



Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Zooplankton community patterns in the Chukchi Sea during summer 2004

Russell R. Hopcroft^{a,*}, Ksenia N. Kosobokova^b, Alexei I. Pinchuk^c^a University of Alaska Fairbanks, PO Box 757220, Fairbanks, AK, 99775-7220, USA^b PP Shirshov Institute of Oceanology, Russian Academy of Sciences, 36 Nakhimova Avenue, 117997 Moscow, Russian Federation^c Seward Marine Center, University of Alaska, 201 Railway Ave, PO Box 730, Seward, AK, 99664-0730, USA

ARTICLE INFO

Keywords:

Zooplankton assemblages
Chukchi Sea
Species composition
Climate change

ABSTRACT

Zooplankton were sampled in the Chukchi Sea along three transects between Alaska and Russia, plus four high-speed transects across the axis of Herald Valley in August of 2004. A total of 50 holoplanktonic species, along with a prominent assemblage of meroplankton were encountered; most were of Pacific Ocean origin. Copepods represented the most diverse group with 23 species, and contributed the bulk (3100 ind. m⁻³, 30 mg dry weight m⁻³) of the total holozooplankton community abundance (3500 ind. m⁻³) and biomass (42 mg DW m⁻³) at most stations. Meroplanktonic larvae were, on average, almost as abundant (2260 ind. m⁻³) as the holozooplankton. Copepods were dominated numerically by four species of *Pseudocalanus*, *Oithona similis*, and the neritic copepods *Acartia longiremis* and *Centropages abdominalis*. The larger-bodied copepods, *Calanus glacialis/marshallae* and three *Neocalanus* species, equalled or exceeded the biomass of *Pseudocalanus*, followed by contributions from *Metridia pacifica* and *Eucalanus bungii*. Considerable abundance (256 ind. m⁻³) and biomass (42 mg DW m⁻³) of the larvacean *Oikopleura vanhoeffeni* was observed throughout the sampling area. The chaetognath *Parasagitta elegans* (4.8 mg DW m⁻³) and a diverse assemblage of cnidarians (~1.2 mg DW m⁻³) comprised the dominant predators. Six major assemblages of zooplankton were identified, and each was closely tied to physical properties of water masses: Euryhaline species in the warm fresh Alaska Coastal Current, a Bering Sea assemblage of both shelf and oceanic species in cool salty Bering Sea Water, a transitional group between these two, a neritic Bering Sea assemblage in cold salty Bering Winter Water, and a small cluster of Arctic Shelf species in cold, fresh Resident Chukchi Water. Ongoing climate change may alter the boundaries, extent of penetration, size spectra, and productivities of these communities, thus warranting regular monitoring of the zooplankton communities of this gateway into the Arctic.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

The Chukchi Sea is one of the Arctic's wide and shallow marginal seas, bordered to the north by the deeper and bathymetrically complex Chukchi Borderlands and the steep continental slopes that separate the shelf from the Arctic Basin proper. The Chukchi Sea represents one of the major gateways into the Arctic where large quantities of Pacific heat, nutrients, phytoplankton and zooplankton enter the region through the shallow (~50 m average deep) Bering Strait in a complicated mixture of water masses (Pickart et al., 2009). Each of these water types—Alaska Coastal, Bering Shelf, and Anadyr—has distinct assemblages and quantities of Pacific-origin zooplankton (e.g. Springer et al., 1989; Coyle et al., 1996). As these waters move northward, they are diluted by Coastal Arctic waters of the East Siberian Current and bifurcate, moving off the shelf through Herald Canyon in the west, through a shallow central channel, and

to the east through Barrow Canyon (Weingartner et al., 1998, 2005; Pickart et al., 2009). Simultaneously, the Pacific planktonic communities acquire more Arctic character as they are diluted by Arctic waters, particularly near the shelf break (e.g. Lane et al., 2008; Llinás et al., 2009).

At present, the high concentration of nutrients in Anadyr waters (Grebmeier and Barry, 1991) stimulate massive sea ice algal and phytoplankton blooms, that cannot be fully exploited by the local zooplankton communities due to temperature-limited growth (Springer et al., 1989; Deibel et al., 2005). Hence, much of this high production is exported unmodified to the benthos (Fukuchi et al., 1993), resulting in impressively high biomass of benthic infauna and epifauna in the southern Chukchi Sea (e.g. Grebmeier et al., 2006a, b; Feder et al., 2005, 2007). In addition to their local importance for the Chukchi shelf, these Pacific inflows are also significant sources of carbon and nutrients to the continental slopes and the deep basin, and play a critical role in structuring the stratification of the Arctic Ocean basins (Grebmeier et al., 1995; Grebmeier and Harvey, 2005).

