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Springtime renewal of zooplankton populations in the Chukchi Sea



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ABSTRACT

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

1. 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 turn-over 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 (Fig. 1). Upon exiting the canyon, a portion of the flow turns eastward to feed the Beaufort Shelfbreak Jet

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(Nikolopoulos et al., 2008), while a larger portion turns westward to form the Chukchi Slope Current (Corlett and Pickart, 2017; Li et al., 2019). The outflow from Herald Canyon feeds the eastward-flowing Chukchi Shelfbreak Jet (Linders et al., 2017).

Different water masses are associated with each of the main advective pathways (Coachman et al., 1975; Gong and Pickart, 2015). Generally, Anadyr Water enters Bering Strait in the west, following the western pathway through the Chukchi Sea. Alaskan Coastal Water enters the eastern side of Bering Strait in summer and is advected in the Alaskan Coastal Current along the eastern pathway to exit the shelf through Barrow Canyon. North of Bering Strait, Anadyr and Bering Shelf Water mix to form what is known as Bering Summer Water (Pisareva et al., 2015), which mostly follows the central pathway northward through the Central Channel, turning to the east north of Hanna Shoal, with several eastward divergences along the way.

Each of these water masses has been associated with characteristic zooplankton communities in recent studies (Wassmann et al., 2015 and references therein; Ershova et al., 2015; Pinchuk and Eisner, 2017; Spear et al., 2019; Xu et al., 2018). Most of the studies have further partitioned the water mass associated species groups into spatially distinct distributions. Furthermore, different nomenclatures for the water masses (e. g., Bering Summer Water vs. Chukchi Summer Water) somewhat complicates the synthesis. However, some generalities for each water mass can be described. Overall, the Bering Summer Water/Chukchi Summer Water (hereafter referred to as Bering Summer Water) is marked by Calanus glacialis, Pacific copepod species such as C. marshallae, Neocalanus spp. and Eucalanus bungii bungii (herein E. bungii) and meroplankton, with the abundances of Pacific species decreasing to the north. Lower abundances of Pacific species and meroplankton and more abundant euphausiids are typical of the Anadyr Water. The Alaskan Coastal Water generally carries more inshore, euryhaline smaller species such as Acartia hudsonica and Centropages abdominalis and is distinct from the neighboring Bering Summer Water. A fourth zooplankton community, dominated by Arctic endemics such as C. hyperboreus, is found along the northern edge of the Chukchi Sea and sometimes extending south through Barrow Canyon after reversal of the prevailing poleward flow there (Pinchuk and Eisner, 2017). While some overlap exists in terms of presence or absence between the water mass types, within a given study the zooplankton communities are distinct. Studies with a broader geographical coverage (e.g., Matsuno et al., 2011; Eisner et al., 2013; Ershova et al., 2015; Pinchuk and Eisner, 2017, Xu et al., 2018) also note both northern-southern and eastern-western transitions, both of which are likely related to the advective pathways, distance from the Bering Sea source, and seasonal evolution of the populations and communities.

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

The objectives of the present study are to describe the abundances and distributions of the copepods *C. glacialis* and *C. marshallae* (copepodid and adult life stages) and of large bodied zooplankton relative to the distribution of water masses and advective pathways during late spring in the northeastern Chukchi Sea. Because *C. glacialis* and *C. marshallae* are extremely difficult to differentiate taxonomically, and because *C. marshallae* is relatively rare, those species were not separated and are herein designated as *C. glacialis* (Plourde et al., 2005; Campbell et al., 2009; Nelson et al., 2009). The work presented here was conducted opportunistically during a cruise to the region that focused on hydrography, sea ice, and primary productivity of the Chukchi Sea in late spring (Arrigo et al., 2017). The goal was to establish information on the zooplankton community of the Chukchi Sea at that time of year and to gain insight into the population dynamics of the copepod *C. glacialis*, a key member of the mesozooplanton community. This is the first



Fig. 1. Geographic place names and major current pathways in the Chukchi Sea. Currents after Corlett and Pickart (2017).

description of these associations and distributions during late spring when the zooplankton community is undergoing a seasonal evolution. It is also the first survey to capture both the overwintering and early summer zooplankton composition of the Chukchi Sea.

