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4 **1 Springtime renewal of zooplankton populations in the Chukchi Sea**

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52 **Key Words:** Zooplankton; Spring; Distributions; Hydrography; Currents; USA, Arctic, Chukchi
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30 **Abstract**

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32 Although considerable work has been done in the Chukchi Sea during summer, much less has
33 been done during other seasons. This has limited our ability to fully understand seasonal cycles
34 and transformations of the Chukchi Sea zooplankton, particularly the key copepod species
35 *Calanus glacialis*. Abundance and distributions of large zooplankton and of all life stages of *C.*
36 *glacialis* in the northeastern Chukchi Sea during May-June 2014 are described. Three main
37 zooplankton communities are identified; “arctic oceanic” along the Chukchi slope associated
38 with off-shelf water masses; Chukchi Sea “overwintering” associated with cold winter water in
39 the northern part of the study area; and Chukchi Sea “spring” associated with early season
40 summer water in the southern portion of the study area. The overwintering and spring
41 communities were distinguished by the near total absence of younger copepodid (CI-CIII) *C.*
42 *glacialis* stages and meroplankton in the overwintering community while older (CV-adult) *C.*
43 *glacialis*, amphipods, and chaetognaths were present in both. The distributions of the
44 communities followed the major circulation pathways in the northeastern Chukchi Sea. Water
45 and plankton flooding in from the northern Bering Sea was filling the Chukchi Sea and
46 replenishing the zooplankton communities as the remnants of the overwintering community was
47 being advected northwards and into the Canadian Basin. A conceptual model of the seasonal
48 evolution of *C. glacialis* populations in the Chukchi Sea, based on the interaction of *C. glacialis*
49 phenology and advective drivers, enfolds both these spring observations and summer
50 observations from numerous previous studies. Because the flushing time of the Chukchi Sea is
51 shorter than the *C. glacialis* generation time, the copepod is unable to establish an endemic
52 population in the Chukchi Sea, hence the population there must be renewed annually from the
53 northern Bering Sea.

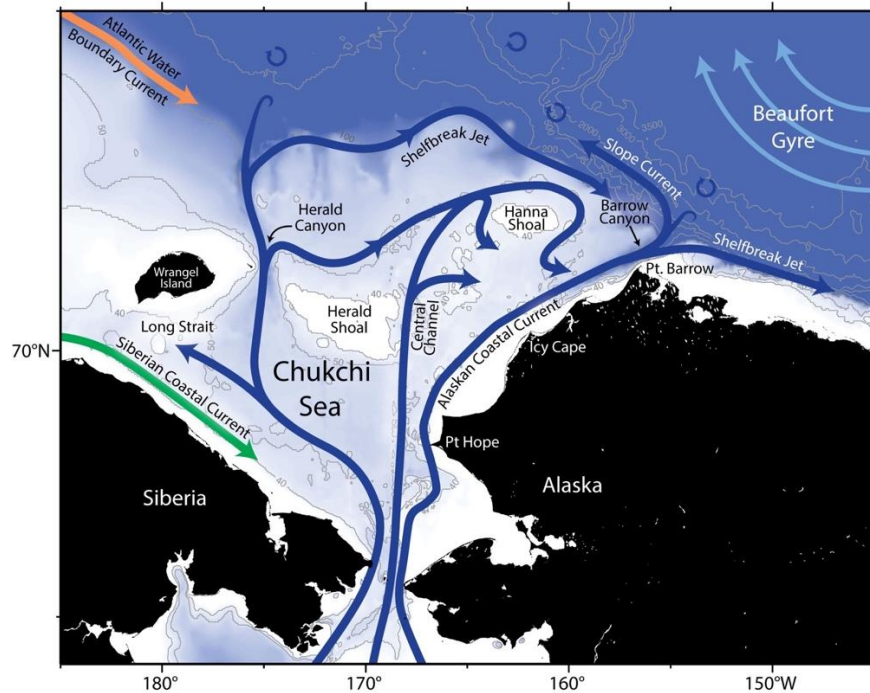
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Introduction

The Chukchi Sea has long been recognized as a flow through system, with multiple lines of evidence demonstrating replacement of water and intrinsic plankton on time scales of order months for most of the region (e.g., Berline et al., 2008; Hopcroft et al., 2010; Wassmann et al., 2015; Stabeno et al., 2018; Woodgate, 2018). Given the relatively short turnover time of the Chukchi Sea (less than a year), it is clear that most if not all zooplankton populations are transient. However, because most previous descriptions of the zooplankton community have been conducted during the summer, only the summertime characteristics have been comprehensively described and there has been little information available from other times of the year to describe the seasonal evolution of the community composition or to track the advective progression of zooplankton through the Chukchi Sea.

Three main pathways carry water northwards through the Chukchi Sea from Bering Strait: through Hope Valley and Herald Canyon in the west, through the Central Channel to the east of Herald Shoal, and in the east along the western coast of Alaska and exiting through Barrow Canyon (Coachman et al., 1975; Weingartner et al., 1998, 2005; Woodgate et al., 2005). The circulation is somewhat complex, as both the western and central pathways branch or bifurcate at points along their pathways. Particularly relevant to the present study is the branching of the Central Channel pathway to the east just north of Herald Shoal and along the southern flank of Hanna Shoal (Pickart et al. 2016; Lin et al., 2019). Much of the outflow from the Chukchi Sea occurs through Barrow Canyon (Figure 1). Upon exiting the canyon, a portion of the flow turns eastward to feed the Beaufort Shelfbreak Jet (Nikolopoulos et al., 2009), while a larger portion turns westward to form the Chukchi Slope Current (Corlett and Pickart, 2017; Li

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4 77 et al., 2019). The outflow from Herald Canyon feeds the eastward-flowing Chukchi Shelfbreak
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6 78 Jet (Linders et al., 2017).
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33 80 Figure 1. Geographic place names and major current pathways in the Chukchi Sea. Currents after
34 81 Corlett and Pickart (2017).
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37 83 Different water masses are associated with each of the main advective pathways
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39 84 (Coachman et al., 1975; Gong and Pickart, 2015). Generally, Anadyr Water enters Bering Strait
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41 85 in the west, following the western pathway through the Chukchi Sea. Alaskan Coastal Water
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43 86 enters the eastern side of Bering Strait in summer and is advected in the Alaskan Coastal Current
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45 87 along the eastern pathway to exit the shelf through Barrow Canyon. North of Bering Strait,
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47 88 Anadyr and Bering Shelf Water mix to form what is known as Bering Summer Water (Pisareva
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49 89 et al., 2015), which mostly follows the central pathway northward through the Central Channel,
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51 90 turning to the east north of Hanna Shoal, with several eastward divergences along the way.
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57 91 Each of these water masses has been associated with characteristic zooplankton
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59 92 communities in recent studies (Wassmann et al., 2015 and references therein; Ershova et al.,
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4 93 2015; Pinchuk and Eisner, 2017; Spear et al., 2018; Xu et al., 2018). Most of the studies have
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6 94 further partitioned the water mass associated species groups into spatially distinct distributions.
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9 95 Furthermore, different nomenclatures for the water masses (e.g., Bering Summer Water vs.
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11 96 Chukchi Summer Water) somewhat complicates the synthesis. However, some generalities for
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14 97 each water mass can be described. Overall, the Bering Summer Water/Chukchi Summer Water
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16 98 (hereafter referred to as Bering Summer Water) is marked by *Calanus glacialis*, Pacific copepod
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19 99 species such as *C. marshallae*, *Neocalanus* spp. and *Eucalanus bungii bungii* (herein *E. bungii*)
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21 100 and meroplankton, with the abundances of Pacific species decreasing to the north. Lower
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24 101 abundances of Pacific species and meroplankton and more abundant euphausiids are typical of
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26 102 the Anadyr Water. The Alaskan Coastal Water generally carries more inshore, euryhaline smaller
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29 103 species such as *Acartia hudsonica* and *Centropages abdominalis* and is distinct from the
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31 104 neighboring Bering Summer Water. A fourth zooplankton community, dominated by Arctic
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33 105 endemics such as *C. hyperboreus*, is found along the northern edge of the Chukchi Sea and
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36 106 sometimes extending south through Barrow Canyon after reversal of the prevailing poleward
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38 107 flow there (Pinchuk and Eisner, 2017). While some overlap exists in terms of presence or
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41 108 absence between the water mass types, within a given study the zooplankton communities are
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43 109 distinct. Studies with a broader geographical coverage (e.g., Matsuno et al., 2011; Eisner et al.,
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46 110 2012; Ershova et al., 2015; Pinchuk and Eisner, 2017, Xu et al., 2018) also note both northern-
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48 111 southern and eastern-western transitions, both of which are likely related to the advective
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51 112 pathways, distance from the Bering Sea source, and seasonal evolution of the populations and
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53 113 communities.

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55 114 Because most of the characterizations of the zooplankton communities have been
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58 115 conducted during summer, relatively little is known about those communities during other
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116 seasons or how the communities change throughout the year, driven by the phenology of the
117 zooplankton themselves and how that phenology is linked to zooplankton advection through the
118 Chukchi Sea. The congeneric large bodied copepods *Calanus glacialis* and *C. marshallae* are of
119 particular interest, since they feature prominently in the zooplankton community and their
120 populations may require re-establishment each year after being flushed out to the north over the
121 winter (Wassmann et al., 2015). These species also are a critical link in the Arctic food chain as
122 prey for planktivorous fish such as arctic cod (Walkusz et al., 2011; Rand et al., 2013).

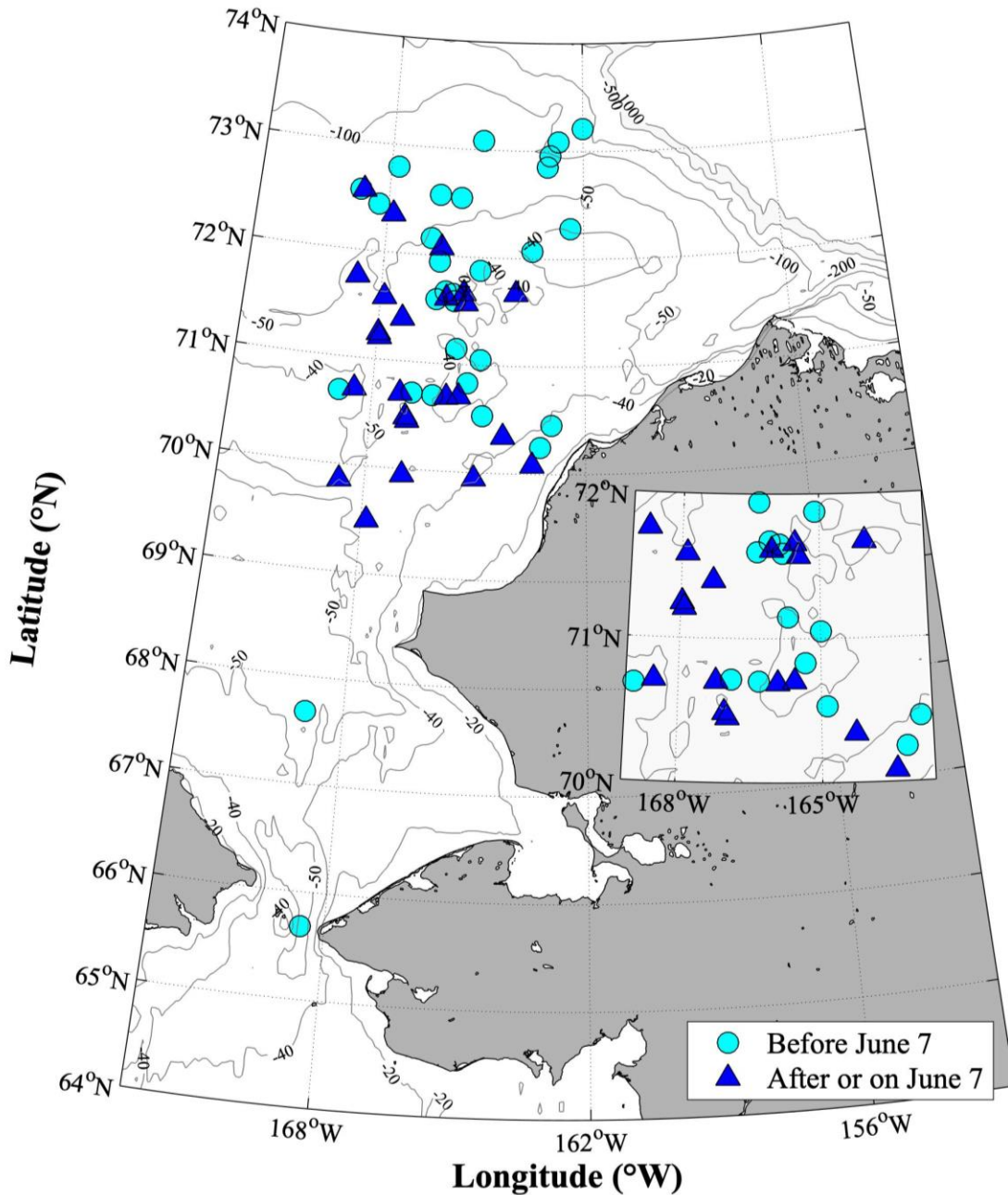
123 The objectives of the present study are to describe the abundances and distributions of the
124 copepods *C. glacialis* and *C. marshallae* (copepodid and adult life stages) and of large bodied
125 zooplankton relative to the distribution of water masses and advective pathways during late
126 spring in the northeastern Chukchi Sea. Because *C. glacialis* and *C. marshallae* are extremely
127 difficult to differentiate taxonomically, and because *C. marshallae* is relatively rare, those
128 species were not separated and are herein designated as *C. glacialis* (Plourde et al. 2004;
129 Campbell et al., 2009; Nelson et al., 2009). The work presented here was conducted
130 opportunistically during a cruise to the region that focused on hydrography, sea ice, and primary
131 productivity of the Chukchi Sea in late spring (Arrigo et al., 2017). The goal was to establish
132 information on the zooplankton community of the Chukchi Sea at that time of year and to gain
133 insight into the population dynamics of the copepod *C. glacialis*, a key member of the
134 mesozooplankton community. This is the first description of these associations and distributions
135 during late spring when the zooplankton community is undergoing a seasonal evolution. It is also
136 the first survey to capture both the overwintering and early summer zooplankton composition of
137 the Chukchi Sea.

