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Potential for resource competition between juvenile groundfishes and salmon in the eastern Gulf of Alaska

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17 ABSTRACT

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19 Ecologically important juvenile groundfishes and salmon co-occur in the upper water column of 20 the eastern Gulf of Alaska during the summer, a period when growth is critical to their survival. We quantified fine-scale spatial and trophic overlap of juvenile groundfishes (arrowtooth 21 flounder, Pacific cod, walleye pollock, and rockfish) and salmon (piscivorous coho and Chinook 22 as well as planktivorous pink, chum, and sockeye) to examine trophic structuring and potential 23 survival bottlenecks for these fishes in the Gulf of Alaska between 2010–14. In general, juvenile 24 groundfish catches had low coherence with station environmental variables with the exception 25 26 that across the years, rockfish were correlated with deeper station bottom depths. Juvenile salmon catches were correlated with station environmental variables such as shallower station 27 depth and when the pycnocline was closer to the surface, higher chlorophyll levels, and lower 28 salinities. The overall fish community in 2011 was disorganized compared to 2010 and 2012-29 30 2014 based on higher ordination stress and had poorer environmental correlations. Fine-scale spatial overlap among juvenile groundfishes and salmon populations was highest in 2011 and 31 32 2012 and lowest in 2013 and 2014. Juvenile rockfish had the least spatial overlap with the juvenile salmon due to their offshore distribution. Fine-scale diet overlap between juvenile 33 groundfishes and planktivorous juvenile salmon species ranged from 0% to 78%, was highest in 34 2012, and was lowest in 2011. Fine-scale diet overlap among juvenile groundfishes and 35 piscivorous juvenile salmon occurred but was typically lower than that with planktivorous 36 juvenile salmon. Additionally, juvenile groundfishes were directly consumed by juvenile salmon. 37 38 Neither the abundance nor stomach fullness of the juvenile planktivorous groundfishes or salmon 39 correlated with station-level zooplankton biomass in 2012–13, suggesting a lack of a resource

40	bottleneck for these planktivores in these 2 years. Juvenile groundfishes were less frequently
41	caught at stations where the highest catches of juvenile piscivorous salmon occurred, which
42	could be due to predation. Overall, during years when juvenile groundfishes survival was high,
43	juvenile salmon survival was also high, suggesting sufficient food resources in the GOA.
44	Alternatively, when food resources are low in the GOA, as seen in 2011, competition for
45	resources by groundfish and salmon was likely, and both appeared to be negatively impacted.
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- 47 Keywords: Juvenile Pacific salmon; Juvenile groundfishes, Gulf of Alaska, Competition,
- 48 Stomach fullness, Plankton biomass, Prey

49 1. Introduction

The Gulf of Alaska (GOA) is a rich and productive marine ecosystem that supports abundant 50 populations of groundfishes and salmon that produce some of the world's largest fisheries 51 (Mundy, 2005; Fissel et al., 2016). In the spring and summer, a number of key groundfishes 52 occupy the upper water column and coastal-shelf waters as larvae and juvenile fish before they 53 settle to the demersal environment of the GOA as adults (Doyle and Mier, 2016). Juvenile 54 55 salmon migrate into the GOA during spring and summer where they occupy the upper water column in coastal waters and out to the continental shelf (Groot and Margolis, 1998). 56 Understanding the potential interactions among juvenile groundfishes and salmon co-occurring 57 in the upper-water column during their critical growth phases could lead to a more 58 comprehensive approach to management of key fisheries in Alaska, such as modifying the 59 production and release of hatchery salmon in the North Pacific, where density-dependent effects 60 have been documented (Batten and Ruggerone, 2018; Ruggerone and Irvine, 2018). Indirect 61 interactions, such as competition for limited prey resources, are difficult to quantify. However, 62 63 the first steps in understanding potential competition is to determine the extent to which fish overlap spatially and trophically (Rand et al., 2012; Link and Auster, 2013). 64 Environmental conditions can influence productivity in the GOA during a critical feeding 65 period for larval and juvenile groundfishes, which in turn can affect their recruitment to the adult 66 population (Brodeur and Wilson, 1996; Mueter et al., 2007; Doyle et al., 2009; Atwood et al., 67 2010; Doyle and Mier, 2012). The primary goal of the GOA Integrated Ecosystem Research 68 Program (GOAIRP) has been to study the determinants of year-class strength for several 69 ecologically and commercially important groundfishes within the GOA in their early life stages. 70 Specifically, the groundfish we examined were: Atheresthes stomias (arrowtooth flounder, 71

72 hereafter referred to as AT_Flounder), Sebastes spp. (rockfish), Gadus macrocephalus (Pacific 73 cod, hereafter referred to as Pcod,) and Gadus chalcogrammus (walleye pollock, hereafter referred to as pollock). In the Gulf of Alaska, adult groundfish release their eggs in offshore 74 spawning locations and the larvae are then transported to nearshore nursery areas, where they 75 continue to feed and grow. The fish remain in nearshore nursery areas before they settle into 76 deeper demersal habitats in offshore waters (Bailey, 1989; Brodeur et al., 2002; Logerwell et al., 77 78 2005). As the larval fish grow into the juvenile stage, the larger fish will start to perform 79 ontogenetic based vertical diel migrations that are thought to be in responses to predator avoidance (Brodeur and Wilson, 1996; Hurst et al., 2009) and feed throughout the diel period 80 81 (Schabetsberger et al., 2000). Successful survival of the early life history stages is known to be affected by transport into suitable nursery habitats, feeding and growth conditions, and predator 82 avoidance, which are all thought to contribute to the establishment of the year-class strength of 83 84 these important fish in the GOA (Ciannelli et al., 2004; Siddon et al., 2013; Doyle et al., 2016; Moss et al., 2016). As such, it is important to understand the interannual variability and to 85 quantify the degree to which early life stages of groundfish interact and overlap with potential 86 competitors and/or predators such as juvenile salmon. 87

