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1 The effect of oceanographic variability on the distribution of larval fishes of the

2 northern Bering and Chukchi seas

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16 ABSTRACT

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18	We investigated the pelagic habitat requirements of Arctic larval fish and the effects of interannual
19	variability of ocean conditions on their distribution. We examined the distribution of larval Arctic cod,
20	Bering flounder, yellowfin sole and capelin in the Chukchi and northern Bering seas during two years with
21	different oceanographic conditions. We found that despite marked changes in water mass distribution,
22	the distributions of larval fishes were not significantly different between the two years. In both years,
23	Arctic cod and Bering flounder were found in cold, high salinity shelf waters advected from the south and
24	influenced by winter cooling (Chukchi Winter Water and Anadyr Water mix). Yellowfin sole and capelin
25	distributions were also similar from year-to-year but they were only found in warm, low salinity Alaska
26	Coastal Water. The cold, high salinity water masses had elevated large copepod biomass, and the Alaska
27	Coastal Water had elevated small copepod biomass. Thus, we propose that these water masses provided
28	different but nonetheless potentially profitable foraging habitat for the four species of larval fishes. We
29	conclude by suggesting that the timing and location of spawning of these species has evolved such that
30	larval offspring are distributed in suitable foraging habitat despite interannual variability in ocean
31	conditions. This study provides a baseline of Arctic larval fish distribution and insight into the degree of
32	climate variability that might be expected to impact early life history stages of larval fish. Our results also
33	increase the knowledge of the mechanistic links between oceanography and the early life history of fish.
34	Because growth and survival of early life stages of fish often drives population change, our results
35	contribute to the understanding of the impacts of climate change on Arctic fish populations.
36	

37 Keywords: USA, Alaska, Chukchi Sea, Fish larvae, Climate changes, Polar waters, Habitat

38 1. Introduction

39

40 The Arctic climate is rapidly changing. Ocean temperatures have been warming at over two times the global rate since the mid-20th century (Huang et al., 2017). Sea ice extent, duration and 41 42 thickness have been declining at an increasing pace (Kwok and Rothrock, 2009; Meier et al., 2012; 43 Wang and Overland, 2015). Embedded within these long-term trends is a high degree of interannual 44 variability in sea ice timing, duration, extent and thickness, as well as ocean temperature and currents 45 (Day et al., 2013; Wang and Overland, 2015; Woodgate et al., 2015). 46 It is not known with certainty how changes in Arctic climate will impact fish, although impacts are 47 expected. Increased water temperatures may affect growth rates negatively or positively depending on 48 the fish's optimum growth temperature and food availability (Björnsson et al., 2001; Laurel et al., 2015). Reductions in sea-ice extent may negatively impact fish that depend on sea ice for spawning, such as 49 50 Arctic cod (Rass, 1968). On the other hand, an increase in the open water period due to loss of sea ice 51 may result in increased primary production which could benefit fish feeding (Arrigo et al., 2008). The 52 timing of spring season sea ice retreat is also an important factor. Earlier sea-ice retreat with ocean 53 warming may change the timing and intensity of the spring bloom of phytoplankton resulting in a 54 reduction in productivity and/or a mismatch between the timing of larval first feeding and the availability 55 of prey (Grebmeier, 2012).

The survival of early life history stages of fish is generally thought to be an important determinant of variability in the abundance of subsequent older age classes (Hjort, 1914; Lasker, 1981). Furthermore, early life stages of fish are particularly sensitive to changes in their environment such as variability in transport to nursery habitat, exposure to predators and changes in food availability (e.g. Siddon et al., 2011). Thus, an understanding of the impacts of interannual variability and long-term climate trends on Arctic fish populations benefits from information on Arctic fish early life history.

Our work was part of the Arctic Ecosystem Integrated Survey (Arctic Eis), a University of Alaska College of Fisheries and Ocean Sciences program conducted in 2012 and 2013 to document physical and biological oceanography, zooplankton, ichthyoplankton, demersal fish and pelagic fish. The overarching goals of the program were to understand the environmental forcing that impacts northern Bering and Chukchi sea ecosystems and to predict the future effects of reduced sea ice and ocean warming on these ecosystems (Mueter et al., 2017). The goal of the work presented here was to study Arctic fish larval distributions and oceanographic habitat associations.

69 The northern Bering and Chukchi seas are mostly shallow shelves (< 60 m depth) with currents typically flowing northward due to the difference in sea level between the Pacific and the Arctic (Aagaard 70 71 et al., 2006). Local winds can slow the northward flow or even redirect the flow to the south or west, depending on the direction of the winds (Panteleev et al., 2010). Water masses in the northern Bering 72 73 and Chukchi seas include warmer, fresher Alaska Coastal Water flowing along the eastern shore and 74 Anadyr/Bering Summer Water flowing across the shelf with moderate temperatures and salinities (Fig. 75 1). The Anadyr/Bering Summer Water transforms to Chukchi Summer Water as it flows north over the 76 Chukchi Sea shelf. Near-bottom cold and salty Bering and Chukchi Winter Waters are the result of 77 previous winter cooling and are resident to each shelf area. Finally, Melt Water is colder, fresher water at 78 the surface formed by melting of sea ice and in summer is only found in the northern Chukchi Sea 79 (Danielson et al., 2017). These different water masses have different nutrient concentrations and 80 productivity. The colder shelf and winter waters are typically nutrient-rich and productive whereas the 81 Alaska Coastal Water is low in nutrients and productivity (Danielson et al., 2017; Springer and McRoy, 82 1993).