2. Methods

Sampling was conducted from May 16 - June 20, 2014 during a cruise on the USCGC Healy to the Chukchi Sea as part of the SUBICE (Study of Under-ice Blooms in the Chukchi Ecosystem) program (Arrigo et al., 2017). The cruise track was centered in the eastern Central Chukchi Sea between Pt. Hope/Cape Lisburne and the Chukchi slope with most work conducted considerably offshore of the Alaskan coast (Fig. 2). The sampling scheme was designed to intercept known and hypothesized advective pathways (Pacini et al., 2019). Most stations were located to the south and west of Hanna Shoal, intersecting the Central Channel flow and the pathway from the Central Channel east towards the Alaskan coast. The zooplankton work was conducted opportunistically to the main objectives of the cruise and was done throughout the study region at a subset of the occupied stations (Fig. 2; Table 1); one station was occupied in Bering Strait, one in the southern Chukchi Sea, and the rest were situated north of Point Hope, AK. Zooplankton samples were collected from the surface to the near bottom without regard to day or night using forty-six vertical hauls of paired 60cm Bongo nets equipped with 150 µm and 500 µm mesh nets and oneway turning flowmeters. The nets were equipped also with a bright strobe to visually stun euphausiids and increase their catch (Wiebe et al., 2004; Ashjian et al., 2017). Zooplankton samples were preserved immediately following collection in 5% formalin seawater. C. glacialis were preserved in ethanol at six stations during the cruise for analysis of the mitochondrial cytochrome c oxidase 1 gene (mtCO1) to determine species and population haplotypes (see methods in Ashjian et al., 2017). Water column hydrography and relative chlorophyll abundance were



Fig. 2. The Chukchi Sea with Bering Sea to the south and the Beaufort Sea to the north and the locations of the net tows used in this study. Topographic lines show bottom depth in meters. Prominent geographic features are marked. Insert shows detail of central study region.

measured at each station using a Seabird 911 + conductivity-temperature-depth (CTD) package equipped with a WET Labs ECO-AFL/FL fluorometer. Velocities along the ship's track were measured using a 150 kHz hull-mounted acoustic Doppler current profiler (ADCP). Additional information on processing of the physical data and the key characteristics of the hydrography and circulation are found in Pacini et al. (2019).

Abundances of different life stages of *Calanus glacialis* were enumerated from the 150 μ m mesh net samples in successive splits until at least 300 *C. glacialis* were identified (*C. glacialis* and *C. marshallae* were not differentiated). Early copepodids stages of *C. glacialis* and *C. hyperboreus* were differentiated based on prosome length (e.g., Lane et al., 2008). Abundances of larger zooplankton, including meroplankton, were enumerated from the 500 μ m mesh net samples. Abundances were calculated as integrated water column abundances to better identify potential "hot spots" of abundance across the shelf and to reflect that the tows sampled a vertical, rather than oblique, body of water.

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

3. Results

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

Zooplankton composition and abundance changed substantially at stations sampled on and after June 7/Station 112 (Table 2; Fig. 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 (Fig. 2).

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 (Figs. 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.

Similar marked changes between the two periods of the cruise were

Dates, position, and bottom depth for the stations at which zooplankton tows were conducted. Station groups identified by principal component analysis also indicated.

Station	Year	Month	Day	Latitude	Longitude	Bottom	Station
Number				(°N)	(°W)	Depth (m)	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
22/	2014	6	20	70.450	166.9642	51	3

observed for several other taxa (Table 2). Very few euphausiids were observed during the first portion of the cruise (Fig. 5A). During the second portion of the cruise, significantly more euphausiids, dominated by pre-furcilia and furcilia, were seen in the southern portion of the study area. There was a west-east shift both in abundance (lower abundances were seen at the western stations) and in stage composition (eastern stations were dominated by furcilia while western stations had more pre-furcilia stages). Pelagic polychaete stages were essentially absent from the Chukchi Sea at stations sampled before June 7 (Fig. 5C). After June 7, however, high abundances of both larvae and trochophores were observed primarily to the southwest of Hanna Shoal. Somewhat reduced abundances were seen along the Alaskan coast. A similar pattern was observed for appendicularians (Fig. 6B) and barnacle nauplii (Fig. 6D).

Both amphipods and chaetognaths were persistent in the zooplankton composition, being present in 96% and 98% of the tows, respectively (Table 2). Similarly to *C. glacialis* AF, chaetognaths did not show changes in abundance between the two periods of the cruise (Fig. 6D). By contrast, amphipods were in low abundance in the southern portion of the study area after June 7 although this difference was not significantly different in the mean (Fig. 6A; Table 2).

Cluster analysis revealed four groups with co-occurring plankton

types (Fig. 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*.

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

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.

	Net	Relative	Before June 7 (N $= 23$)		On or After June	e 7 (N = 23)	<i>t</i> -test
	Mesh	Occurrence	Mean Abd.	Std. Dev.	Mean Abd.	Std. Dev.	р
Taxonomic Category	(µm)		(# m ⁻²)	(# m ⁻²)	(# m ⁻²)	(# m ⁻²)	
Calanus glacialis CI	150	0.48	5	15	1154	1573	0.00
C. glacialis CII	150	0.43	1	4	412	806	0.02
C. glacialis CIII	150	0.46	10	37	74	165	0.09
C. glacialis CIV	150	0.33	35	132	7	25	0.35
C. glacialis CV	150	0.50	41	67	11	29	0.06
C. glacialis AM	150	0.46	4	6	4	8	0.98
C. glacialis AF	150	1.00	359	336	218	217	0.10
C. hyperboreus	150	0.04	74	336	0	0	0.29
Metridia longa CV-AM	500	0.28	5	12	1	2	0.12
Neocalanus sp.	500	0.13	7	31	1	5	0.42
Eucalanus bungii b. CII-AM	500	0.11	3	11	1	2	0.36
Paraeuchaeta 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
Limacina 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

eigenvalues.