Juvenile pink (*Oncorhynchus gorbuscha*), chum (*O. gorbuscha*), and sockeye (*O. nerka*) salmon are primarily planktivorous salmon and the most numerous salmon in the GOA (Cooney and Brodeur, 1998; Landingham et al., 1998; Fisher et al., 2007), and interannual changes in their abundance as juveniles have been shown to be correlated (Stachura et al., 2013; Ruggerone and Connors, 2015; Ruggerone et al., 2016; Kohan et al., this issue). In years when juvenile planktivorous salmon abundance in the GOA was high, prey resources may become limited for all planktivores in the surface waters (Shiomoto et al., 1997), although some studies indicate that

food is not limited in the GOA (Auburn and Ignell, 1996; Boldt and Haldorson, 2002). Still other 95 studies have shown that food competition is more prevalent among adult predators (Springer and 96 van Vliet, 2014; Ruggerone et al., 2016). Juvenile groundfishes also have substantial interannual 97 variability in their abundance. While the impact that high numbers of juvenile groundfishes can 98 have on localized prey resources has been documented in the southeast Bering Sea (Ciannelli et 99 al., 2004), juvenile groundfishes are a small fraction of the body sizes of the juvenile 100 101 planktivorous salmon and therefore consume relatively less prey. While changes in 102 environmental conditions have been shown to affect the success of young groundfishes (Doyle et al., 2009; Moss et al., 2016; Coffin and Mueter, 2016), it is thought to be more from 103 104 environmental limitations of prey production versus the potential for top-down over-grazing (Kendall et al., 1987). Top-down overgrazing may occur with the larger juvenile and adult 105 106 planktivorous salmon, albeit the salmon are also affected by bottom-up processes of zooplankton 107 production (Ruggerone and Nielsen, 2004; Springer and van Vliet, 2014; Kohan et al., this issue). 108 There is variability in how these juvenile groundfishes distribute across the GOA. In general, 109

pollock tend to be distributed consistently inshore to offshore (Doyle et al., 2016) but exhibit
interannual variability longitudinally across the GOA (Brodeur and Wilson, 1996; Moss et al.,
2016; McGowan et al., this issue). Juvenile Pcod are principally found in the central GOA, and
lower numbers are found in the eastern GOA (EGOA). AT_Flounder are principally found in the
EGOA (Spies and Palsson, 2018). Juvenile rockfishes are distributed across the GOA, especially
in the offshore waters (Doyle et al., 2016; Siddon et al., this issue). As pelagic juveniles, these
groundfishes are primarily planktivorous and feed on copepods, early stages of euphausiids, and

117 fish larvae (prey listed in decreasing order of importance; Rose, 1980; Wilson et al., 2011;

118 Strasburger et al., 2014; Moss et al., 2016; Debenham et al., this issue).

Similar to juvenile groundfishes, the early marine feeding period is also critical to the growth 119 and survival of juvenile salmon (Fisher and Pearcy, 1988; Pearcy, 1992; Orsi et al., 2014; Daly 120 and Brodeur, 2015). Juvenile salmon generally occupy the upper water column within coastal 121 waters (Fisher et al., 2007). Juvenile Oncorhynchus tshawystscha (Chinook salmon) are typically 122 123 most abundant closest to shore, juvenile O. kisutch (coho salmon) are found in the nearshore 124 waters out to deeper depths. Juvenile chum, pink, and sockeye salmon are abundant in GOA waters that are deeper with lower salinity (Fisher et al., 2007). Juvenile Chinook and coho 125 126 salmon prey upon larval and juvenile fishes (including juvenile groundfishes), squids, decapods, and adult euphausiids (Landingham et al., 1998; Brodeur et al., 2007; Weitkamp and Sturdevant, 127 2008; Johnson and Schindler, 2009; Hertz et al., 2015; Daly et al., this issue). In contrast, 128 129 juvenile chum, pink, and sockeye salmon are highly planktivorous, eating copepods, pteropods, early-stage euphausiids, amphipods, and fish eggs and larvae (Landingham et al., 1998; 130 Kaeriyama et al., 2004; Armstrong et al., 2005, 2008; Brodeur et al., 2007; Daly et al., this 131 issue). 132

In wild fish populations, the abundance, size, health, and age of the adult population can determine fluctuations in annual spawning biomass of eggs and larvae (Berkeley et al., 2004; Marshall et al., 2008; Hixon et al., 2014). For wild salmon populations, annual fluctuations in eggs and fry occur, but each year this number is augmented by hatcheries that release older stages of fish. On average, 67 million hatchery salmon smolts are released into Alaska waters each year (Stopha, 2017) in addition to those from the wild populations. With the consistent annual release of high numbers of planktivorous and piscivorous salmon into the GOA 140 regardless of environmental conditions, competition and predation may potentially occur 141 between juvenile salmon and groundfishes. Predation and competition for resources would occur only when competitors, either interspecific or intraspecific, rely on the same limited resource and 142 overlap in time and space. Our goal was to determine if there were trophic structuring and 143 survival bottlenecks of juvenile groundfishes with juvenile salmon as both competitors and 144 predators. To accomplish this, fine-scale spatial and dietary overlap among juvenile groundfishes 145 and salmon in the EGOA was quantified. Additionally, we examined the frequency of juvenile 146 147 salmon predation on juvenile groundfishes and whether food resources were limited where high numbers of juvenile groundfishes or salmon were caught. 148

150 2. Methods

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152 2.1. Field and laboratory sampling

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154 Annual fisheries oceanographic surveys were conducted by the Auke Bay Laboratory, Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration, in the 155 156 coastal regions of the EGOA during the summers of 2010-2014. Juvenile salmon and groundfishes were captured in 2010 using a Nordic trawl and in 2011-2014 with a Cantrawl, both 157 with a 1.2 mm mesh codend liner and fished at the surface (see Straburger et al. (2018) for 158 sampling details). Daytime tows were made at stations along transects (Fig. 1) for 30 minutes at 159 approximately 3.3–7.0 km h⁻¹ with the net towed at or near the surface to an average of 19-m 160 depth. Sampling station locations and number of stations sampled varied slightly from year to 161 year, and the sampling map (Fig. 1) is a generalized map of the station locations that were 162 sampled from 2010-2014. Juvenile salmon and groundfishes collected in the trawl were 163 identified, counted, weighed, and measured (up to 50 per station per species). A maximum of 10 164 juvenile groundfishes and salmon per species from each sampling station were frozen at sea 165 166 (except for juvenile Chinook salmon, which were all retained) and brought back to the laboratory for diet analysis 167

