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TROPHIC NICHE SEPARATION BETWEEN SYMPATRIC SIBLING FLATFISHES IN  
RELATION TO GILL RAKER MORPHOLOGY

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ABSTRACT

Arrowtooth Flounder *Atheresthes stomias* and Kamchatka Flounder *Atheresthes evermanni* are upper trophic level predators which have been considered trophically equivalent in their

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30 sympatric range. Here, we present evidence against trophic equivalence of these sibling species  
31 based on flounder size and space-stratified analyses of stomach contents data from 5,724  
32 flounders sampled from the eastern Bering Sea (EBS) during summer 2007-2016. We found  
33 interspecific trophic niche separation occurred between flounders  $\leq 39$  cm fork length, before  
34 convergence at larger size classes. Our findings are consistent with the hypothesis that foraging  
35 efficiency differences arise due to divergence in gill raker counts. Arrowtooth Flounder have  
36 more gill rakers than Kamchatka Flounder and consistently consumed more zooplankton than  
37 Kamchatka Flounder, while Kamchatka Flounder typically consumed more benthic fishes. While  
38 a benthivory-zooplanktivory axis of resource partitioning is common among sympatric trophic  
39 polymorphs in freshwater ecosystems, our findings are novel for marine sibling species and  
40 flatfishes (Pleuronectiformes). Abundance estimates for both Arrowtooth Flounder and  
41 Kamchatka Flounder have substantially increased in Alaska in recent years, and we suggest  
42 trophic niche separation alleviates interspecific competition, which may buffer sympatric  
43 carrying capacities for Arrowtooth Flounder and Kamchatka Flounder.

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45

## 46 INTRODUCTION

47 Arrowtooth Flounder, *Atheresthes stomias* and Kamchatka Flounder, *Atheresthes*  
48 *evermanni* are large-mouth flatfishes, sympatric in the Bering Sea, Aleutian Islands and  
49 southwestern Gulf of Alaska. Morphological differences between species are subtle, such that  
50 field identification confidence during stock assessment surveys conducted by the National  
51 Marine Fisheries Service was only moderate through 2008 (Stevenson and Hoff 2009). The  
52 primary morphological differences are the position of the left eye, which is on the dorsal margin  
53 of the body in Arrowtooth Flounder and below the dorsal margin in Kamchatka Flounder, and  
54 higher gill raker counts on each of the first three gill arches in Arrowtooth Flounder  
55 (Wilimovsky et al. 1967; Yang 1988). Gill rakers of both species are lathe-shaped and of  
56 moderate length (Yang 1991), but Arrowtooth Flounder have a combined 28-37 gill rakers on the  
57 first three gill arches (mean: 31.4), while Kamchatka Flounder have 19-29 gill rakers (mean:  
58 24.8; Yang 1988; M.S. Yang, unpublished data).

59 Interspecific morphological differences suggest foraging capabilities are likely to differ  
60 between Arrowtooth Flounder and Kamchatka Flounder which, hypothetically, could confer a

61 mutually beneficial ecological advantage where they co-occur. Phenotypic divergence of feeding  
62 structures is common among sympatric sibling species and conspecific polymorphs (Smith and  
63 Skúalson 1996; Ward et al. 2006), and can facilitate alleviation of resource competition through  
64 resource specialization (Swanson et al. 2003). A common pattern of niche separation occurs  
65 between sympatric benthic specialists and zooplankton specialists, where zooplankton specialists  
66 have higher gill raker counts (Wimberger 1994; Smith and Skúalson 1996) that increase capture  
67 efficiency for small-bodied zooplankton prey (MacNeill and Brand 1990; Sanderson et al. 1991;  
68 Link and Hoff 1998; Roesch et al. 2013). Thus, Arrowtooth Flounder may be more efficient  
69 zooplankton consumers than Kamchatka Flounder. However, the only prior comparative diet  
70 study between species concluded Arrowtooth Flounder and Kamchatka Flounder are “trophically  
71 equivalent,” and that interspecific competition was unlikely to be important due to a high  
72 abundance of prey resources in the eastern Bering Sea (Yang and Livingston 1986).

73 In this paper, we re-examine the trophic equivalency of Arrowtooth Flounder and  
74 Kamchatka Flounder in the eastern Bering Sea (EBS) using a larger data set than was available  
75 for the earlier comparative diet study. Yang and Livingston's (1986) study design may not have  
76 allowed detection of interspecific trophic niche differences because their available sample size  
77 was relatively small, covered a limited spatial extent, and was collected during a two-week  
78 period in a single year. In addition, the importance of resource competition between *Atheresthes*  
79 has likely increased since Yang and Livingston's (1986) study because aggregate Arrowtooth  
80 Flounder and Kamchatka Flounder biomass has increased four-fold within their sympatric range  
81 (Spies et al. 2016; Wilderbuer et al. 2016). Based on spatial biomass trends, Zador et al. (2011)  
82 suggested that Arrowtooth Flounder may be near carrying capacity in some parts of the EBS.  
83 Under these conditions, resource competition may have increased, and the expression of  
84 morphology-based resource partitioning, or trophic niche separation, between Arrowtooth  
85 Flounder and Kamchatka Flounder may be more pronounced (Svanbäck and Bolnick 2007). As  
86 such, we address three main questions:

- 87 1. Do the trophic niches of Arrowtooth Flounder and Kamchatka Flounder differ within  
88 their sympatric range?
- 89 2. If so, does trophic niche separation persist spatially and across predator size classes?
- 90 3. Are patterns of trophic niche partitioning consistent with expectation based on  
91 interspecific differences in feeding structure morphology?

92

## 93 METHODS

94

### 95 *Study area and sample collection*

96 The eastern Bering Sea (EBS) is a large coastal ecosystem with a broad (~500 km)  
97 continental shelf that gradually increases in depth to ~200 m, before an abrupt depth increase  
98 along the continental slope into the deep Aleutian Basin (Fig. 1). Strong seasonal dynamics and  
99 inter-annual environmental variability influence EBS community spatial structure.

100 Diet data used in this study were collected during summer (June-August) bottom-trawl  
101 surveys conducted by NOAA's Alaska Fisheries Science Center from 2007 through 2016.  
102 Bottom-trawl surveys of the EBS shelf were conducted annually (e.g., see Conner et al. 2017),  
103 and bottom-trawl surveys of the EBS slope were conducted biennially, except 2014 (Hoff 2016).  
104 Survey designs and sampling gear differed for the EBS shelf and EBS slope due to differences in  
105 stock assessment needs and substrate types. The EBS shelf survey sampled across a regularly-  
106 spaced grid (20 nmi x 20 nmi) of 376 stations, at ~15-200 m bottom depth, with higher density  
107 sampling in areas of historically high crab abundance around St. Matthew, St. Paul and St.  
108 George Islands (Lauth and Nichol 2013). EBS slope survey samples were randomly stratified by  
109 sub-areas and depth (200-1200 m), and ~200 stations were sampled per survey (Hoff 2013).

110 Stomachs were collected from specimens of *Atheresthes* at a subset of survey stations  
111 following a size-stratified sampling scheme (Livingston et al. 2017). Up to 15 stomachs were  
112 collected per station. Fish were examined for evidence of regurgitation (i.e., prey in the mouth,  
113 flaccid stomach) or net-feeding (i.e., undigested prey in the mouth), and whole stomachs were  
114 sampled from fish not displaying evidence of regurgitation or net-feeding. Predator species, fork  
115 length (cm), sex and collection location were recorded for each sample. Stomachs were fixed in  
116 neutral-buffered 10% formalin, then transferred to 70% ethanol for storage prior to stomach  
117 contents analysis. Stomach samples used for this study were collected during 2007-2016 EBS  
118 shelf surveys, and 2008, 2010, 2012 and 2016 EBS slope surveys. An average of 518 non-empty  
119 *Atheresthes* stomachs were sampled per EBS shelf survey, and an average of 137 non-empty  
120 stomachs were sampled per EBS slope survey (Table 1).

121 Stomach contents analysis was performed by analysts in the Resource Ecology and  
122 Ecosystem Modeling Task Trophic Interactions Laboratory at NOAA's Alaska Fisheries Science

123 Center (AFSC; Seattle, WA) following standardized laboratory protocols (Livingston et al. 2017).  
124 Briefly, prey items were identified to the lowest practical taxon, fish and crab prey were  
125 enumerated, and prey weights were recorded to the nearest milligram.

