), and year (2010-2014) with survey dates. Surveys with less than 4 sampling stations are denoted with an * and were not included in the trophic analysis.

	Summer								**Fall**		
	EGOA					**CGOA**			**EGOA**		**CGOA**
	2010	**2011**	**2012**	**2013**	**2014**	**2011**	**2012**	**2013**	**2011**	**2013**	**2011**
dates	July 5-22	July 3-19, Aug 2-4	July 3-21, Aug 3-4	July 3-21, Aug 3-4	July 7-24, Aug 5-25	Aug 5-20	Aug 5-21	Aug 6-15	Sept 11-22	Sept 6-24	Sept 26-Oct 8
Chinook Adult		7*	26	24	43	56			9*		6
Chinook Juvenile	23	88	62	82	114	3*		17*	8*	25*	2*
Coho Adult		38	30	43	74	18			34		1*
Coho Juvenile	98	437	70	125		312	72				
Sockeye Juvenile	173	275	42	26	58	230	75	36	25*		93
Chum Juvenile	184	164	44	27	147	164	43	2*	23*		135
Pink Adult		249	258	375	85	115			45		
Pink Juvenile	363	170	44	9*	243	293	75	40	62		297
Total	**841**	**1428**	**576**	**711**	**764**	**1191**	**265**	**95**	**206**	**25**	**534**

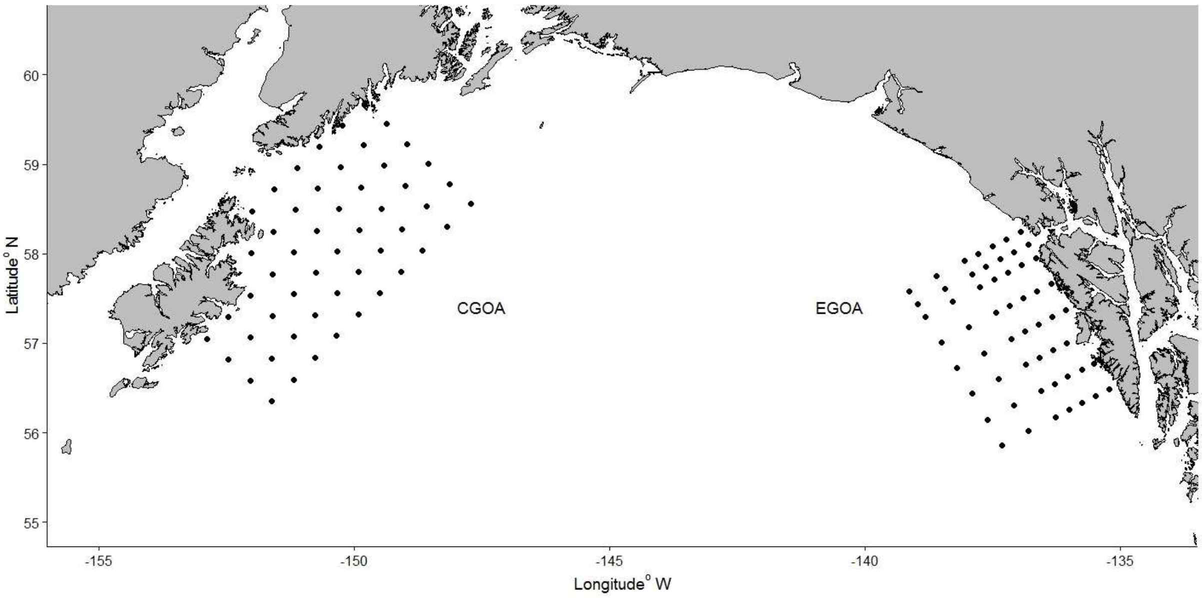
Table 2. Global R values of significant Analysis of Similarity (ANOSIM) test results of diet differences between each salmon/age-class. Values greater than 0.4 are indicated in bold. A = adult, J = juvenile.

	chinook A	Chinook J	Coho A	Coho J	Sockeye J	Chum J	Pink A
Chinook A							
Chinook J	0.159						
Coho A	0.055	0.061					
Coho J	0.275	0.089	0.202				
Sockeye J	**0.601**	**0.417**	**0.485**	0.263			
Chum J	**0.476**	0.366	0.343	0.266	0.033		
Pink A	**0.503**	0.348	0.341	0.223	0.079	0.109	
Pink J	**0.625**	**0.439**	**0.523**	0.260	n.s.	0.057	0.053

Table 3. Global R values of significant Analysis of Similarity (ANOSIM) test results of annual, regional, seasonal, and ontogenetic diet differences for Chinook, coho, sockeye, chum and pink adults (A) and juveniles (J). Values greater than 0.4 are indicated in bold.