On each survey, a Seabird Electronics CTD was deployed throughout the water column
to determine temperature (°C) and salinity at various depths (m). Water samples were taken
using 5-L Niskin bottles to measure chlorophyll-*a* every 10 m from the surface to 50 m.
Zooplankton samples were taken with a 60-cm bongo net (505 μm mesh) towed obliquely from
the surface to 200 m depth or within 20 m of the bottom, at ~ 2 knots. A calibrated General

samples were preserved in 10% formalin-seawater solution for later analysis in the laboratory. 174 The mean temperature, salinity, and chlorophyll-a were calculated from the top 20 m at 175 each station. In the lab, chlorophyll-a samples were processed using standard fluorometric 176 analysis (Parsons et al. 1984). Station pycnocline depths were estimated using the station CTD 177 cast data based on the depth where the density gradient was at a maximum (Thomson and Fine 178 179 2003). The depth of the layer of water above where the density gradient was at a maximum, 180 known as the pycnocline depth, was included as an environmental variable as a shallow pycnocline in the North Pacific has been shown to be associated with increased primarily 181 182 production that would support food resources important to larval and juvenile fishes (Eisner et al., 2016). 183

Oceanics flowmeter was used in the bongo nets to determine the volume of water filtered, and

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184 In the laboratory, individual fish were thawed, measured (nearest mm), and weighed 185 (nearest mg). Fish stomachs were removed, weighed full, emptied of contents, and weighed empty. Stomach contents were identified to the lowest possible taxonomic category using a 186 dissecting scope and taxa were weighed (nearest mg). Taxonomic categories of the diets were 187 grouped as follows and were the top prey for both juvenile salmon and groundfishes: capelin 188 (Mallotus villosus), Sebastes spp., flatfishes, fishes (all other rarely consumed taxa), 189 cephalopods, copepods, decapods, euphausiids, hyperiid amphipods, amphipods (non-hyperiid), 190 pteropods, shrimp, and "other" which were the rarely consumed taxa (barnacle larvae, 191 chaetognaths, eggs, insects, isopods, gelatinous zooplankton, mysids, tunicates, polychaetes). 192 Percent stomach fullness was calculated as the (total prey weight) / (predator's weight – total 193 prey weight). The biomass of zooplankton biomass available at each station in 2012-2013 only, 194 and was calculated from the zooplankton samples that were split using a Folsom splitter to obtain 195

196 a subsample of \geq 200 individuals. Detailed species composition was determined microscopically, and zooplankton were identified and counted to the lowest possible taxonomic level including 197 sex and stage, when applicable (Kimmel et al., 2018). The zooplankton were summed into the 198 same taxonomic groupings as the juvenile groundfishes and salmon diets. Prey counts were 199 converted to prey wet weight using both literature and unpublished values (E. Fergusson, 200 personal communication) and the total station biomass of prev was calculated as the sum total of 201 202 the estimated wet weights per volume of water filtered. Fish larvae were excluded from the 203 biomass, and zooplankton samples were only available from 2012-13.

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205 2.2. Juvenile groundfishes and salmon annual spatial patterns with environmental overlay
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To determine catch per unit effort (CPUE) for each species, counts of juvenile 207 208 groundfishes and salmon at each station were divided by the area trawled (km²), which was estimated as the product of the width of the net spread (km) and the distance the net was towed 209 (km). General patterns in CPUE by year and species were plotted for each station, with the 210 stations ranked by the bottom depth (m) from shallow to deep to display spatial patterns. We also 211 analyzed the spatial organization of the fish CPUE at each sampled station using non-metric 212 multidimensional scaling (NMDS) ordination plots constructed from Bray-Curtis dissimilarity 213 matrices by year. NMDS ordination plots with generated stress values < 0.15 were considered 214 ecologically significant and interpretable (Clark 1993). Environmental conditions variables 215 measured at each station were overlain as vectors in correlation (with corresponding R² value) to 216 the fish CPUE. Station environmental variables of bottom depth, pycnocline depth, mean salinity 217 (20 m), mean temperature (20 m), and mean chlorophyll-a (20 m) were utilized. The average 218

219	environmental variable from the top 20 meters was used because this was the depth range of the
220	trawl net utilized to collect the juvenile groundfishes and salmon. Environmental variables were
221	standardized and the CPUE values were transformed (ln(CPUE +1)). The NMDS analysis was
222	completed using the vegan, mass, permute, labdsv packages in R (R Core Team 2019).

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224 2.3. Statistical analysis of spatial overlap

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226 To test if juvenile groundfishes and salmon had different fine-scale spatial distribution patterns, we used the Cramér-von Mises non-parametric test (Syrjala, 1996). The test accounts 227 228 for spatial differences in population abundance, but is insensitive to the differences in abundance of each population and was chosen because of the observed population size differences between 229 the fish. For the analysis, a single test statistic Ψ was calculated for each year between the CPUE 230 231 of each species of juvenile salmon and each species of groundfish. The test is calculated as the square of the differences between the cumulative distributions of the two groups, summed over 232 all the sampled stations, and it is sensitive to differences in the way groups are distributed across 233 the study area regardless of differences in abundance. A p-value was computed based on 9999 234 random permutations of the data using the Syrjala routine in the ecespa package in R (R Core 235 Team 2019). 236

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238 2.4. Juvenile groundfishes and salmon diet overlap and community analysis

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240 To identify whether juvenile groundfishes and salmon had diet composition differences241 by weight of prey eaten, we summarized the diet composition for each individual species at each

sampling station by taxonomic groupings listed in the diet methods (see above), then averaged
the diets for each species at each station. Trophic relationships were analyzed by calculating the
degree of diet similarity, or diet overlap, between each pairwise species of juvenile groundfishes
and salmon at all sampling stations when data were available, using the Percent Similarity Index
(PSI):

$$\mathsf{PSI} = \left(1 - 0.5 \sum_{i=1}^{n} \left| p_{ik} - p_{jk} \right| \right) \times 100$$

where p_{ik} is the proportion by weight of prey item *k* found in the diet of predator *i*, p_{jk} is the proportion by weight of prey item *k* found in the diet of predator *j*, and n is the total number of prey categories (Wallace and Ramsay, 1983).

To display the diet community of the planktivorous groundfishes relative to the juvenile salmon, we utilized NMDS ordinations constructed from Bray-Curtis dissimilarity matrices to plot the station diet composition for each planktivorous salmon and groundfishes by year. Differences in diet composition were tested using a Multi-Response Permutation Procedure (MRPP; McCune and Mefford, 1999) which is a multivariate equivalent to analysis of variance (ANOVA) based on a matrix of pairwise Bray-Curtis similarity coefficients, and the significance is determined by permutation where P < 0.05.