## 126 127 *Data analysis*

128 Multivariate analyses were used to compare trophic niche variation between species, over  
129 flounder size and space, based on broad prey categories. Prey categories were assigned based on  
130 *a priori* knowledge of important prey categories identified in previous diet studies of Arrowtooth  
131 Flounder and Kamchatka Flounder: benthic fishes, assorted pelagic fishes and squids, gadids  
132 (Family Gadidae, mostly Walleye Pollock), shrimp (Suborders Dendrobranchiata and  
133 Pleocyemata), unidentified fishes, non-shrimp benthic invertebrates, zooplankton (mostly Order  
134 Euphausiacea), and “other.” Stomachs containing fisheries discards (offal) were omitted prior to  
135 analysis (1.6% of stomachs). Flounder groups were aggregated by species, size and spatial area.  
136 Flounders were divided into five size classes based on fork length ( $\leq 19$  cm, 20-29 cm, 30-39 cm,  
137 40-49 cm, and  $\geq 50$  cm) to allow interspecific comparisons between flounders expected to have  
138 similar stomach capacity and diet composition. Size classes were informed by the four size  
139 classes ( $\leq 200$  mm, 201-300 mm, 301-400 mm,  $> 400$  mm) used by Yang and Livingston (1986),  
140 but were adjusted based on size class designations used in NOAA’s standardized stomach  
141 sampling protocol (Livingston et al. 2017), along with the availability of more samples from  
142 larger-sized flounders for our analysis. Spatial areas were designated using five EBS shelf strata  
143 (A-E) roughly delineating areas with distinct oceanographic features and community  
144 composition (Stauffer 2004), and a 200-600 m bottom depth stratum along the EBS slope  
145 (stratum F; Fig. 1). Flounder groups from areas where *Atheresthes* were scarce, sympatry was  
146 weak, or sample sizes were small ( $< 10$  non-empty stomachs) were excluded from analysis.  
147 Overall, 10,110 specimens were assigned among 56 groups, of which 5,762 specimens from 55  
148 groups had non-empty stomachs (Table 2). Adequate sample sizes for analyses were available  
149 for 46 groups containing 5,724 non-empty stomachs (Table 2). Proportional wet weights of prey  
150 were calculated for the groups of non-empty flounder stomachs ( $\%W_{i,k,l,s}$ ):

$$\%W_{i,k,l,s} = \frac{\sum_{j=1}^{n_j} W_{i,j,k,l,s}}{\sum_{j=1}^{n_j} \sum_{i=1}^{n_i} W_{i,j,k,l,s}}$$

151 where  $W$  is wet weight of prey category  $i$ , from the stomach of flounder  $j$ , flounder size class  $l$ ,  
152 flounder species  $s$ , and spatial stratum  $k$ ;  $n_i$  is the number of prey categories, and  $n_j$  is the number  
153 of non-empty stomachs collected for the flounder group. A Bray-Curtis diet dissimilarity matrix  
154 (Bray and Curtis 1957) was calculated from the flounder group proportional diet data for  
155 multivariate statistical analysis.

156 Hierarchical clustering and ordination were used for multivariate statistical analysis of  
157 diet data. Hierarchical clustering was conducted to determine which flounder groups had  
158 greatest diet similarity and to evaluate which group dimensions (size, stratum, or flounder  
159 species) influenced diet similarity. Ordination was performed to determine the relative influence  
160 of prey categories on differences between flounder groups.

161 Similar-sized flounders have more similar diets than different-sized flounders, and a  
162 strong ontogenetic shift from shrimp prey to fish prey has been identified for *Atheresthes* in the  
163 EBS (Yang and Livingston 1986). Since the purpose of this analysis was to identify descriptive  
164 differences in flounder group association, rather than synoptic patterns of ontogenetic diet shift,  
165 we used space-dilating hierarchical clustering algorithms (flexible beta with  $\beta$  parameter varying  
166 from -0.5 to -1.0, and complete linkage clustering) to increase contrast within size classes.  
167 Space-dilating algorithms may increase the likelihood of producing small or orphan clusters, but  
168 they can also preserve ecologically meaningful differences by requiring a more stringent  
169 criterion for assigning cluster membership (Legendre and Legendre 2012). We used cophenetic  
170 correlation to compare clustering algorithm performance. An appropriate number of clusters was  
171 determined from examination of a scree plot of cluster dissimilarity attained across a range of  
172 clusters, and through index-based evaluation of relevant clusters using R package 'NbClust'  
173 (Charrad et al. 2014).

174 After relevant clusters were identified, an ANOSIM test was used to test statistical  
175 significance of global clusters. ANOSIM is a non-parametric rank-based permutation test which  
176 compares within-cluster similarity to between cluster similarity (Clarke 1993). The ANOSIM  $R$   
177 statistic ranges from -1 to 1 and indicates the level of similarity between clusters, where 1  
178 indicates all flounder groups within a cluster are more similar to each other than to groups from  
179 other clusters, while an  $R$  of 0 indicates no difference between clusters. Significant differences  
180 between clusters were also tested using pairwise ANOSIM tests. Global and pairwise ANOSIM  
181 tests used 999 random permutations to generate sample distributions for significance tests.

182 SIMPER analysis (Clarke 1993) was then used to determine which prey categories were most  
183 different between clusters.

184 Non-metric multidimensional scaling (NMDS) ordination (Kruskal 1964) was performed  
185 on the diet dissimilarity matrix to determine which prey categories were associated with flounder  
186 group dissimilarity. NMDS was chosen over other ordination methods because predator group  
187 diet data were not multivariate normally distributed, and relative differences between groups  
188 were more important than absolute differences. Random starting placements (up to 100) were  
189 used to find a convergent ordination solution, and an appropriate number of dimensions for the  
190 ordination ( $k$ ) was determined by examining stress values on a scree plots for 1-8  $k$ -dimensions.  
191 Statistical significance of the final ordination was tested using a random permutation test (999  
192 permutations) and goodness-of-fit was evaluated based on the correlation between the observed  
193 dissimilarity and ordination distance on a Shephard diagram. Prey loadings in ordination space  
194 were calculated using linear correlation analysis, and statistical significance of prey category  
195 loadings were tested using a random permutation test. Differences between flounder groups were  
196 evaluated from visual inspection of NMDS plots. If NMDS plots indicated a consistent diet  
197 difference between interspecific flounder pairs sharing size class and stratum, a two-tailed sign  
198 test was conducted to test the null hypothesis of interspecific trophic equivalence (Zar 1999).  
199 Under the null hypothesis, a flounder group would be equally likely to have a higher or lower  
200 proportion of a prey type as its interspecific counterpart from the same size class and stratum.

201 Proportional wet weight of prey provides a relative measure of prey contribution to diet,  
202 but does not reflect absolute consumption of a prey type. To ensure that results of multivariate  
203 analyses were not simply a reflection of interspecific biases in overall prey consumption, we  
204 compared stomach fullness indices and prey frequency of occurrence ( $\%F$ ) among non-empty  
205 stomachs to make interspecific comparisons of consumption. Fullness indices followed Lilly  
206 (1991) except in lieu of cubed length ( $L^3$ ), we used estimated flounder biomass calculated from  
207 length-weight regressions ( $M_j$ ), available from NOAA/AFSC's Groundfish Trophic Interactions  
208 Database (Livingston et al. 2017). Total fullness index ( $TFI$ ) was calculated as:  $TFI_j =$   
209  $\sum_{i=1}^Q W_{ij} M_j^{-1} \cdot 10^4$ , where  $W_{ij}$  is the wet weight of prey type  $i$  in flounder stomach  $j$ ,  $M_j$  is  
210 estimated biomass of the flounder  $j$ , and  $Q$  is the number of prey categories.  $PFI$  was calculated  
211 as:  $PFI_{i,j} = W_{i,j} M_j^{-1} \cdot 10^4$ . Prey types for  $PFI$  calculations were the same as for multivariate  
212 analyses. When adequate sample sizes were available ( $\geq 10$  non-empty stomachs), tested for

213 significant interspecific differences between fullness indices for size class-stratum flounder pairs  
214 using the two-tailed Mann-Whitney test. We used the non-parametric Mann-Whitney test  
215 because fullness index distributions were non-normal and *PFI* had a high proportion of zeroes.