Atmospheric and oceanographic conditions observed during the Arctic Eis surveys were different
between 2012 and 2013, leading to subsequent variations in water mass distribution (Danielson et al.,
2017). Sea level pressure and the resulting wind fields strongly contrasted between years. In 2012, low
pressure was centered over the northwestern Chukchi Sea resulting in the typical winds from the

87	southwest. In 2013, zonally (longitudinally) elongated low pressure over the Bering Sea resulted in zonal
88	winds from the east. Drifter and high-frequency radar data suggest that the result of these wind
89	differences was that the freshwater core of the Alaska Coastal Current was mostly absent from the
90	Northeast Chukchi Sea during 2013. These differences in winds and currents resulted in pronounced
91	differences in the distribution of water masses. In 2012, Alaska Coastal Water was observed close to
92	shore from the northern Bering Sea all the way to the Northeast Chukchi Sea (Point Barrow). In contrast,
93	in 2013, Alaska Coastal Water was only observed as far north as Ledyard Bay in the Chukchi Sea; and it
94	spread at least 100 km farther offshore in the Northern Bering Sea compared to 2012. Along with more
95	extensive northerly distribution of Alaska Coastal Water in 2012 the Anadyr/Bering Summer
96	Water/Chukchi Summer Water mix extended farther north in 2012 than in 2013.
97	There were also interannual differences in temperature, salinity, nutrients and chlorophyll
98	biomass (Danielson et al., 2017). Surface waters were warmer and near-bottom waters were less saline in
99	2013 than 2012. Macronutrients, particularly in surface waters, were also different between years: there
100	was less surface nitrate, ammonium and phosphate in 2013 than in 2012, likely leading to nutrient
101	limitation of phytoplankton growth in 2013. In fact, average integrated chlorophyll was lower in 2013
102	than in 2012 (Danielson et al. 2017). Sea-ice conditions in 2012 and 2013 were similar. Winter sea ice was
103	relatively high but June sea-ice concentrations were below normal in both years.
104	To investigate the potential impact of interannual variability in water mass distribution, we
105	compared the spatial distribution of fish larvae collected in the northern Bering and Chukchi seas in 2012
106	and 2013. Our expectation was that larvae would be distributed farther north in 2012, and farther
107	offshore in 2013. We propose that this would be a result of spawning location and subsequent advection
108	within the water masses. To understand larval fish habitat associations, we mapped the distribution of
109	larvae relative to water mass and to explore the potential foraging value of water masses, we examined
110	their biological characteristics in terms of chlorophyll and zooplankton biomass. We also mapped the
111	distribution of eggs and compared larval length frequency distributions for clues about spawn timing and 5

112 location. The overall goal of our research presented here is to define larval oceanographic habitat and to 113 improve our understanding of the mechanisms and the magnitude of climate variability that impact Arctic 114 fish early life history. 115 116 117 2. Methods 118 119 Ichthyoplankton and oceanographic data were collected at stations spaced 28 or 55 km apart, 120 depending on location, over a survey grid that spanned the U.S. northeastern Bering Sea and Chukchi Sea 121 shelves (157–170°W, 60–72°N, Fig. 2). Sampling occurred from 7 August – 24 September in both years, 122 with a similar order of station occupations. 123 Ichthyoplankton were collected at the primary stations (55-km spacing) and at the higher 124 resolution stations (28-km) with a 60-cm bongo sampler fitted with two 0.505 mm mesh nets with 125 detachable codends at 138 stations in 2012 and 143 stations in 2013. During all cruises, quantitative 126 oblique tows were made to a maximum depth of 200 m (or to within 10 m of the substratum), resulting 127 in vertically integrated estimates of larval fish abundance. The ship speed was monitored and adjusted 128 (1.5 to 2.5 knots) throughout each tow to maintain a wire angle of 45° from the ship to the bongo net. 129 The nets were equipped with a calibrated flow meter; therefore, catch rates were standardized to 130 effort and converted to catch 10 m⁻² of sea surface area (CPUE; number 10 m⁻²). Sampling occurred 131 during daylight hours as per ship protocol. Samples were preserved in 5% formaldehyde-sea water 132 solution buffered with sodium borate. 133 Samples were sorted and fish eggs, larvae and juveniles identified to the lowest taxonomic level possible at the Plankton Sorting and Identification Center in Szczecin, Poland. Taxonomic identifications 134 135 were verified at the Alaska Fisheries Science Center (AFSC) in Seattle, WA, following Matarese et al. 136 (1989), Busby et al. (2017), and the Ichthyoplankton Information System

137 (https://access.afsc.noaa.gov/ichthyo/). Some fish eggs and larvae were categorized as taxonomic groups 138 (e.g. Limanda spp., Liparis spp.) due to limitations associated with identifying egg and larval stages to the 139 species level. In the case of Limanda spp. eggs, Limanda aspera were by far the most common species of 140 Limanda larvae, so we treated Limanda spp. eggs as L. aspera in the analyses. In some cases, 141 identifications of damaged specimens were made at the family level. In these instances, the 142 identifications were not included in counts of species richness or diversity because they were considered 143 to be of taxa that could normally be successfully identified. Taxonomic nomenclature follows 144 (Mecklenburg et al., 2018), except for Bering flounder (*Hippoglossoides robustus*) which, according to 145 Mecklenburg et al. should now be classified as flathead sole (*Hippoglossoides elassadon*) in the Arctic. 146 However, the American Fisheries Society (Page et al., 2013) still lists the occurrence of flathead sole as 147 Pacific only, and Bering flounder as Pacific and Arctic. We defer to the latter source and use Bering 148 flounder in this paper. We use Arctic cod for the common name of *Boreogadus saida* after Mecklenburg 149 and Steinke (2015).

Fish were measured for standard length (SL) to the nearest 1.0 mm. The separation point between the larval and juvenile stages for *B. saida* is 25.0 mm standard length (SL) based on the size at transformation of *Gadus chalcogrammus* determined by Brown et al. (2001). For other taxa, definition of the juvenile stage follows Kendall et al. (1984) as a fish having complete adult complements of fin elements, scales and "the appearance of a small adult". The only taxa for which we caught juveniles was *B. saida*.