The prevalence of juvenile salmon consuming juvenile groundfishes was calculated as the percent frequency of occurrence (%FO) that the prey occurred in station-averaged diets for each juvenile salmon species by year. Fish prey were grouped by taxonomic family and included: cod (pollock and Pcod), rockfish, and flatfish (including AT_Flounder). Fish prey were primarily identified as "unidentified fish" due to the digestion of identifiable characteristics; therefore, %FO of juvenile groundfishes in juvenile salmon diets was a minimal estimate of
juvenile salmon predation on juvenile groundfishes.

To look for fine-scale prey resource bottlenecks, we examined the relationship between 266 prey biomass and the abundance of predators by testing if the station prey biomass changed 267 relative to stations grouped into predator CPUE quartiles. Juvenile groundfish were tested 268 separately from the juvenile salmon. We expected prey resources not to differ relative to fish 269 270 abundances. Prey resources for both juvenile groundfishes and planktivorous juvenile salmon 271 were measured as the station biomass of zooplankton taxa, and the prey resources for the piscivorous salmon were measured as the total combined CPUE of juvenile groundfishes at a 272 273 station. We utilized three predator groups as follows: the sum total station CPUE of juvenile groundfishes categorized into four quartiles (Q1-4), the sum total station CPUE of juvenile 274 planktivorous salmon categorized into four quartiles (Q1-4), and the sum total station CPUE of 275 276 the juvenile piscivorous salmon, which were grouped into three quartiles (Q1-2, 3, 4). Three quartiles were used in the case of the juvenile piscivorous salmon because ~50% of the stations 277 did not have any juvenile salmon; therefore, the first two quartiles were merged. We then tested 278 if there were statistically different amounts of prey biomass at stations for each quartile of 279 juvenile groundfishes (Q1-4) or salmon (Q1-2, 3, 4) with the nonparametric Kruskal-Wallis test 280 for each year with significance of P < 0.05. The nonparametric test was utilized due to the lack of 281 normally distributed data. 282

To identify whether there were any prey resource bottlenecks, we tested if there was a relationship between prey biomass and the percent stomach fullness of juvenile groundfishes or salmon as it related to their station prey resources (zooplankton biomass for the planktivores, and CPUE of groundfishes for the piscivores) using linear regression analysis. We also tested if the

287	station average percent stomach fullness was affected by the abundance of potential competitors.
288	Potential competitors for juvenile groundfishes were the CPUE of the planktivorous salmon, and
289	we did not have available potential competitor data for the piscivorous salmon. We expected
290	stomach fullness not to change, dependent upon the amount of prey or abundances of potential
291	competitors. Tests were done at the station level for each year using linear regression analysis
292	with significance of $P < 0.05$.
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295	3. Results
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297	3.1. Juvenile groundfishes and salmon annual spatial patterns with environmental overlay
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299	Total catches of juvenile groundfishes and salmon were among the highest in 2010 and
300	lowest in 2011 (Fig. 2). Of the groundfish taxa, juvenile rockfish and pollock were caught in the
301	highest numbers, especially at deeper bottom depths (Fig. 2-3). There were high catches of
302	rockfishes at many of the sampling stations in 2010 and especially 2014 (Fig. 2). Juvenile
303	pollock were caught at ~75% of the sampled stations in 2013, dominating the catch relative to
304	the other juvenile fishes (groundfishes and salmon). Pollock were also caught in high abundance
305	in 2014, but were absent in 2011 (Fig. 2). Pcod were typically caught in low numbers at a few
306	stations (or none in 2011), and were caught in their highest frequency in 2014. AT_Flounder
307	were caught in EGOA in relatively low numbers, except in 2010 and 2012 (Fig. 2). For the
308	juvenile salmon, pink salmon were the dominate species caught, especially in 2010, and were
309	caught notably reduced in numbers in 2013. Juvenile Chinook salmon were caught in the lowest

numbers of the juvenile salmon, and at typically < 30% of the stations in any given year (Fig. 2).
Juvenile coho salmon were caught at 86% of the sampled stations in 2011, and were caught in
relatively high numbers in 2013.

For the ordination plots, there were 393 sampling stations where fish were caught and the 313 full suite of environmental data was available for analysis. Overall, the stations with the highest 314 catches of juvenile groundfishes or salmon did not overlap, as can be seen by the separation 315 316 between the two groups of fishes in the annual NMDS ordination plots (Fig 3). Juvenile 317 groundfishes were associated along the positive side of NMDS axis 1, and the juvenile salmon on the negative side (Fig. 3). The environmental variable that consistently showed the highest 318 319 correlation with the fish community was the bottom depth of the station (Table 1), which was aligned along the positive axis 1. In all years except 2011, the correlation of depth was greater 320 than $R^2 = 0.50$ (Table 1). In 2014, there was a negative correlation with station temperature for 321 Pcod and pollock ($R^2 = -0.30$). AT Flounder were commonly associated with higher salinity 322 values (Fig. 3). Juvenile salmon abundance was correlated with lower salinity and higher 323 chlorophyll-a levels, and rockfishes were typically associated with greater bottom and 324 pycnocline depths. The NMDS plots for each year had organized structure with low to moderate 325 stress (< 15.0) for the first two axes, except for 2011. In 2011, the stress was higher than the 326 other years at 18.6, indicating a poorly organized random fish community with low 327 328 environmental correlation (Table 1).

In 2011, AT_Flounder and rockfishes, the only juvenile groundfishes present in sufficient numbers to test, overlapped spatially with all the juvenile salmon. In 2012, when there were sufficient numbers of all juvenile groundfishes and salmon present for analysis, there was high spatial overlap (Cramér-von Mises; P < 0.05; Table 2; dark gray cells). However, in 2013 and 2014 spatial overlap was substantially lower (Cramér-von Mises; P < 0.05; Table 2; dark gray
cells). Overall, juvenile rockfishes had the lowest spatial overlap with the juvenile salmon except
in 2011 and 2012. For the juvenile salmon, only the chum and pink salmon were consistently in
significant spatial overlap with each juvenile groundfish, except for rockfishes (Cramér-von
Mises; P < 0.05; Table 2; dark gray cells).