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139 **Methods**

140 Sampling was conducted from May 16 – June 20, 2014 during a cruise on the *USCGC*
141 *Healy* to the Chukchi Sea as part of the SUBICE (Study of Under-ice Blooms in the Chukchi
142 Ecosystem) program (Arrigo et al., 2017). The cruise track was centered in the eastern Central
143 Chukchi Sea between Pt. Hope/Cape Lisburne and the Chukchi slope with most work conducted
144 considerably offshore of the Alaskan coast (Figure 2). The sampling scheme was designed to
145 intercept known and hypothesized advective pathways (Pacini et al., 2019). Most stations were
146 located to the south and west of Hanna Shoal, intersecting the Central Channel flow and the
147 pathway from the Central Channel east towards the Alaskan coast. The zooplankton work was
148 conducted opportunistically to the main objectives of the cruise and was done throughout the
149 study region at a subset of the occupied stations (Figure 2; Table 1); one station was occupied in
150 Bering Strait, one in the southern Chukchi Sea, and the rest were situated north of Point Hope,
151 AK. Zooplankton samples were collected from the surface to the near bottom without regard to
152 day or night using forty-six vertical hauls of paired 60-cm Bongo nets equipped with 150 µm and
153 500 µm mesh nets and one-way turning flowmeters. The nets were equipped also with a bright
154 strobe to visually stun euphausiids and increase their catch (Wiebe et al., 2004; Ashjian et al.,
155 2017). Zooplankton samples were preserved immediately following collection in 5% formalin
156 seawater. *C. glacialis* were preserved in ethanol at six stations during the cruise for analysis of
157 the mitochondrial cytochrome c oxidase 1 gene (mtCO1) to determine species and population
158 haplotypes (see methods in Ashjian et al., 2017). Water column hydrography and relative
159 chlorophyll abundance were measured at each station using a Seabird 911+ conductivity-
160 temperature-depth (CTD) package equipped with a WET Labs ECO-AFL/FL fluorometer.
161 Velocities along the ship’s track were measured using a 150 kHz hull-mounted acoustic Doppler

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4 162 current profiler (ADCP). Additional information on processing of the physical data and the key
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7 163 characteristics of the hydrography and circulation are found in Pacini et al. (2019).
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166 Figure 2. The Chukchi Sea with Bering Sea to the south and the Beaufort Sea to the north and the
167 locations of the net tows used in this study. Topographic lines show bottom depth in meters.
168 Prominent geographic features are marked. Insert shows detail of central study region.
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171 Table 1. Dates, position, and bottom depth for the stations at which zooplankton tows were
 172 conducted. Station groups identified by principal component analysis also indicated.

Station Number	Year	Month	Day	Latitude (°N)	Longitude (°W)	Bottom Depth (m)	Station Group
5	2014	5	15	65.680	168.5436	55	5
10	2014	5	18	70.685	168.9338	38	2
19	2014	5	18	70.702	166.3079	43	4
24	2014	5	19	70.530	164.8796	47	5
29	2014	5	20	70.247	163.2462	31.6	2
31	2014	5	21	70.455	162.9482	36	2
33	2014	5	22	70.828	165.3290	44	2
36	2014	5	23	71.047	164.9906	40	2
44	2014	5	24	71.876	165.0956	43	2
51	2014	5	24	72.563	166.4093	50	2
56	2014	5	26	72.796	167.7767	59	2
57	2014	5	26	72.559	168.8819	62	2
59	2014	5	26	72.438	168.2956	55	4
64	2014	5	27	72.160	166.6102	49	4
70	2014	5	28	72.066	163.5498	41.7	4
75	2014	5	28	72.282	162.4067	38.5	4
80	2014	5	29	72.957	163.0336	86	2
81	2014	5	30	73.084	162.7759	120	1
83	2014	5	30	73.211	162.0117	182	1
96	2014	6	2	72.547	165.7605	53	4
99	2014	6	2	71.943	166.3229	46	2
104	2014	6	4	71.596	166.3611	45	2
105	2014	6	4	71.672	166.0906	45	4
112	2014	6	7	71.145	165.6964	42	2
120	2014	6	7	70.701	165.5588	45	3
124	2014	6	8	70.341	164.2880	40	5
127	2014	6	8	70.080	163.4647	28	3
132	2014	6	8	69.942	165.0439	40	3
137	2014	6	9	69.944	167.0018	50	3
141	2014	6	9	69.497	167.8457	51	3
142	2014	6	9	69.853	168.6869	49	3
151	2014	6	10	70.485	167.0255	50	3
152	2014	6	11	70.688	165.9077	44	3
156	2014	6	11	70.699	167.2102	55	3
160	2014	6	11	70.708	168.5115	42	3
168	2014	6	12	71.760	168.7236	51	2
175	2014	6	13	72.557	168.7795	62	2
178	2014	6	13	72.354	167.8162	54	2
182	2014	6	14	72.072	166.2800	48	2
188	2014	6	14	71.670	164.0167	40	2
201	2014	6	16	71.206	167.9234	49	3
205	2014	6	17	71.583	167.8803	50	5
209	2014	6	17	71.660	165.5426	42	2
215	2014	6	18	71.398	167.3046	50	3
221	2014	6	19	71.245	167.9652	50	3
227	2014	6	20	70.450	166.9642	51	3

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174 Abundances of different life stages of *Calanus glacialis* were enumerated from the 150

175 μm mesh net samples in successive splits until at least 300 *C. glacialis* were identified (*C.*

176 *glacialis* and *C. marshallae* were not differentiated). Early copepodids stages of *C. glacialis* and

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177 *C. hyperboreus* were differentiated based on prosome length (e.g., Lane et al., 2008).
178 Abundances of larger zooplankton, including meroplankton, were enumerated from the 500 µm
179 mesh net samples. Abundances were calculated as integrated water column abundances to better
180 identify potential “hot spots” of abundance across the shelf and to reflect that the tows sampled a
181 vertical, rather than oblique, body of water.

182 Groups of co-occurring species and taxa were identified using hierarchical cluster
183 analysis based on Euclidian distance between Spearman Rank Correlations, modified to range
184 between 0 and 2, between plankton types. Total abundances across life stages were used for all
185 species and types with the exception of *C. glacialis* and euphausiids for which individual life
186 stages were used. The different plankton groups then were used to identify stations with similar
187 plankton compositions using principal component analysis (PCA) based on $\log_{10}(x + 1)$ group
188 abundances. All calculations were conducted in Matlab (Mathworks, Inc.).

189
190 **Results**

191 Twenty-three zooplankton types, including life stages of *C. glacialis*, euphausiids, and
192 meroplankton, were differentiated (Table 2). Smaller copepods such as *Oithona* spp. and
193 *Pseudocalanus* spp. were collected with the 500 µm mesh net and were ubiquitous in the study
194 area but were not sampled quantitatively with that large mesh-size net and are not included in the
195 present analysis. Both spatial and temporal variability in the abundances of different taxa were
196 observed. Some types were wide-spread throughout the study area, such as *C. glacialis* AF,
197 chaetognaths, and amphipods (*T. abyssorum*) (Figure 3). Other types were present primarily in
198 particular locations, such as *C. hyperboreus* that was seen only in the two most northern stations
199 (Stns. 81 and 83; not shown in Figure 3).

Zooplankton composition and abundance changed substantially at stations sampled on and after June 7/Station 112 (Table 2; Figure 3). Before that date, this community contained primarily *C. glacialis* AF, amphipods, and chaetognaths (note, here the “community” is defined by the mesh size of net used). However, at many stations sampled after that date the plankton composition was dominated by younger stages of *C. glacialis* (CI-CIII), euphausiid furcilia, and meroplankton (barnacle nauplii, polychaete larvae and trochophores). For most of these taxa, significant differences in abundance were found between the two periods (Table 2). It is important to note that here time/date and location are inextricably interconnected, with later dates corresponding to more southerly locations and earlier dates covering both southern and northern locations (Figure 2).

Table 2. Taxa differentiated in the net tows. The proportion of nets in which each was collected (relative occurrence), the mean and standard deviation of the water column abundance from all stations conducted before and on or after June 7, and the p-value for the t-test comparing those means is noted for each taxon. Significant differences ($p < 0.05$ or better) between the two times denoted by bold type for the p-value.

Taxonomic Category	Net Mesh (μm)	Relative Occurrence	Before June 7 (N=23)		On or After June 7 (N=23)		t-test p
			Mean Abd. ($\# \text{ m}^{-2}$)	Std. Dev. ($\# \text{ m}^{-2}$)	Mean Abd. ($\# \text{ m}^{-2}$)	Std. Dev. ($\# \text{ m}^{-2}$)	
<i>Calanus glacialis</i> CI	150	0.48	5	15	1154	1573	0.00
<i>C. glacialis</i> CII	150	0.43	1	4	412	806	0.02
<i>C. glacialis</i> CIII	150	0.46	10	37	74	165	0.09
<i>C. glacialis</i> CIV	150	0.33	35	132	7	25	0.35
<i>C. glacialis</i> CV	150	0.50	41	67	11	29	0.06
<i>C. glacialis</i> AM	150	0.46	4	6	4	8	0.98
<i>C. glacialis</i> AF	150	1.00	359	336	218	217	0.10
<i>C. hyperboreus</i>	150	0.04	74	336	0	0	0.29
<i>Metridia longa</i> CV-AM	500	0.28	5	12	1	2	0.12
<i>Neocalanus</i> sp.	500	0.13	7	31	1	5	0.42
<i>Eucalanus bungii</i> b. CII-AM	500	0.11	3	11	1	2	0.36
<i>Paraeuchaeta</i> sp. CIII-AM	500	0.04	19	78	0	0	0.27
Euphausiid Pre-Furcilia	500	0.43	2	5	6	7	0.09
Euphausiid Furcilia	500	0.41	3	6	10	17	0.03
Euphausiid Juveniles & Adults	500	0.33	2	5	2	3	0.76
Amphipods	500	0.96	162	132	90	139	0.07
Appendicularians	500	0.54	40	96	111	194	0.16
Chaetognaths	500	0.98	201	130	179	122	0.52
<i>Limacina</i> sp.	500	0.50	11	26	6	8	0.37
Polychaete Larvae	500	0.46	2	8	303	411	0.00
Polychaete Trochophores	500	0.39	1	3	108	149	0.00
Barnacle Nauplii	500	0.59	1	3	3051	5214	0.01