Macro- and mesozooplankton were also collected with the 60-cm bongo frame (505 um mesh). Meso- and microzooplankton were sampled with a 20-cm PairVet net with 150 µm mesh attached to the array with the 60-cm frame. PairVet samples were only analyzed for the 2012 cruise, due to loss of data sheets at sea during 2013. All samples were preserved in 5% formalin, buffered with seawater for later processing. In the laboratory, each net sample was subsampled and taxa were identified, staged, counted and weighed. All animals in the samples were identified to the lowest taxonomic category possible.

Sibling species *Calanus marshallae* and *C. glacialis* co-occurring in the Bering and Chukchi seas (e.g.
Nelson et al., 2009) were not discriminated and are named as *C. glacialis* hereafter. Recent studies
confirm that the vast majority of *Calanus* spp. in the northern Bering Sea are *C. glacialis* (Campbell et al.,
2014). Copepodites stages were identified and recorded. Biomass values by station were computed for
each species in grams m⁻³. See Pinchuk and Eisner (2016) for details of zooplankton sampling and
laboratory analyses.

At the primary stations (55-km spaced), ocean temperature and salinity were determined from conductivity-temperature-depth measurements collected with a Sea-Bird (SBE) 911 or SBE 25 CTD equipped with a Wetlabs Wet-Star fluorimeter to estimate in vivo Chla. In addition, a SBE 49 or SBR19+ CTD was towed with the bongo net to obtain hydrographic data at higher spatial resolution (between primary stations). At the primary stations, water samples for total Chla were collected at ~10 m depth intervals.

174 Danielson et al. (2017) identified four different bottom water masses-based on T/S diagrams derived _ 175 from the survey oceanographic data: Alaska Coastal Water (ACW), Anadyr Water/Bering Shelf 176 Water/Chukchi Shelf Water (AW Mix), Bering Winter Water (BWW) and Chukchi Winter Water (CWW). 177 ACW was the warmest and freshest (7 - 12 °C; 20 - 32 salinity). CWW and BWW were the coldest and most saline (-2.0 to 0 °C; 30 – 33.5 salinity). The AW Mix was intermediate in temperature and high in 178 179 salinity (0 – 7 °C; 30-33.5 salinity). Surface water masses were: Melt Water, which was relatively cool 180 and fresh (-2 - 7 °C; 25 - 30 salinity); and AW Mix and ACW (as defined above). Ichthyoplankton 181 distributions were overlaid on water mass distributions using ArcMap 10.5 (ver 10.5.0.6491). 182 A statistical test based on a generalized two-sample Cramér-von Mises test was employed to test 183 for differences between the spatial distributions of ichthyoplankton between years (Syrjala, 1996). The 184 null hypothesis for this specific test is that across the study area, the distributions of the populations are 185 the same. The alternative hypothesis for this test is that there is some unspecified difference in the 186 underlying distributions. The distributions are normalized so the test is sensitive to differences in the way

187	populations are distributed across space, but insensitive to differences in abundance. The test is
188	nonparametric, so no assumptions are required about the distributions of the populations. The test was
189	implemented in R version 3.3.2 (R Core Team, 2016) using the "syrjala" function. The Kruskal-Wallis rank
190	sum test was employed to test for differences in chlorophyll and zooplankton biomass density among
191	water masses. A non-parametric test was used because the skewed distributions and heterogeneity of
192	variances could not be remedied by data transformation. The test was implemented in R version 3.3.2 (R
193	Core Team 2016).
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196	3. Results
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198	A total of 1057 individuals and 31 taxa of larvae and juveniles were sampled by the ichthyoplankton nets
199	in 2012 and 2013 (Table 1). The four most abundant taxa collected were Pacific capelin (Mallotus
200	catervarius), Arctic cod (Boreogadus saida), Bering flounder (Hippoglossoides robustus) and yellowfin sole
201	(Limanda aspera). These four taxa were the focus of further analysis. Juvenile fish caught in the nets were
202	all Arctic cod. Eggs of only 5 taxa were caught, mostly Bering flounder and yellowfin sole. Walleye pollock
203	(Gadus chalcogrammus) eggs were only caught in the northern Bering Sea.
204	Bering flounder eggs were distributed in the north Chukchi Sea over the shelf during 2012 (Fig. 3
205	a). Very few eggs were caught in 2013, but they were found in a similar area as in 2012 (Fig. 3 b). In
206	contrast, yellowfin sole eggs were found farther south, in the northern Bering Sea, and in the
207	south/central Chukchi Sea, and relatively close to shore compared to Bering flounder (Fig. 4). No eggs of
208	either Arctic cod or Pacific capelin were caught during the surveys.
209	Arctic cod larvae and juveniles were distributed in the north and northeast area of the survey in
210	both years (Fig. 5a, b.). Arctic cod were the only taxa for which we caught juvenile fish. The distributions
211	of the two life stages overlapped, such that for further analyses, we combined the data. The Cramer von- 9

Mises test indicated that there was not enough evidence to support a statistically significant difference in the distribution of Arctic cod between years (ψ =3.233, *P*=0.165). Bering flounder larvae were distributed throughout the Chukchi Sea, and in the northern Bering Sea (Fig. 5b, c). The catch density of Bering flounder in 2013 was much less than 2012. Similar to Arctic cod, the Cramer von-Mises test indicated that there was not enough evidence to support a statistically significant difference in the distributions between 2012 and 2013 (ψ =1.498, *P*=0.767).

218 Yellowfin sole and capelin larvae had more southerly distributions than Arctic cod and Bering 219 flounder (Fig. 6). Similar to the other two taxa, there was no statistically significant difference in the 220 distributions between 2012 and 2013 (yellowfin sole: ψ =3.216, P=0.065; capelin: ψ =2.462, P=0.779). 221 Flatfish larval length-frequency distributions were examined along with their egg distributions 222 (reported above) for information on spawning locations that could explain the distribution of larvae. No 223 eggs of either Arctic cod or capelin were caught. Bering flounder larvae distribution was discontinuous 224 around 70°N in 2012 (Fig. 5c). Very few larvae were caught in 2013. There was little overlap in the length-225 frequency distributions north and south of 70°N (Fig. 7) – larvae were smaller north of 70°N and larger 226 south. Yellowfin sole larvae distribution was discontinuous at around 65.5°N (Fig. 6a, b). However, in 227 contrast with Bering flounder, the length- frequency distributions of yellowfin sole larvae were similar 228 north and south of 65.5°N in both years (Fig. 8).