The station groups were identified based primarily on the first two principal components (Fig. 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 -2to 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 be positive with high abundances of Group C plankton types. Station Group 4 had the most negative PC1s. These were stations that had compositions similar to those of Station Group 2 (low abundances of plankton Group C) but also low abundances of plankton Group D. Four stations lay between Station Group 2 and Station Group 3 in PC space (Fig. 8), suggesting either low abundances of all plankton groups or high abundances of all plankton groups. One station appeared, on the basis of PC1 vs. PC2, to be grouped with Station Group 4 but was placed in Station Group 2 on the basis of principal component 3 (not shown) for which plankton group D was the strongest determinant.

Plankton abundances, plankton groups, and station groups were embodied in a heat map (*sensu* Hopcroft et al., 2010) to better illustrate the relationships between the three (Fig. 9). Station Group 1 included



Fig. 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.



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



Fig. 5. Integrated water column abundances of life stages of euphausiids (A, B) and polychaetes (C, D) at locations north of Pt. Hope, AK. A and C: Abundances from before June 7, 2014. B and D: Abundances from on or after June 7, 2014. Crosses (+) denote locations for which no animals were observed. Different life stages denoted by different colored shading. JAD = Juveniles and Adults. Data from station in Bering Strait not shown.

two stations that were located on the Chukchi Slope (Fig. 10), the only stations where oceanic Arctic plankton that are part of plankton Group A were found (note abundances of zero for those plankton types at all stations outside of those in station group 1). Moderate abundances of CIII-adult *C. glacialis* also were present at those two stations.

Station Group 2 was distributed primarily along a swath extending northwest from Icy Cape (Fig. 10). Many, but not all, of these stations



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

were sampled prior to June 7 (Table 1). *C. glacialis* AF, chaetognaths, and amphipods were prominent at these stations (Fig. 8); most other plankton types were present in low abundance or not at all. Group 3 stations lay to the south of Group 2 stations, along a swath with the same northwest-southeast orientation (Fig. 10). These stations all were sampled on or after June 7 (Table 1) and had high abundances of the Group C plankton, young *C. glacialis*, meroplankton, and euphausiid



Fig. 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".

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

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

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



Fig. 8. Stations grouped according to principal components 1 and 2.

species in Species Group C, early stage *C. glacialis*, meroplankton, and appendicularians, were significantly greater (Kruskal Wallis, $p \ll 0.01$) for the Group 3 stations than for the other station groups (Table 4). These are the plankton types that were important for Mode 1 of the PCA,



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



Fig. 10. A) Locations of stations by group. The station located in Bering Strait (Fig. 2) is in the "No Group" category and not in the geographic range of this figure. B) Mean water column velocity averaged over 24 h prior to the time that net sample was collected. Velocity vectors are color coded by station group. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

with high positive PC1. Note also that the mean abundances of Group C species in Group 5 stations were intermediate between those seen in Group 3 stations and Groups 2 and 4 stations, consistent with the spatial distribution of Group 5 stations between the southern Group 3 stations and the northern Groups 2 and 4 stations (Fig. 10) and with the magnitude of Principal Component 1 (Fig. 8). Mean Group 1 station abundances (note, n = 2) were significantly greater (Kruskal Wallis, p < 0.05) for the oceanic arctic species (*C. hyperboreus, Paraeuchaeta*, foraminifera) and for *Neocalanus* spp. Greater Group 2 station mean abundances that were not necessarily significantly different from other group station means also were seen for all stages of *C. glacialis*, including CIV and CV that were generally much less important elsewhere. Amphipods

had significantly greater mean abundance for Group 2 stations than for other station groups. For other plankton types, no difference in mean abundance was seen between station groups or the abundances were too low and too variable to detect a difference.

Although Pacini et al. (2019) provided a comprehensive description of the hydrographic characteristics and circulation encountered during the cruise, aspects of these are here presented to provide appropriate context for the interpretation of the zooplankton distributions. Differences in hydrography and water column fluorescence (a measure of chlorophyll *a* concentration) were seen between the different station types (Figs. 9, 11). Five water masses were identified following previous definitions (e.g. Gong and Pickart, 2015; Pacini et al., 2019). These are:

Mean integrated water column zooplankton abundances (# m^{-2}) for stations in each station group. Significant Kruskal-Wallis *p* values denoted by bold type (last column). Bold mean abundances show those significantly different from the others (Tukey-Kramer post hoc test, p < 0.05). Mean and standard deviations (std) of abundance shown for each group.