Foraminifera 500 0.04 120 399 0 0 0.16

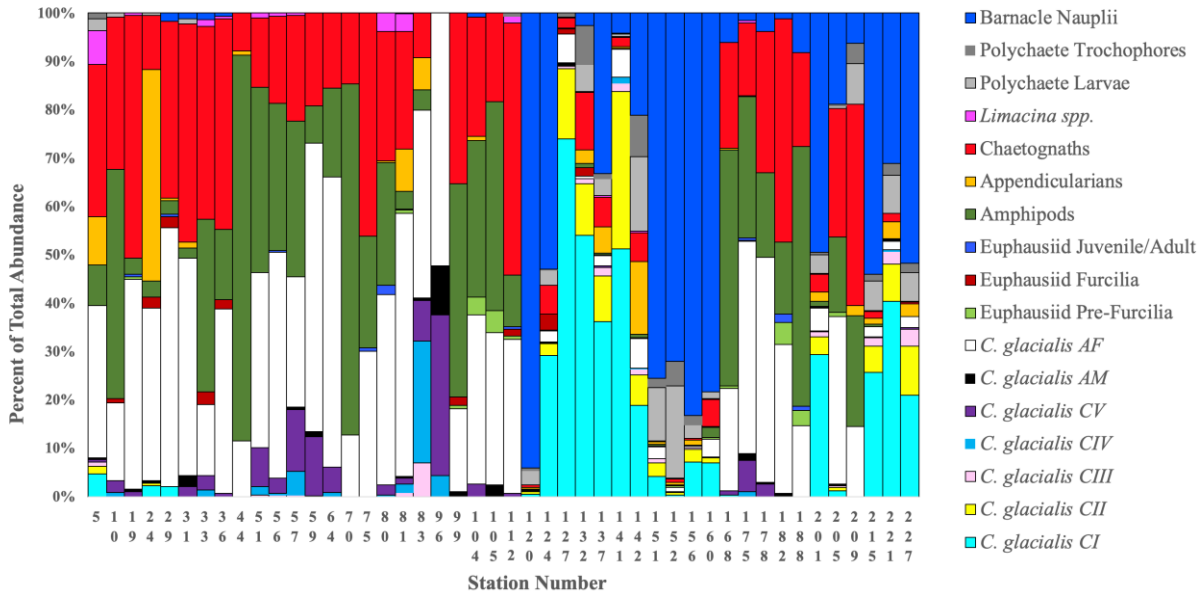
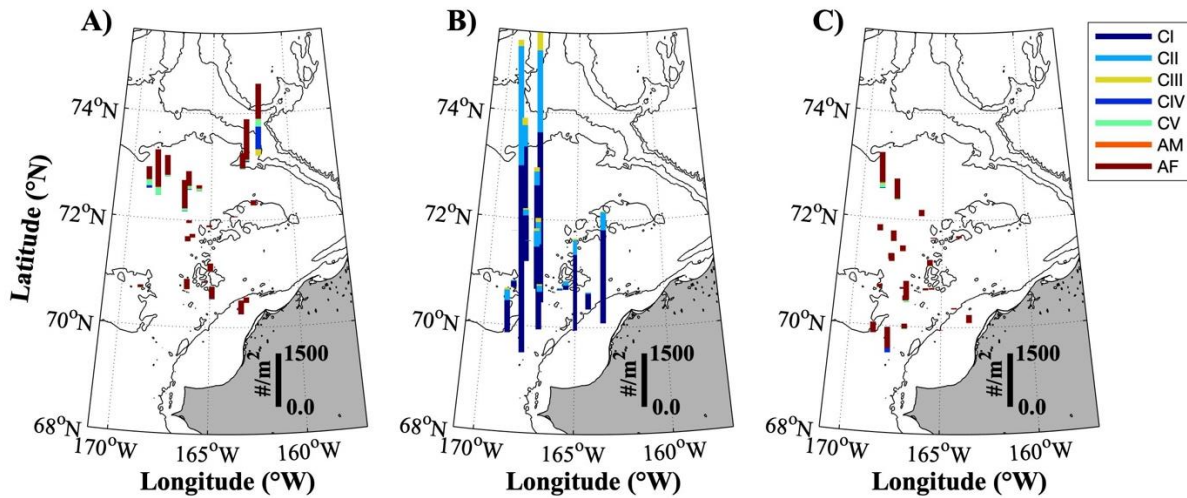


Figure 3. Percentage of total abundance of zooplankton types by station. Zooplankton species or taxa that were present in only trace abundances or observed only at 1-2 stations are not included. The break in time between the first part and second part of the cruise (June 7) occurred between stations 105 and 120.

Distribution plots are presented only for taxa that occurred in more than 30% of the tows (Table 2). *C. glacialis* was widespread throughout the study area, although abundances varied by location and by life stage (Figures 3 and 4). Before June 7, *C. glacialis* AF was present at every net tow in approximately equivalent abundances and dominated the stage proportions. After June 7, many of the stations, especially those in the southern portion of the study area, had high abundances of younger copepodid stages (I-III). Females were still present but CIV and CV were essentially absent.

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7 235 other taxa (Table 2). Very few euphausiids were observed during the first portion of the cruise
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9 236 (Figure 5A). During the second portion of the cruise, significantly more euphausiids, dominated



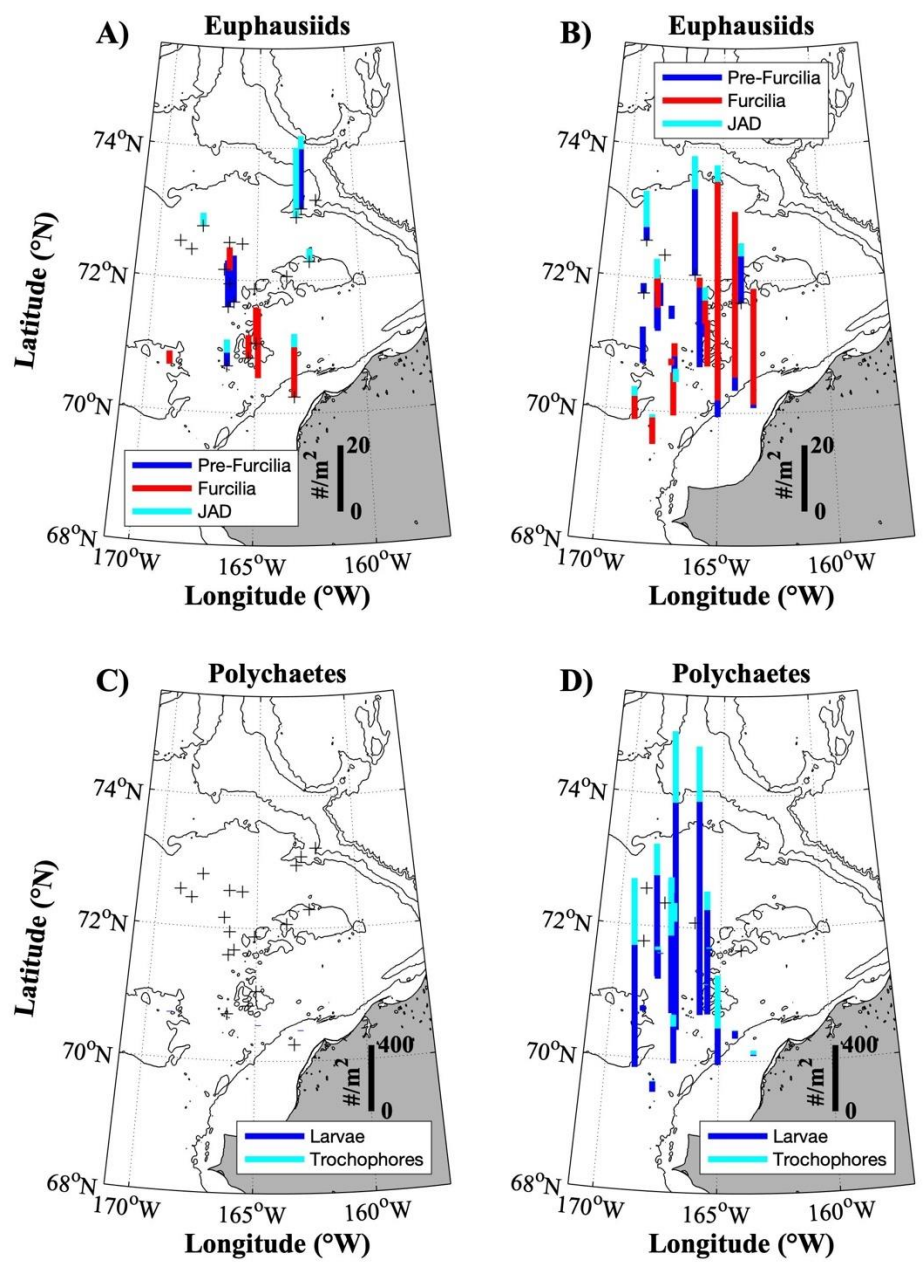
237
238 Figure 4. Integrated water column abundances of life stages of *C. glacialis* at locations north of
239 Pt. Hope, AK. A) Abundances from before June 7, 2014. B) Abundances of CI-CIII on or after
240 June 7, 2014. C) Abundances of CIV-AF on or after June 7, 2014. Data from station in Bering
241 Strait not shown.
242

243 by pre-furcilia and furcilia, were seen in the southern portion of the study area. There was a
244 west-east shift both in abundance (lower abundances were seen at the western stations) and in
245 stage composition (eastern stations were dominated by furcilia while western stations had more
246 pre-furcilia stages). Pelagic polychaete stages were essentially absent from the Chukchi Sea at
247 stations sampled before June 7 (Figure 5C). After June 7, however, high abundances of both
248 larvae and trochophores were observed primarily to the southwest of Hanna Shoal. Somewhat
249 reduced abundances were seen along the Alaskan coast. A similar pattern was observed for
250 appendicularians (Figure 6B) and barnacle nauplii (Figure 6D).

251 Both amphipods and chaetognaths were persistent in the zooplankton composition, being
252 present in 96% and 98% of the tows, respectively (Table 2). Similarly to *C. glacialis* AF,

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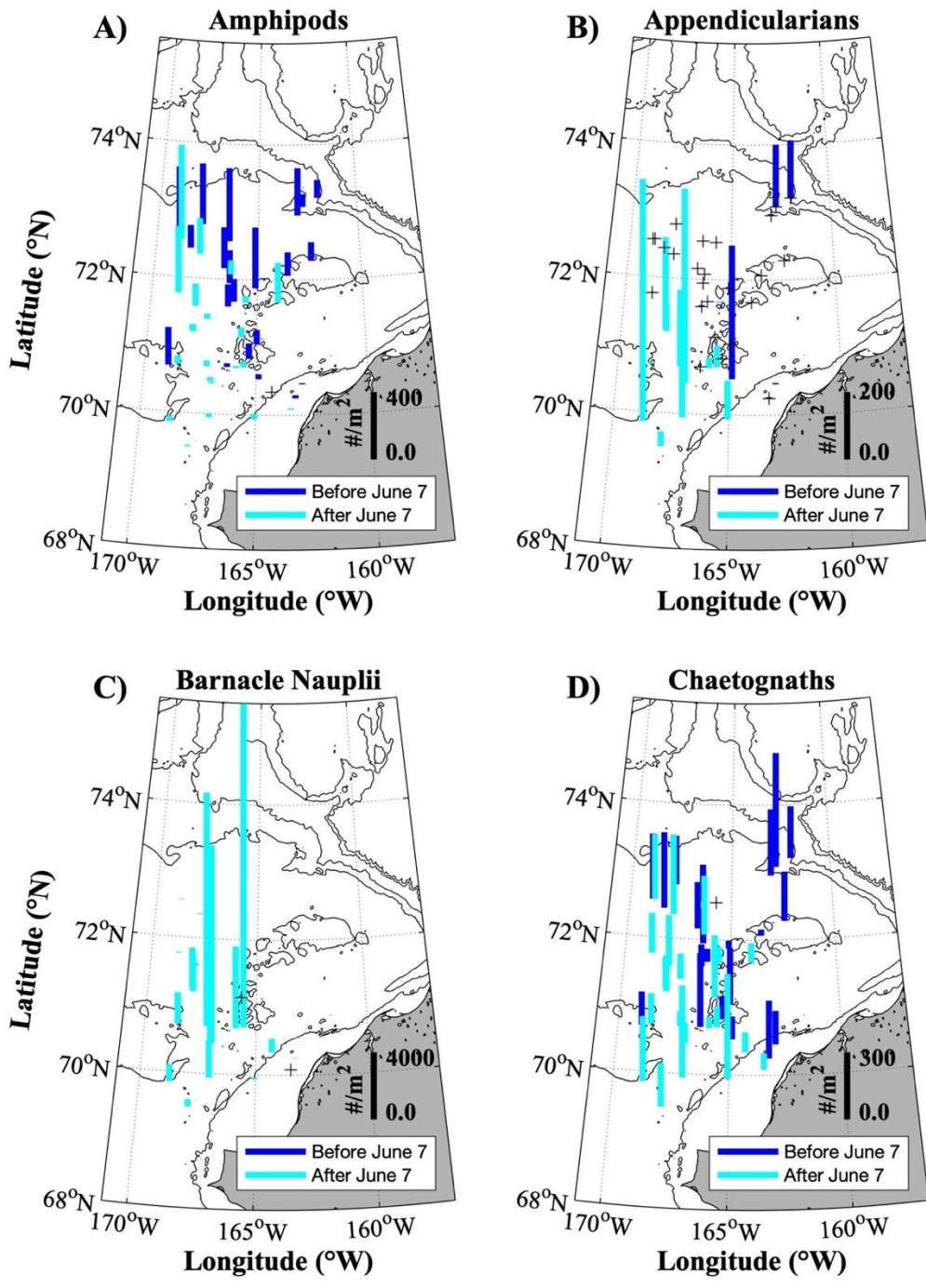
253 chaetognaths did not show changes in abundance between the two periods of the cruise (Figure
254 6D). By contrast, amphipods were in low abundance in the southern portion of the study area
255 after June 7 although this difference was not significantly different in the mean (Figure 6A;
256 Table 2).