229 Overlaying the distribution of ichthyoplankton on bottom water masses shows that Arctic cod 230 were only present in the CWW and AW Mix in both years (Fig. 5a, b). Similarly, Bering flounder were most 231 abundant in the CWW and AW Mix (Fig. 5c, d). The relatively northerly extension of the AW Mix and ACW 232 in 2012, reported by Danielson et al. (2017), is also evident. The distributions of yellowfin sole and 233 capelin (Fig. 6) are shown overlaid on surface water mass distributions because there was spatial 234 coherence between larvae and both bottom and surface ACW and the oceanographic signal of ACW was 235 more pronounced in surface waters. BWW and CWW were not evident in surface waters (Fig. 6), only in 236 waters at depth (Fig. 5). The ichthyoplankton tows were not depth-discrete, so it is unknown at which

237 depths the larvae occurred. Yellowfin sole and capelin were distributed in the southern two-thirds of the 238 study area and were virtually restricted to ACW in both years (Fig. 6), in contrast to the more northerly 239 Arctic cod and Bering flounder, which occurred in the cold, high salinity water masses as described above. 240 The difference in integrated chlorophyll biomass among water masses was statistically significant 241 in 2012 (Kruskal-Wallis Chi-squared = 12.085, p-value = 0.002), but not in 2013 (Kruskal-Wallis Chi-242 squared = 3.4023, p-value = 0.182) (Fig. 9 a, b). Post-hoc tests showed that chlorophyll biomass was 243 significantly greater in ACW compared to CWW and greater in AW Mix compared to CWW in 2012 (Fig 9 244 a). There was no significant difference in chlorophyll biomass between ACW and AWMix. Post-hoc tests 245 comparing BWW with other water masses were not conducted, because BWW was only observed at one 246 station (n=1).

The difference in *Calanus glacialis* biomass density among all water masses was significant in 2012 (Kruskal-Wallis Chi-squared = 25.724, p-value <0.001), and marginally significant in 2013 (Kruskal-Wallis Chi-squared = 4.5013, p-value = 0.10) (Fig. 9 c, d). Post-hoc tests showed that *Calanus glacialis* biomass density was significantly greater in AW Mix than ACW in both years; and significantly greater in CWW than ACW in 2012. The smaller-sized stages of *Calanus glacialis* copepodites (C2 and C3) were proportionally most abundant in CWW in 2012 (Fig. 10) and even more so in 2013 (Fig. 11). C2 stages were only found in CWW in both years.

254 In contrast to Calanus glacialis, the biomass density of nauplii and smaller taxa of copepods 255 (sampled with the PairVet net) was similar or higher in ACW compared to the other water masses in 256 2012. The PairVet net samples collected in 2013 were not analyzed due to loss of data sheets at sea. 257 Calanoida nauplii biomass density was significantly different among water masses (Fig. 12 a; Kruskal-258 Wallis Chi-squared = 8.1041, p- value < 0.05). Post-hoc tests showed that nauplii biomass density was 259 significantly greater in ACW compared to AW Mix. Pseudocalanus spp. biomass density was not 260 significantly different among water masses (Fig. 12 b; Kruskal- Wallis Chi-squared = 1.8085, p-value = 261 0.40). Acartia spp. and Oithona spp. biomass densities were significantly different among water masses

262	(<i>Acartia</i> : Kruskal-Wallis Chi-squared = 34.34, p-value < 0.001. <i>Oithona</i> : Kruskal-Wallis Chi-squared = 32.5,
263	p-value < 0.001) (Fig 12 c, d). Post-hoc tests showed that Acartia and Oithona biomass densities were
264	greater in ACW compared to AW Mix and compared to CWW. Oithona biomass density was also
265	significantly greater in AW Mix compared to CWW.
266	In summary, Arctic cod and Bering flounder were most abundant in cold, high salinity water
267	masses (AW Mix and CWW), which had elevated large copepod (Calanus glacialis) biomass density
268	compared to Alaska Coastal Water. In contrast, yellowfin sole and capelin were only found in warm,
269	low salinity Alaska Coastal Water that was high in Calanoida nauplii and small copepod biomass
270	density (Acartia spp. and Oithona spp.) compared to the cold, high salinity water masses (AW Mix and
271	CWW).
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274	4.0 Discussion
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276	Arctic cod, Bering flounder, yellowfin sole and capelin were the four most abundant species in the
277	ichthyoplankton catch during the 2012 and 2013 Arctic EIS surveys. Previous ichthyoplankton surveys
278	have caught a similar mix of species (Busby et al., in review; Norcross et al., 2010; Randall et al., 2019;
279	Wyllie-Echeverria et al., 1997), although Randall et al. (2019) also caught relatively high numbers of Arctic
280	sand lance (Ammodytes hexapterus) and Arctic shanny (Stichaeus punctatus); and Busby et al. (in review)
281	caught relatively high numbers of snailfish (Liparis gibbus).
282	Arctic cod and capelin are important energy-rich prey for upper trophic level predators (Hop
283	and Gjøsæter, 2013). Arctic cod are consumed by beluga whales (Delphinapterus leucas), ringed seals
284	(Pusa hispida), bearded seals (Erignathus barbatus), harp seals (Pagophilus groenlandicus), black
285	guillemot (<i>Cepphus grylle</i>) and thick-billed murres (<i>Urig lomvig</i>) (Bradstreet, 1976; Bradstreet et al.,

1986; Bradstreet and Cross, 1982; Huntington and The communities of Buckland, Elim, Koyuk, Point
Lay, 1999).