	Annual		Region				Season		Ontogenetic				
	EGOA	CGOA	Summer			Fall	EGOA	CGOA	EGOA				CGOA
	2010-2014	2011-2013	2011	2012	2013	2011	2011	2011	2011	2012	2013	2014	2011
Chinook A	**0.403**		n.s.					n.s.		**0.439**	0.232	**0.477**	
Chinook J	0.187						n.s.						
Coho A	0.207		n.s.				0.115		**0.613**	0.273	0.175		0.370
Coho J	0.329	**0.405**	0.252	n.s.									
Sockeye J	0.304	0.307	0.351	0.137	n.s.			n.s.					
Chum J	**0.546**	0.322	n.s.	0.176				0.174					
Pink A	**0.401**		0.256				0.240		0.372	0.349		0.092	0.156
Pink J	**0.509**	0.316	0.238	n.s.	n.s.	0.293	0.323	0.284					

627 Fig. 1. Sampling map of the eastern Gulf of Alaska (EGOA) and central Gulf of Alaska
628 (CGOA).



629

Fig. 2. General diets of juvenile (_J) and adult (_A) salmon in the Gulf of Alaska based on diet composition by weight of prey consumed with sample size.

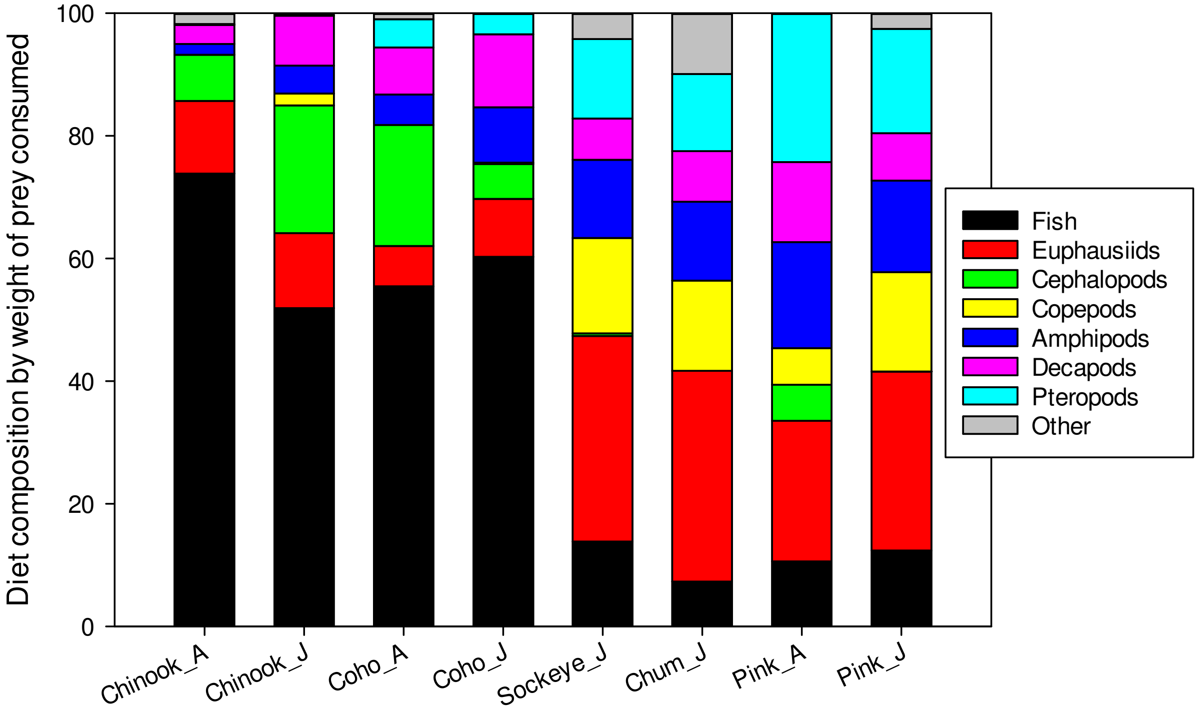


Fig. 3. Shade plot of EGOA average summer interannual diets with prey type on left, and across the top the year and salmon. Salmon followed by _J are juvenile, and by _A are adult. Color scale represents the percent diet composition by weight of prey on average for the salmon for each year. Dashed line in each annual rectangle is the separation between piscivorous (left of line) and planktivorous salmon (right of line).