257
258 Figure 5. Integrated water column abundances of life stages of euphausiids (A, B) and
259 polychaetes (C, D) at locations north of Pt. Hope, AK. A and C: Abundances from before June 7,

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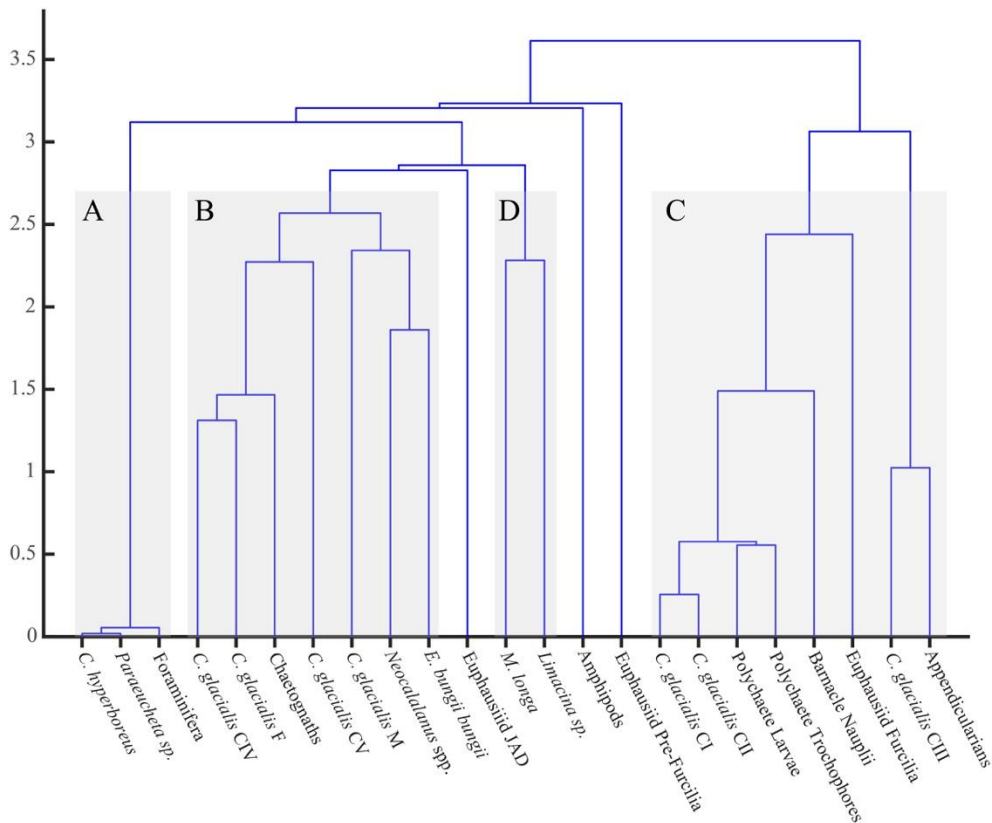
260 2014. B and D: Abundances from on or after June 7, 2014. Crosses (+) denote locations for
261 which no animals were observed. Different life stages denoted by different colored shading. JAD
262 = Juveniles and Adults. Data from station in Bering Strait not shown.



263
264 Figure 6. Integrated water column abundances of all life stages of A) amphipods, B)
265 appendicularians, C) barnacle nauplii, and D) chaetognaths. Crosses denote locations for which
266 no animals were observed. Abundances from before June 7, 2014 and on or after June 7, 2014
267 differentiated by the different colored bars. Data from station in Bering Strait not shown.

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Cluster analysis revealed four groups with co-occurring plankton types (Figure 7). Three plankton types (euphausiid pre-furcilia, euphausiid juveniles/adults and amphipods) were only loosely associated with other types and were not included in a group. Group A was composed of three types (*C. hyperboreus* (CI, CII, AF), *Paraeuchaeta* sp., foraminifera) typical of deeper Arctic oceanic regions. Group B constituted types that were present throughout the study region for the entire period of the study and included older life stages of *C. glacialis*, chaetognaths, and the Pacific copepod species *Neocalanus* spp. and *E. bungii*. Group C included plankton types that showed much higher abundances in the southern region of the study area after June 7 and included younger stages of *C. glacialis*, meroplankton, and appendicularians. Group D comprised only two plankton types; *Limacina* sp. and *M. longa*.



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Figure 7. Dendrogram showing taxa groups identified by cluster analysis. Gray shading separates groups. Unless noted, all stages of a species are combined. “JAD” refers to “Juveniles and Adults”.

Principal component analysis based on the abundances of the four different plankton groups revealed five groups of stations that corresponded to the spatial and temporal variation in the relative abundances of the plankton types. The first three principal components explained a total of 97% of the variation (Table 3). Mode 1 (PC1) was dominated by the relative abundance of plankton Group C (young *C. glacialis*, meroplankton). The second mode was driven by the relative abundance of plankton Group A, the oceanic arctic species. Mode 3 was dominated by plankton Group D that included *Limacina* sp. and *M. longa*, indicating that stations with those types would have more negative third mode eigenvalues.

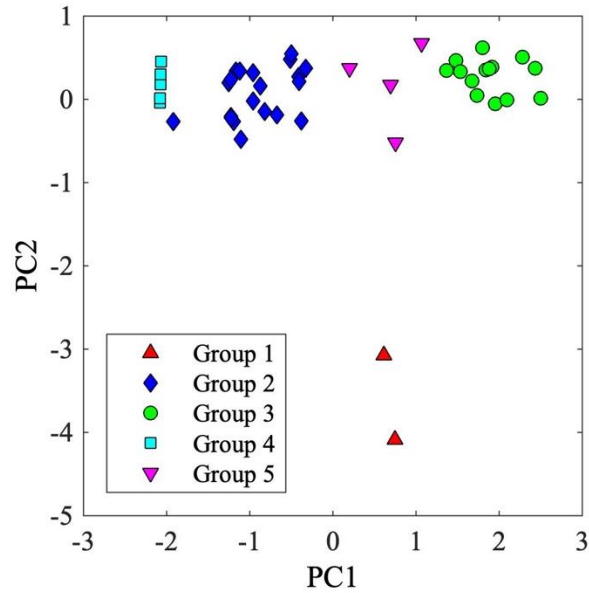
Table 3. Eigenvectors for the first three principal components (PC1-PC3) and the proportion of the variation explained by each component. Coefficients for each plankton group (GP) of the eigenvectors have been standardized to the absolute value of the maximum coefficient for each vector.

	PC1	PC2	PC3
GP-A	0.048	-1.000	0.450
GP-B	0.009	-0.344	-0.158
GP-C	1.000	0.108	0.143
GP-D	0.166	-0.381	-1.000
Prop. Variation	0.69	0.17	0.10

The station groups were identified based primarily on the first two principal components (Figure 8). Station Group 1 included two stations with very negative PC2s resulting from high abundances of plankton Group A and a negative, most heavily weighted coefficient for that plankton group. Station Group 2 were those with PC1 ranging from -2 to 0. Based on the eigenvectors, stations with low abundances of plankton Group C would have negative PC1, since that principal component is positively dependent on abundances of those plankton types. Station Group 3 was differentiated on the basis of very positive (>1) PC1. Principal component 1 would

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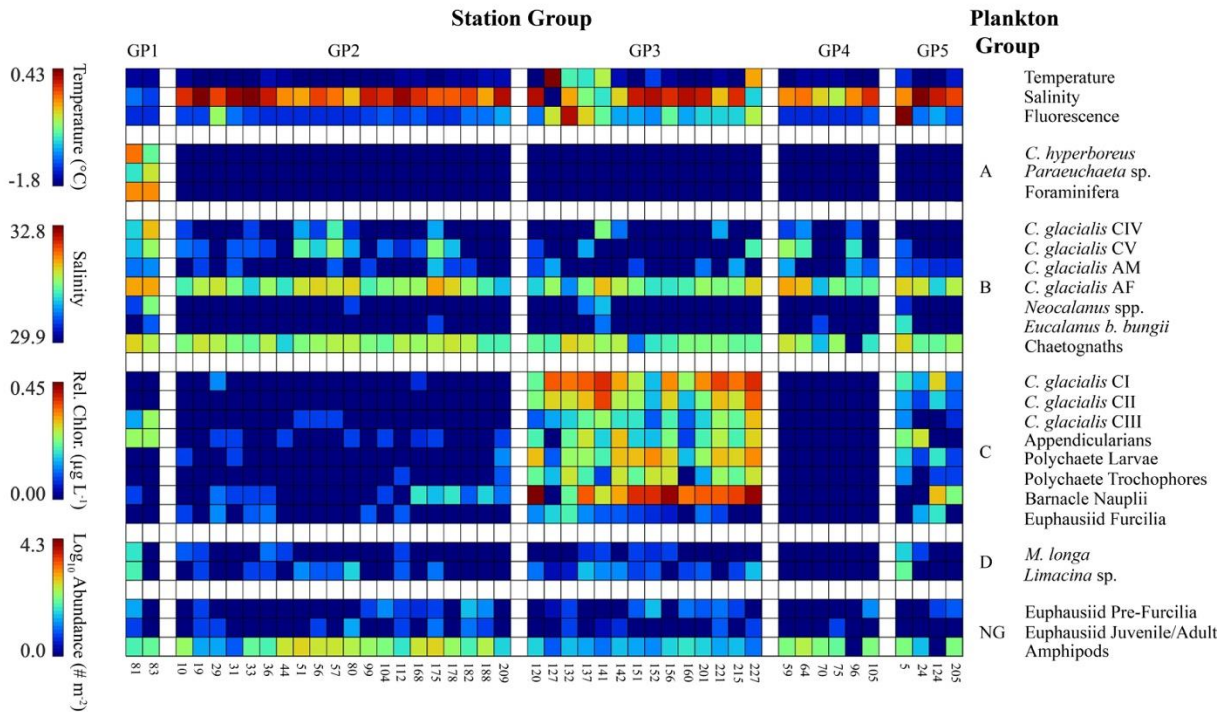
305 be positive with high abundances of Group C plankton types. Station Group 4 had the most
306 negative PC1s. These were stations that had compositions similar to those of Station Group 2
307 (low abundances of plankton Group C) but also low abundances of plankton Group D. Four
308 stations lay between Station Group 2 and Station Group 3 in PC space (Figure 8), suggesting
309 either low abundances of all plankton groups or high abundances of all plankton groups. One
310 station appeared, on the basis of PC1 vs. PC2, to be grouped with Station Group 4 but was
311 placed in Station Group 2 on the basis of principal component 3 (not shown) for which plankton
312 group D was the strongest determinant.



313
314 Figure 8. Stations grouped according to principal components 1 and 2.
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316 Plankton abundances, plankton groups, and station groups were embodied in a heat map
317 (*sensu* Hopcroft et al., 2010) to better illustrate the relationships between the three (Figure 9).
318 Station Group 1 included two stations that were located on the Chukchi Slope (Figure 10), the
319 only stations where oceanic Arctic plankton that are part of plankton Group A were found (note

320 abundances of zero for those plankton types at all stations outside of those in station group 1).
 321 Moderate abundances of CIII-adult *C. glacialis* also were present at those two stations.