216

## 217 RESULTS

218 Prey types consumed by Arrowtooth Flounder and Kamchatka Flounder were  
219 qualitatively similar and four hierarchical clusters were relevant for describing predator diets  
220 (Fig. 2). Complete linkage clustering (Sørensen 1948) provided the best hierarchical clustering  
221 performance (cophenetic correlation  $r^2 = 0.89$ ). Cluster W included mostly predators in 20-29 cm  
222 and 30-39 cm size classes, but also included Stratum C Arrowtooth Flounder  $\leq 19$  cm and  
223 Stratum F Kamchatka Flounder  $\geq 50$  cm. Cluster X had the largest group membership, including  
224 all large size classes (40-49 cm,  $\geq 50$  cm) except Cluster F Kamchatka Flounder  $\geq 50$  cm. Six  
225 small and medium size classes were also in Cluster X. Cluster Y only contained the smallest size  
226 class ( $\leq 19$  cm), and included both species. Cluster Z contained only smaller size classes ( $\leq 19$  cm,  
227 20-29 cm) of Kamchatka Flounder. All stratum B size class pairs showed concordant cluster  
228 membership, indicating greater interspecific diet overlap than in other strata for which at least  
229 three size classes were represented. Among small and medium size classes ( $\leq 19$  cm, 20-29 cm,  
230 30-39 cm), the only interspecific predator group pair sharing cluster membership, aside from  
231 stratum B, were 30-39 cm size classes in stratum D. Overall, interspecific pairs of small and  
232 medium size class predator groups were in different clusters 63.6% (7/11) of the time. Within  
233 Cluster W, there was a considerable distance between a branch where seven out of eight leaves  
234 were medium size class Arrowtooth Flounder, and a monospecific Kamchatka Flounder branch.  
235 This difference occurred at a dissimilarity of 0.56, slightly below the phenon line at 0.6.

236 Gadids, shrimp, zooplankton and benthic fishes contributed most ( $\geq 70\%$ ) to between  
237 cluster dissimilarity, but ranked contribution to differences varied among cluster pairs (Table 3).  
238 A global ANOSIM test revealed significant differences across clusters ( $R = 0.96$ ,  $P = 0.001$ ), and  
239 five out of six pairwise ANOSIM tests identified significant and substantial diet differences  
240 between clusters ( $0.91 \leq R \leq 1.00$ ; Table 3). Clusters Y and Z were not significantly different,  
241 although an ecological difference was not convincingly rejected due to small cluster membership  
242 and a low p-value ( $P = 0.09$ ).



243 Important prey categories in the best NMDS ordination were consistent with the prey  
244 categories that contributed most to hierarchical cluster dissimilarity (Table 3; Fig. 3). NMDS  
245 diagnostics indicated a two-dimensional ( $k = 2$ ) ordination was appropriate, and the ordination  
246 resulted in a stress value of 0.09 (Fig. 4). More of the variation was explained by the ordination  
247 than expected by random chance ( $P < 0.001$ ) and fit to the data was good (non-metric  $r^2 = 0.99$ ).  
248 Benthic fishes ( $P < 0.001$ ,  $r^2 = 0.37$ ), gadids ( $P < 0.001$ ,  $r^2 = 0.91$ ), shrimp ( $P < 0.001$ ,  $r^2 = 0.71$ )  
249 and zooplankton ( $P < 0.001$ ,  $r^2 = 0.50$ ) categories had highly significant vector loadings. Benthic  
250 invertebrates ( $P = 0.01$ ,  $r^2 = 0.06$ ), unidentified fishes ( $P = 0.04$ ,  $r^2 = 0.02$ ), and other ( $P = 0.01$ ,  
251  $r^2 = 0.05$ ) prey categories had statistically significant vector loadings but, compared to the highly  
252 significant prey vectors, did not account for much of the variation in ordination space (low  $r^2$ -  
253 values) so were omitted from the NMDS plot (Fig. 3). Miscellaneous pelagic fishes and squids  
254 were not significant ( $P = 0.31$ ,  $r^2 = 0$ ).

255 Shrimp and gadid vectors were divergent and were associated with an ontogenetic shift in  
256 diet (Fig. 3). Smaller *Atheresthes* were more strongly associated with the shrimp vector, while  
257 larger *Atheresthes* had a higher proportion of gadids in their diet. Zooplankton and benthic fish  
258 prey categories were divergent and were associated with trophic niche separation between  
259 Arrowtooth Flounder and Kamchatka Flounder. Among small and medium flounder size classes  
260 ( $\leq 19$  cm, 20-29 cm, 30-39 cm) there was a consistent within-stratum difference between 11 size  
261 class pairs of Arrowtooth Flounder and Kamchatka Flounder. Arrowtooth flounder were more  
262 strongly associated with zooplankton prey, and Kamchatka Flounder were more strongly  
263 associated with benthic fish prey, suggesting interspecific trophic niche separation occurred  
264 along a benthic fish-zooplankton prey gradient. The same benthic fish-zooplankton arrangement  
265 also occurred in some larger size classes (40-49 cm in strata B, C, E and A;  $\geq 50$  cm in strata A, B  
266 and F), but not for 40-49 cm size classes in stratum D and E. Stratum F Kamchatka Flounder  $\geq 50$   
267 cm were dissimilar from other  $\geq 50$  cm groups and were associated with the benthic fishes vector.

268 Arrowtooth Flounder groups consumed higher proportions of zooplankton than  
269 Kamchatka Flounder in 100% of pairwise comparisons (sign-test;  $P < 0.001$ ,  $n = 19$ ). Stratum A  
270 pairs were tied and omitted from sign-tests because neither group consumed zooplankton.  
271 Kamchatka Flounder were more likely to have a higher proportion of benthic fishes in the diet  
272 than Arrowtooth Flounder (sign test;  $P < 0.05$ ,  $n = 21$ ). Kamchatka Flounder groups had a higher  
273 proportion of benthic fishes in their diet than Arrowtooth Flounder in 76.2% (16/21) of pairwise

274 comparisons. There were no evident size or stratum trend for the 23.8% (5/21) of pairs where  
275 Arrowtooth Flounder consumed more benthic fishes.

276 Interspecific differences in  $PFI_i$  and  $\%F_i$  were generally consistent with patterns of  
277 trophic niche separation observed in multivariate analyses. Significant differences ( $P < 0.05$ ) in  
278  $PFI_i$  were detected in 31 out of 154 flounder group comparisons (Fig. 4; Table S.1). Mean  
279  $PFI_{zooplankton}$  and  $\%F_{zooplankton}$  were higher for Arrowtooth Flounder than Kamchatka Flounder for  
280 100% (19/19) of pairwise comparisons, and there were 11 statistically significant differences in  
281  $PFI_{zooplankton}$ . Mean  $PFI_{benthic\_fishes}$  was higher for Kamchatka Flounder in 76.2% (16/21) of group  
282 comparisons, there were seven statistically significant differences in  $PFI_{benthic\_fishes}$ ,  
283 and  $\%F_{benthic\_fishes}$  was higher in Kamchatka Flounder for 76.2% (16/21) of comparisons.  
284 Significant differences in  $PFI$  were also identified for shrimp, Gadidae, benthic invertebrates,  
285 miscellaneous pelagic, and unidentified fishes. Kamchatka Flounder  $\leq 39$  cm had higher mean  
286  $PFI_{shrimp}$  and  $\%F_{shrimp}$  in 90.9% (10/11) of group comparisons, among which five statistically  
287 significant differences in  $PFI_{shrimp}$  were observed.  $PFI_{shrimp}$  was significantly higher for 40-49  
288 cm Arrowtooth Flounder in stratum A, but shrimp were only a minor contributor to total  
289 consumption.  $PFI_{Gadidae}$  was higher for Arrowtooth Flounder in one comparison, and higher for  
290 Kamchatka Flounder in two comparisons.  $PFI_{benthic.inverts}$  was higher for 30-39 cm Kamchatka  
291 Flounder in stratum E, but contributed very little to overall consumption.  $PFI_{misc\_pelagic}$  was  
292 significantly higher for  $\geq 50$  cm Kamchatka Flounder in stratum F.  $PFI_{fish\_unid}$  was higher for 20-  
293 29 cm Arrowtooth Flounder in stratum E, and higher for  $\geq 50$  cm Kamchatka Flounder in stratum  
294 F. Despite the preponderance of significant differences in  $PFI$ , significant interspecific  
295 differences in  $TFI$  only occurred in stratum B, for 30-39 cm, 40-49 cm and  $\geq 50$  cm size classes  
296 (Table S.2).