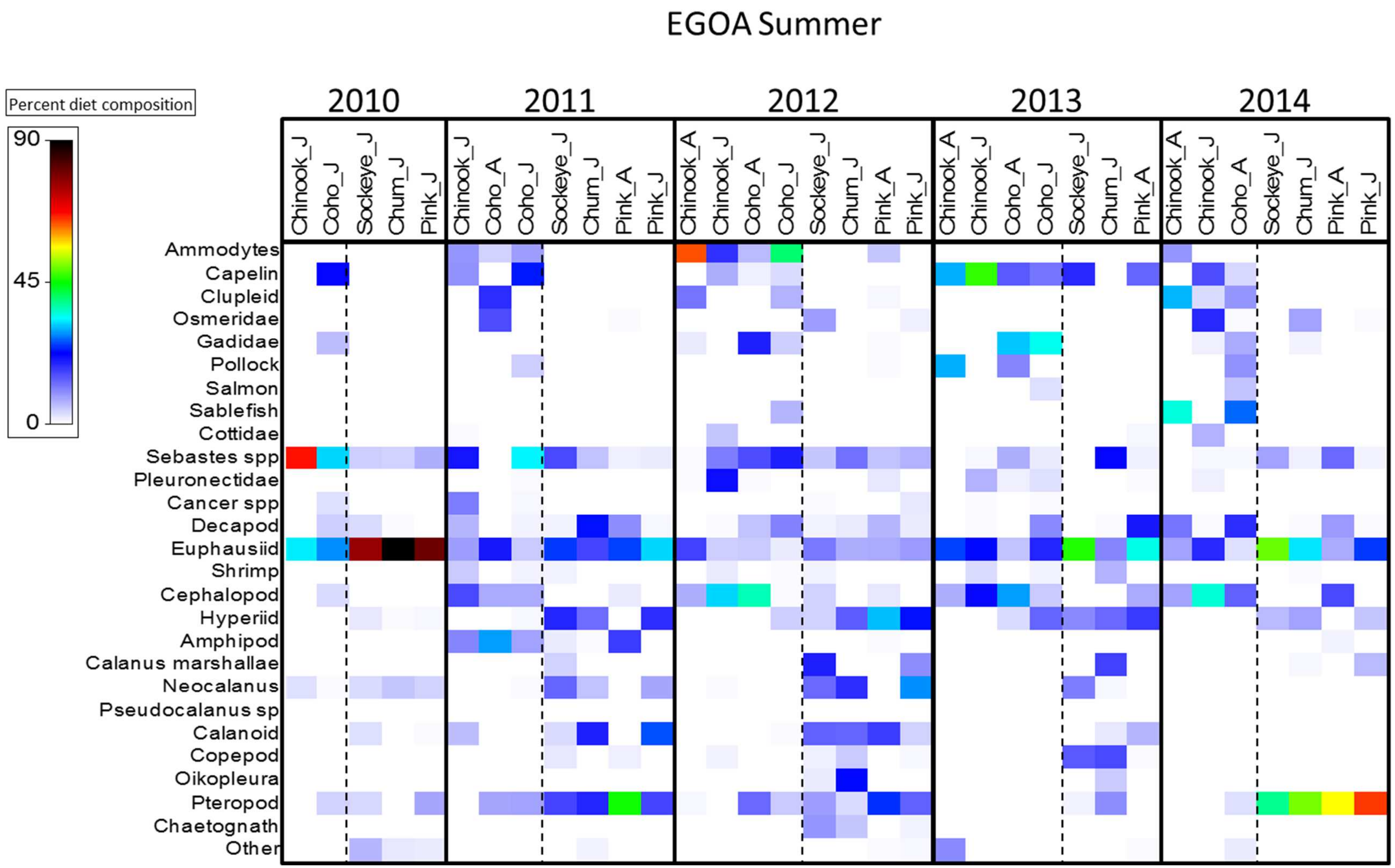


Fig. 4. Shade plot of CGOA average summer interannual diets with prey type on left, and across the top the year and juvenile salmon. Color scale represents the percent diet composition by weight of prey on average for the salmon for each year. Dashed line in each annual rectangle is the separation between piscivorous (left of line) and planktivorous salmon (right of line).