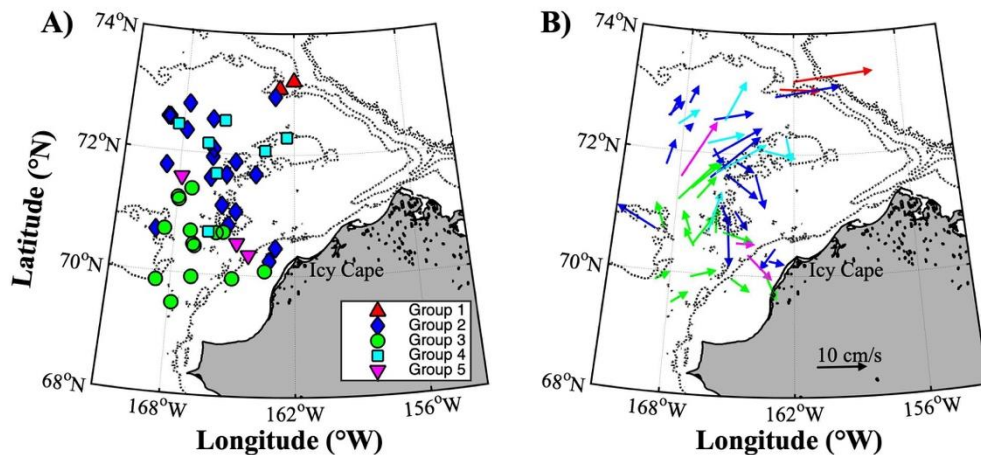


322
 323 Figure 9. Heat map showing relationships between plankton abundances, plankton groups, and
 324 station groups. Temperature and salinity at 8-m and mean water column uncalibrated chlorophyll
 325 (from fluorescence) also shown for each tow. Each column shows data from a different tow; each
 326 row shows abundance data (plankton) or environmental data from each tow. Unless noted, all
 327 plankton life stages enumerated for each type are combined. Station numbers are noted along the
 328 bottom axis. Within a station group, stations are sorted chronologically from earliest (lowest
 329 station number) to latest (highest station number). Station groups (GP1-GP4) are separated along
 330 the horizontal axis; plankton groups and environmental characteristics are separated along the
 331 vertical axis.

333 Station Group 2 was distributed primarily along a swath extending northwest from Icy Cape
 334 (Figure 10). Many, but not all, of these stations were sampled prior to June 7 (Table 1). *C.*
 335 *glacialis* AF, chaetognaths, and amphipods were prominent at these stations (Figure 8); most
 336 other plankton types were present in low abundance or not at all. Group 3 stations lay to the
 337 south of Group 2 stations, along a swath with the same northwest-southeast orientation (Figure
 338 10). These stations all were sampled on or after June 7 (Table 1) and had high abundances of the

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339 Group C plankton, young *C. glacialis*, meroplankton, and euphausiid furcilia, and relatively
340 lower abundances of amphipods. There was little spatial overlap, with one exception, between
341 Station Group 2 (early) and Station Group 3 (late) locations (Figure 10), although latitudinally
342 the two groups co-occurred between 70.23°N and 71.40°N. Station Group 4 was mostly co-
343 located with the northern part of Station Group 2. These stations had no individuals from
344 plankton groups C or D. All of these stations were occupied prior to June 7. Three of the Group 5
345 stations were found geographically along the interface between the locations of Group 2 and
346 Group 3 stations and the fourth was located in Bering Strait (Table 1). These stations had
347 intermediate abundances of the early *C. glacialis* copepodids and of meroplankton. There was no
348 consistent pattern in the timing of the stations (e.g., early vs. late in the cruise).



349
350 Figure 10. A) Locations of stations by group. The station located in Bering Strait (Figure 2) is in
351 the “No Group” category and not in the geographic range of this figure. B) Mean water column
352 velocity averaged over 24 hours prior to the time that net sample was collected. Velocity vectors
353 are color coded by station group.

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355 Mean abundances of plankton types within each station group showed significant
356 differences between groups for plankton types that were important drivers of variability (and the
357 eigenvectors of the PC analysis) in the plankton community. The mean abundances of most

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4 358 species in Species Group C, early stage *C. glacialis*, meroplankton, and appendicularians, were
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6 359 significantly greater (Kruskal Wallis, $p < 0.01$) for the Group 3 stations than for the other station
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9 360 groups (Table 4). These are the plankton types that were important for Mode 1 of the PCA, with
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11 361 high positive PC1. Note also that the mean abundances of Group C species in Group 5 stations
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14 362 were intermediate between those seen in Group 3 stations and Groups 2 and 4 stations, consistent
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16 363 with the spatial distribution of Group 5 stations between the southern Group 3 stations and the
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19 364 northern Groups 2 and 4 stations (Figure 10) and with the magnitude of Principal Component 1
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21 365 (Figure 8). Mean Group 1 station abundances (note, $n=2$) were significantly greater (Kruskal
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23 366 Wallis, $p < 0.05$) for the oceanic arctic species (*C. hyperboreus*, *Paraeuchaeta*, foraminifera) and
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26 367 for *Neocalanus* spp. Greater Group 2 station mean abundances that were not necessarily
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29 368 significantly different from other group station means also were seen for all stages of *C.*
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31 369 *glacialis*, including CIV and CV that were generally much less important elsewhere. Amphipods
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33 370 had significantly greater mean abundance for Group 2 stations than for other station groups. For
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36 371 other plankton types, no difference in mean abundance was seen between station groups or the
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38 372 abundances were too low and too variable to detect a difference.

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41 373 Although Pacini et al. (2019) provided a comprehensive description of the hydrographic
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43 374 characteristics and circulation encountered during the cruise, aspects of these are here presented
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46 375 to provide appropriate context for the interpretation of the zooplankton distributions. Differences
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48 376 in hydrography and water column fluorescence (a measure of chlorophyll *a* concentration) were
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51 377 seen between the different station types (Figures 9, 11). Five water masses were identified
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53 378 following previous definitions (e.g. Gong and Pickart, 2016; Pacini et al., 2019). These are: (i)
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55 379 Newly Ventilated Winter Water (NVWW), which is cold, weakly stratified water near the
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58 380 freezing point; (ii) Remnant Winter Water (RWW), which is NVWW that has been moderated

381 either by solar heating or mixing with warmer water (e.g. Gong and Pickart, 2015); (iii) Chukchi
 382 Summer Water (CSW), which is one of the Pacific-origin summer waters (also referred to
 383 Table 4. Mean integrated water column zooplankton abundances (# m⁻²) for stations in each
 384 station group. Significant Kruskal-Wallis *p* values denoted by bold type (last column). Bold
 385 mean abundances show those significantly different from the others (Tukey-Kramer post hoc
 386 test, *p*<0.05). Mean and standard deviations (std) of abundance shown for each group.
 387

Taxonomic Category	Group 1 (n=2)		Group 2 (n=19)		Group 3 (n=14)		Group 4 (n=7)		Group 5 (n=4)		Kruskal- Wallis <i>p</i>
	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	
<i>Calanus glacialis</i> CI	0	0	1	3	1864	1670	0	0	134	203	6.5 x 10⁻⁸
<i>C. glacialis</i> CII	0	0	0	0	675	953	0	0	17	15	1.7 x 10⁻⁸
<i>C. glacialis</i> CIII	98	112	1	1	122	199	0	0	4	7	2.0 x 10⁻⁷
<i>C. glacialis</i> CIV	336	425	6	16	11	32	3	5	0	0	0.05
<i>C. glacialis</i> CV	119	132	28	48	7	19	49	78	2	4	0.02
<i>C. glacialis</i> AM	11	2	3	6	4	7	7	8	4	2	0.11
<i>C. glacialis</i> AF	1054	108	258	224	191	176	355	403	276	175	0.16
<i>C. hyperboreus</i>	855	1069	0	0	0	0	0	0	0	0	6.5 x 10⁻⁹
<i>Metridia longa</i> CV-AM	23	33	1	3	1	2	1	2	11	19	0.47
<i>Neocalanus</i> sp.	77	103	0	1	2	7	0	0	1	2	0.003
<i>Eucalanus bungii</i> CII-AM	4	5	0	1	1	2	1	2	13	26	0.28
<i>Paraeuchaeta</i> sp. CIII-AM	214	228	0	0	0	0	0	0	0	0	4.0 x 10⁻⁹
Euphausiid Pre-Furcilia	9	13	4	7	5	7	3	5	3	3	0.41
Euphausiid Furcilia	0	0	3	5	12	19	0	0	18	24	0.008
Euphausiid Juveniles/Adults	2	3	3	6	1	2	1	2	0	0	0.64
Amphipods	90	23	221	164	26	13	112	81	70	65	0.002
Appendicularians	177	10	2	2	181	223	0	0	135	187	2.5 x 10⁻⁵
Chaetognaths	368	195	193	91	164	134	167	140	218	169	0.37
<i>Limacina</i> sp.	37	52	5	10	8	9	1	2	25	50	0.06
Polychaete Larvae	0	0	1	3	494	430	0	0	23	22	8.3 x 10⁻⁸
Polychaete Trochophores	0	0	1	2	176	157	0	0	6	6	7.9 x 10⁻⁷
Barnacle Nauplii	2	3	11	16	4832	6020	0	0	237	376	3.0 x 10⁻⁶
Foraminifera	1386	77	0	0	0	0	0	0	0	0	4.0 x 10⁻⁹

388
 389 as Bering Summer Water, e.g. Lin et al., 2019). This is a mixture of northern Bering Shelf water
 390 and Anadyr water (Pisareva et al., 2017); (iv) Melt Water / River runoff (MWR), which derives
 391 from a combination of ice melt and fluvial runoff; and (v) Atlantic Water, which is the warm,
 392 salty water of Atlantic origin found along the continental slope.

393 Winter Water (NVWW and/or RWW, T<-1°C, 31.5<S) was present at all stations (Figure
 394 11), with a very tight TS envelope at Group 4 stations, but with seasonal transformations and
 395 mixing with other water masses at Group 1 and Group 3 stations (see also Pacini et al., 2019).

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396 No other water mass types were present at Group 2 and Group 4 stations. AW ($T > -1$, $S > 33.6$)
397 was present only at the single deep station along the Chukchi slope (Station 83) that was part of
398 Group 1. Group 1 stations also had MWR; this was absent at the other types of stations and was
399 due to early-season ice melt seaward of the shelf. CSW ($-1 < T < 3$; $30 < S < 33.6$) was present at only
400 Group 3 stations. Because Winter Water was observed at depth at all stations (Pacini et al, 2019,
401 Figure 11), near-surface water characteristics were used as a simple indicator of water mass
402 types between the different stations for Figure 9. The water at 8 m depth was warmer and fresher
403 for the southern Group 3 stations (Figure 9, stations located in the left of the Group 3 block).
404 Mean water column fluorescence was greater for Group 3 stations than for all other stations with
405 the exception of the Bering Strait station (left most station in the Group 5 station block). Pacini
406 et al. (2019) described the temporal evolution in sea ice cover during the cruise. Accordingly,
407 Group 1, 2, 4, and 5 stations were all well to the north of ice edge while Group 3 stations were
408 much closer or at the ice edge (defined by 80% sea ice cover).

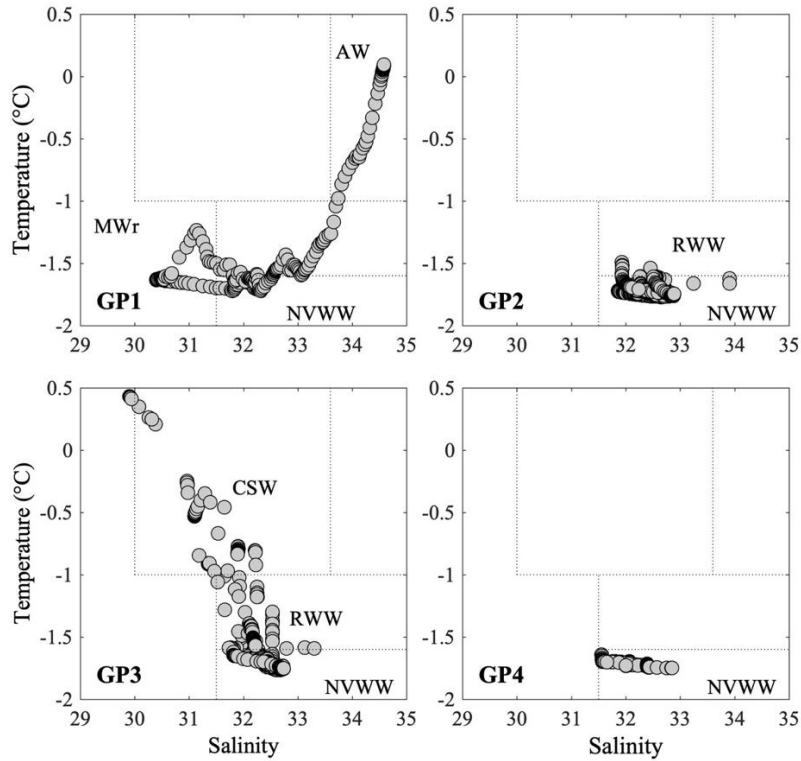


Figure 11. Temperature-salinity characteristics at all the stations from which net tows were used, with stations from each station group (GP) plotted on the different panels. Data averaged into 1-m depth bins. Lines denote limits of the different water mass types: NVWW = Newly Ventilated Winter Water; RWW = Remnant Winter Water; CSW = Chukchi Summer Water; MWR = Melt Water / river runoff; AW = Atlantic Water.