Recent and projected changes in the extent and timing of the ice cover in the Arctic are expected to have profound impact on

* Corresponding author.

E-mail address: hopcroft@ims.uaf.edu (R.R. Hopcroft).

arctic marine ecosystems (ACIA, 2004; Carmack et al., 2006). Zooplankton communities may be particularly sensitive to such changes as seasonal life cycles are intricately coupled to the timing of ice-breakup and phytoplankton blooms (Smith and Schnack-Schiel, 1990; Deibel and Daly, 2007). There is significant discussion that the Chukchi Sea may be undergoing an enhancement of energy utilization within its pelagic realm as zooplankton populations respond with faster growth in warmer waters, with a consequent decline in the phytoplankton production made available to the benthic communities (Feder et al., 2005; Grebmeier et al., 2006a). Such changes will propagate through the system, ultimately affecting all trophic levels and leading to changes in the pathways and magnitude of energy flow into upper trophic levels such as fish, sea-birds and marine mammals, and consequently their abundance and distribution. These changes in prey base have already been documented for the northern Bering Sea (Grebmeier et al., 2006b; Coyle et al., 2007).

There is a long and scattered history of work in the Chukchi Sea, even the earliest of which noted the significant influence of Pacific fauna on its ecosystem (Johnson, 1934; Stepanova, 1937a, b; Bogorov, 1939; Jaschnov, 1940). Further Russian studies in the Far Eastern Seas laid the foundation for our understanding of this broad region (Brodsky, 1950, 1957), along with work more specific to the Chukchi Sea (Virketis, 1952; Pavshits, 1984). North American work in the region began with both a quantitative and taxonomic dimension (Johnson, 1953, 1956, 1958), followed by the Alaskan Outer Continental Shelf Environmental Assessment Program (OCSEAP) with a variety of more regional surveys (English, 1966; Wing, 1974; Cooney, 1977; English and Horner, 1977). It was 1985–1986 before broader scale multidisciplinary zooplankton sampling resumed in the Bering Strait and Chukchi Sea with the Inner Shelf Transfer and Recycling (ISHTAR) program (Springer et al., 1989). Subsequent programs have typically concentrated on deeper waters to the north (Thibault et al., 1999; Ashjian et al., 2003; Lane et al., 2008). A notable exception to the political boundaries imposed on most post-WWII sampling in the Bering and Chukchi Seas has been the Joint US–USSR BERPAC program (Tsyban, 1999), from which BERPAC 1988 encompassed a significant number of stations from the southern Bering Sea through to the mid-Chukchi Sea (Kulikov, 1992). Direct comparison between these studies is hampered to various extents by the lack of access to the original data, changes in taxonomy and differences in gear type.

In order to detect and quantify any future or ongoing changes in Arctic zooplankton, it is essential that we form detailed and extensive baseline information on the current state of these communities. Given the oceanographic complexity of the region, simultaneous estimates of the zooplankton entering from both sides of the Bering Strait are essential; with the lack of cross basin coverage limiting the ability of most prior studies to adequately describe this region. In 2004, we began to address this need by a survey of zooplankton communities across the Bering Strait, and both sides of the Chukchi Sea, in conjunction with physical and chemical oceanographic characterization as part of the Russian American Long-term Census of the Arctic (RUSALCA) program.

2. Methods

The RUSALCA expedition consisted of 22 stations along 3 transects lines between Alaska and Russia, plus 4 high-speed transects across the axis of Herald Valley in the northwestern part of the study area (Fig. 1). Station depths typically varied between 40 and 55 m, except in the center of Herald Valley where the depth was as much as 100 m in the northern transect (see sections in Pickart et al., 2009). Quantitative zooplankton sampling was