297

## 298 DISCUSSION

299 Our findings indicate trophic niche separation occurs between Arrowtooth Flounder and  
300 Kamchatka Flounder at smaller sizes ( $\leq 39$  cm) until trophic niches converge ontogenetically.  
301 Trophic niche partitioning is consistent with hypothesized differences in foraging efficiency due  
302 to gill raker functional morphology. Arrowtooth Flounder examined for this study consumed  
303 more zooplankton than Kamchatka Flounder, and small-sized to medium-sized Kamchatka  
304 Flounder consumed more benthic fish than small-sized to medium-sized Arrowtooth Flounder.

305 Some diet overlap occurred between species of the same size class and the degree of  
306 trophic niche separation between species varied among strata. Multiple factors likely contributed  
307 to spatial variation in trophic niche separation. Diet overlap is common among allied resource  
308 competitors because diet is jointly influenced by foraging capability and prey availability  
309 (Amundsen et al. 2004; Chavarie et al. 2016). Greater diet overlap often occurs when a shared  
310 prey resource is abundant and available. As resource competition increases, aggregate trophic  
311 niche breadth can increase (Svanbäck and Persson 2004) and morphology-based resource  
312 partitioning can become more pronounced (Svanbäck and Bolnick 2007). Hypothetically, this  
313 would increase trophic niche separation between Arrowtooth Flounder and Kamchatka Flounder.  
314 However, causes of spatial variation in niche separation cannot be determined because prey  
315 abundances are not known. Thus, in stratum B, the comparatively high trophic niche overlap  
316 could be due to either an abundance of preferred resources, or a scarcity of alternate resources.

317 A notable exception to the shrimp-gadid ontogenetic shift was evident for Stratum F  
318 Kamchatka Flounder  $\geq 50$  cm, which may reflect a non-trophic dimension of ecological niche  
319 separation between Arrowtooth Flounder and Kamchatka Flounder. With increasing depth,  
320 Kamchatka Flounder abundance increases relative to Arrowtooth Flounder abundance on the  
321 continental slope, and Arrowtooth Flounder become scarce on the outer continental slope (600-  
322 1200 m; Zimmermann and Goddard 1996). Consequently, Stratum F Kamchatka Flounder  $\geq 50$   
323 cm were sampled from deeper (mean: 474 m, SD: 72 m) than Stratum F Arrowtooth Flounder  
324  $\geq 50$  cm (mean: 405 m, SD: 98 m), so interspecific diet differences may reflect depth-dependent  
325 changes in prey availability, including the lower  $PFI_{Gadidae}$  for stratum F Kamchatka Flounder.  
326 The primary aim of this analysis was to determine whether trophic niche separation occurs in  
327 sympatry, so the outer continental slope was excluded from analysis. However, the Kamchatka  
328 Flounder diet on the outer continental slope (600-1200 m) is distinct from strata included in this  
329 analysis, and the stratum F diet may resemble a transitional diet between the inner and outer  
330 continental slope. On the outer slope, the diet of Kamchatka Flounder  $\geq 50$  cm is dominated by  
331 deep-water benthic fishes (Fig. S.1; *Bothrocara* spp., Macrouridae).

332 Interspecific differences in fullness indices and prey frequency of occurrence were  
333 consistent with our finding of trophic niche divergence linked to morphology, but also produced  
334 two surprising outcomes which may warrant further investigation of interspecific ecological  
335 differences. While the large number of comparisons we made increased the potential for Type I

336 errors, repeat differences in prey-specific *PFI* comparisons and highly significant differences in  
337 *PFI* for important prey types are noteworthy. Higher *PFI*<sub>shrimp</sub> and %*F*<sub>shrimp</sub> for Kamchatka  
338 Flounder  $\leq 39$  cm may be due to greater benthivory by Kamchatka Flounder, although we were  
339 unable to determine whether differences were due to consumption of greater numbers of the  
340 same shrimp taxa, larger shrimp, a broader diversity of shrimp taxa, or a combination of factors.  
341 Counting prey shrimp was not a standard protocol for laboratory analysis, the number of  
342 available prey size measurements was not adequate to make interspecific comparisons of shrimp  
343 size, and an insufficient proportion of shrimp were identified to a taxonomic level suitable for  
344 more detailed prey categories. Dominant EBS shrimp taxa include a combination of benthic  
345 (families Crangonidae, Hippolytidae), pelagic (family Pasiphaeidae, Sergestidae), and semi-  
346 pelagic (family Pandalidae) taxa (Wicksten 2012), and both flounders consume shrimp from all  
347 major EBS families (Yang and Livingston 1986; Yang 1995; Orlov and Moukhametov 2004).  
348 For larger-sized flounders (40-49 cm,  $\geq 50$  cm) in Stratum B, interspecific differences in  
349 *PFI*<sub>Gadidae</sub> were explained by higher %*F*<sub>Gadidae</sub> in non-empty Kamchatka Flounder stomachs, but  
350 we were unable to determine why the difference in %*F*<sub>Gadidae</sub> occurred. Potential explanations  
351 include interspecific differences in allometric scaling of size-structured interactions, feeding  
352 activity level, aspects of the prey search-detection-capture sequence, rates of digestion, feeding  
353 chronology, or spatial overlap with prey on a finer spatial scale than we considered in our  
354 analysis.

355 Environmental variation influences community spatial structure in the EBS across  
356 seasonal and inter-annual temporal scales (e.g. Mueter and Litzow 2008; Kotwicki and Lauth  
357 2013; Barbeaux 2017). During summer months, the spatial distribution of many commercially  
358 and ecologically important species is influenced by the cold pool, an area with near bottom water  
359 temperatures  $\leq 2^{\circ}\text{C}$  which approximately reflects the southern extent of winter sea ice and  
360 persists through summer months (Mueter and Litzow 2008). During some years, this limits  
361 distributions of Arrowtooth Flounder and Kamchatka Flounder to the outer continental shelf,  
362 because they avoid the cold pool (Spencer 2008; Barbeaux and Hollowed 2018). On the EBS  
363 shelf (but not the slope), Kamchatka Flounder  $\geq 40$  cm tend to occupy slightly colder habitat than  
364 Arrowtooth Flounder  $\geq 42$  cm (Barbeaux 2017; Barbeaux and Hollowed 2018). Hypothetically,  
365 during cold years, this may allow comparatively higher overlap of large Kamchatka Flounder  
366 with cold-tolerant Gadid prey (Walleye Pollock), than for large Arrowtooth Flounder. While diet

367 data in the present study included both cold (2007-2013) and warm (2014-2016) years,  
368 Kamchatka Flounder sample sizes were not sufficient to compare concurrent interspecific shifts  
369 in diet over time.

370 It is unclear how Arrowtooth Flounder diet shifts relative to Kamchatka Flounder diet as  
371 the environment and prey availability change. Discrete sampling of Arrowtooth Flounder and  
372 Kamchatka Flounder would improve understanding of how environmental variability influences  
373 diet composition. In the Gulf of Alaska, zooplankton contribution to Arrowtooth Flounder diet is  
374 highest during spring, when zooplankton are most abundant (Knoth and Foy 2008). No  
375 analogous seasonal comparison of Kamchatka Flounder diet has been conducted. Stable isotope  
376 analysis would extend the temporal range of summer sampling, improve understanding of  
377 benthic and pelagic trophic pathway duration, and provide a relative measure of trophic position  
378 between species. In the Gulf of Alaska, Arrowtooth Flounder trophic position, inferred from bulk  
379  $\delta^{15}\text{N}$  ratios was lower during years when euphausiids were unusually abundant in stomach  
380 samples (Marsh et al. 2015).

381 Support for the hypothesized association between morphology and diet is ample.  
382 Sympatric benthivore and planktivore polymorphs have been identified in gasterosteids (McPhail  
383 1984; Taylor and McPhail 2000), osmerids (Taylor and Bentzen 1993), salmonids (Foote et al.  
384 1999; Guiguer et al. 2002; Chavarie et al. 2016), and coregonids (Amundsen et al. 2004; Østbye  
385 et al. 2005; Gowell et al. 2012). Gill raker functional morphology has repeatedly been linked to  
386 adaptive resource partitioning between benthivore and zooplanktivore polymorphs in freshwater  
387 ecosystems (Schluter and McPhail 1992; Wimberger 1994; Smith and Skúalson 1996). In marine  
388 systems, gill raker functional morphology has been linked to prey size divergence between  
389 sibling planktivores (e.g. Castillo-Rivera et al. 1996), but had not previously been linked to  
390 benthivory-zooplanktivory resource partitioning. Regardless of prey type consumed, foraging by  
391 both species of *Atheresthes* likely occurs near-bottom, in contrast with common patterns of  
392 habitat partitioning between demersal foraging benthivore morphs and pelagic foraging  
393 zooplanktivore morphs in freshwater systems.