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339 *3.2. Juvenile groundfishes and salmon diet overlap and diet composition community*

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Diets of juvenile groundfishes and juvenile planktivorous salmon were similar when fish 341 342 were caught concurrently. The diet overlap based on the average Percent Similarity Index (PSI) ranged from 0% to a maximum of 66.6% (Fig. 4; Table 2). Diet overlaps between the juvenile 343 groundfishes and piscivorous juvenile salmon were lower than those for juvenile planktivorous 344 345 salmon (Fig. 4). Average diet overlap in 2011 was relatively low between juvenile groundfishes and salmon, except at one station between pink salmon and AT_Flounder (Table 2). In 2010, 346 average diet overlap was relatively high between the juvenile rockfishes and planktivorous 347 salmon, yet these populations were not in significant spatial overlap. AT_Flounder consistently 348 had some diet overlap with the juvenile planktivorous salmon, and pink salmon had some of the 349 highest average diet overlap with all four juvenile groundfishes (Fig. 4). Overall, the highest 350 spatial and average trophic overlap occurred in 2012 between the juvenile groundfishes and 351 salmon (Table 2). 352

The diet composition community of the juvenile groundfishes were different from those of the juvenile planktivorous salmon primarily due to higher amounts of copepods being eaten by the groundfishes relative to the salmon. The diet ordination plots showed that the juvenile 356 groundfish diets were grouped on the negative side of NMDS axis 1, and the juvenile planktivorous juvenile salmon were on the positive side, illustrating diet separation between 357 these fish groups. The exception was 2010 when rockfish diets overlapped in ordination space 358 with the salmon (Fig. 5). However, only the ordination in 2010 had a stress of < 0.1; the stress 359 for the other years was > 0.2 suggesting low community structure as the diets were highly 360 variable between stations. In 2013 and 2014, almost all juvenile groundfishes ate different prev 361 362 types and amounts than juvenile planktivorous salmon, and all comparisons showed highly significant diet differences (Fig. 5; MRPP; P < 0.001). Rockfish diets were not significantly 363 different from chum or pink salmon diets in 2010, nor were AT Flounder from chum salmon in 364 365 2011 (Fig. 5; MRPP; P > 0.05). The diet community in 2012 had the least separation in diets between the juvenile groundfishes and salmon, yet it still showed significantly different diets 366 (MRPP; P < 0.05). As there was low diet overlap between the juvenile piscivorous salmon and 367 368 groundfishes, we omitted them from the NMDS plots.

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370 *3.3. Juvenile salmon predation on juvenile groundfishes*

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Coho and Chinook salmon had higher frequency of occurrence (%FO) of juvenile groundfishes in their diets relative to the planktivorous salmon, and the frequency varied from year to year (Table 3). The juvenile groundfishes eaten by salmon in highest FO were rockfish in 2010 when 20% to 68.4% of the juvenile salmon diets had juvenile rockfishes in them, which was a year in which rockfishes were not in spatial overlap with the salmon (Table 2), but were caught in high numbers (Fig. 2). Juvenile Chinook, coho, and sockeye salmon regularly had rockfish in their diets in all other years (Table 3), again, with low spatial overlap between the populations (Table 2). Flatfish were eaten frequently by juvenile Chinook salmon in 2012. Both
cod were infrequently eaten in any given year, but were consumed slightly more frequently by
juvenile coho salmon than the other salmon (Table 3).

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383 *3.4. Relation between prey amount and predator CPUE*

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385 Generally, the number of zooplankton available to planktivores was lower in 2013 386 relative to 2012 (Fig. 6a-d). In looking for potential prey-limitation bottlenecks, we examined the relation between the available zooplankton biomass relative to the station CPUE of juvenile 387 388 groundfishes or planktivorous salmon grouped into quartiles for the years 2012 and 2013. In 2013, zooplankton biomass was lowest for the 25% of stations with the highest CPUE of juvenile 389 groundfishes, and in 2012, zooplankton was highest for the 25% of stations with the highest 390 391 CPUE of juvenile planktivorous salmon; however, neither of these relationships were significantly lower (Fig. 6a-d; Kruskal-Wallis test, P > 0.05). In 2013, there were higher amounts 392 of zooplankton biomass at the higher CPUE quantile of juvenile planktivorous salmon, although 393 not significantly more (Fig. 6d; Kruskal-Wallis test, P > 0.05). 394 Lastly, in all five years of the study, there were higher abundances of juvenile 395 groundfishes at stations with the fewest amount of juvenile piscivorous salmon (Fig. 7 a-f; 396 Kruskal-Wallis test, P < 0.05). There were significantly more juvenile groundfishes at the 397 stations with the least amount of piscivores in 2010 and 2011 and there was the least amount of 398 juvenile groundfishes at the stations with the highest amount of piscivores in 2012 (Kruskal-399

- 400 Wallis test, P < 0.05). In 2014, there were no differences between the quartiles. In summary,
- 401 based on the available biomass of zooplankton, there did not appear to be any indication that

planktivorous juvenile fish grazed down the available prey where they were most abundant.
However, there were significantly more juvenile groundfishes in 2010-2012 when there were
fewer numbers of juvenile piscivorous salmon, possibly due to predation.

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406 *3.5. Predator stomach fullness relative to prey or potential competitors*

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408 We did not find significant relationships between any of the juvenile groundfishes' 409 average station stomach fullness and their food based on the station zooplankton biomass in either 2012 or 2013 (P > 0.05). In 2012, juvenile rockfish stomachs were significantly less full 410 when there was a higher CPUE of planktivores (P=0.02, $R^2=0.299$), suggesting a decrease in 411 prey resources for rockfish when there were many juvenile planktivorous salmon co-occurring. 412 In 2014, juvenile Pcod and pollock stomach fullness was significantly higher when there were 413 more planktivores at a station (P = 0.03; R²= 0.358, P = 0.03, R²= 0.078, respectively), 414 suggesting that there was sufficient prey for these groundfishes even at high abundances of 415 juvenile salmon. Lastly, there were no significant relationships between the station average 416 stomach fullness of the juvenile piscivorous salmon and the sum total CPUE of all juvenile 417 groundfishes in any of the study years (P > 0.05). 418