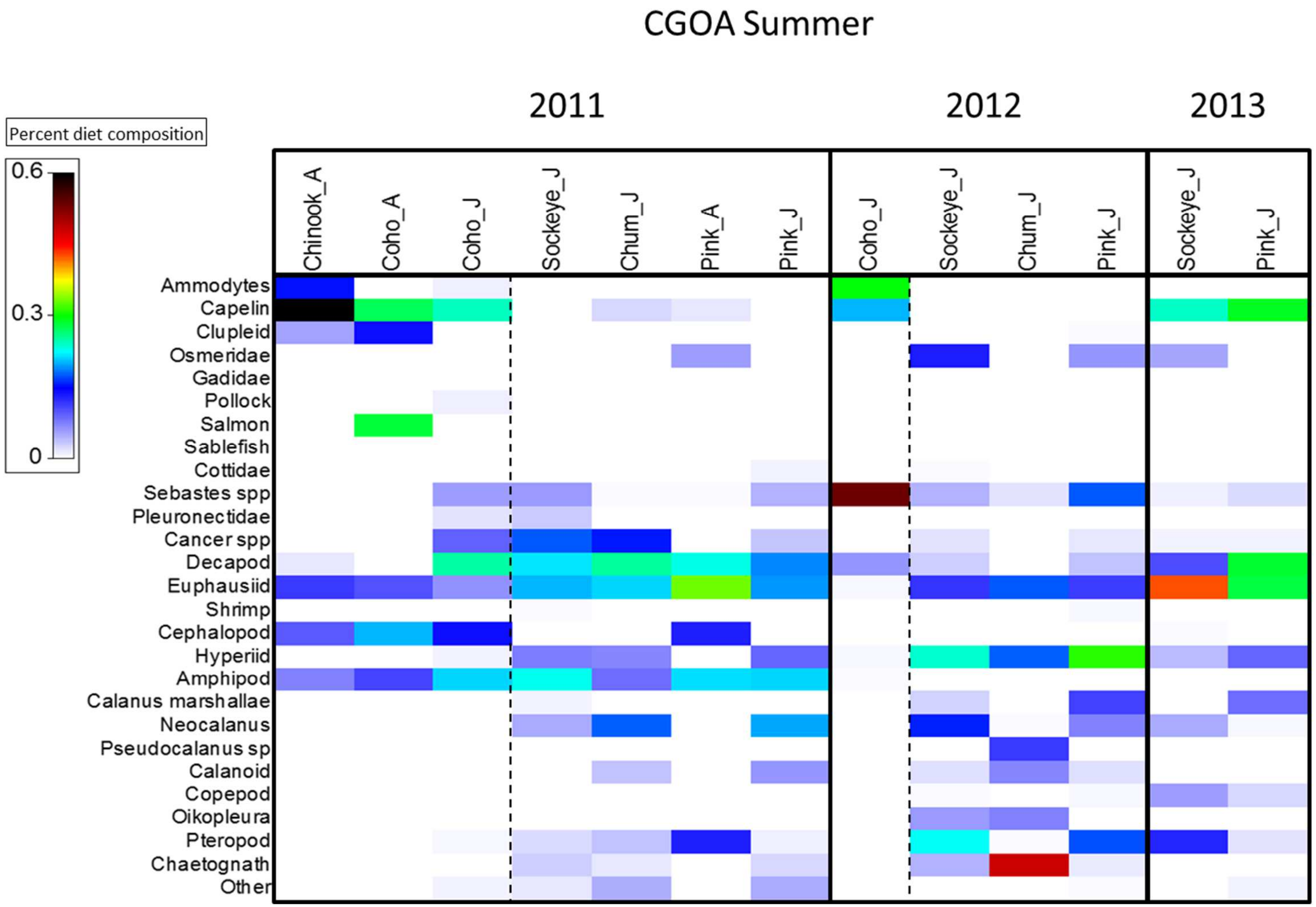


Fig. 5. Shade plot of CGOA and EGOA average fall 2011 diets with prey type on left, and across the top the region and juvenile salmon. Color scale represents the percent diet composition by weight of prey on average for the salmon for each region. Dashed line in each region rectangle is the separation between piscivorous (left of line) and planktivorous salmon (right of line).