	Group 1 ($n = 2$)		Group 2 (n = 19)		Group 3	Group 3 (n = 14)		Group 4 (n = 7)		(n = 4)	Kruskal-Wallis p
Taxonomic Category	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	
Calanus glacialis CI	0	0	1	3	1864	1670	0	0	134	203	$6.5 imes10^{-8}$
C. glacialis CII	0	0	0	0	675	953	0	0	17	15	$1.7 imes 10^{-8}$
C. glacialis CIII	98	112	1	1	122	199	0	0	4	7	$2.0 imes10^{-7}$
C. glacialis CIV	336	425	6	16	11	32	3	5	0	0	0.05
C. glacialis CV	119	132	28	48	7	19	49	78	2	4	0.02
C. glacialis AM	11	2	3	6	4	7	7	8	4	2	0.11
C. glacialis AF	1054	108	258	224	191	176	355	403	276	175	0.16
C. hyperboreus	855	1069	0	0	0	0	0	0	0	0	$6.5 imes10^{-9}$
Metridia longa CV-AM	23	33	1	3	1	2	1	2	11	19	0.47
Neocalanus sp.	77	103	0	1	2	7	0	0	1	2	0.003
Eucalanus bungii CII-AM	4	5	0	1	1	2	1	2	13	26	0.28
Paraeuchaeta sp. CIII-AM	214	228	0	0	0	0	0	0	0	0	$4.0 imes10^{-9}$
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	$2.5 imes10^{-5}$
Chaetognaths	368	195	193	91	164	134	167	140	218	169	0.37
Limacina 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	$8.3 imes10^{-8}$
Polychaete Trochophores	0	0	1	2	176	157	0	0	6	6	$7.9 imes10^{-7}$
Barnacle Nauplii	2	3	11	16	4832	6020	0	0	237	376	$3.0 imes10^{-6}$
Foraminifera	1386	77	0	0	0	0	0	0	0	0	$4.0 imes10^{-9}$



Fig. 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.

(i) Newly Ventilated Winter Water (NVWW), which is cold, weakly stratified water near the freezing point; (ii) Remnant Winter Water (RWW), which is NVWW that has been moderated either by solar heating or mixing with warmer water (e.g. Gong and Pickart, 2015); (iii) Chukchi Summer Water (CSW), which is one of the Pacific-origin summer waters (also referred to as Bering Summer Water, e.g. Lin et al., 2019). This is a mixture of northern Bering Shelf water and Anadyr water (Pisareva et al., 2015); (iv) Melt Water / River runoff (MWR), which derives from a combination of ice melt and fluvial runoff; and (v) Atlantic Water, which is the warm, salty water of Atlantic origin found along the continental slope.

Winter Water (NVWW and/or RWW, T < -1 °C, 31.5 < S) was present at all stations (Fig. 11), with a very tight TS envelope at Group 4 stations, but with seasonal transformations and mixing with other water masses at Group 1 and Group 3 stations (see also Pacini et al., 2019). No other water mass types were present at Group 2 and Group 4 stations. AW (T > -1, S > 33.6) was present only at the single deep station along the Chukchi slope (Station 83) that was part of Group 1. Group 1 stations also had MWR; this was absent at the other types of stations and was due to early-season ice melt seaward of the shelf. CSW (-1 < T < 3; 30 < S <33.6) was present at only Group 3 stations. Because Winter Water was observed at depth at all stations (Pacini et al, 2019, Fig. 11), near-surface water characteristics were used as a simple indicator of water mass types between the different stations for Fig. 9. The water at 8 m depth was warmer and fresher for the southern Group 3 stations (Fig. 9, stations located in the left of the Group 3 block). Mean water column fluorescence was greater for Group 3 stations than for all other stations with the exception of the Bering Strait station (left most station in the Group 5 station block). Pacini et al. (2019) described the temporal evolution in sea ice cover during the cruise. Accordingly, Group 1, 2, 4, and 5 stations were all well to the north of ice edge while Group 3 stations were much closer or at the ice edge (defined by 80% sea ice cover).

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 h previous to each net tow and a description of the general features are presented here to provide context for the discussion (Fig. 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 northwestern Group 2 stations were in the outflow from Central Channel headed towards the northern side of Hanna Shoal, while the southeastern Group 2 stations were in the Central Channel outflow headed towards the Alaska coast; a similar pattern was seen for the Group 4 stations. Group 3 stations were in the northward Central Channel flow or in the flow diverging from there towards the coast in the southern portion of the study region.

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

4. Discussion

Zooplankton abundances and composition and *C. glacialis* population structure together revealed that there were three zooplankton



Fig. 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).