420 4. Discussion

421

422 *4.1. Interannual CPUE and spatial overlap*

423

Our study documents that juvenile, groundfishes and salmon have fine-scale spatial, 424 425 temporal, and trophic overlap in the GOA and therefore these abundant juvenile fish have the 426 potential to impact one another during periods of low prey abundance and/or from top-down predation. We also identify that these interactions varied in intensity from year to year. Juvenile 427 groundfishes and salmon exhibit different spatial differences and the correlations of 428 environmental variables with the CPUE of juvenile groundfishes and salmon during our study 429 430 were similar to those found in other studies (Morris et al., 2007; Orsi et al., 2007; Weitkamp et 431 al., 2011; Doyle and Mier, 2016). The highest abundances of juvenile groundfishes were caught farther offshore, which had deeper pycnocline depths and warmer temperatures. Generally, the 432 juvenile salmon were caught in nearshore waters of the GOA relative to the juvenile 433 groundfishes, and the planktivorous salmon were caught together in less saline waters (this 434 study; Fisher et al., 2007; Echave et al., 2012). Juvenile coho and Chinook salmon were usually 435 436 caught together but coho salmon were also caught farther offshore (but not as far as the juvenile 437 groundfishes), and both were positively correlated with chlorophyll-a levels in some years. Juvenile Chinook and coho salmon along the Washington and Oregon coast and Bering Sea have 438 also been shown to have spatial distributions influenced by increased levels of chlorophyll-a, 439 most likely due to the increased levels of prey associated with higher primary production (Pearcy 440 and Fisher, 1990; Cieciel et al., 2009). Lastly, the 2011 overall fish community structure based 441 on the ordination had the highest stress value, indicating a poorly organized community and very 442 poor correlations to environmental variables. Ecologically, 2011 was quite different from other 443 years in the GOA, with low productivity (Waite and Meuter, 2013; Moss et al., 2016; Strom et 444

al., 2016), and the high stress in the community ordination indicated an unusual lack of a spatialstructure of the fish community.

Juvenile groundfishes and salmon were often caught together in fine-scale spatial 447 overlap. Other studies have noted general spatial overlap between these fishes during summer 448 within the GOA (Mecklenburg et al., 2002; Echave et al., 2012; Martinson et al., 2012; Moss et 449 al., 2016; McGowan et al., this issue). Our study indicated interannual variability in intensity of 450 451 fine-scale spatial overlap between juvenile groundfishes and salmon, with years of higher or 452 lower spatial overlap and therefore opportunity for resource competition. Few studies have documented the interannual changes in spatial overlap between potential competitors (Brodeur et 453 454 al., 2014). In the Mediterranean Sea, the spatial overlap between two fish populations increased in years with increased numbers of one fish, sardines, but decreased in years with increased 455 numbers of the other fish, anchovies (Barra et al., 2015). In 2013, there were consistent high 456 457 catches of pollock across the EGOA, yet low spatial overlap occurred with the salmon, and in 2012, there were good catches of both groundfishes and salmon, and the highest spatial overlap 458 between fish. Further investigation of the interannual variability in the strength of fine-scale 459 spatial (and diet) overlap would be of interest due to the potential for competition, especially in 460 years of low productivity when resources are restricted. There also could be a seasonal 461 component to the amount of spatial and diet overlap between fish populations, as identified in 462 Kemp et al. (2013), which warrants further study. Annual variability in the degree of fine-scale 463 spatial overlap of populations is important to our understanding the potential for increased or 464 decreased competition and population structures within the GOA. 465

466

467 4.2. Fine-scale diet overlap and predation between juvenile groundfishes and salmon468

469 When juvenile groundfishes and salmon were caught together, there was, in general, 470 moderate diet overlap. While our study focused on fine-scale diet overlap between juvenile groundfishes and salmon, diet overlap between juvenile non-salmonid fishes in Alaska waters 471 has been studied but on a limited basis. The diet overlap between pollock and herring 472 (Sturdevant et al., 2001), pollock and Pcod (Strasburger et al., 2014), and pollock and capelin 473 (Wilson et al., 2006) has been shown to occur. Diet overlap between juvenile pink salmon and 474 475 pollock (as well as jellyfish) has been shown to be low due to the high amounts of larvaceans 476 eaten by pink salmon relative to pollock, although the comparisons were made using diets from two different years (Purcell and Sturdevant, 2001). Monthly diet overlap analysis of juvenile 477 478 Pcod, pollock, pink, sockeye, and chum salmon revealed that these fishes had moderate to significant levels of diet overlap (Sturdevant and Willette, 1999). The diet overlap among salmon 479 480 has been well studied in the North Pacific, with the highest overlap being between the 481 planktivorous salmon and the piscivorous salmon (Sturdevant et al., 1997; Davis et al., 2004; Ruggerone and Nielsen, 2004; Blikshteyn, 2005; Brodeur et al., 2007; Weitkamp and Sturdevant, 482 483 2008; Daly et al., this issue). Overall, our study confirms, along with other studies, that juvenile salmon and groundfishes do have some similarities in their diets. 484

The highest rates of diet overlap in our analysis occurred primarily due to the high planktivory rates of juvenile groundfishes and juvenile pink, chum, and sockeye salmon. Finescale diet overlap between the planktivores during the study period was typically between 20– 50% of their diets being comprised of similar taxa, and there was modest interannual variability. Diets can vary even over small distances due to changes in the prey community, and diets of fishes caught at the same location and time usually have the most diet similarity (Weitkamp and Sturdevant, 2008). Even though we analyzed the spatial and diet overlap between the fish at the 492 station level, the finest spatial scale possible, each trawl still sampled several kilometers of
493 water. While juvenile groundfish and salmon were consistently caught together during the
494 sampling effort, they may not actually be overlapping in the water column or even near each
495 other along the transect, reducing competition of common prey resources.

Not only did groundfishes and salmon show some spatial and trophic overlap, but also 496 the juvenile groundfishes were directly consumed by juvenile salmon. Of the groundfishes, 497 498 juvenile rockfishes were most frequently found in salmon stomachs, particularly in 2010, when 499 our analysis showed low spatial overlap between juvenile salmon and rockfishes. Juvenile Chinook and coho salmon also frequently consumed rockfishes in 2011, when these groups 500 501 exhibited significant spatial overlap. Both cods were eaten with low frequency by the juvenile salmon (< 17%) in all years, while flatfishes were eaten just in 2012–13. Overall, rockfishes 502 503 were the most frequently-eaten groundfish taxa by the juvenile salmon, yet had the least spatial 504 overlap. Juvenile rockfish are darkly pigmented, and the salmon may be highly selective in their consumption of rockfishes (Schabetsberger et al., 2005) even with low spatial overlap. 505

506

507 4.3. Prey bottlenecks

508

With the spatial and trophic overlap between juvenile planktivorous groundfishes and salmon, there may have been competition for prey resources if limitations existed (Link and Auster, 2013). Competition could ultimately impact growth and survival of these fishes during their early marine period. In 2012, there was high CPUE of the fish in our study, as well as significant diet and spatial overlap, but there was no evidence in either year when we had zooplankton data, that prey consumption and growth were limited. Adult pink salmon that were juveniles in 2012 returned in record numbers the following year, and were noted to be heavier than usual (Orsi et al., 2016). Both pollock and Pcod that were juveniles in 2012, had a higher
than average recruitment to the adult population from that year class (Barbeaux et al., 2017;
Dorn et al., 2016). Additionally, our data suggest that plankton biomass in 2012 was not
diminished at the stations with the highest catches of juvenile planktivorous salmon or
groundfishes.