288 Alaska Arctic communities on the Chukchi Sea coast rely on many of these marine mammal 289 species for subsistence use (Hovelsrud et al., 2008; Huntington and The communities of Buckland, Elim, 290 Koyuk, Point Lay, 1999). Capelin are preyed upon by mammal, bird and fish predators such as harp seals 291 (Stenson et al., 1997), thick-billed murres (Provencher et al., 2012) and Atlantic cod (Mehl and Sunnana, 292 1991; Rose and O'Driscoll, 2002). Flatfishes are also important subsistence and ecological resources in 293 the Arctic (Grebmeier et al., 2006a). Furthermore, yellowfin sole is one of the most abundant flatfish 294 species in the eastern Bering Sea and currently is the target of the largest flatfish fishery in the world 295 (Wilderbuer et al., 2017).

296 There were no statistically significant differences between 2012 and 2013 in the distributions of 297 Arctic cod, Bering flounder, yellowfin sole and capelin larvae. This was observed despite wind-driven 298 changes in water mass distribution between 2012 and 2013 (Danielson et al., 2017). We expected that 299 larvae would be distributed less far north and further offshore in 2013 due to the reduced northerly 300 extension of the Alaska Coastal Water and Anadyr Water Mix; and the offshore spread of Alaska Coastal 301 Water. We did observe fewer Bering flounder larvae in 2013 compared to 2012. Perhaps the lower 302 nutrient concentration and phytoplankton biomass observed in 2013 (Danielson et al., 2017) reduced the 303 magnitude or delayed the timing of Bering flounder spawning and/or negatively impacted the survival of 304 early larvae. The larval densities of the three other species were similar during the two years. 305 In both years, Arctic cod and Bering flounder larvae were found in cold water masses that we

306 suggest provided good foraging opportunities. Arctic cod were only found in the northern third of the 307 survey area in the Anadyr Water/Bering Shelf Water/Chukchi Shelf Water Mix (AW Mix) and Chukchi 308 Winter Water (CWW). Bering flounder were similarly virtually restricted to these two cold and high 309 salinity water masses. We suggest that the association of larval fish with particular water masses is the 310 result of spawning location and subsequent entrainment of eggs and larvae in the currents that are

311 associated with the water masses. Arctic cod spawn under the ice in late winter. Eggs are buoyant and 312 develop near the surface, beginning under the ice cover and ending near the surface in ice-free areas 313 after melting of the ice cover (Rass, 1968). Bering flounder spawn from April to June on the Bering and 314 Chukchi sea shelves (Stark, 2004). It is not surprising that Arctic cod larvae are found in the north, given 315 that they spawn under the ice in late winter. In addition, Arctic cod and Bering flounder were not found 316 in Alaska Coastal Water which was expected given that they spawn in shelf waters.

317 AW Mix is formed from Bering Shelf Water, Chukchi Shelf Water and Anadyr Water. Anadyr Water is cold, saline and nutrient-rich that is delivered across the Gulf of Anadyr to the Bering Strait. This 318 319 exogenous nutrient supply fuels much of the summer production on the Chukchi Sea shelf (Danielson et 320 al., 2017). The two other components of the AW Mix, Bering Shelf Water and Chukchi Shelf Water, are 321 cold and saline because of cycles of freezing, brine rejection and then summer warming (Danielson et al., 322 2017). Chukchi Winter Water (CWW) is the cold remnant of the previous winter's heat loss (Danielson et 323 al., 2017). We found that these two cold water masses (AW Mix and CWW) had elevated large copepod 324 (Calanus glacialis) biomass, compared to the warmer, fresher Alaska Coastal Water (ACW). The smallest 325 stages of *Calanus* (C2) were proportionally most abundant in CWW.

326 Published information about the diets of larval Arctic cod supports the idea that the colder water 327 masses were good foraging areas. We caught Arctic cod larvae from 10 mm to 55 mm SL, spanning flexion 328 larvae to post-flexion larvae to juvenile stages (Ponomarenko, 2000). Arctic cod flexion larvae sampled 329 from the Canadian Beaufort Sea consumed copepod nauplii and C1-C2 Calanus glacialis copepodites. 330 Post-flexion larvae consumed copepod nauplii, Pseudocalanus spp. and C1-C2 Calanus glacialis 331 copepodites. Arctic cod juveniles (26-55 mm length) consumed C2-C4 Calanus glacialis copepodites 332 (Walkusz et al., 2011). No Arctic cod larval diet data are available for the Chukchi Sea, but if larval diets 333 are comparable across adjacent seas, then the AW Mix and CWW could be hypothesized to be good 334 foraging areas for Arctic cod larvae in the Chukchi Sea.

335 There is no published information on larval Bering flounder diets. In a review of latitudinal and

336 taxonomic patterns in larval feeding ecology, Llopiz (2013) found that 85% of the diet of flatfish (Order: 337 Pleuronectiformes) was comprised of appendicularians, nauplii, and calanoids. Other studies of specific 338 flatfish taxa showed similar results. American plaice (*Hippoglossoides platessoides*) and Yellowtail 339 flounder (Limanda ferruginea) relied on nauplii and copepodites of Pseudocalanus, Oithona similis and 340 Temora longicornis (Pepin and Penney, 1997). Copepods (Copepoda) have been found to make up 88% 341 to 99% of the total gut contents of Greenland halibut (*Rheinhardtius hippoglossoides*) (Simonsen et al., 342 2006). Bering flounder likely consume smaller prey than Arctic cod, however the colder water masses 343 could provide sufficient biomass of some smaller prey taxa such as *Pseudocalanus* spp. and C2 stages of 344 Calanus glacialis.