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

It is widely believed that *C. glacialis* in the Chukchi Sea originate from the south, with young-of-the year either spawned in the Bering Sea or spawned in the southern Chukchi Sea from females advected in from the northern Bering Sea (e.g., Hopcroft et al., 2010; Ershova et al., 2015; Wassmann et al., 2015; Pinchuk and Eisner, 2017 and others). It is also believed that there are both Arctic Ocean and Bering/Chukchi Sea populations of *C. glacialis*, with differing phenologies and genetic characteristics (Nelson et al., 2009; Ershova et al., 2015; Wassmann et al., 2015; Ashjian et al., 2017; Pinchuk and Eisner, 2017; Xu et al., 2018). The findings of the present study, renewal of *C. glacialis* populations with young-of-the year from the northern Bering Sea/southern Chukchi Sea and distinct Arctic vs. Chukchi/Bering haplotype frequencies and communities, support those paradigms.

4.1. Biogeography, pathways of advection, and replenishment of the Chukchi Sea zooplankton community

The community at the two most northern stations (Group 1stations) constituted species endemic to the Arctic Basin, including CI and CII of C. hyperborus, life stages CIII and later of C. glacialis, amphipods, and chaetognaths. There were no meroplankton at these sites. Advection at the time of sampling was predominantly to the east along the isobaths of the Chukchi Slope north of Hanna Shoal, indicating that the stations were located in the shelf break jet (Corlett and Pickart, 2017). The northernmost station was deep enough to sample AW. The C. hyperboreus early copepodids stages likely resulted from lipid-based reproduction in late winter. The presence of C. glacialis CIII and CIV so early in the season suggests that those individuals represent an overwintering population. The species is believed to overwinter at copepodid Stage IV in the Arctic as part of a two-year life history (Falk-Petersen et al., 2009; Daase et al., 2013). However, Daase et al. (2013) observed both CIII and CIV copepodids in Franklin Bay and Amundsen Gulf in May and June and attributed their presence to overwintering. Different population structures between Chukchi Sea and Arctic Basin C. glacialis have been observed previously, with Arctic populations believed to overwinter at CIV and the subarctic populations at CV (Falk-Petersen et al., 2009; Ershova et al., 2015; Pinchuk and Eisner, 2017). Furthermore, genetic haplotype frequencies from this (Fig. 12) and previous studies (Nelson et al., 2009; Ashjian et al., 2017) support there being genetically distinct Arctic and sub-arctic populations of C. glacialis.

The northern study region community (excluding the two northernmost stations) was dominated by adult C. glacialis, chaetognaths, and amphipods and marked by the near absence of meroplankton and younger C. glacialis copepodids. It extended spatially from offshore of Icy Cape to the northwest. Stations at which this community was found were categorized on the basis of plankton composition as being either station Group 2 or station Group 4, with Group 4 stations differing only in their lack of M. longa and Limacina spp. and a total absence (vs. low abundances) of early stage C. glacialis copepodids. Only Winter Water was present at these locations, with little evolution in hydrographic characteristics through ice melt, heating, or advection from the south (Pacini et al., 2019). These stations were located in the northward Central Channel flow or in the southeastern arm of that flow that diverges south of Hanna Shoal and eventually joins the eastern coastal branch. Although adult female C. glacialis were present, reproduction does not appear to have occurred in time for eggs to develop to the early copepodid stages. This was not surprising, given the low fluorescently detected chlorophyll concentration, since C. glacialis primarily reproduces based on available food (Daase et al., 2013). This community can be considered the overwintering Chukchi Sea community.

High numbers of younger copepodid stage *C. glacialis* and meroplankton, the presence of euphausiid furcilia, and lower abundances of amphipods characterized the southern study region community, in addition to the ubiquitous chaetognaths and adult female *C. glacialis*. Abundances of *C. glacialis* AF were equivalent to those observed in the overwintering community. This community (Group 3 stations) was found to the south of the first community (Group 2 and Group 4 stations), with the two distributions juxtaposing with little spatial overlap. Hydrographically, some of the southern locations had warmer, fresher water characteristic of CSW, indicating that this water, and intrinsic plankton, had been advected to those locations from the northern Bering Sea following winter. Elevated levels of fluorescently detected chlorophyll also were present, together with a depletion of nitrate presumably due to drawdown during photosynthesis and reduced sea ice cover (Arrigo et al., 2017; Pacini et al., 2019). Most of these locations were located in the northward flow of the Central Channel with the exception of those in the southeastern portion of the study area which were located where the Central Channel flow had split, with a portion diverging to the east to join the eastern coastal branch.