Prey resources did not appear to be limiting in 2013. The salmon and groundfish were not 521 522 in high spatial or diet overlap, except for AT_Flounder, and recruitment levels of juvenile fishes 523 from 2013 were average (McGowan et al., this issue; Orsi et al., 2016). Even with a lower biomass of zooplankton in 2013 relative to 2012, we did not observe a significant reduction of 524 525 food resources even at stations with high fish catches. Similar to 2012, there were high CPUE of juvenile groundfishes and salmon in 2014, when pollock were the only juvenile groundfish in 526 spatial and trophic overlap with salmon. However, stock assessment data reflect that recruitment 527 528 during 2014 was low (Dorn et al., 2018) possibly due to competition. In 2011, a year with documented low primary production (Stabeno et al., 2015) and plankton resources (Hopcroft et 529 530 al., 2016), there was spatial and diet overlap between juvenile planktivorous salmon and rockfishes and AT_Flounder. Having more than just two years of zooplankton data, especially in 531 a year of low productivity like 2011, could be useful in understanding prey resource bottlenecks 532 in the GOA. The year 2011 was an anomalously poor year for juvenile Pcod and pollock, which 533 534 were largely absent in the GOA (McGowan et al., this issue; and this study), and the North Pacific groundfish stock assessments confirm poor recruitment success for both these stocks for 535 the year class of 2011 (Dorn et al., 2014; Barbeaux et al., 2017). Juvenile salmon in 2011 were 536 537 thin and small, and there were poor returns of pink salmon the following year (Orsi et al., 2016; Daly et al., this issue). Finally, in 2010, when above average catches of rockfishes were present 538

with high diet overlap with the juvenile planktivorous salmon, but low spatial overlap,
competition was not likely present. Overall, the conditions in the GOA during our study period
were not consistent, and as such, it is difficult to draw conclusions on competition between
juvenile groundfish and planktivorous salmon, but most likely, in 2011, there was competition
that negatively affected both salmon and groundfishes, and in 2012, there were likely sufficient
food resources that competition was not an issue.

545 Catches of juvenile groundfishes were higher at stations where there were less piscivorous salmon in all years of our study, possibly due to increased juvenile salmon predation. 546 In most years, juvenile Chinook and coho salmon had significant spatial overlap with the 547 548 juvenile groundfishes, and directly consumed juvenile groundfishes in their diets. However, with the exception of rockfishes, they ate higher proportions of other juvenile fish such as sandlance 549 (Ammodytes personatus) or capelin (Weitkamp and Sturdevant, 2008; Daly et al., this issue). The 550 551 reduction of juvenile groundfishes co-occurring with piscivorous salmon could have been due to predation. Predation by salmon would negatively affect the recruitment success of these 552 economically important fishes especially if most of their population were in direct overlap in the 553 GOA. Overall, juvenile Pcod, pollock, and in some years, rockfishes, had higher CPUE in the 554 CGOA versus EGOA (Siddon et al., this issue), whereas juvenile Chinook salmon have higher 555 CPUE in EGOA than CGOA, albeit a low overall CPUE relative to coho salmon and the 556 557 groundfish. Coho salmon do utilize, in relatively high abundances, the EGOA and CGOA and therefore could have an impact on juvenile groundfishes recruitment success, especially 558 rockfishes, which coho salmon ate in highest frequency of the four juvenile groundfish. 559 The stomach fullness of the juvenile groundfishes and juvenile piscivorous salmon were 560 not related to the amount of prey available, as indicated by the zooplankton biomass or the 561

562 CPUE of juvenile groundfishes. In the summer of 2012 or 2013, plankton prey did not appear to be limited in the EGOA. Stomach fullness of the juvenile planktivores was minimally related to 563 the abundance of other planktivores; in only one case negatively, and two cases positively, and 564 for the juvenile piscivorous salmon, not in any case. These results were different from what was 565 observed in several other studies in the region. In a study by Sturdevant and Willette (1999), 566 planktivorous fish caught in the same location as other planktivorous fish had less full stomachs 567 568 then when caught in allopatric aggregations (regardless of aggregation size), which suggested 569 competition when mixed planktivores were sympatric. Steelhead (O. mykiss) had less full stomachs when there were higher catches of pink salmon in the oceanic Gulf of Alaska 570 571 (Atcheson et al., 2012). The effect that high abundances of pink salmon have on grazing down the plankton community may occur in their second year, as adult fish returning across the GOA, 572 versus during their juvenile stage, as noted in Springer and van Vliet (2014) and Ruggerone et al. 573 574 (2016). For example, in 2013, there were high numbers of juvenile pollock that did not appear to survive (Dorn et al., 2014), and there were record numbers of adult pink salmon returning across 575 576 the GOA at the same time.

Identifying whether juvenile groundfishes and salmon had a negative impact on each 577 other due to prey competition or direct predation is complex. Overall, juvenile groundfishes and 578 salmon frequently occupied the same place at the same time and showed some diet overlap, and 579 salmon also preyed directly upon juvenile groundfishes. When juvenile groundfishes 580 experienced high recruitment rates during their first marine summer, as they did during 2012, 581 there is evidence that juvenile salmon did so as well. We did not identify that food resources 582 were depleted in 2012 causing survival bottlenecks, and even in 2013 when there was less food, 583 recruitment was not poor. Increased growth of juvenile salmon has been shown to be a positive 584

585	predictor of favorable conditions for young pollock (Martinson et al., 2012). This suggests that
586	when conditions are good for groundfishes, they are good for salmon. In conditions, such as were
587	found in 2011, when there was evidence that prey resources were limited and the fishes
588	overlapped spatially and trophically, juvenile salmon and groundfish were both negatively
589	affected indicating trophic bottlenecks (Orsi, 2016; Moss et al., 2016). Predation of juvenile
590	groundfish by piscivorous salmon occurred, with significantly fewer groundfishes where larger
591	abundances of coho and Chinook salmon were located. Overall, quantifying interannual changes
592	in fine-scale spatial and trophic overlap between juvenile groundfishes and salmon can allow
593	fisheries managers to better identify survival bottlenecks in the GOA and understanding
594	recruitment variability for these important fish stocks.
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Table 1. Sampling station environmental correlation R^2 values relative to the non-metric

multidimensional scaling (NMDS) community analysis of juvenile groundfishes and salmon
CPUE by year.