345 Advection and the timing of seasonal sea-ice retreat contribute to the formation and 346 productivity of the cold, high salinity water masses (AW Mix and CWW), which we suggest are good 347 foraging habitat for Arctic cod and Bering flounder. Advection through the Bering Strait brings nutrients 348 and plankton-rich Pacific Ocean water into the Chukchi Sea, across the shelf and through Barrow Canyon 349 (Pickart et al., 2005; Woodgate et al., 2015). The seasonal sea-ice zone provides ice algae and early 350 stabilization of the water column by melting ice, which initiates a spring bloom of phytoplankton. Both of 351 these features, advection and sea ice retreat, have been shown to be impacted by global climate change. 352 Ocean warming has resulted in reduction in seasonal sea-ice extent and earlier sea-ice retreat (Frey et 353 al., 2014; Grebmeier et al., 2006b). This change in timing of ice break up means that although ice melt 354 still stabilizes the water column, sunlight is not sufficient to initiate an intense spring bloom (Clement, 355 2004), suggesting a lowering of overall primary production. Alternatively, earlier sea-ice breakup could 356 result in increased primary production due to a longer growing season, as has been observed in the 357 Arctic Ocean (Arrigo et al., 2008). The second process of interest here, advection through the Bering 358 Strait, has increased by almost 50% from 2001 to the present (Woodgate et al., 2015). A larger-scale 359 analysis of flow patterns from 1979 to 2014 shows, in contrast, that there was slightly less poleward 360 advection across the Chukchi Sea shelf since the turn of the century (Bond et al., 2018). Although the

361 present study from two years' surveys suggests some potential mechanisms, further research over 362 multiple years and over a broader study area is needed to confirm how the dynamics of advection and 363 sea-ice retreat impact the habitat of larval fishes.

364 In contrast to Arctic cod and Bering flounder, yellowfin sole and capelin larvae were found more 365 towards the south and exclusively in nearshore Alaska Coastal Water (ACW) in both years. Yellowfin sole 366 spawn in June and July in nearshore waters (Nichol and Acuna, 2001), and capelin spawn in summer on 367 beaches (Frost and Lowry, 1987). So it is perhaps not surprising that the larvae of both species would be 368 entrained in the ACW. Alaska Coastal Water was the warmest and freshest water observed in the survey, 369 and it is typically low in nutrients, chlorophyll-a and phytoplankton productivity after the spring bloom of 370 phytoplankton and associated nutrient depletion (Springer and McRoy, 1993). We observed reduced 371 large copepod (Calanus glacialis) biomass in ACW during our surveys. However, copepod nauplii and 372 small copepod biomass (Acartia spp. and Oithona spp.) were relatively high, compared to the other water 373 masses.

374 Due to a paucity of relevant published diet information, it is difficult to assess whether ACW 375 could be good foraging habitat for larval yellowfin sole and capelin. There are no published diet data for 376 yellowfin sole larvae. The larval diets of a related species, common dab (Limanda limanda) collected in 377 the southern North Sea, were comprised mainly of nauplii and copepodites of the copepod Temora 378 longicornis (Last, 1978). Yellowtail flounder (Limanda ferruginea) caught off the coast of Newfoundland 379 similarly relied on nauplii and copepodites of Pseudocalanus, Oithona similis and Temora longicornis 380 (Pepin and Penney, 1997). There are no studies of capelin diets in the Pacific arctic or subarctic. Studies 381 of capelin diets in the Barents and Norwegian seas showed that larvae were feeding on Calanus eggs 382 and nauplii (Bjorke, 1976; Karamushko and Reshetnikov, 1994). Capelin diets off the coast of 383 Newfoundland were comprised of nauplii and copepodites of Pseudocalanus, Oithona similis and 384 Temora longicornis (Pepin and Penney, 1997). Other forage fish taxa, such as Pacific herring (Clupea 385 harengus) and sandlance (Ammodytes spp.) similarly consume copepod nauplii and copepodites,

including *Acartia* spp. (Fortier et al., 1995; Robert et al., 2013). If copepod nauplii and small copepods
such as *Acartia* and *Oithona* are suitable prey for yellowfin sole and capelin larvae in the Chukchi Sea
and Northern Bering Sea, then the ACW could provide good foraging habitat.

389 Previous ichthyoplankton surveys of the Chukchi Sea have made similar conclusions about the 390 distribution of Arctic fish larvae in relation to water masses. Surveys in 1990-1991 (Wyllie-Echeverria et 391 al., 1997) and in 2004 (Norcross et al., 2010) found Arctic cod in cold offshore water and yellowfin sole in 392 nearshore ACW. Wyllie-Echeverria et al. (1997) also found capelin in ACW; Norcross et al. (2010) did not 393 catch any capelin in 2004. One conflict among these results is that Norcross et al. (2010) found Bering 394 flounder larvae in cold offshore waters, similar to what we observed, but Wyllie-Echeverria et al. (1997) 395 showed Bering flounder associated with ACW. Randall et al. (2019) documented species assemblages of 396 ichthyoplankton during marine mammal and plankton surveys in 2010-2015 and found interannual 397 associations between communities and the dominant water masses similar to our results. For instance, in 398 years where ACW occupied more of the study area, the ichthyofauna was characterized by a yellowfin 399 sole-driven community. In years when there was more cold water on the shelf, a community typified by 400 Arctic cod was present at most stations.

The distribution and large size of Arctic cod larvae was expected given what is known about the timing and location of Arctic cod spawning. The transport pathways between Arctic cod hatching locations and larval distributions have been investigated using a biophysical transport model that simulates larval growth and dispersal (Vestfals et al., in prep). The results of this modeling effort indicate that Arctic cod larvae caught during the Arctic Eis surveys were likely spawned in the northern Bering Sea or southern Chukchi Sea in winter and then transported to the north by late summer.