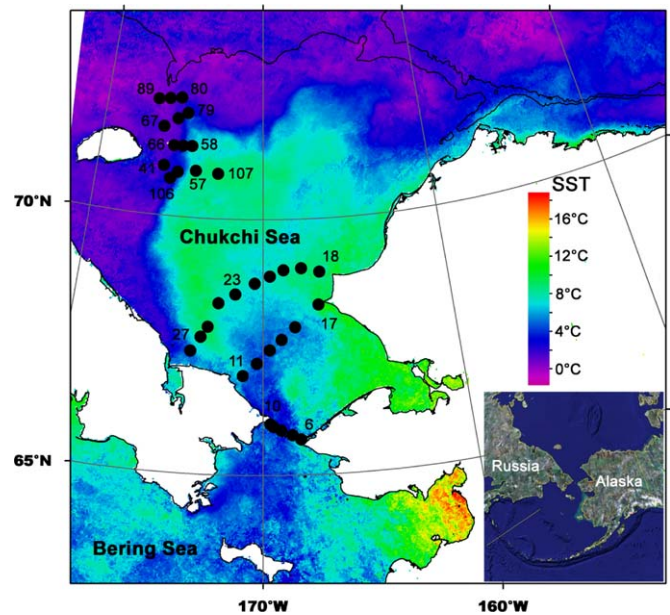


Fig. 1. Station map overlain on the 7-day composite AVHRR sea-surface temperature during the sampling period (August 11–17, 2004). The 100 and 500 m contours indicated. Numbers indicate station numbers at the beginning and the end of each transect.

conducted at all stations on the lower 3 transects, end and midpoints of the upper transects, plus 2 additional stations for a total of 36 zooplankton sampling sites. Zooplankton were collected by a package of two 150 μm -mesh, MARMAP-design, Bongo nets of 60 cm diameter. Nets were hauled vertically from within 3 m of the bottom to the surface at 0.5 m s^{-1} , and the volume of water filtered was measured by General Oceanics flow meters in the mouth of each net rigged not to spin during descent. Upon retrieval, one sample of each mesh size was preserved in 10% formalin containing Rose Bengal stain, and the other sample was preserved in 100% non-denatured ethanol (Bucklin, 2000). Weather prevented collection of a sample at station 16.

In the laboratory, survey samples were first scanned for larger and rarer species that were enumerated and measured in the sample's entirety. For more abundant species, subsampling was conducted by a combination of Folsom splits and Stempel pipettes, such that at least 50 of the most abundant taxa were in the smallest fraction examined. Increasingly larger fractions were examined, with no more than 100 of any single taxa measured, and a minimum of 300 animals measured in each sample. The copepods were staged, enumerated and their prosome length measured using a computer-assisted measurement system and ZoopBiom software (Roff and Hopcroft, 1986), except for *Oncaea*, where staging of the copepodites proved problematic. For some congeneric species, where earlier copepodites could not be distinguished, they have been grouped with the sibling species. Adults were identified to species. In the case of *Calanus*, excessive stain in several samples made it difficult to view the ocellus which could distinguish *C. marshallae* from *C. glacialis*, and other features used to separate the adults are difficult to employ routinely, thus the species were grouped for consistency. The larger *C. hyperboreus* would have been distinguished by size (e.g. Unstad and Tande, 1991; Hirche et al., 1994), but was not encountered. The weight of each specimen was predicted from species-specific relationships, or from those of a morphologically similar species of holozooplankton (Table 1). Such relationships were unavailable for merozooplankton. Notably, although a relationship has been published for *Oithona*

Table 1

Relationships employed to predict weight from length for the holozooplankton encountered in the study region.