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

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

The overall picture, then, was of two Chukchi Sea faunal communities separated by a distinctive faunal front that also corresponded to a seasonal transition in hydrography, influenced by the prevailing circulation. The northern community was present over the winter (herein overwintering community). Younger stages of C. glacialis or meroplankton were not found because those produced the prior year had all developed to older stages (copepods) or settled out of the plankton (meroplankton) by fall of the previous year. Presumably the overwintering community had filled the shelf during the winter but now, in spring, it had been partially replaced by a new community, the southern community, coming in from the northern Bering Sea (herein spring community). The spring community contained high abundances of young-of-the year of the copepod C. glacialis, benthic polychaetes, and barnacles. These resulted from reproduction in the northern Bering Sea or southern Chukchi Sea where the seasonal cycle in primary production (ice algae and then phytoplankton), in response to reduction in sea ice and snow cover, is initiated earlier than in the northeastern Chukchi Sea. Barnacle nauplii could have originated along rocky shorelines where the sessile adult barnacles have settled; the region around Bering Strait and the Diomede Islands provide suitable habitat. Alternatively, they could have originated from adults settled on hard-bodied benthic organisms in the Chukchi Sea (Slattery and Oliver, 1987). Of note, no barnacle nauplii were present at the Bering Strait Station, suggesting that the nauplii observed in this study originated north of the Strait (by contrast, polychaete larvae and trochophores were present at that station). A back-ofthe-envelope calculation of the transit time between the Bering Strait station and the southernmost Group 3 station (#141), assuming straightline advection and current speeds of 10 or 15 cm/sec (Stabeno et al., 2018), yields 33 (at 15 cm/sec) and 50 (at 10 cm/sec) days, considerably longer than the difference between the two sampling dates (25 days) and supporting the hypothesis that the barnacle nauplii likely originated somewhere to the north of Bering Strait.

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

This scenario of community replacement would require that the Chukchi Sea continue to flush northward through the winter and spring, and that the prevailing circulation pathways would essentially persist through the year. Evidence from moorings (Fang et al., 2020; Tian et al., 2021) suggests that this is the case. The essential features of the circulation remain the same in winter as in other seasons, although with reduced northward transport through Bering Strait (Woodgate, 2018) and more frequent and prolonged encroachments of water from the Canada Basin onto the Chukchi Shelf through Barrow Canyon in the northeast (Weingartner et al., 2017; Stabeno et al., 2018; Pisareva et al., 2019).

The distributions of the two faunal communities also track the circulation pathways through the eastern Chukchi Sea. North of ~71.5, the overwintering community is seen advected anti-cyclonically around the north side of Hanna Shoal; south of that latitude it has been replaced by the spring community advected from the south. The overwintering community also follows southeasterly pathways of flow from south of Hanna Shoal towards Icy Cape and joining with the coastal flow adjacent to Alaska. This contributes to the NW-SE latitudinal gradient seen in the faunal boundary between the two communities. The spring community is found further to the north in the west, associated with the persistent northward Central Channel flow, than in the east where it is found in the flow divergence from the Central Channel towards the coast at the southern portion of the study area (Pacini et al., 2019). The transit time for parcels to advect from Bering Strait to Barrow Canyon is estimated to be 3-6 months, with the shorter time corresponding to the coastal pathway, and the longer time associated with the central pathway around the north side of Hanna Shoal (Weingartner et al., 1998; Stabeno et al. 2018; Tian et al., 2021). This is consistent with the overall flushing time of 4.5 months estimated by Woodgate (2018) and suggests that the faunal community observed in the northern Chukchi Sea in early June might have entered through Bering Strait in early March; however, since the northward transport on the Chukchi shelf is generally reduced during winter (Tian et al., 2021), 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 circulation pathways, rather than that circulation feature itself persistently defining different communities.

Although numerous previous studies have described zooplankton community compositions and their associations with hydrographic characteristics in the Chukchi Sea (e.g., Hopcroft et al. 2010 and earlier studies described therein; Eisner et al., 2013; Ershova et al., 2015; Matsuno et al., 2011, 2016; Pinchuk and Eisner, 2017; Spear et al., 2019; Xu et al., 2018), this study stands out as the only survey of the Chukchi shelf conducted during late spring; all other studies were conducted during mid-late summer or early fall. Furthermore, of recent summerfall surveys, only the work of Matsuno et al. (2011, 2016), Pinchuk and Eisner (2017), Spear et al. (2019), and Xu et al. (2018) overlap spatially to any great extent with the present study area. Nonetheless, it is useful to compare the observations herein with those from the summer-fall surveys to better infer the seasonal transitions in zooplankton composition in the entire Chukchi Sea and how water mass distributions and circulation influence the observed zooplankton distributions.