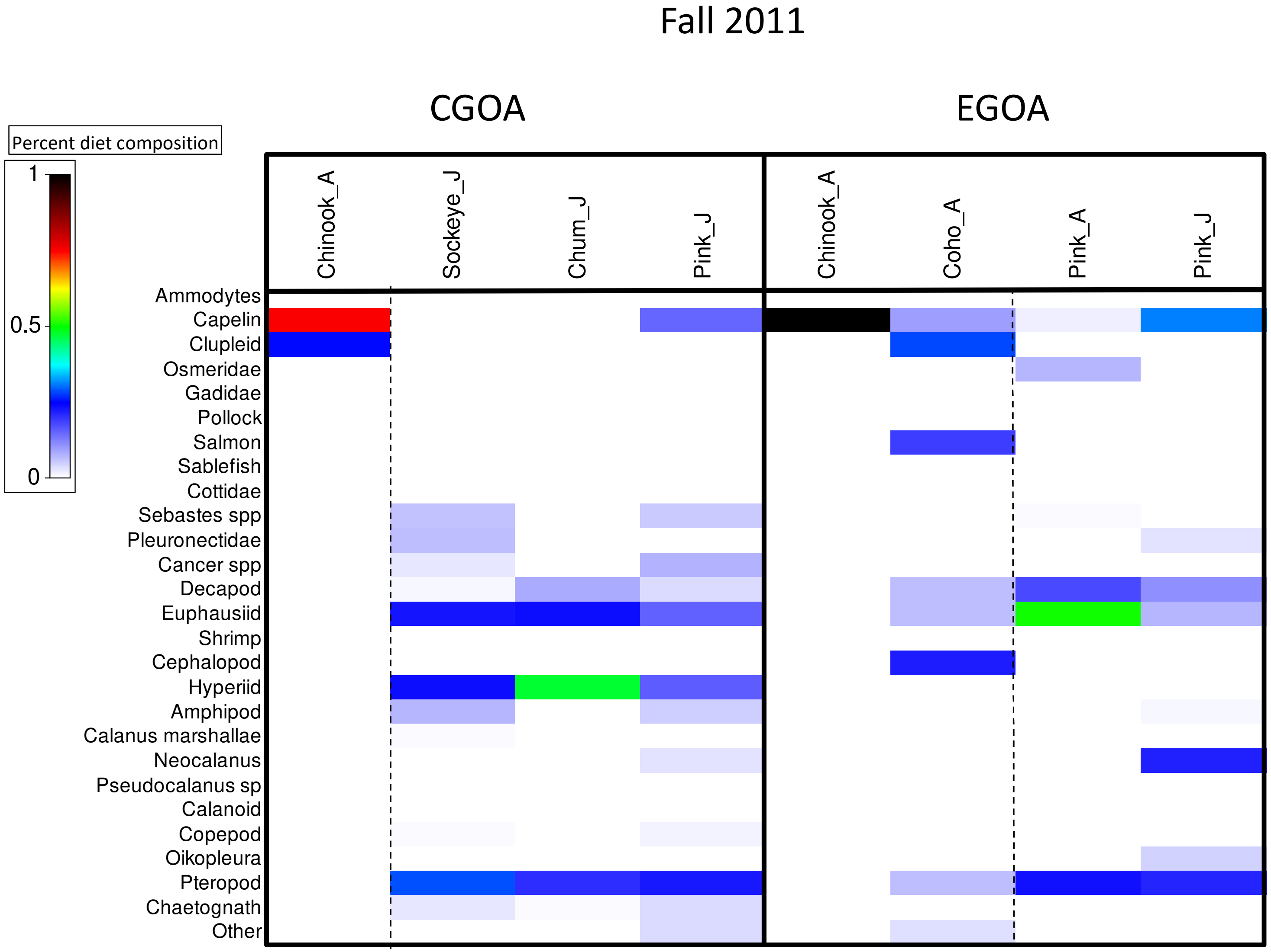


Figure 6. Interannual differences in stomach fullness (as a percentage of the salmon body weight; % BW) for juvenile (J) salmon with standard error bars in eastern Gulf of Alaska (EGOA; a) and central Gulf of Alaska (CGOA; b) during summer. Sample size listed below each bar, and different superscripts indicate significant differences (Kruskal-Wallis test P < 0.05).