394 A morphological mechanism for trophic niche separation implies niche specialization  
395 should persist across the ranges of Arrowtooth Flounder and Kamchatka Flounder. Throughout  
396 the range of Arrowtooth Flounder, euphausiids (zooplankton) are frequent prey and often  
397 contribute substantially to overall diet, especially among Arrowtooth Flounder  $\leq 39$  cm (Gotshall

398 1969; Rose 1980; Yang and Livingston 1986; Yang 1995; Buckley et al. 1999; Knoth and Foy  
399 2008). By contrast, euphausiids are uncommon or unimportant in Kamchatka Flounder diet  
400 (Yang and Livingston 1986; Orlov 1997; Orlov and Moukhametov 2004). While ecosystem  
401 dynamics and prey availability certainly vary across the North Pacific, diet differences  
402 throughout the species' ranges support the association between gill raker morphology and trophic  
403 niche separation.

404 Unlike gill rakers, the morphological difference in left-eye position between the two  
405 species does not have a clear association with the observed pattern in benthivory-zooplanktivory  
406 resource partitioning. The position of the left eye of Arrowtooth Flounder (more  
407 zooplanktivorous), intersecting the dorsal margin (Yang 1988), suggests a field of view that may  
408 encompass more of the benthos than that of Kamchatka Flounder (more benthivorous). The eye  
409 position in flatfish is less indicative of specific feeding behaviors than other morphological  
410 characteristics and specializations (Gibb 1997; Bergstrom and Palmer 2007), so this may be due  
411 to random phenotypic divergence. However, we speculate on the possibility that the marginal  
412 position of the left eye in Arrowtooth Flounder may result from parasite mediated selection by  
413 the pathologic copepod, *Phrixocephalus cincinnatus* (Wilson, 1908). A high percentage of  
414 Arrowtooth Flounder off British Columbia, Canada, become infected with this parasite (Kabata  
415 1969; Blaylock et al. 2005). The right eye was more commonly infected than the left eye (the eye  
416 nearer the dorsal margin) in Arrowtooth Flounder (Kabata 1969; Blaylock et al. 2005), but  
417 infection rates of Pacific Sanddab *Citharichthys sordidus*, having eyes located nearly level on the  
418 eyed-side of the head, have similar infection rates of the left and right eyes (Perkins and Gartman  
419 1997). Binocular infections by this copepod certainly lead to death (Kabata 1969; Perkins and  
420 Gartman 1997) while monocular infections may also result in substantial impairment of the host  
421 (Blaylock et al. 2005). However, a captured Pacific Sanddab, was observed to survive the  
422 monocular infection and completion of the life cycle (death) of the parasite, and it grew as fast as  
423 uninfected Pacific Sanddabs also in captivity (Perkins and Gartman 1997). There are no reports  
424 in the literature of a similar pathology for Kamchatka Flounder in the western North Pacific  
425 Ocean. If marginal eye position imparts increased host-survival of infections by pathologic  
426 copepods at minimal or no associated energetic cost, the trait would be beneficial to a population  
427 that suffers high rates of infection and could be maintained in the absence of the parasite (Ebert  
428 2005).

429 Evolutionary mechanisms which initially led to trophic niche separation between  
430 Arrowtooth Flounder and Kamchatka Flounder are unclear because the evolutionary history of  
431 the genus *Atheresthes* is not known. Sympatric speciation caused by resource-driven character  
432 displacement may be possible, although an allopatric origin is more likely considering the glacial  
433 history of the North Pacific. Glacial isolation during the Pleistocene epoch has been suggested as  
434 the reason for east-west genetic population structures in Pacific Cod (Canino et al. 2010) and  
435 Pacific Herring (Liu et al. 2011) in the North Pacific. There is a clear genetic difference between  
436 Arrowtooth Flounder and Kamchatka Flounder and no evidence of interspecific hybridization  
437 (Ranck et al. 1986; De Forest et al. 2014). However, the genetic difference between species is  
438 minor, suggesting recent speciation (Ranck et al. 1986). Although genetic studies have been  
439 conducted to validate species identities in *Atheresthes*, more thorough investigation of genetic  
440 population structure is necessary to elucidate patterns of phylogenetic divergence.

441 Ecological niche width imposes a constraint on population growth (Hutchinson 1957;  
442 Schoener 1974), so a broader combined trophic niche for smaller Arrowtooth Flounder and  
443 Kamchatka Flounder size classes may facilitate a higher carrying capacity than might be  
444 expected under trophic niche equivalence. An important consequence of higher *Atheresthes*  
445 carrying capacity is elevated predation pressure, which may dampen recruitment of  
446 commercially important Walleye Pollock in the EBS (Mueter et al. 2011; Holsman et al. 2015;  
447 Spencer et al. 2016). Predation on Walleye Pollock may be especially impactful during warm  
448 years, when higher bottom temperatures allow greater Arrowtooth Flounder and Kamchatka  
449 Flounder spatial overlap with juvenile Walleye Pollock (Mueter et al. 2006; Kotwicki and Lauth  
450 2013; Spencer et al. 2016; Barbeaux 2017). Warm year frequency is expected to increase due to  
451 climate change, and the potential corollary of increased predation on Walleye Pollock is a  
452 management concern, so modeling efforts have sought to forecast climate-mediated shifts in  
453 Walleye Pollock predation mortality (Mueter et al. 2011; Holsman et al. 2015; Spencer et al.  
454 2016). Separately considering demographic changes and diet compositions for Arrowtooth  
455 Flounder and Kamchatka Flounder could improve ecosystem (energy flow) models. While  
456 abundances of sympatric Arrowtooth Flounder and Kamchatka Flounder increased concurrently  
457 in recent decades, ecological niche partitioning, including trophic niche divergence, suggests  
458 future responses to ecosystem change may differ between species.

459 Our study contributes to understanding of interspecific differences in the life history and  
460 ecology of Arrowtooth Flounder and Kamchatka Flounder in their sympatric range. Although  
461 larval traits and spatial-temporal dispersal patterns overlap (De Forest et al. 2014) and both  
462 species exhibit a shift towards deeper water with increasing size and age (Zimmermann and  
463 Goddard 1996), Arrowtooth Flounder grow faster and mature at a smaller size and younger age  
464 than Kamchatka Flounder (Stark 2012). In addition, large Kamchatka Flounder tend to be  
465 distributed at greater depths and in warmer oceanic waters than large Arrowtooth Flounder  
466 (Zimmermann and Goddard 1996). Through an accumulation of dietary data (Livingston et al.  
467 2017), we find evidence against trophic equivalence between species, and identify an  
468 interspecific difference in trophic niche consistent with hypothesized variation in foraging  
469 efficiency due to divergent gill raker morphology.

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706

707

708 TABLE CAPTIONS

709 Table 1. Sample sizes stomachs sampled per year, by species and survey. Numerator indicates  
710 the number of non-empty stomachs, denominator indicates total number of stomachs, number in  
711 parentheses indicates percentage of non-empty stomachs. Dashes (-) indicate no bottom-trawl  
712 survey was conducted.

713

714 Table 2. Sample sizes of stomachs for flounder groups, assigned by species, spatial stratum, and  
715 size class. Numerator indicates the number of non-empty stomachs, denominator indicates total  
716 number of stomachs, number in parentheses indicates percentage of non-empty stomachs.

717 *Italicized groups, with sample sizes <10, were excluded from analysis.*

718

719 Table 3. Pairwise ANOSIM R statistics (lower diagonal) for the four relevant predator clusters  
720 (W, X, Y, Z) identified using complete linkage clustering. Significance levels denoted by:  $P <$   
721  $0.1$  (^),  $P < 0.05$  (\*),  $P < 0.01$  (\*\*),  $P < 0.001$  (\*\*\*). SIMPER results (upper diagonal) indicate  
722 which prey categories cumulatively contribute  $\geq 70\%$  of between-cluster dissimilarity, ranked by  
723 contribution. Prey categories are: BF – Benthic fish, GA – Gadidae, SH – Shrimp, ZP –  
724 Zooplankton.