Species	Regression	Units	Source
<i>Themisto pacifica</i> *	DW = 0.0049TL ^{2.957}	mm, µg	Ikeda and Shiga (1999)
<i>Themisto libellula</i>	DW = 0.006TL ^{2.821}	mm, µg	Auel and Werner (2003)
<i>Acartia longiremis</i>	CW = 1.023 × 10 ⁻⁸ PL ^{2.906}	µm, µg	Hansen et al. (1999)
<i>Calanus glacialis/marshallae</i>	Log DW = 4.034 log PL – 11.561	µm, µg	Liu and Hopcroft (2007)
<i>Centropages abdominalis</i>	Log DW = 3.00 log PL – 7.89	µm, µg	Uye (1982)
<i>Eucalanus bungii</i>	Log DW = 3.091 log PL – 0.0026	mm, µg	Hopcroft et al. (2002)
<i>Eurytemora hermani</i>	Log DW = 2.96 log PL – 7.60	µm, µg	Middlebrook and Roff (1986)
<i>Microsetella</i> **	Log AFDW = 2.52 log PL – 16.03	µm, µg	Webber and Roff (1995)
<i>Metridia pacifica</i>	Log DW = 3.29 log PL – 8.75	µm, µg	Liu and Hopcroft (2006b)
<i>Neocalanus plumchrus/flemingeri</i>	Log DW = 3.56 log PL – 2.32	mm, mg	Liu and Hopcroft (2006a)
<i>Neocalanus cristatus</i>	Log DW = 4.001 log PL – 11.776	µm, µg	Kobari et al. (2003)
<i>Paraeuchaeta</i> spp.	AFDW = 0.0075 PL ^{3.274}	mm, mg	Mumm (1991)
<i>Pseudocalanus</i> spp.	Log DW = –2.85 log PL – 7.62	µm, µg	Liu and Hopcroft (2008)
<i>Oithona similis</i> ***	Log AFDW = 3.16 log PL – 8.18	µm, µg	Hopcroft et al. (1998)
<i>Oncaea</i> spp.***	Log AFDW = 3.16 log PL – 8.18	µm, µg	Hopcroft et al. (1998)
<i>Oikopleura vanhoeffeni</i>	Log C = 3.20 log TL – 8.93	µm, µg	Deibel (1986)
<i>Fritillaria borealis</i> *	Log DW = 3.21 log TL – 9.11	µm, µg	Fenaux (1976)
Other calanoids** <i>Micro-calanus</i> , <i>Jaschnovia</i>	Log DW = –2.85 log PL – 7.62	µm, µg	Liu and Hopcroft (2008)
Ostracods	AFDW = 0.0228PL ^{2.3698}	mm, mg	Mumm (1991)
<i>Thysanoessa inermis</i> (<i>T. rachii</i>)	Log DW = 2.50 log CL – 1.162	mm, mg	Pinchuk and Hopcroft (2007)
<i>Evadne</i> & <i>Podon</i>	Log DW = 4.0 log TL – 10.5	µm, µg	Uye (1982)
<i>Tomopteris</i>	DW = 0.005L ^{2.25}	mm, mg	Matthews and Hestad (1977)
<i>Eukrohnia hamata</i>	DW = 0.00032PL ^{3.00}	mm, mg	Matthews and Hestad (1977)
<i>Parasagitta elegans</i>	DW = 0.000064PL ^{3.30}	mm, mg	Matthews and Hestad (1977)
<i>Aglantha digitale</i> & other jellies	DW = 0.00194PL ^{3.05}	mm, mg	Matthews and Hestad (1977)

Where species-specific relations were not employed we used relationships from: **T. japonica*, ***Macrosetella*, ****Oithona nana*, **F. pellucida*, ***Pseudocalanus*. DW—dry weight, AFDW—ash-free dry weight, CW—carbon weight, TL—total body length, PL—prosoma length, CL—carapace length.

similis (Sabatini and Kiørboe, 1994), its slope of 2.16 is unrealistically shallow and thus overestimates weights for early stages, hence we use that for a congeneric species of similar body form. Where necessary, ash-free dry weight (AFDW) was converted to dry weight (DW) assuming 10% ash (Båmstedt, 1986). A carbon weight (CW) to DW conversion does not exist for larvae, so we assumed it to be 40% of DW for *Oikopleura vanhoeffeni*, as is typical of many copepods (Båmstedt, 1986). For *Acartia longiremis* where CW was 50% of DW, weights were more consistent with other relationships determined for this genus (e.g. Uye, 1982).

Community patterns were explored using the Primer (V6) software package which has been shown to reveal patterns in zooplankton communities (e.g. Clarke and Warwick, 2001; Wishner et al., 2008). Analyses were performed independently for abundance and biomass data. Data sets were power transformed (4th root), and the Bray–Curtis similarity index between stations was calculated employing all taxonomic categories that contributed at least 3% to any sample in that dataset. Significant groups within the hierarchical clustering were established with the SIMPROF routine, and these clusters were superimposed on the 2D and 3D plots of the multi-dimensional scaled (MDS) datasets, as well as spatial plots of the data. The SIMPER routine was used to provide insight into the species combinations responsible for each species group, as well as by performing cluster analysis similar to above, among the species (rather than among stations).