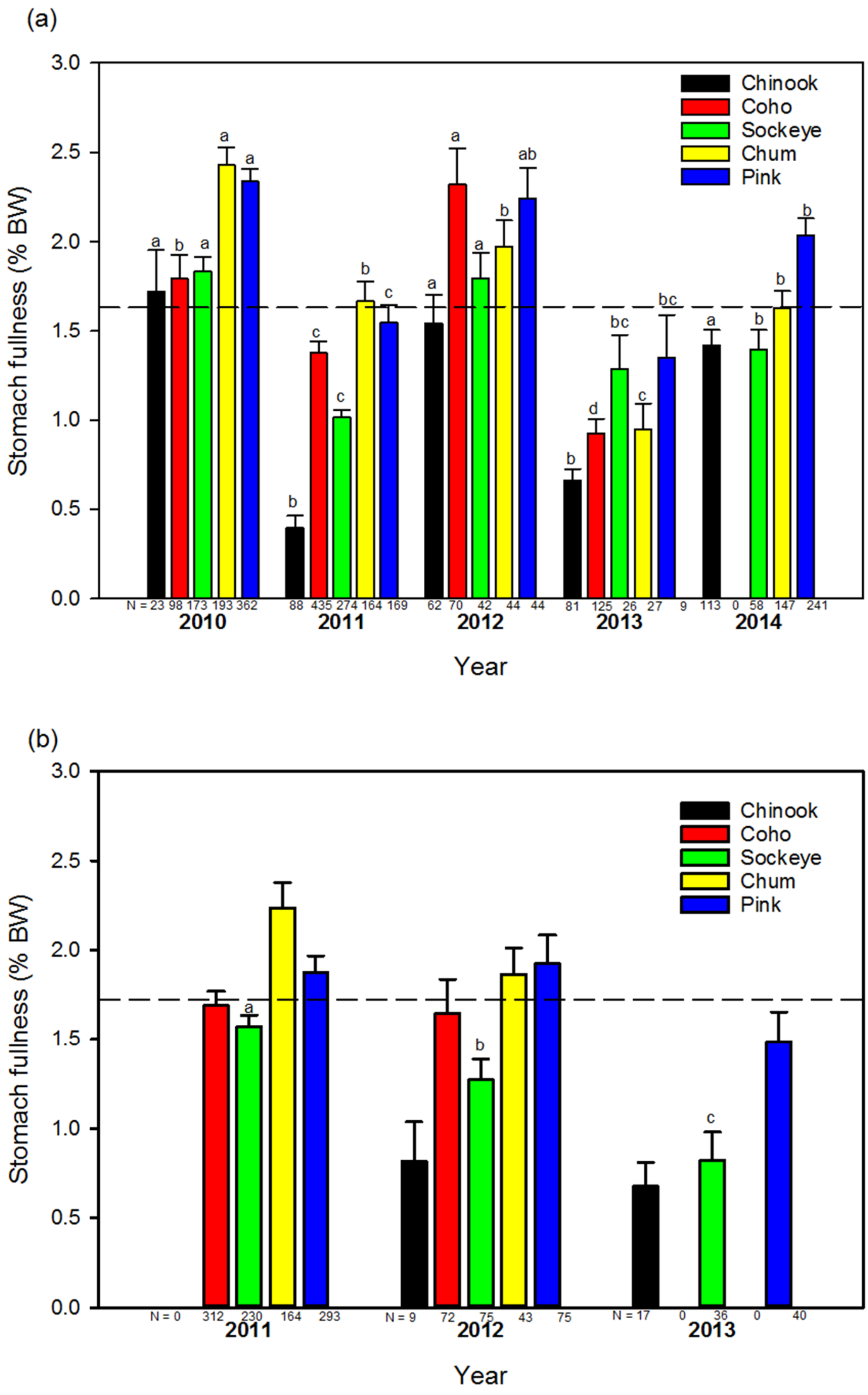


Fig. 7. Regional differences in stomach fullness (as a percentage of the salmon body weight; % BW) for juvenile (J) salmon with standard error bars for central Gulf of Alaska (CGOA; in yellow) and eastern Gulf of Alaska (EGOA; in green) in summer 2011 (a), summer 2012 (b), summer 2013 (c), and (d) fall 2011. Asterisk (*) denotes significant regional differences (CGOA x EGOA) for the juvenile salmon.