725

726 TABLES

727 Table 1.

Year	Arrowtooth		Kamchatka	
	Shelf	Slope	Shelf	Slope
2007	582/789 (73.8)	-	18/18 (100)	-
2008	313/568 (55.1)	67/270 (24.8)	124/156 (79.5)	42/97 (43.3)
2009	191/388 (49.2)	-	21/27 (77.8)	-
2010	395/628 (62.9)	122/197 (61.9)	20/34 (58.8)	49/78 (62.8)
2011	493/881 (56)	-	24/46 (52.2)	-
2012	365/585 (62.4)	96/202 (47.5)	145/190 (76.3)	45/88 (51.1)
2013	418/733 (57)	-	75/102 (73.5)	-
2014	442/607 (72.8)	-	49/68 (72.1)	-



2015	456/948 (48.1)	-	164/246 (66.7)	-
2016	722/1,411 (51.2)	106/320 (33.1)	181/289 (62.6)	37/144 (25.7)
Overall	4,377/7,538 (58.1)	391/989 (39.5)	821/1,176 (69.8)	173/407 (42.5)

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Predator	Stratum					
	A	B	C	D	E	F
Arrowtooth flounder						
≤19 cm		133/158 (84.2)	55/88 (62.5)	127/165 (77.0)	120/178 (67.4)	
20-29 cm	1/1 (100.0)	179/260 (68.8)	97/174 (55.7)	200/387 (51.7)	260/501 (51.9)	4/7 (57.1)
30-39 cm	6/8 (75.0)	336/470 (71.5)	116/180 (64.4)	194/396 (49.0)	202/484 (41.7)	64/120 (53.3)
40-49 cm	19/21 (90.5)	560/748 (74.9)	161/242 (66.5)	152/352 (43.2)	227/513 (44.2)	105/316 (33.2)
≥50 cm	12/18 (66.7)	674/1015 (66.4)	155/252 (61.5)	131/379 (34.6)	260/548 (47.4)	218/546 (39.9)
Kamchatka flounder						
≤19 cm		20/26 (76.9)	1/3 (33.3)	21/31 (67.7)	15/28 (53.6)	0/1 (0.0)
20-29 cm		60/83 (72.3)	11/18 (61.1)	21/32 (65.6)	31/50 (62.0)	3/6 (50.0)
30-39 cm	7/7 (100.0)	88/124 (71.0)	35/55 (63.6)	31/57 (54.4)	25/63 (39.7)	8/27 (29.6)
40-49 cm	23/29 (79.3)	164/198 (82.8)	74/104 (71.2)	11/18 (61.1)	19/33 (57.6)	49/143 (34.3)
≥50 cm	21/26 (80.8)	87/105 (82.9)	48/63 (76.2)	5/9 (55.6)	3/14 (21.4)	113/230 (49.1)

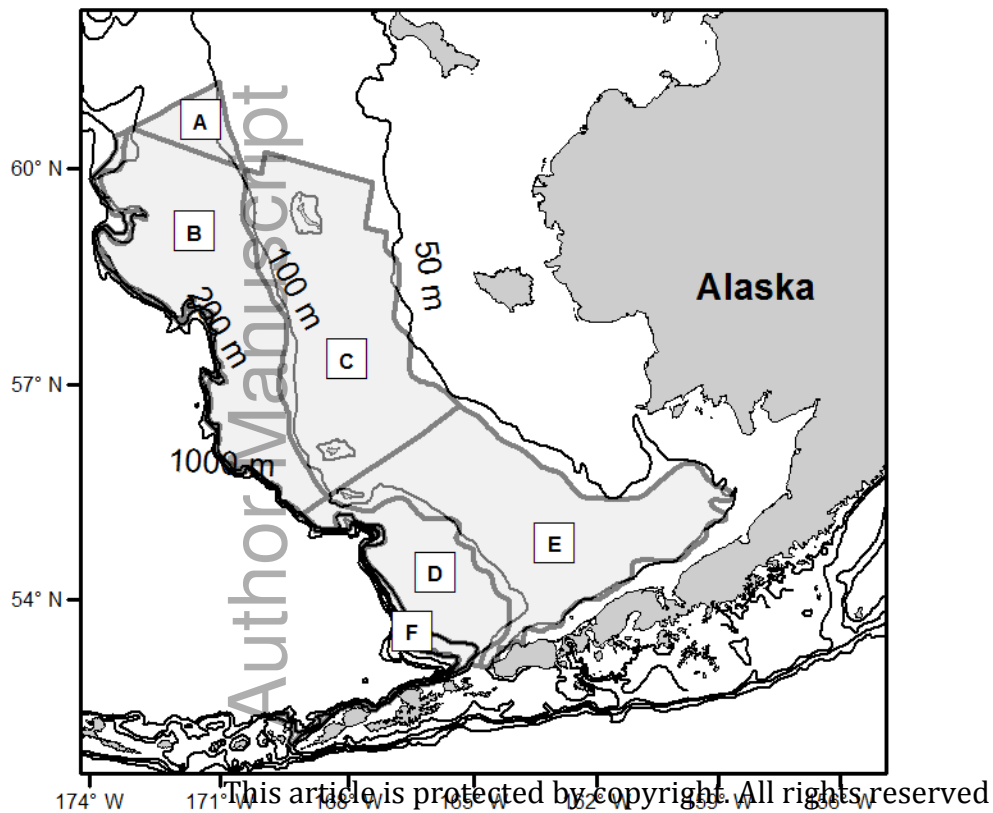
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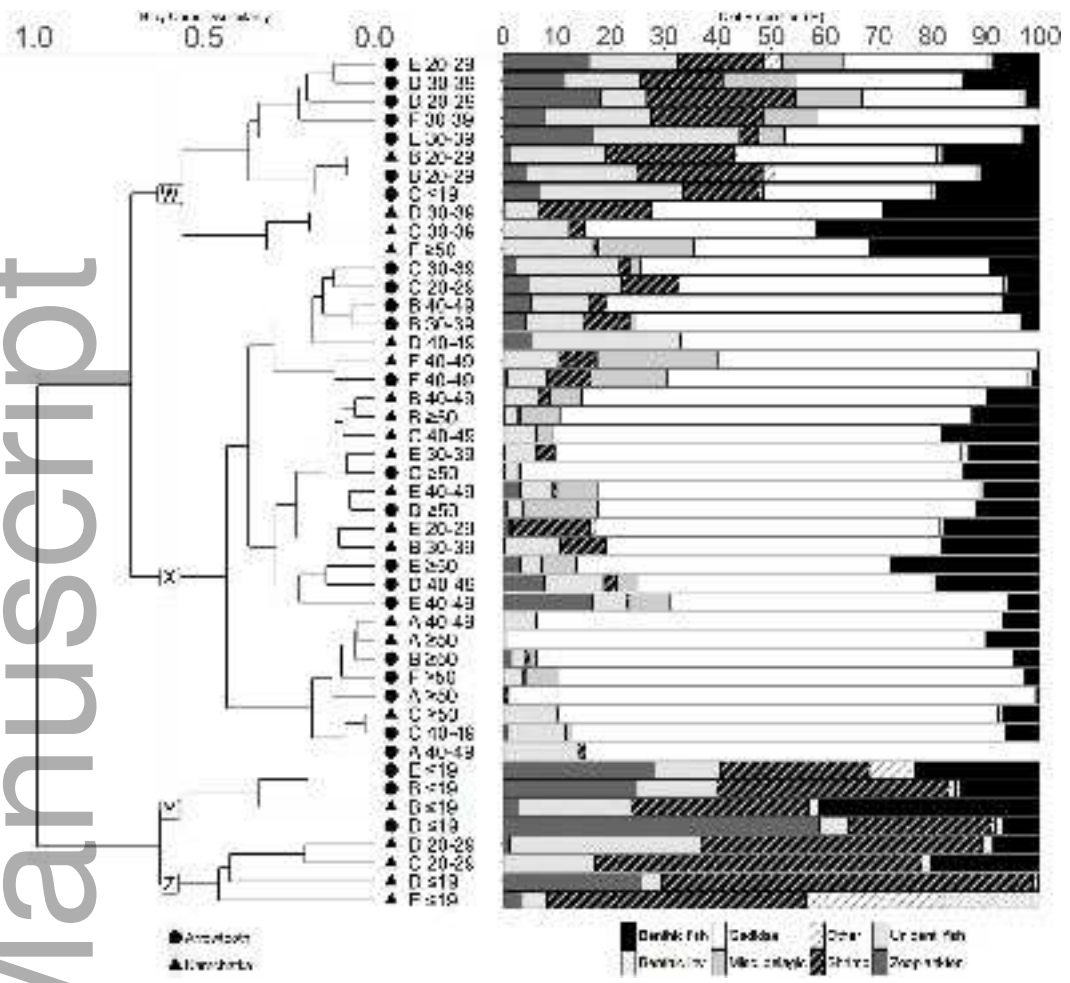
732 Table 3.