The circulation described by the ADCP velocities also has been presented previously by Pacini et al. (2019) and followed patterns typical of the Chukchi Sea (Lin et al., 2019). Average velocities for the 6 hours previous to each net tow and a description of the general features are presented here to provide context for the discussion (Figure 10). Northward flow emanating from Central Channel and turning to the east along the northern edge of Hanna Shoal is seen in the western portion of the region. A portion of this flow diverges towards the Alaska coast in the southern portion of the study region. Southeastward flow towards Icy Cape also was seen between 71 and 72°N at about 166°W; Pacini et al. (2019) interpret this as two separate pathways. Group 1 stations were clearly in the eastward flow north of Hanna Shoal. The

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425 northwestern Group 2 stations were in the outflow from Central Channel headed towards the
426 northern side of Hanna Shoal, while the southeastern Group 2 stations were in the Central
427 Channel outflow headed towards the Alaska coast; a similar pattern was seen for the Group 4
428 stations. Group 3 stations were in the northward Central Channel flow or in the flow diverging
429 from there towards the coast in the southern portion of the study region.

430 Mitochondrial COI analysis from a limited subset of stations (Figure 12) revealed a
431 diverse set of haplotypes in *C. glacialis* and *C. marshallae*. Five *C. glacialis* Arctic haplotypes
432 and fifteen *C. glacialis* Bering Sea haplotypes were detected. In addition, four haplotypes of the
433 congener *C. marshallae* were detected. Haplotype proportions, combined by region type,
434 demonstrated that most of the individuals were of the Bering Sea haplotype of *C. glacialis* except
435 at the northernmost station where ~37% of the individuals were of the Arctic haplotype (Figure
436 12). Few *C. marshallae* were detected (<5%) except at the northwesternmost station (~14% *C.*
437 *marshallae*).

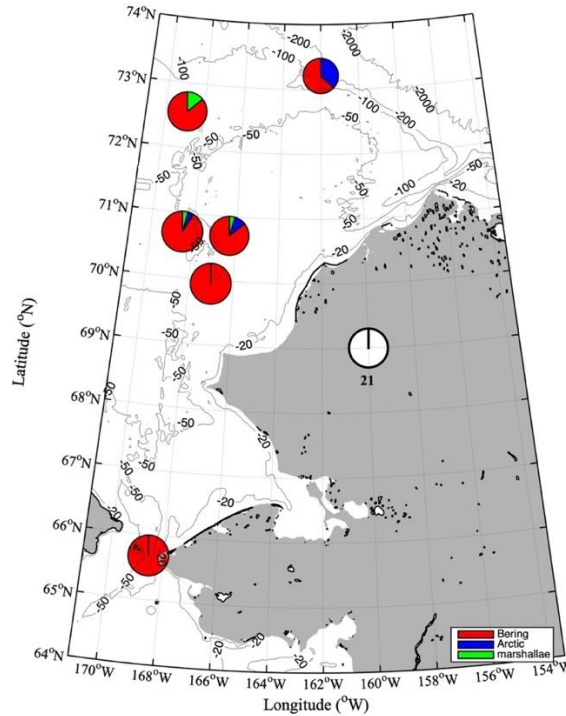


Figure 12. Haplotype frequencies of the mtCOI gene from *C. glacialis*. Two *C. glacialis* haplotypes and one *C. marshallae* haplotype are shown. Circles scaled to the number of individual copepods (19-21 individuals/station).

Discussion

Zooplankton abundances and composition and *C. glacialis* population structure together revealed that there were three zooplankton communities, corresponding to three of the station groups (Group 1-Group 3), present in the northeastern Chukchi Sea during May-June 2014, one each found in the northern and southern portion of the study region and one at the northernmost stations, all associated with different water mass characteristics and with their distributions impacted by the prevailing current pathways. Five station groups were identified, three of which corresponded to the three station communities while the other two (Group 4, Group 5) had compositions intermediate between the northern and southern Chukchi communities. Spatial and temporal patterns are intertwined in the data and can best be untangled through consideration of

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4 456 the prevailing circulation. What emerges from the analysis is a conceptual model of the spring
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6 457 transition of the northeastern, and indeed entire, Chukchi Sea zooplankton community between
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9 458 the overwintering and summer states and of a springtime renewal of zooplankton, including *C.*
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11 459 *glacialis* populations, driven by flooding of the Chukchi Sea with water, and intrinsic plankton,
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14 460 from the south. Although only a single species, *C. glacialis*, was enumerated from the 150 µm
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16 461 net samples, it is considered here as a tracer for the mesozooplankton community. Associations
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19 462 between zooplankton community compositions and abundances in the Chukchi Sea have been
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21 463 described previously (e.g., Hopcroft et al., 2010 and references therein, Matsuno et al., 2011,
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23 464 2016; Eisner et al., 2013; Ershova et al., 2015; Pinchuk and Eisner, 2017; Xu et al., 2018),
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26 465 however this is the first description of these associations and distributions during late-spring
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29 466 when the zooplankton community is undergoing a seasonal evolution. It is also the first survey to
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31 467 capture both the overwintering and spring zooplankton compositions.

32
33 468 It is widely believed that *C. glacialis* in the Chukchi Sea originate from the south, with
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36 469 young-of-the year either spawned in the Bering Sea or spawned in the southern Chukchi Sea
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38 470 from females advected in from the northern Bering Sea (e.g., Hopcroft et al., 2010; Ershova et
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40 471 al., 2015; Wassmann et al., 2015; Pinchuk and Eisner, 2017 and others). It is also believed that
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43 472 there are both Arctic Ocean and Bering/Chukchi Sea populations of *C. glacialis*, with differing
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46 473 phenologies and genetic characteristics (Nelson et al., 2009; Ershova et al., 2015; Wassmann et
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48 474 al., 2017; Ashjian et al., 2017; Pinchuk and Eisner, 2017; Xu et al., 2018). The findings of the
49
50 475 present study, renewal of *C. glacialis* populations with young-of-the year from the northern
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53 476 Bering Sea/southern Chukchi Sea and distinct Arctic vs. Chukchi/Bering haplotype frequencies
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55 477 and communities, support those paradigms.

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4 479 *Biogeography, Pathways of Advection, and Replenishment of the Chukchi Sea Zooplankton*

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7 480 *Community*

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9 481 The community at the two most northern stations (Group 1 stations) constituted species
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11 482 endemic to the Arctic Basin, including CI and CII of *C. hyperboreus*, life stages CIII and later of
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13 483 *C. glacialis*, amphipods, and chaetognaths. There were no meroplankton at these sites. Advection
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16 484 at the time of sampling was predominantly to the east along the isobaths of the Chukchi Slope
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19 485 north of Hanna Shoal, indicating that the stations were located in the shelf break jet (Corlett and
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21 486 Pickart, 2017). The northernmost station was deep enough to sample AW. The *C. hyperboreus*
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24 487 early copepodids stages likely resulted from lipid-based reproduction in late winter. The
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26 488 presence of *C. glacialis* CIII and CIV so early in the season suggests that those individuals
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29 489 represent an overwintering population. The species is believed to overwinter at copepodid Stage
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31 490 IV in the Arctic as part of a two-year life history (Falk-Peterson et al., 2009; Daase et al., 2013).
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33 491 However, Daase et al. (2013) observed both CIII and CIV copepodids in Franklin Bay and
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36 492 Amundsen Gulf in May and June and attributed their presence to overwintering. Different
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38 493 population structures between Chukchi Sea and Arctic Basin *C. glacialis* have been observed
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41 494 previously, with Arctic populations believed to overwinter at CIV and the subarctic populations
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43 495 at CV (Falk-Peterson et al., 2009; Ershova et al., 2015; Pinchuk and Eisner, 2017). Furthermore,
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46 496 genetic haplotype frequencies from this (Figure 12) and previous studies (Nelson et al., 2009;
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48 497 Ashjian et al., 2017) support there being genetically distinct Arctic and sub-arctic populations of
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51 498 *C. glacialis*.

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53 499 The northern study region community (excluding the two northernmost stations) was
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55 500 dominated by adult *C. glacialis*, chaetognaths, and amphipods and marked by the near absence
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58 501 of meroplankton and younger *C. glacialis* copepodids. It extended spatially from offshore of Icy
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4 502 Cape to the northwest. Stations at which this community was found were categorized on the
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6 503 basis of plankton composition as being either station Group 2 or station Group 4, with Group 4
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8 504 stations differing only in their lack of *M. longa* and *Limacina* spp. and a total absence (vs. low
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10 abundances) of early stage *C. glacialis* copepodids. Only Winter Water was present at these
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12 505 locations, with little evolution in hydrographic characteristics through ice melt, heating, or
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14 506 advection from the south (Pacini et al., 2019). These stations were located in the northward
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16 507 Central Channel flow or in the southeastern arm of that flow that diverges south of Hanna Shoal
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18 508 and eventually joins the eastern coastal branch. Although adult female *C. glacialis* were present,
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20 509 reproduction does not appear to have occurred in time for eggs to develop to the early copepodid
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22 510 stages. This was not surprising, given the low fluorescently detected chlorophyll concentration,
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24 511 since *C. glacialis* primarily reproduces based on available food (Daase et al., 2013). This
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26 512 community can be considered the overwintering Chukchi Sea community.
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33 514 High numbers of younger copepodid stage *C. glacialis* and meroplankton, the presence of
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35 euphausiid furcilia, and lower abundances of amphipods characterized the southern study region
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37 515 community, in addition to the ubiquitous chaetognaths and adult female *C. glacialis*.
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39 516 Abundances of *C. glacialis* AF were equivalent to those observed in the overwintering
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41 517 community. This community (Group 3 stations) was found to the south of the first community
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43 518 (Group 2 and Group 4 stations), with the two distributions juxtaposing with little spatial overlap.
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45 519 Hydrographically, some of the southern locations had warmer, fresher water characteristic of
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47 520 CSW, indicating that this water, and intrinsic plankton, had been advected to those locations
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49 521 from the northern Bering Sea following winter. Elevated levels of fluorescently detected
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51 522 chlorophyll also were present, together with a depletion of nitrate presumably due to drawdown
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53 523 during photosynthesis and reduced sea ice cover (Arrigo et al., 2017; Pacini et al., 2019). Most
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525 of these locations were located in the northward flow of the Central Channel with the exception
526 of those in the southeastern portion of the study area which were located where the Central
527 Channel flow had split, with a portion diverging to the east to join the eastern coastal branch.

528 Could the younger *C. glacialis* observed in the southern community have resulted from
529 in-situ reproduction and development during the period of the cruise? Two nearly co-located
530 stations on the western side of Central Channel provide the opportunity for a back-of-the
531 envelope calculation of the time required for development to CI at that location. The first station
532 (Stn. 10) was occupied on May 18 and classified as Species Group 2, while the second station
533 (Stn. 160) was occupied on June 11 and classified as Species Group 3 (Table 1). Near-surface
534 water temperature for both stations was very low (~-1.8°C); in fact, the range of water
535 temperatures on the shelf, where zooplankton was sampled, ranged from -1.8°C to 0.5 °C for the
536 period of the cruise (Figure 11). At -1.8°C, ~75 days are required for development of *C. glacialis*
537 from hatching to naupliar stage 6 (N6) (Ji et al., 2012) – a period of time that is over double the
538 time between the sampling dates of the two stations (32 days) (Table 1). Even at 0.5°C,
539 development to N6 requires a longer period of time than the entire sampling period in the
540 Chukchi Sea (34 days). It is therefore unlikely that the CI-CIII observed in the study were
541 produced *in-situ*.

542 Intermediate zooplankton community compositions were seen at a few locations (station
543 group 5) that lay along the faunal front between the northern and southern regions. There the
544 abundances of the newly advected *C. glacialis* and meroplankton were reduced relative to those
545 present in the Pacific-origin community, and amphipod abundances remained as high as seen in
546 the overwintering community.