Flatfish larvae in the Chukchi Sea could have resulted from local (Chukchi Sea) or remote (Bering Sea) spawning. Our data on egg distributions and larval length-frequency patterns provided clues about flatfish spawning areas. Bering flounder eggs were caught in the northern Chukchi Sea and there was an aggregation of larvae in the same area. There were also Bering flounder larvae in the southern Chukchi 411 Sea and northern Bering Sea, but no eggs were found in those areas. The length-frequency distributions 412 of the northern versus the southern Bering flounder larvae were different. The larvae to the north were 413 smaller, consistent with later spawning and/or slower larval growth rates. The larvae to the south were 414 larger, consistent with earlier spawning and/or faster growth rates. These patterns in egg distribution 415 and larval length-frequencies could indicate that Bering flounder larvae in the northern Chukchi Sea were 416 spawned locally, in the northern Chukchi Sea, later than flounder to the south and in colder water 417 resulting in slower growth and smaller size. In contrast, larvae in the southern Chukchi Sea could have 418 been spawned to the south in the Bering Sea earlier and in warmer water resulting in faster growth rate, 419 and were then transported north, in the Bering Shelf and/or Anadyr Current. It is unlikely that larvae in 420 the south were advected from the north where we caught eggs because this is in the opposite direction 421 of the prevailing currents. An alternative mechanism is that Bering flounder larvae in the southern 422 Chukchi Sea were spawned locally, but sufficiently earlier that eggs were no longer present when that 423 area was surveyed.

Yellowfin sole eggs were found throughout the survey area and larval length-frequency
distributions were similar to the north and south. This is consistent with local spawning of yellowfin sole
larvae in the southern Chukchi Sea and northern Bering Sea at the same time of year. An alternative
mechanism is that yellowfin sole spawning only occurred in the southern Bering Sea and their eggs and
larvae were transported to the northern Bering Sea and Chukchi Sea in the Alaska Coastal Current.

429 Currents across the Chukchi Sea shelf are slow, on average, around 5 cm s⁻¹ (Stabeno et al., 2018; 430 Weingartner et al., 2005; Woodgate et al., 2005), such that it is less likely that larval flatfish found in the 431 Chukchi Sea were transported from the south. At 5 cm s⁻¹ (4.32 km day⁻¹), it would take an egg or larvae 432 179 days to transit the 777 km from the Bering Strait to the northernmost station in the survey. Pelagic 433 durations of flatfish larvae are less than that transit time, on the order of 30-60 days for yellowfin sole in 434 the Gulf of Alaska, and 30-120 days for *Hippoglossoides platessoides* (American plaice) in the North 435 Atlantic (Duffy-Anderson et al., 2015). Randall et al. (2019), analyzing data from a collection of other

436 ichthyoplankton surveys conducted in 2010-2015 as part of marine mammal studies (CHAOZ and
437 ArcWest), similarly concluded that Bering flounder in the Chukchi Sea were likely to have been spawned
438 locally.

- 439
- 440
- 441 **5.** Conclusions
- 442

443 The distributions of Arctic fish larvae were not statistically different between 2012 and 2013 despite the differences in water mass distribution between the two years. Larvae of Arctic cod, Bering 444 445 flounder, yellowfin sole and capelin were found in similar locations in both years and were associated 446 with water masses that had elevated biomass of zooplankton taxa that could potentially have been prey. 447 We suggest that the distribution of larvae is a product of spawning behavior that results in the larvae 448 being located in habitat suitable for successful foraging even as oceanographic processes vary from year-449 to-year. In other words, Arctic fishes have evolved spawn timing and location such that larval 450 distributions are resilient to the degree of interannual climate variability observed between 2012 and 451 2013. Biophysical transport models such as Vestfals, et al. (in prep) can demonstrate the advective 452 connections between spawning location and larval distribution and can be used to explore this 453 hypothesis. This study describes the habitat for larval Arctic cod, Bering flounder, capelin and yellowfin 454 sole and provides baseline information on their early life history. Understanding the associations 455 between larval oceanographic habitat and spawning-related resilience helps us to better understand the 456 mechanisms and the degree of oceanographic change due to ocean warming and loss of sea ice which 457 may have the potential to impact the early life histories of Arctic fishes.

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660 Figure and table legends

Table 1. Numbers of fish eggs, larvae, and juveniles collected in bongo tows from the Chukchi and

northern Bering seas (NBS) during the 2012 and 2013 Arctic Ecosystem Integrated Survey (Arctic Eis)

664 surveys.

661

Fig. 1. Study area map with bathymetric depths and overview of general currents in the region.

666 Mean flow pathways are color coded to denote current systems. Yellow=Bering Slope Current

and Beaufort Gyre; Black=Alaska Coastal Current; Brown=Siberian Coastal Current;

668 Purple=pathways of Bering shelf, Anadyr, and Chukchi shelf waters (Danielson et al. 2017).

669 Fig. 2. Survey area and stations sampled in 2012 (x-symbols) and 2013 (solid circles). Depth

670 contours in meters.

Fig. 3. Distribution of Bering flounder egg catch density (No./10 m²) in a) 2012 and b) 2013.

Fig. 4. Distribution of yellowfin sole egg catch density (No./10 m²) in a) 2012 and b) 2013.

Fig. 5. Distribution of ichthyoplankton catch density (No./10 m²) overlaid on bottom water mass

type. a) 2012 Arctic cod, b) 2013 Arctic cod, c) 2012 Bering flounder, and d) 2013 Bering

flounder. Open circles are larval fish, filled circles are juvenile fish. Arctic cod were the only taxa

676 for which juvenile fish were caught. Water mass data courtesy of S. Danielson.

Fig. 6. Distribution of ichthyoplankton catch density (No./10 m²) overlaid on surface water mass

type. a) 2012 yellowfin sole, b) 2013 yellowfin sole, c) 2012 capelin, and d) 2013 capelin

679 ichthyoplankton. Water mass data courtesy of S. Danielson.

Fig. 7. Length-frequency distributions (number of fish) of Bering flounder larvae from 2012: a)

north of 70° latitude (n=8) and b) south of 70° latitude (n=52).

Fig. 8. Length-frequency distributions (number of fish) of yellowfin sole larvae from: a) 2012,

683 north of 65.5° latitude (n=71); b) 2012, south of 65.5° latitude (n=295); c) 2013, north of north of

684 65.5° latitude (n=53); and d) 2013, south of 65.5° (n=181).