All of the previous studies identified different species compositions/ groups that were associated with hydrography throughout the Chukchi Sea, although the degree of granularity of the group distributions varied between studies. Where study regions overlap spatially, some similarities in species composition and groups between studies exist, however each study identified a unique set of species or hydrographic groups depending on the mesh size net utilized, the level of taxonomic detail utilized, and the range of biological (e.g., taxa, fluorescence) and physical variables enfolded in the analyses. Overall, however, all of the studies in late summer and early fall indicate that the eastern Chukchi Sea, from Bering Strait to Hanna Shoal, was occupied by a zooplankton community similar in composition to the replenishment community here described. Accordingly, C. glacialis was widespread, with most life stages observed in all studies (some studies did not report copepodid Stage I, but this could have resulted from the use of larger mesh nets, e. g., Xu et al., 2018). Barnacle nauplii and cyprids also were pervasive. Appendicularians, polychaete larvae or trochophores, and euphausiid furcilia were less often reported, however their absence might have resulted from methodological or reporting approaches rather than their absence. Abundances of individual taxa were highly variable between summer studies of the northeastern Chukchi Sea (Pinchuk and Eisner, 2017; Spear et al., 2019; Xu et al., 2018). The abundances from this spring study for C. glacialis, barnacle nauplii, and polychaete larvae/ trochophores in the replenishment community were within the range of variability reported for the summer studies, however abundances of the Pacific copepod species E. bungii and Neocalanus spp. were much reduced relative to those seen in summer. A clear distinction in the faunal composition and abundances between Arctic Ocean and Chukchi Sea was seen consistently in all studies, with the Arctic community intermittently extending south onto the Chukchi Shelf in association with southern advection (e.g., Ershova et al., 2015; Pinchuk and Eisner, 2017; Xu et al., 2018).

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

Surveys with substantial spatial overlap with the present study often described longitudinal gradients in species composition associated with changing water mass types (Alaskan Coastal Water in the east; CSW in the west) north of Cape Lisburne (Matsuno et al., 2011; Pinchuk and Eisner, 2017; Spear et al., 2019; Xu et al., 2018), similar to what was seen in the present study between the overwintering and replenishment communities. Some studies also reported latitudinal faunal boundaries that approximately overlapped with the distinct faunal front seen in the present study (Matsuno et al., 2011; Pinchuk and Eisner, 2017; Spear et al., 2011; Pinchuk and Eisner, 2017; Spear et al., 2011; Pinchuk and Eisner, 2017; Spear et al., 2019). They did not associate those boundaries with circulation patterns but rather with differences in hydrography (which of course is related to the circulation).

4.2. C. glacialis phenology

The high abundances of C. glacialis early copepodids so far north into the Chukchi and the widespread Bering Sea haplotype (Fig. 12; Nelson et al., 2009; Ashjian et al., 2017) supports the paradigm that a great proportion of the C. glacialis found in the Chukchi Sea originate south of Bering Strait and are not endemic to the Chukchi Sea (e.g., Ershova et al., 2015; Wassmann et al. 2015). Despite nearly continuously being advected across the Chukchi shelf, C. glacialis apparently has not established a population of Bering/Southern Chukchi Sea endemics in the Arctic Ocean, since both molecular and population structure point to there being distinct populations between the regions. The distribution of haplotype frequencies shows a differentiation between Arctic and Bering Sea populations (Nelson et al., 2009; Ashjian et al., 2017; this study), but not between the Chukchi Sea and the Bering Sea, with the frequency of Bering Sea haplotypes decreasing with distance into the Arctic Ocean from the Chukchi Sea source (Nelson et al., 2009). Population stage structure of C. glacialis differs across the faunal front between Arctic and Chukchi populations and the two apparently follow different phenologies, with Bering/Chukchi C. glacialis developing to copepodid stage V and Arctic C. glacialis developing to copepodid stage IV prior to diapause (Lane et al., 2008; Ershova et al., 2015; Pinchuk and Eisner, 2017). Because of earlier sea ice retreat and primary production, the Bering/ Chukchi populations initiate reproduction earlier in the year (e.g., Baier and Napp, 2003). They also have faster development times in the warmer temperatures of the northern Bering Sea and southern Chukchi Sea than in Arctic waters and thus, at a given date in summer, older stages might be observed in the Bering/Chukchi population than in the Arctic population.

The presence of younger copepodid stages of *C. glacialis* in the spring community provided the opportunity, using biological-physical modeling, to track plankton, and thus water, of Pacific origin flooding the Chukchi Sea in spring, as well as to identify the spawning locations for the individuals there. The spawning locations of younger stages of *C. glacialis* observed in the net tows were estimated using modeled backwards advection. Temperature and velocity from a coupled atmosphere-sea ice-ocean model (BIOMAS; Zhang et al., 2010, 2015) were coupled with an individual based model of *C. glacialis* temperature-dependent development rates (Ji et al., 2012) and run backwards in time, from the collection locations, until the copepods reached the egg stage and thus the spawning location. Modeled temperature dependent development times provide a duration for the backward advection. Trajectories and spawning locations revealed three different patterns

(Fig. 13). For the first, individuals were spawned south of Bering Strait and advected northwards through the Central Channel route where they were collected as CI, CII, and CIII between 69 and 70°N. For the second, individuals were spawned north of Bering Strait in a known Chukchi Sea production and benthic hotspot (e.g., Grebmeier, 2012; Grebmeier et al., 2015) along the eastern Chukchi Sea flow pathway and advected northwards in that eastern pathway to be collected off of Icy Cape. Finally, some individuals were spawned north of (CI, CII) or near (CIII) 69°N in the Central Channel pathway and advected to north of 71°N where they were collected. For this latter pattern, the length of the trajectory was shorter due either to slower velocities or to faster development times in response to warmer water temperatures.