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547 The overall picture, then, was of two Chukchi Sea faunal communities separated by a
548 distinctive faunal front that also corresponded to a seasonal transition in hydrography, influenced
549 by the prevailing circulation. The northern community was present over the winter (herein
550 overwintering community). Younger stages of *C. glacialis* or meroplankton were not found
551 because those produced the prior year had all developed to older stages (copepods) or settled out
552 of the plankton (meroplankton) by fall of the previous year. Presumably the overwintering
553 community had filled the shelf during the winter but now, in spring, it had been partially
554 replaced by a new community, the southern community, coming in from the northern Bering Sea
555 (herein spring community). The spring community contained high abundances of young-of-the
556 year of the copepod *C. glacialis*, benthic polychaetes, and barnacles. These resulted from
557 reproduction in the northern Bering Sea or southern Chukchi Sea where the seasonal cycle in
558 primary production (ice algae and then phytoplankton), in response to reduction in sea ice and
559 snow cover, is initiated earlier than in the northeastern Chukchi Sea. Barnacle nauplii could have
560 originated along rocky shorelines where the sessile adult barnacles have settled; the region
561 around Bering Strait and the Diomed Islands provide suitable habitat. Alternatively, they could
562 have originated from adults settled on hard-bodied benthic organisms in the Chukchi Sea
563 (Slattery and Oliver, 1987). Of note, no barnacle nauplii were present at the Bering Strait Station,
564 suggesting that the nauplii observed in this study originated north of the Strait (by contrast,
565 polychaete larvae and trochophores were present at that station). A back-of-the-envelope
566 calculation of the transit time between the Bering Strait station and the southernmost Group 3
567 station (#141), assuming straight-line advection and current speeds of 10 or 15 cm/sec (Stabeno
568 et al., 2018), yields 33 (at 15 cm/sec) and 50 (at 10 cm/sec) days, considerably longer than the

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4 569 difference between the two sampling dates (25 days) and supporting the hypothesis that the
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7 570 barnacle nauplii likely originated somewhere to the north of Bering Strait.

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9 571 Water mass characteristics associated with each of the two faunal communities supports
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11 572 the model of the spring community being advected in from the Bering Sea, since CSW,
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14 573 associated with the spring community, is a combination of two northern Bering Sea water types.
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16 574 This water mass (and other summer water) is transformed into NVWW in late-autumn and
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19 575 disappears from the Chukchi Sea at that time, so its presence requires renewed input through
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21 576 Bering Strait. Elevated chlorophyll also was present associated with the spring community but
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24 577 this might have resulted in-situ in the southern Chukchi Sea in response to reduction in sea ice
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26 578 cover; this is supported by the low levels of nitrate suggesting depletion during photosynthesis.
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29 579 A similar evolution in water mass characteristics and replenishment of nutrients from the south
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31 580 was observed in a five-year study using moored CTDs and nitrate sensors along a transect
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33 581 extending the NW from Icy Cape (Mordy et al., 2020).

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36 582 This scenario of community replacement would require that the Chukchi Sea continue to
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38 583 flush northward through the winter and spring, and that the prevailing circulation pathways
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41 584 would essentially persist through the year. Evidence from moorings (Fang et al., 2020; Tian et
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43 585 al., submitted) suggests that this is the case. The essential features of the circulation remain the
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46 586 same in winter as in other seasons, although with reduced northward transport through Bering
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48 587 Strait (Woodgate, 2018) and more frequent and prolonged encroachments of water from the
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51 588 Canada Basin onto the Chukchi Shelf through Barrow Canyon in the northeast (Weingartner et
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53 589 al., 2017; Stabeno et al., 2018; Pisareva et al., 2019).

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55 590 The distributions of the two faunal communities also track the circulation pathways
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58 591 through the eastern Chukchi Sea. North of ~71.5, the overwintering community is seen advected
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592 anti-cyclonically around the north side of Hanna Shoal; south of that latitude it has been replaced
593 by the spring community advected from the south. The overwintering community also follows
594 southeasterly pathways of flow from south of Hanna Shoal towards Icy Cape and joining with
595 the coastal flow adjacent to Alaska. This contributes to the NW-SE latitudinal gradient seen in
596 the faunal boundary between the two communities. The spring community is found further to the
597 north in the west, associated with the persistent northward Central Channel flow, than in the east
598 where it is found in the flow divergence from the Central Channel towards the coast at the
599 southern portion of the study area (Pacini et al., 2019). The transit time for parcels to advect from
600 Bering Strait to Barrow Canyon is estimated to be 3-6 months, with the shorter time
601 corresponding to the coastal pathway, and the longer time associated with the central pathway
602 around the north side of Hanna Shoal (Weingartner et al., 1999; Stabeno et al. 2018; Tian et al.,
603 submitted). This is consistent with the overall flushing time of 4.5 months estimated by
604 Woodgate (2018) and suggests that the faunal community observed in the northern Chukchi Sea
605 in early June might have entered through Bering Strait in early March; however, since the
606 northward transport on the Chukchi shelf is generally reduced during winter (Tian et al.,
607 submitted), it could have been earlier.

It is likely that the distinct faunal boundary associated with the location of the
southeastward divergence of the Central Channel flow pathway resulted from the seasonal
progression of water across the Chukchi shelf, rather than spatial differences in the circulation.
Three stations, characterized by the overwintering community (Stns. 10 and 19) or the transition
community (Stn. 24), were sampled early in the cruise and were co-located with stations showing
the replenishment communities later in the cruise. This suggests that the faunal distinction was
established by the inflow of the replenishment community with the early season CSW along the

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4 615 circulation pathways, rather than that circulation feature itself persistently defining different
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6 616 communities.

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9 617 Although numerous previous studies have described zooplankton community
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11 618 compositions and their associations with hydrographic characteristics in the Chukchi Sea (e.g.,
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14 619 Hopcroft et al. 2010 and earlier studies described therein; Matsuno et al., 2011, 2016; Eisner et
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16 620 al., 2013; Ershova et al., 2015; Pinchuk and Eisner, 2017; Spear et al., 2018; Xu et al., 2018) ,
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19 621 this study stands out as the only survey of the Chukchi shelf conducted during late spring; all
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21 622 other studies were conducted during mid-late summer or early fall. Furthermore, of recent
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24 623 summer-fall surveys, only the work of Matsuno et al. (2011, 2016), Pinchuk and Eisner (2017),
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26 624 Spear et al. (2018), and Xu et al. (2018) overlap spatially to any great extent with the present
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29 625 study area. Nonetheless, it is useful to compare the observations herein with those from the
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31 626 summer-fall surveys to better infer the seasonal transitions in zooplankton composition in the
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33 627 entire Chukchi Sea and how water mass distributions and circulation influence the observed
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36 628 zooplankton distributions.

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38 629 All of the previous studies identified different species compositions/groups that were
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41 630 associated with hydrography throughout the Chukchi Sea, although the degree of granularity of
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43 631 the group distributions varied between studies. Where study regions overlap spatially, some
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46 632 similarities in species composition and groups between studies exist, however each study
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48 633 identified a unique set of species or hydrographic groups depending on the mesh size net utilized,
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51 634 the level of taxonomic detail utilized, and the range of biological (e.g., taxa, fluorescence) and
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53 635 physical variables enfolded in the analyses. Overall, however, all of the studies in late summer
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56 636 and early fall indicate that the eastern Chukchi Sea, from Bering Strait to Hanna Shoal, was
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58 637 occupied by a zooplankton community similar in composition to the replenishment community
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4 638 here described. Accordingly, *C. glacialis* was widespread, with most life stages observed in all
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6 639 studies (some studies did not report copepodid Stage I, but this could have resulted from the use
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9 640 of larger mesh nets, e.g., Xu et al., 2018). Barnacle nauplii and cyprids also were pervasive.
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11 641 Appendicularians, polychaete larvae or trochophores, and euphausiid furcilia were less often
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14 642 reported, however their absence might have resulted from methodological or reporting
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16 643 approaches rather than their absence. Abundances of individual taxa were highly variable
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19 644 between summer studies of the northeastern Chukchi Sea (Pinchuk and Eisner, 2017; Spear et
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21 645 al., 2017; Xu et al., 2018). The abundances from this spring study for *C. glacialis*, barnacle
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23 646 nauplii, and polychaete larvae/trochophores in the replenishment community were within the
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26 647 range of variability reported for the summer studies, however abundances of the Pacific copepod
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29 648 species *E. bungii* and *Neocalanus* spp. were much reduced relative to those seen in summer. A
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31 649 clear distinction in the faunal composition and abundances between Arctic Ocean and Chukchi
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33 650 Sea was seen consistently in all studies, with the Arctic community intermittently extending
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36 651 south onto the Chukchi Shelf in association with southern advection (e.g., Ershova et al., 2015;
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38 652 Pinchuk and Eisner, 2017; Xu et al., 2018).

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41 653 Barnacle nauplii and/or cyprids were found throughout the eastern Chukchi Sea during
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43 654 summer, including regions near and on Hanna Shoal (Questel et al., 2013; Ashjian et al., 2017).
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46 655 That broad spatial distribution of barnacle nauplii and/or cyprids contrasts with the present
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48 656 spring study in which they were seen only in the southwestern portion of the study area. These
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51 657 observations indicate that barnacle nauplii and cyprids are persistent members of the summer
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53 658 zooplankton community, despite interannual variations in abundance. Their absence during
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55 659 winter is likely because they have either matured and settled out or been advected northward off
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660 the Chukchi shelf, and that they are re-introduced from the south in spring following spawning in
661 the Bering Sea or rocky coasts of the southern Chukchi Sea.

662 Surveys with substantial spatial overlap with the present study often described
663 longitudinal gradients in species composition associated with changing water mass types
664 (Alaskan Coastal Water in the east; CSW in the west) north of Cape Lisburne (Matsuno et al.,
665 2011; Pinchuk and Eisner, 2017; Spear et al., 2018; Xu et al., 2018), similar to what was seen in
666 the present study between the overwintering and replenishment communities. Some studies also
667 reported latitudinal faunal boundaries that approximately overlapped with the distinct faunal
668 front seen in the present study (Matsuno et al., 2011; Pinchuk and Eisner, 2017; Spear et al.,
669 2018). They did not associate those boundaries with circulation patterns but rather with
670 differences in hydrography (which of course is related to the circulation).

671

672 *C. glacialis* Phenology

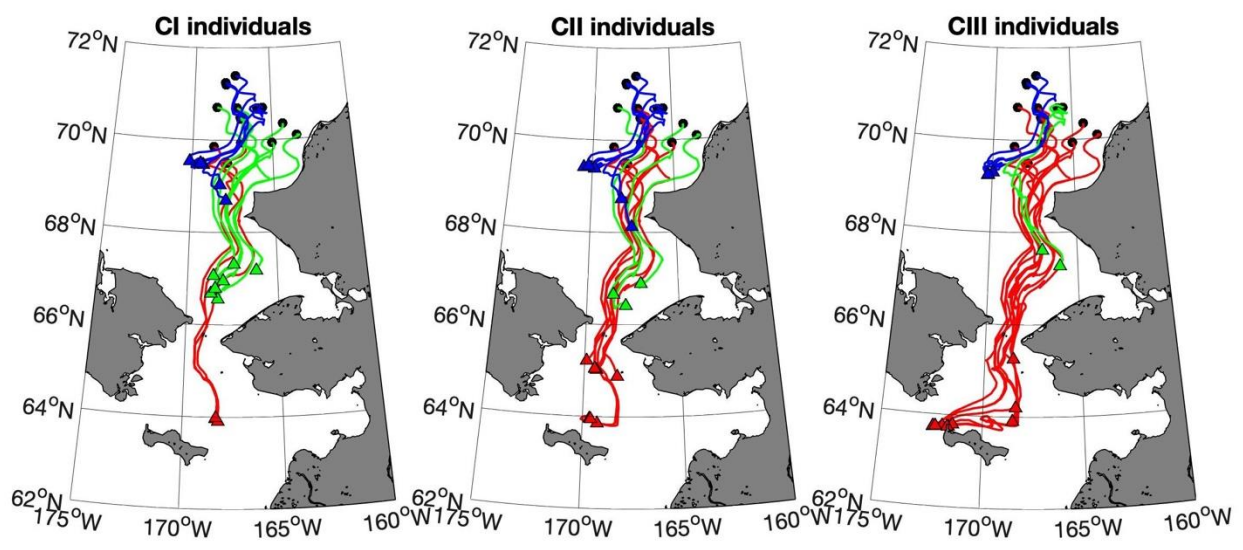
673 The high abundances of *C. glacialis* early copepodids so far north into the Chukchi and
674 the widespread Bering Sea haplotype (Figure 12; Nelson et al., 2009; Ashjian et al., 2017)
675 supports the paradigm that a great proportion of the *C. glacialis* found in the Chukchi Sea
676 originate south of Bering Strait and are not endemic to the Chukchi Sea (e.g., Ershova et al.,
677 2015; Wassmann et al. 2015). Despite nearly continuously being advected across the Chukchi
678 shelf, *C. glacialis* apparently has not established a population of Bering/Southern Chukchi Sea
679 endemics in the Arctic Ocean, since both molecular and population structure point to there being
680 distinct populations between the regions. The distribution of haplotype frequencies shows a
681 differentiation between Arctic and Bering Sea populations (Nelson et al., 2009; Ashjian et al.,
682 2017; this study), but not between the Chukchi Sea and the Bering Sea, with the frequency of