Fig. 9. Water mass characteristics for Alaska Coastal Water (ACW) at the surface; and Anadyr

686 Water/Bering Shelf Water/Chukchi Shelf Water (AW Mix), Chukchi Winter Water (CWW) and

687 Bering Winter Water (BWW) at depth. Box plots show median (horizontal line), first and third

688 quartile (box), minimum and maximum (whiskers) and outliers (points). p-value from Kruskal-

689 Wallis rank sum test for comparisons among all water masses is shown at upper right of each

690 box plot. Significant p-values for post-hoc Kruskal-Wallis rank sum test comparisons between

pairs of water masses are indicated by bars and asterix. * p<0.05, **p<0.01, ***p<0.001; a) 2012

692 integrated chlorophyll (mg m⁻²), b) 2013 integrated chlorophyll (mg m⁻²), c) 2012 Calanus

693 glacialis (mg m⁻³), and d) 2013 Calanus glacialis (mg m⁻³).

Fig. 10. Proportion of *Calanus glacialis* copepodite stages C2-C6 in each water mass in 2012: a)

Alaska Coastal Water (ACW), b) Chukchi Winter Water (CWW), c) Anadyr Water/Bering Shelf

696 Water/Chukchi Shelf Water (AW Mix), d) Bering Winter Water.

697 Fig. 11. Proportion of *Calanus glacialis* copepodite stages C2-C6 in each water mass in 2013: a)

Alaska Coastal Water (ACW), b) Chukchi Winter Water (CWW), c) Anadyr Water/Bering Shelf

699 Water/Chukchi Shelf Water (AW Mix), d) Bering Winter Water.

702	Fig. 12. Biomass density (mg m ⁻³) of small copepods in Alaska Coastal Water (ACW), Anadyr
703	Water/Bering Shelf Water/Chukchi Shelf Water (AW Mix), Chukchi Winter Water (CWW) and
704	Bering Winter Water (BWW) in 2012. No small (20-mm) PairVet net samples were analyzed for
705	2013 due to loss of data sheets at sea. Box plots show median (horizontal line), first and third
706	quartile (box), minimum and maximum (whiskers) and outliers (points). p-value from Kruskal-
707	Wallis rank sum test for comparisons among all water masses is shown at upper right of each
708	box plot. Significant p-values for post-hoc Kruskal-Wallis rank sum test for comparisons between
709	pairs of water masses are indicated by bars and asterix. * p<0.05, **p<0.01, ***p<0.001; a)
710	Calanoida nauplii, b) Pseudocalanus sp., c) Acartia spp., and d) Oithona spp.
711	



Fig. 1





Fig. 3



Fig. 4















Fig. 8





Fig. 9



b. **CWW**









Fig. 10



C2

C3

C4

C5

C6

C2

C3

C4

C5

C6









p < 0.001

BWW

***0

808

AW Mix

cww

Water Mass

*



Fig. 12

			Chukchi			NBS			Chukchi				NBS				
			7 August - 9 September			10-24 September			7 August - 8 September			7 August, 10-24 September					
			20	12 (<i>n</i> =100 st	ations)	2012 (n=38 stations)			2013 (<i>n</i> =100 stations)			2013 (<i>n</i> =43 stations)			Totals		
Family	Scientific Name	Common Name	Eggs Larvae Juveniles		Eggs	Eggs Larvae Juveniles		Eggs Larvae Juveniles		Juveniles	Eggs	Eggs Larvae Juveniles		Larvae + Eggs Juveniles			
Clupeidae	Clupea pallasi	Pacific herring					2									2	
Osmeridae	Mallotus catervarius	Pacific capelin		22			16			7			3			48	
Gadidae		unidentified cods								1						1	
	Boreogadus saida	Arctic cod		9	4					22	15					50	
	Eleginus gracilis	saffron cod		1						1	5					7	
	Gadus chalcogrammus	walleye pollock		1		25		1		2		1	1		26	5	
Gasterosteidae	Pungitius pungitius	ninespine stickleback						1								1	
Hexagrammidae	Hexagrammos stelleri	whitespotted greenling											1			1	
Cottidae	Gymnocanthus tricuspis	Arctic stagehorn sculpin		2						6						8	
	Hemilepidotus papilio	butterfly sculpin					3									3	
	lcelus spatual Aspidophoroides	spatulate sculpin		1												1	
Agonidae	monopterygius	alligatorfish		1												1	
	Aspidophoroides olrikii	Arctic alligatorfish		2						1						3	
	Podothecus veternus	veteran poacher								1						1	
Liparidae	Liparis spp.	unidentified snailfish		3						2						5	
	Liparis fabricii	gelatinous seasnail		1						2						3	
	Liparis gibbus1	variegated snailfish		13						7						20	
	Liparis tunicatus	kelp snailfish unidentified		3			1			11						15	
Stichaeidae		pricklebacks		1												1	
	Acantholumpenus mackayi Eumocoarammus	blackline prickleback					1									1	
	praecisus	fourline snakeblenny		7						1						8	
	, Anisarchus medius	stout eelblenny		1						2						3	
	Leptoclinus maculatus	, daubed shanny		2						3						5	
	Lumpenus fabricii	, slender eelblenny		1						1						2	
	Stichaeus punctatus	Arctic shanny		17						19						36	
Ammodytidae	Ammodytes hexapterus	Arctic sand lance		4						13			1			18	
		unidentified flounders	6						1				2		7	2	
Pleuronectidae	Hippoglossoides robustus	Bering flounder	156	66			7		3	10			1		159	84	
	Lepidopsetta polyxystra	northern rock sole		1												1	
	Limanda spp.	unidentified Limanda	370						333			10	1		713	1	
	Limanda aspera	yellowfin sole		76		1	321			36			221		1	654	
	Limanda proboscidea	longhead dab		15									4			19	
	Limanda sakhalinensis Pleuronectes	Sakhalin sole		9						1						10	
	quadrituberculatus	Alaska plaice		5						1						6	
		total number of taxa total number of	3	25	1	2	7	2	3	21	2	2	8	0	5	31	
		individuals	532	264	4	16	351	2	337	150	30	11	235	0	906	1057	