Cluster	W	X	Y	Z
W		GA,SH,BF	GA,ZP,SH	SH,GA,BF
X	0.92***		GA,SH,ZP	GA,SH
Y	0.91***	1.00**		SH,ZP,BF
Z	0.98**	1.00***	0.33^	

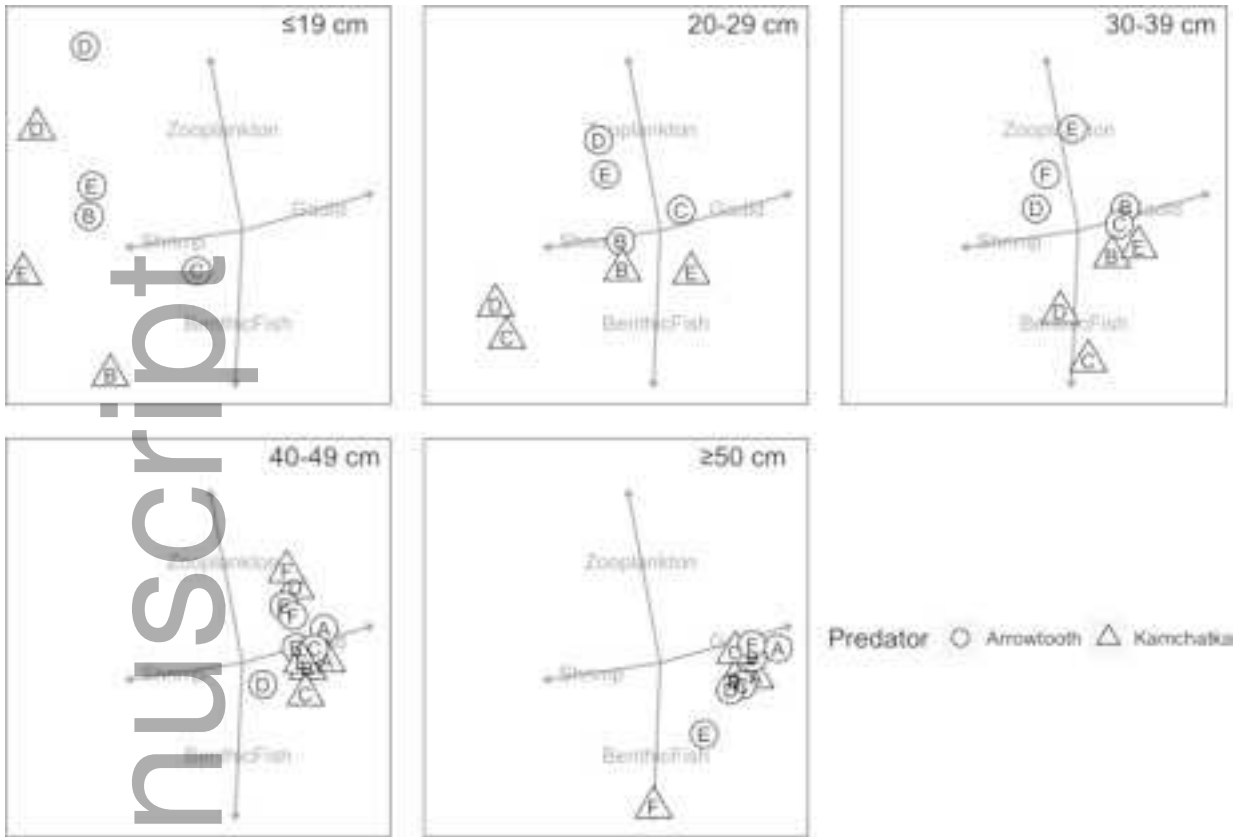
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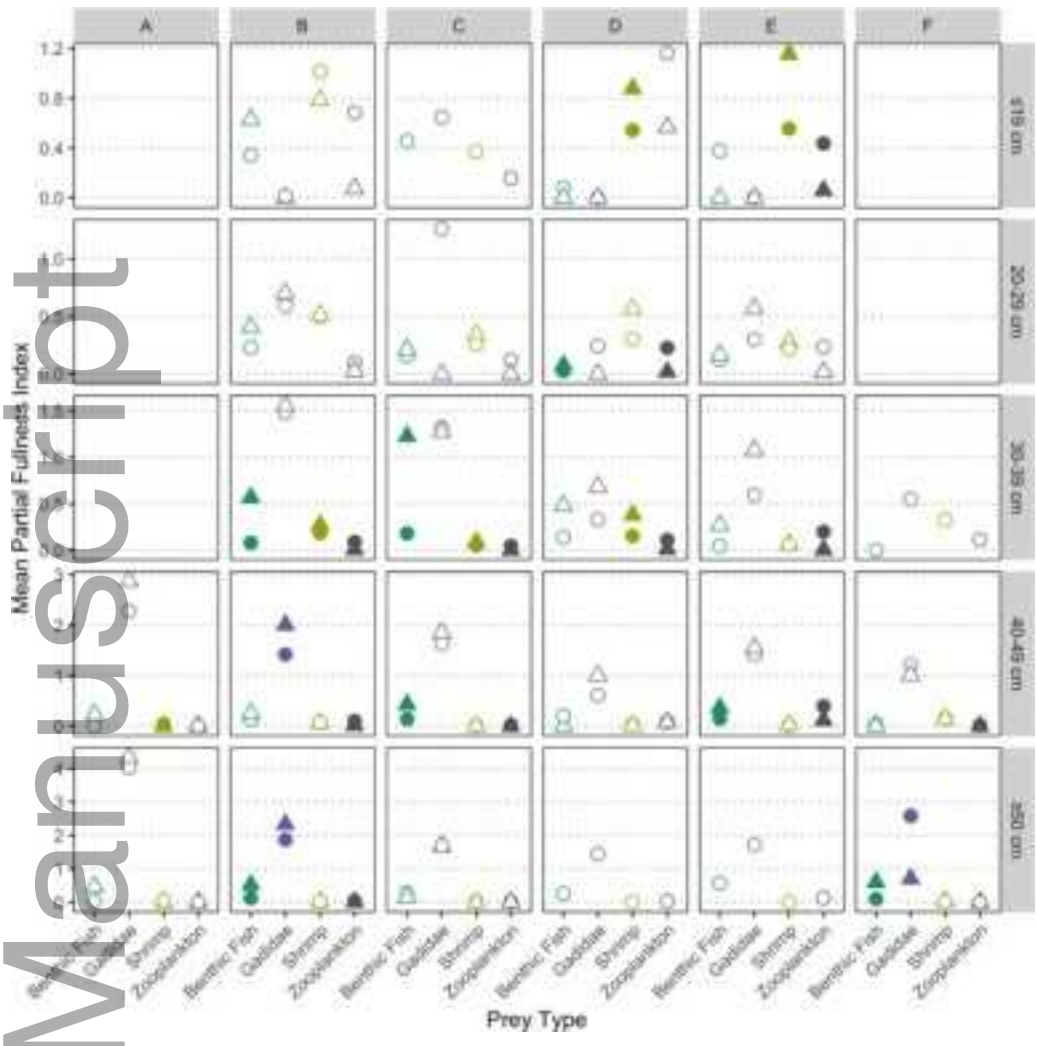