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4 683 Bering Sea haplotypes decreasing with distance into the Arctic Ocean from the Chukchi Sea
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6 684 source (Nelson et al., 2009). Population stage structure of *C. glacialis* differs across the faunal
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9 685 front between Arctic and Chukchi populations and the two apparently follow different
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12 686 phenologies, with Bering/Chukchi *C. glacialis* developing to copepodid stage V and Arctic *C.*
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14 687 *glacialis* developing to copepodid stage IV prior to diapause (Lane et al., 2008; Ershova et al.,
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16 688 2015; Pinchuk and Eisner, 2017). Because of earlier sea ice retreat and primary production, the
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19 689 Bering/Chukchi populations initiate reproduction earlier in the year (e.g., Baier and Napp, 2003).
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21 690 They also have faster development times in the warmer temperatures of the northern Bering Sea
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24 691 and southern Chukchi Sea than in Arctic waters and thus, at a given date in summer, older stages
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26 692 might be observed in the Bering/Chukchi population than in the Arctic population.
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29 693 The presence of younger copepodid stages of *C. glacialis* in the spring community
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31 694 provided the opportunity, using biological-physical modeling, to track plankton, and thus water,
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33 695 of Pacific origin flooding the Chukchi Sea in spring, as well as to identify the spawning locations
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36 696 for the individuals there. The spawning locations of younger stages of *C. glacialis* observed in
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38 697 the net tows were estimated using modeled backwards advection. Temperature and velocity from
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41 698 a coupled atmosphere-sea ice-ocean model (BIOMAS; Zhang et al., 2010, 2014) were coupled
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43 699 with an individual based model of *C. glacialis* temperature-dependent development rates (Ji et
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45 700 al., 2012) and run backwards in time, from the collection locations, until the copepods reached
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48 701 the egg stage and thus the spawning location. Modeled temperature dependent development
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51 702 times provide a duration for the backward advection. Trajectories and spawning locations
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53 703 revealed three different patterns (Figure 13). For the first, individuals were spawned south of
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55 704 Bering Strait and advected northwards through the Central Channel route where they were
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58 705 collected as CI, CII, and CIII between 69-70°N. For the second, individuals were spawned north
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706 of Bering Strait in a known Chukchi Sea production and benthic hotspot (e.g., Grebmeier, 2012;
707 Grebmeier et al., 2015) along the eastern Chukchi Sea flow pathway and advected northwards in
708 that eastern pathway to be collected off of Icy Cape. Finally, some individuals were spawned
709 north of (CI, CII) or near (CIII) 69°N in the Central Channel pathway and advected to north of
710 71°N where they were collected. For this latter pattern, the length of the trajectory was shorter
711 due either to slower velocities or to faster development times in response to warmer water
712 temperatures.



715 Figure 13. Simulations showing backtracking of *C. glacialis* CI, CII, and CIII from their
716 collection location (black dots) southwards to their spawning location (triangles). Each track
717 shows the path of a theoretical copepod that is backwards developed from the observed stage
718 through younger stages to egg at ambient water temperatures and using modeled velocity. The
719 different colors represent the three different spawning locations (Bering Sea – red, southern
720 Chukchi Sea – green, near/north of 69°N – blue).

722 A previous modeling study of *C. glacialis* populations on Hanna Shoal in August 2012
723 and 2013 concluded, based on backwards tracking coupled with development time, that the
724 majority of the adult *C. glacialis* originated in the southern Chukchi Sea and northern Bering Sea
725 and that the younger stages had been spawned primarily at the northern end of the Central

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4 726 Channel by May 1 (Elliott et al., 2017). The distributions of young stages of *C. glacialis*
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6 727 observed in the present study may be consistent with these predictions, since the youngest life
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9 728 stage enumerated in the present study, CI, requires ~75 days to mature (Ji et al., 2012). With a
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12 729 spawning date of May 1 (Elliott et al., 2017), copepodid stage I would be achieved in mid-July.
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14 730 This in turn predicts that the sampling in the present study should not have observed copepodid
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16 731 stage I or later in the northern Chukchi Sea, since any individuals spawned on May 1 should not
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19 732 have developed to a stage that would have been collected using the 150 µm mesh net of this
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21 733 study. Note that since the Elliott et al. (2017) study was focusing on source populations for
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24 734 Hanna Shoal, the simulations are not as relevant to the remainder of the Chukchi Sea. However,
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26 735 based on simulations of both source and sinks for Hanna Shoal *C. glacialis*, Elliott et al. (2017)
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29 736 similarly concluded that *C. glacialis* populations in the Chukchi Sea are advected off the
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31 737 Chukchi shelf to the north over winter and must be replenished annually from the south.

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33 738 Similar to results of the modeling simulations identifying the spawning locations, a
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36 739 number of studies concluded that *C. glacialis* populations are replenished from the south and that
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38 740 the observed young-of-the year originated either in the very Southern Chukchi Sea or the
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41 741 northern Bering Sea. Based on estimated development times at temperatures ranging from -1.8 to
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43 742 12 °C and drifter velocities, Spear et al. (2018) concluded that *C. glacialis* copepodids collected
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46 743 north of Cape Lisburne in August were spawned in the Chukchi Sea. Ershova et al. (2015) in
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48 744 summer found Arctic populations primarily at copepodid stages I-III, suggesting that these are
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51 745 young-of-the-year developing to the overwintering CIV stage. By contrast, the Bering/Pacific
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53 746 populations were more developed at stages CIV and CV, resulting from earlier reproduction due
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56 747 to earlier ice retreat and a productive season and faster development times in warmer
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58 748 temperatures of the northern Bering and southern Chukchi Seas than in Arctic waters. Pinchuk
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4 749 and Eisner (2017) observed increasing mean life stage with time and latitude through the
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6 750 Chukchi Sea, with older CV observed in mid-late August in the northeastern Chukchi Sea and
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9 751 higher proportions of younger CIV in early August in the southern Chukchi Sea. This pattern
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11 752 likely reflected temporal changes along the northward advection pathways, so that the older CV
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14 753 were observed later due to maturation. Matsuno et al. (2016) observed few early stage
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16 754 copepodids and low *C. glacialis* biomass in the northeastern Chukchi Sea and concluded that
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19 755 reproduction was not ongoing. The present study found that, in spring, the populations advected
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21 756 into the Chukchi Sea from the northern Bering Sea were dominated by copepodid CI-CIII. Since
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24 757 the development time of *C. glacialis* from CI - CV is ~90 days at 0°C and faster at warmer
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26 758 temperatures (Ji et al., 2012), copepodid stages CI-CIII observed in June in the present study
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28
29 759 could easily have developed to CIV and CV by August, in accord with the findings of these
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31 760 previous studies.

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33 761 Both Ashjian et al. (2017) and Pinchuk and Eisner (2017) noted high proportions of *C.*
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36 762 *glacialis* copepodid III or younger on Hanna Shoal in August of 2012 and 2013. Pinchuk and
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38 763 Eisner (2017) concluded that these young copepodids were part of an Arctic population of *C.*
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41 764 *glacialis* that had been advected over Hanna Shoal. This contradicts the findings of Elliott et al.
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43 765 (2017), who estimated spawning locations for those animals farther south in the Chukchi Sea. It
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46 766 is also at odds with the genetic analyses presented in Ashjian et al. (2017) showing that, although
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48 767 Arctic animals were present on northeastern Hanna Shoal, only over the Chukchi Slope did their
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51 768 frequencies approach fifty percent. It could be that the high abundances of young copepodids
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53 769 observed on Hanna Shoal in the two studies resulted from reproduction by *C. glacialis* in the
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55 770 middle-northern Chukchi Sea, as estimated by Elliott et al. (2017), while the older copepodids
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58 771 observed farther to the south by Pinchuk and Eisner (2017) were advected into the Chukchi Sea
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772 earlier in spring, as seen for the renewal population in the present study, and had developed to
773 copepodid V by mid-late August.

774 Together, the observations suggest a conceptual model for *C. glacialis* phenology in the
775 Chukchi Sea that incorporates a year-round “conveyer belt” supply of animals. Central to the
776 model is the observation that *C. glacialis* generation time (~ 1-year; Falk-Peterson et al., 2009) in
777 this region is longer than the flushing time of the Chukchi Sea (~ 4.5 months; Woodgate, 2018)
778 so that individuals spawned in the Chukchi Sea will not remain there until adulthood. *C. glacialis*
779 overwinters in the Chukchi Sea primarily as copepodid Stage V or perhaps as adult females, with
780 continuous inputs of stage CV from the northern Bering Sea. Whether substantial portions of the
781 population can successfully diapause in the very shallow northern Bering Sea and Chukchi Sea
782 remains in question. Regardless, adult females dominate the remaining animals by spring (either
783 through differential mortality of the CV stages or by molting from CV to AF); this is the
784 population structure of the May-June overwintering community observed here. In the northern
785 Bering Sea and eventually southern Chukchi Sea, sea ice extent diminishes starting in March-
786 April, permitting the initiation of primary production, the availability of algal food for the adult
787 females, and food-dependent spawning by females. Those communities spill into the Chukchi
788 Sea through Bering Strait and move northwards in CSW, filling the southern Chukchi Sea with
789 newly hatched *C. glacialis*. As the water moves north, the copepods continue to develop,
790 reaching the younger copepodid stages by the time the water reaches the northeastern Chukchi
791 Sea. This is the replenishment community observed in the present study.

792 Simultaneously with the northern advection, sea ice continues to retreat to the north,
793 exposing greater portions of the Chukchi Sea to sunlight and initiating primary production and
794 reproduction by the overwintering community of *C. glacialis*. However, because of the relatively

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4 795 strong advective pathways, the overwintering community is swept out of the Chukchi Sea into
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7 796 the Arctic basin except for regions such as Hanna Shoal where the circulation is more sluggish
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9 797 (e.g. Martin and Drucker, 1997). In those regions, the progeny of the overwintering community
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12 798 reaches the early copepodid stages later in the summer, as seen by Ashjian et al. (2017) and
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14 799 Pinchuk and Eisner (2017). Because of their later spawning date, these animals may need to
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16 800 overwinter as copepodid stage IV, similar to the Arctic Ocean populations, if they have the
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19 801 plasticity. Alternatively, *C. glacialis* on Hanna Shoal do not overwinter successfully and must be
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21 802 replaced each year by the northward flowing Bering/Chukchi sea populations (since haplotypes
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24 803 on Hanna Shoal are of the Bering Sea type; Ashjian et al., 2017).

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27 28 805 **Concluding Remarks**

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31 806 Although associations between zooplankton community compositions and abundances in
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33 807 the Chukchi Sea have been described previously, this is the first description of these associations
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36 808 and distributions during late spring when the zooplankton community is undergoing a seasonal
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38 809 evolution. It is also the first survey to capture both the overwintering and summer zooplankton
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41 810 composition offshore of the Alaskan coast. A conceptual model describing the evolution of *C.*
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43 811 *glacialis* populations in the Chukchi Sea explains the replenishment of those populations from
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46 812 the Bering Sea and serves also as a model for how other plankton are similarly supplied by the
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48 813 Bering Sea.

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50 814 At present, it appears that zooplankton from the Bering Sea are transient in the Chukchi
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53 815 Sea and do not establish populations there. Given the persistent northward advection and
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55 816 relatively short turnover time of the Chukchi Sea, it appears unlikely that there could be endemic
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58 817 Chukchi Sea populations, except perhaps in coastal bays or lagoons, because the animals are

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818 continuously flushed out to the north. Therefore, even if summer conditions under environmental
819 warming permit successful recruitment by Pacific species, those animals would not remain in the
820 Chukchi Sea. Furthermore, the inevitable return of winter conditions and the shallow depth of the
821 Chukchi shelf would likely preclude successful overwintering by many Pacific zooplankton
822 species. Consequently, it is likely that, in the future, annual differences in the abundance and
823 biomass of zooplankton in the Chukchi Sea will continue, but the community composition will
824 likely remain similar to what it is today. Perhaps more interesting is if any of the species could
825 successfully persist in the Arctic oceanic regions to the north, potentially competing with the
826 endemic Arctic species and significantly changing the community composition there. This could
827 have substantial impacts to multiple components and functions of the western Arctic ecosystem,
828 from prey availability for Arctic cod to utilization of primary production to carbon flux to the
829 seafloor.

830

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