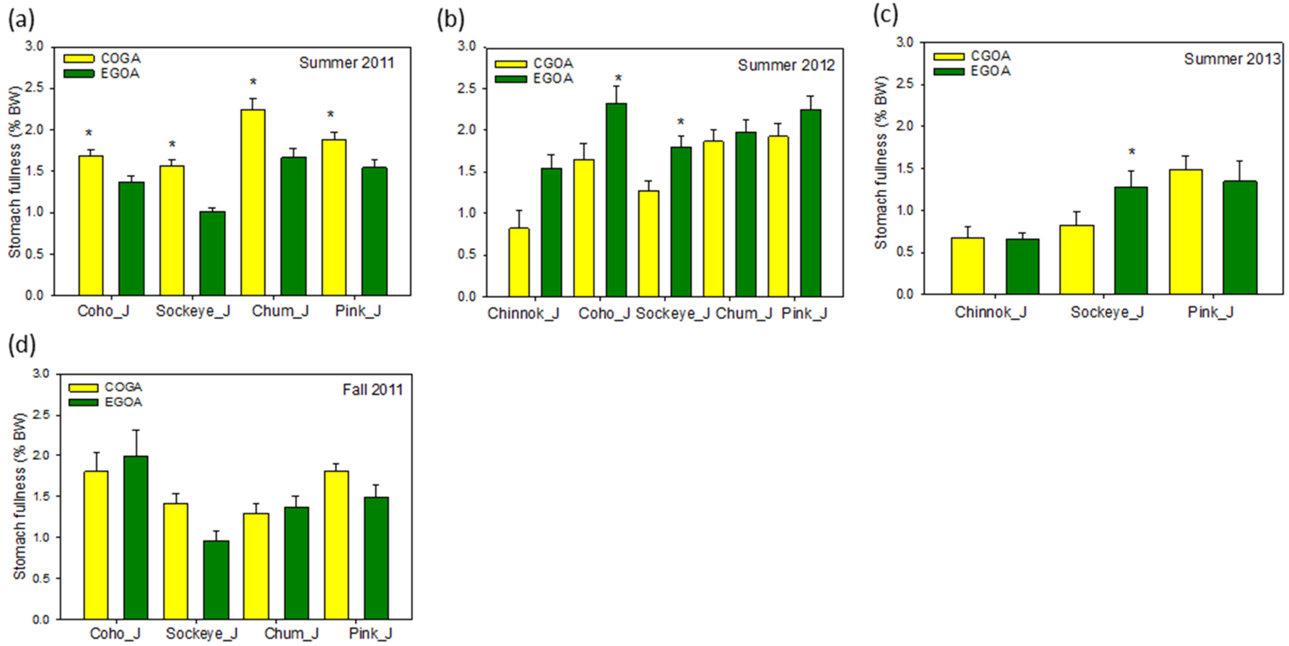


Fig. 8. Interannual differences in condition based on length-weight residuals for juvenile (J) salmon with standard error bars in eastern Gulf of Alaska (EGOA; a) and central Gulf of Alaska (CGOA; b) during summer. Sample size listed below each bar, and different superscripts indicate significant differences (Kruskal-Wallis test P < 0.05).