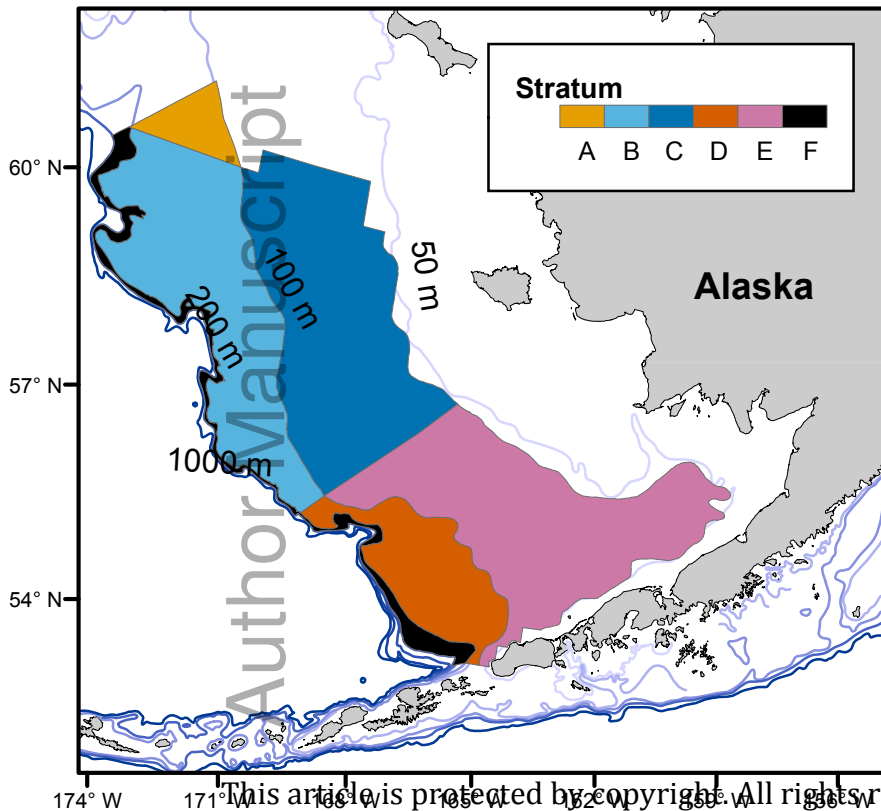
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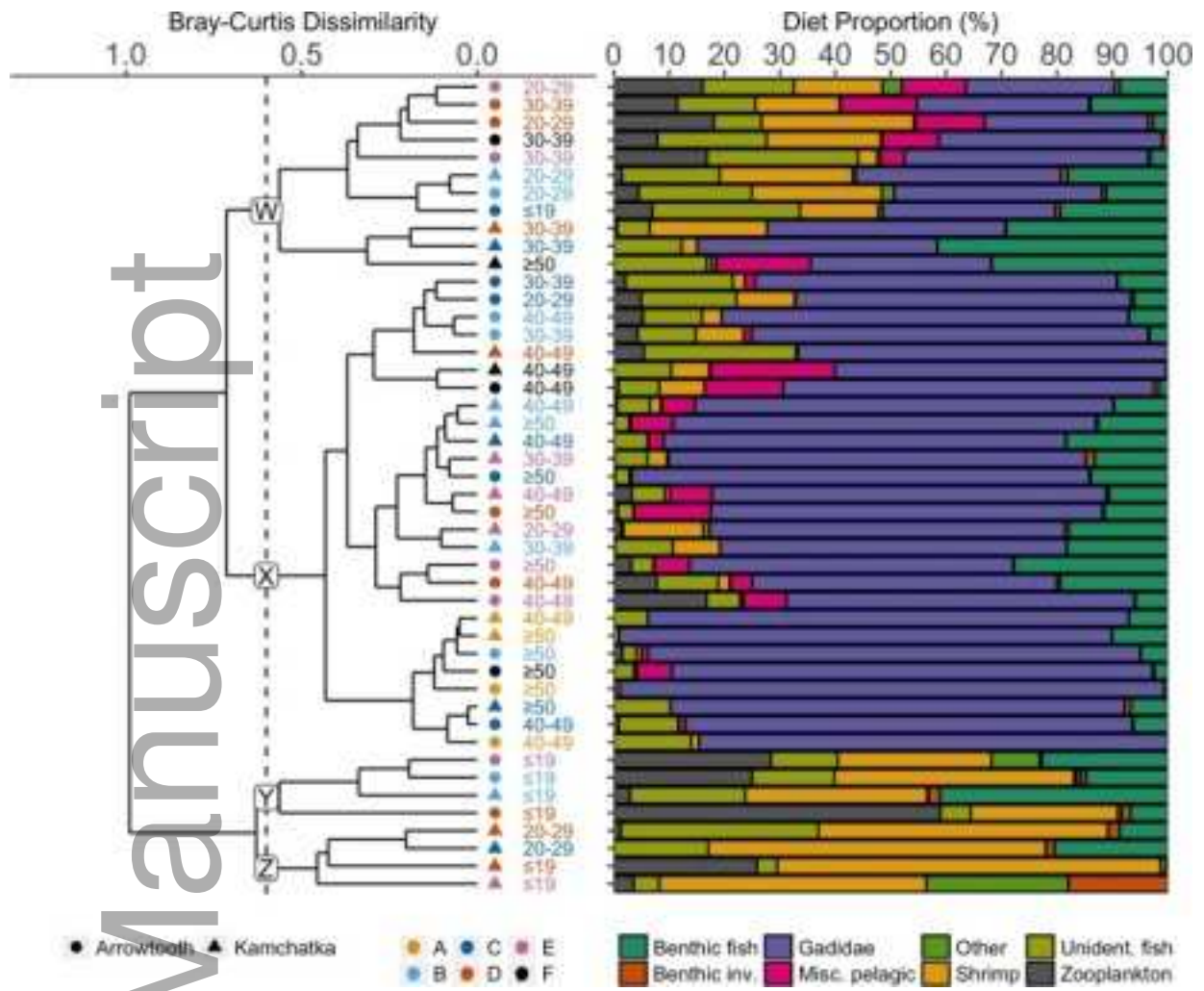


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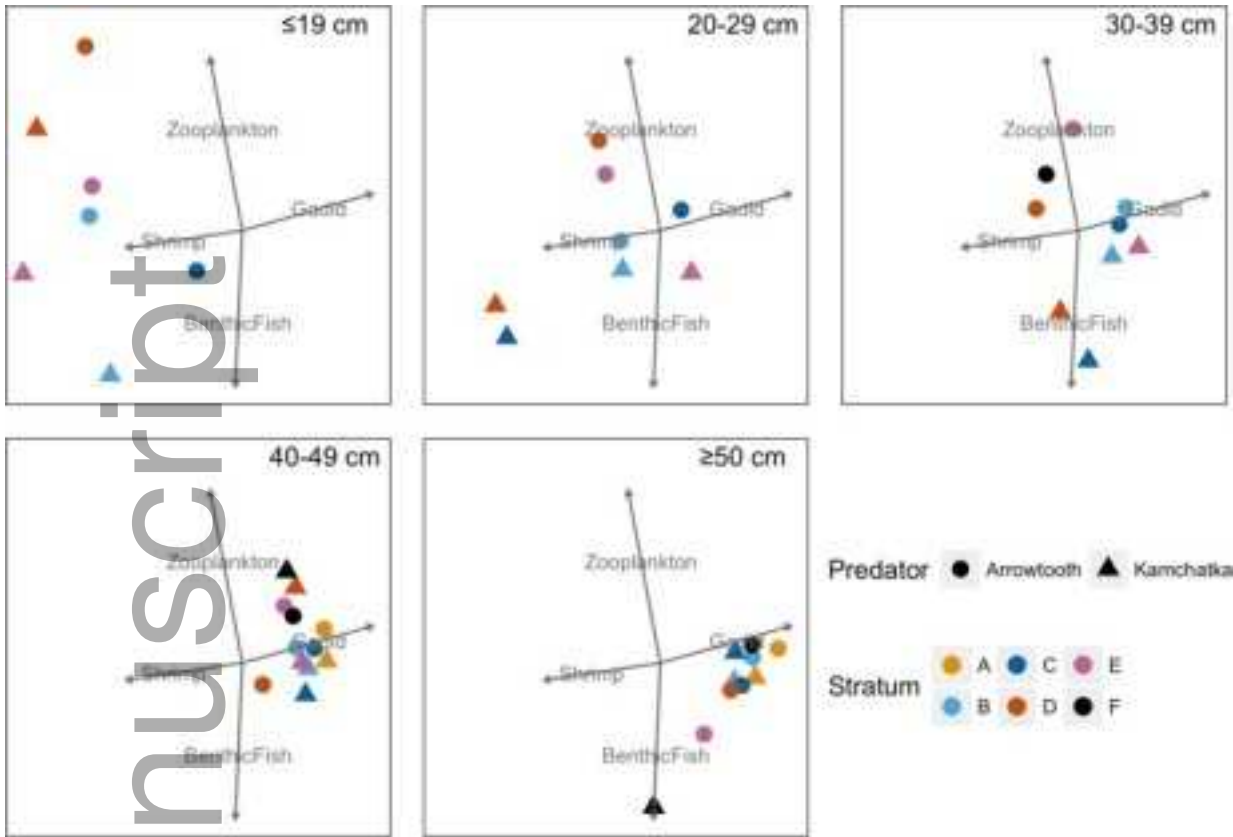




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