Year	Station Depth (m)	Top 20 m Temperature (°C)	Top 20 m Salinity	Top 20 m total Chlorophyll- <i>a</i>	Pycnocline depth (m)
2010	0.52	0.16	0.28	0.20	ns
2011	0.15	ns	ns	ns	0.12
2012	0.72	ns	ns	ns	ns
2013	0.67	0.11	0.30	0.31	0.18
2014	0.57	0.30	0.15	0.10	0.09

Table 2. Spatial and diet overlap between juvenile groundfish and salmon by year. Cell color
represents the results of Cramér-von Mises test on spatial overlap; dark gray cells:
represents significant spatial overlap between the populations, represents non-significant
spatial overlap between the populations, and represents insufficient sample size of the
populations to test for differences. Text in cells is the average percent diet overlap (± SD)
between juvenile groundfishes and salmon by year. Text without (± SD) represent just one
station and therefore not an average.

Sockeye Chinook Coho Chum Pink 2010 Arrowtooth Pcod Pollock Rockfish 49.7 (±41.1%) 66.5 (±31.5%) 66.58(±31.9%) 2011 Arrowtooth 16.5% (±4.7%) 78.10% 44.90% 0% 0% Pcod Pollock Rockfish 30.8% (±24.9%) 3.30% 0% 14.7 (±16.1%) 2012 0.0 (±0.1%) 53.8% (±40.0%) 44.0 (±43.5%) 47.4 (±38.5%) Arrowtooth 0.8 (±2.4%) Pcod 4.3 (±7.5%) 9.8% 10.4 (±14.8%) 49.4 (±46.9%) 1.1 (±2.5%) 32.5% (±22.4%) 39.3 (±37.2%) 30.1 (±45.5%) Pollock 10.6 (±12.2%) 18.3% (±3.6%) 53.0 (±62.0%) 26.0 (±33.3%) Rockfish 0% 0% 2013 Arrowtooth 19.2 (±27.2%) 10.2 (±30.6%) 44.3 (±51.0%) Pcod 0.7% 1.70% 0% Pollock 0% 2.1 (±7.1%) 20.5 (±44.0%) 94.90% Rockfish 2014 Arrowtooth Pcod 1.9 (±2.7%) 15.5 (±26.6%) 27.5 (±31.1%) 47.4 (±43.3%) Pollock 11.7 (±13.3%) 20.0 (±34.3%) 24.1 (±30.2%) 32.9 (±38.3%) Rockfish

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Table 3. Juvenile salmon predation upon juvenile groundfishes by percent frequency of

914 occurrence for each year. Cod included both Pcod and pollock, and flatfish included

915 AT_Flounder. Shaded cell reflect values above zero.

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	Chinook	Coho	Chum	Pink	Sockeye
2010					
Flatfish	0.0%	0.0%	0.0%	0.0%	0.0%
Cod	0.0%	10.5%	0.0%	0.0%	0.0%
Rockfish	20.0%	68.4%	24.1%	28.2%	20.7%
2011					
Flatfish	0.0%	0.0%	0.0%	0.0%	0.0%
Cod	13.0%	0.0%	0.0%	0.0%	0.0%
Rockfish	47.8%	67.6%	0.0%	7.1%	23.1%
2012	-	-	-		-
Flatfish	50.0%	0.0%	0.0%	0.0%	0.0%
Cod	0.0%	9.1%	0.0%	0.0%	0.0%
Rockfish	38.9%	22.7%	0.0%	15.8%	42.1%
2013					
Flatfish	28.6%	8.0%	0.0%	0.0%	0.0%
Cod	0.0%	16.0%	0.0%	0.0%	0.0%
Rockfish	14.3%	16.0%	0.0%	0.0%	0.0%
2014					
Flatfish	0.0%		0.0%	0.0%	0.0%
Cod	9.1%		10.5%	0.0%	0.0%
Rockfish	18.2%		10.5%	8.3%	11.8%

Figure 1. Map of the eastern Gulf of Alaska (EGOA) and the general station locations (red circles) during 2010-2014. Not all stations were sampled each year.



Figure 2. Log scale catch per unit effort (log(CPUE)) at each sampling station ranked by bottom
depth (m) of juvenile groundfishes and salmon for each year, note the y-scale is different.



923

Station ranked by depth (m)

- 924 Figure 3. Non-metric multidimensional scaling (NMDS) plots of catch per unit effort (CPUE) of juvenile groundfishes and salmon
- species for each year with vectors of physical variables overlaid on each plot. Each point represents station CPUE of the juvenile
- 926 groundfishes and salmon. The temperature (°C), salinity units and total chlorophyll a (CHL) levels were average station values from
- 927 the top 20 m, depth represents station depth (m), and pycnocline was an estimated depth (m) where the change in density was at
- 928 maximum.



Figure 4. Average percent diet overlap of the four groundfish species with each juvenile 930 salmonid for all years combined. 931



- 934 Figure 5. Non-metric multidimensional scaling (NMDS) plots of juvenile groundfishes and salmon diets by year. Each colored symbol
- represents diets of juvenile fishes averaged at each sampling station. Abbreviations of the predator taxa are as follows: Arrowtooth
- flounder (ATF), chum (CH), Pacific cod (Pcod), pink salmon (PK), walleye pollock (pollock), rockfish (RF), and sockeye salmon
- 937 (SO). Ellipses encompass the major and minor axes of each species diet deviation.



Figure 6. Average zooplankton food biomass (± SE) at each sampling station grouped by
juvenile groundfishes CPUE quartiles and year (a-b) and by juvenile piscivorous salmon CPUE
quantiles and year (c-d). There were no significant pairs based on the Kruskal-Wallis test; P <
0.05.



Figure 7. Average groundfishes CPUE (\pm SE) at each sampling station grouped by juvenile piscivorous salmon CPUE quartile and year. Letters above error bar represent significantly different groups based on the Kruskal-Wallis test; P < 0.05.