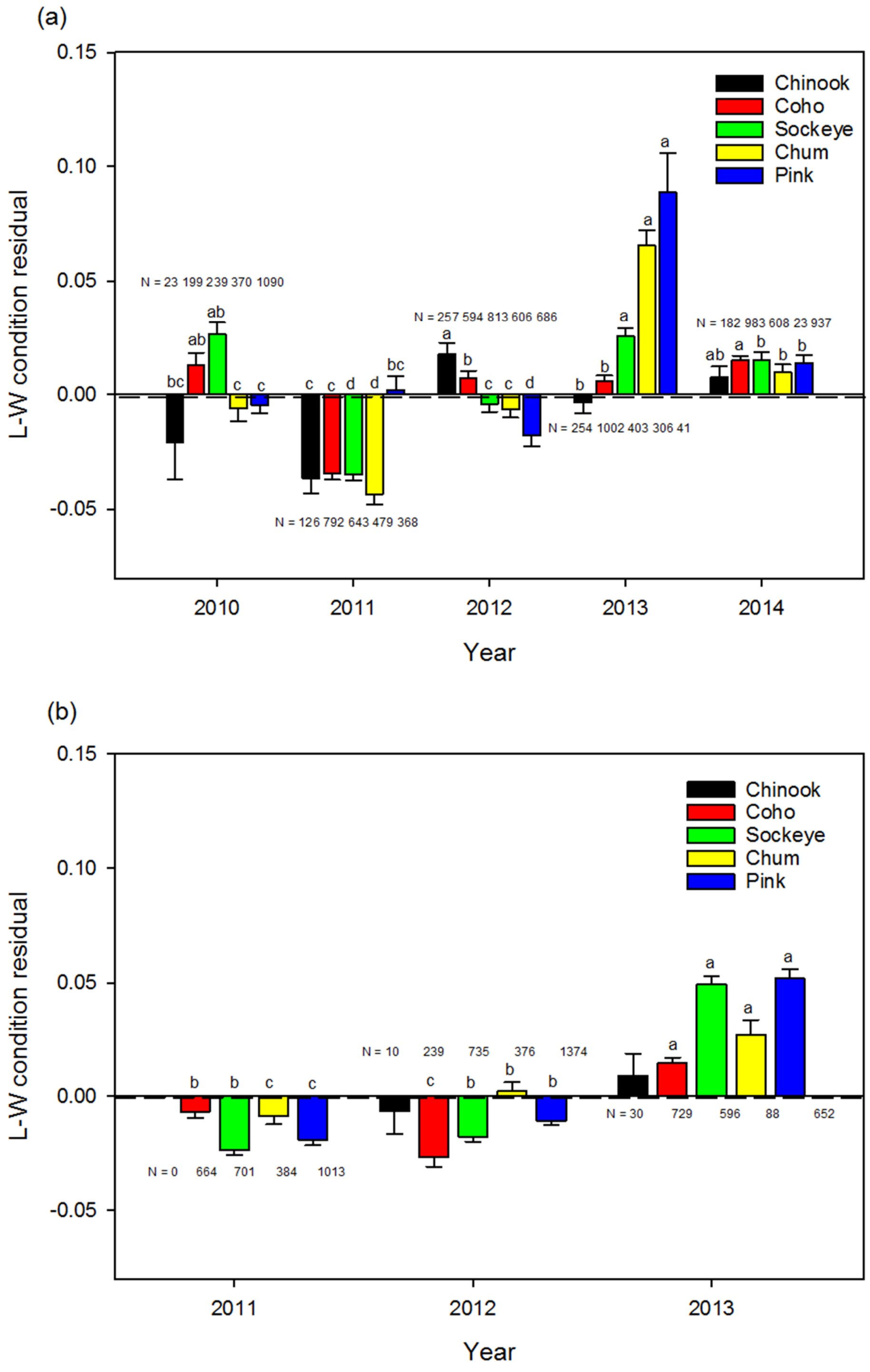


Fig. 9. Regional differences in condition based on length-weight residuals for juvenile (J) salmon with standard error bars for central Gulf of Alaska (CGOA; in yellow) and eastern Gulf of Alaska (EGOA; in green) in summer 2011 (a), summer 2012 (b), summer 2013 (c), and (d) fall 2011. Asterisk (*) denotes significant regional differences (CGOA x EGOA) for the juvenile salmon.