A previous modeling study of C. glacialis populations on Hanna Shoal in August 2012 and 2013 concluded, based on backwards tracking coupled with development time, that the majority of the adult C. glacialis originated in the southern Chukchi Sea and northern Bering Sea and that the younger stages had been spawned primarily at the northern end of the Central Channel by May 1 (Elliott et al., 2017). The distributions of young stages of C. glacialis observed in the present study may be consistent with these predictions, since the youngest life stage enumerated in the present study, CI, requires \sim 75 days to mature (Ji et al., 2012). With a spawning date of May 1 (Elliott et al., 2017), copepodid stage I would be achieved in mid-July. This in turn predicts that the sampling in the present study should not have observed copepodid stage I or later in the northern Chukchi Sea, since any individuals spawned on May 1 should not have developed to a stage that would have been collected using the 150 µm mesh net of this study. Note that since the Elliott et al. (2017) study was focusing on source populations for Hanna Shoal, the simulations are not as relevant to the remainder of the Chukchi Sea. However, based on simulations of both source and sinks for Hanna Shoal C. glacialis, Elliott et al. (2017) similarly concluded that C. glacialis populations in the Chukchi Sea are advected off the Chukchi shelf to the north over winter and must be replenished annually from the south.

Similar to results of the modeling simulations identifying the spawning locations, a number of studies concluded that *C. glacialis* populations are replenished from the south and that the observed youngof-the year originated either in the very Southern Chukchi Sea or the northern Bering Sea. Based on estimated development times at temperatures ranging from -1.8 to $12 \degree$ C and drifter velocities, Spear et al. (2019) concluded that *C. glacialis* copepodids collected north of Cape Lisburne in August were spawned in the Chukchi Sea. Ershova et al. (2015) in summer found Arctic populations primarily at copepodid stages I-III, suggesting that these are young-of-the-year developing to



Fig. 13. Simulations showing backtracking of *C. glacialis* CI, CII, and CIII from their collection location (black dots) southwards to their spawning location (triangles). Each track shows the path of a theoretical copepod that is backwards developed from the observed stage through younger stages to egg at ambient water temperatures and using modeled velocity. The different colors represent the three different spawning locations (Bering Sea – red, southern Chukchi Sea – green, near/ north of 69° N – blue). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the overwintering CIV stage. By contrast, the Bering/Pacific populations were more developed at stages CIV and CV, resulting from earlier reproduction due to earlier ice retreat and a productive season and faster development times in warmer temperatures of the northern Bering and southern Chukchi Seas than in Arctic waters. Pinchuk and Eisner (2017) observed increasing mean life stage with time and latitude through the Chukchi Sea, with older CV observed in mid-late August in the northeastern Chukchi Sea and higher proportions of younger CIV in early August in the southern Chukchi Sea. This pattern likely reflected temporal changes along the northward advection pathways, so that the older CV were observed later due to maturation. Matsuno et al. (2016) observed few early stage copepodids and low C. glacialis biomass in the northeastern Chukchi Sea and concluded that reproduction was not ongoing. The present study found that, in spring, the populations advected into the Chukchi Sea from the northern Bering Sea were dominated by copepodid CI-CIII. Since the development time of C. glacialis from CI - CV is \sim 90 days at 0 °C and faster at warmer temperatures (Ji et al., 2012), copepodid stages CI-CIII observed in June in the present study could easily have developed to CIV and CV by August, in accord with the findings of these previous studies.

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

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

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

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

5. Concluding remarks

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

At present, it appears that zooplankton from the Bering Sea are transient in the Chukchi Sea and do not establish populations there. Given the persistent northward advection and relatively short turnover time of the Chukchi Sea, it appears unlikely that there could be endemic Chukchi Sea populations, except perhaps in coastal bays or lagoons, because the animals are continuously flushed out to the north. Therefore, even if summer conditions under environmental warming permit successful recruitment by Pacific species, those animals would not remain in the Chukchi Sea. Furthermore, the inevitable return of winter conditions and the shallow depth of the Chukchi shelf would likely preclude successful overwintering by many Pacific zooplankton species. Consequently, it is likely that, in the future, annual differences in the abundance and biomass of zooplankton in the Chukchi Sea will continue, but the community composition will likely remain similar to what it is today. Perhaps more interesting is if any of the species could successfully persist in the Arctic oceanic regions to the north, potentially competing with the endemic Arctic species and significantly changing the community composition there. This could have substantial impacts to multiple components and functions of the western Arctic ecosystem, from prev availability for Arctic cod to utilization of primary production to carbon flux to the seafloor.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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