Concurrent physical oceanographic data were collected with a Seabird 911+ equipped with an oxygen sensor, transmissometer and fluorometer (Pickart et al., 2009) with data binned into 1 m intervals. Chlorophyll was collected by Niskin bottles on the CTD rosette every 5 m starting at the surface, filtered at low pressure onto GF/F filters and analyzed fluorometrically (Lee et al., 2007). Water masses were identified by cluster analysis using the SIMPROF routine, employing Euclidean distances on the normalized average temperature and salinity from the surface to the just

above the bottom, or to a maximum of 50 m at deeper stations in Herald Valley to avoid excessive weighting of very cold bottom waters at those locations. The 2-D MDS representation from this approach yields a plot similar to a traditional T–S diagram shown below, with quantitative separation. Established terminology is employed for the observed water masses (Weingartner et al., 1998; Pickart et al., 2009). Relationships between zooplankton community composition and these variables were explored with Primer's BEST routine using normalized physical and chlorophyll data that had been averaged over the upper 10 and 50 m. For physical data we also considered averages of the upper 25 m, the layer between 10 and 50 m, and the layer between 25 and 50 m, to determine if the stratified aspect of some variables was a determinant of community composition (e.g. Lane et al., 2008).

3. Results

A total of 50 holoplanktonic species, along with a prominent assemblage of 12 meroplanktonic taxa, were encountered during the RUSALCA survey (Table 2). The copepods represented 23 of the holoplanktonic species, and contributed the bulk of the zooplankton community abundance (Fig. 2) and biomass (Fig. 3) at most stations. Numerically, both the holozooplankton and copepod communities were dominated by a suite of four species of *Pseudocalanus*: *P. minutus*, *P. mimus*, *P. acuspes* and *P. newmani*, with the former two not consistently separated. These were followed by *Oithona similis*, and then the neritic copepods *A. longiremis* and *Centropages abdominalis*. The less abundant but larger-bodied copepods *Calanus glacialis/marshallae*, and the three *Neocalanus* species, equalled or exceeded the biomass of *Pseudocalanus*, followed by contributions from *Metridia pacifica* and *Eucalanus bungii*. Abundance of copepods declined rapidly with body size (as prosoma length), and began to level-out at ~1.5 mm, with the largest individuals approaching 9 mm (Fig. 4). The corresponding biomass spectrum was multi-modal with

Table 2
List of planktonic taxa collected during the 2004 RUSALCA cruise, with their average abundance and dry-weight biomass over the study area.

	Num m ⁻³	mg m ⁻³		Num m ⁻³	mg m ⁻³
Copepods			Chaetognaths		
<i>Acartia longiremis</i>	199.1	0.41	<i>Eukrohnia hamata</i>	0.4	0.34
<i>Acartia hudsonica</i>	2.5	0.01	<i>Parasagitta elegans</i>	5.7	4.77
<i>Acartia tumida</i>	0.4	<0.01	Amphipods		
<i>Calanus glacialis/marshallae</i>	36.1	6.71	Amphipod (misc)	<0.1	0.14
<i>Centropages abdominalis</i>	190.8	0.74	<i>Primno macropa</i>	Trace	
<i>Eucalanus bungii</i>	14.5	1.31	<i>Themisto pacifica</i>	<0.1	0.06
<i>Euchaeta elongata</i>	Observed		<i>Themisto libellula</i>	<0.1	<0.01
<i>Eurytemora herdmani</i>	6.9	0.02	Ctenophores		
<i>Eurytemora pacifica</i>			<i>Bolinopsis infundibulum</i>	Observed	
<i>Jaschnovia tolli</i>	0.3	0.01	<i>Mertensia ovum</i>	Observed	
<i>Microcalanus pygmeus</i>	8.2	0.03	Cnidarians		
<i>Microsetella norvegica</i>	19.3	0.09	<i>Aeginopsis laurentii</i>	Observed	
<i>Metridia pacifica</i>	39.7	1.45	<i>Aglantha digitale</i>	5.4	0.95
<i>Neocalanus flemingeri</i>	7.1	4.50	<i>Chrysaora melanaster</i>	Observed	
<i>Neocalanus plumchrus</i>	2.1	1.42	<i>Euphysa flamma</i>	<0.1	0.08
<i>Neocalanus cristatus</i>	0.9	6.38	<i>Melicertum octocostatum</i>	<0.1	<0.01
<i>Oithona similis</i>	703.4	0.77	<i>Melicertum campanula</i>	<0.1	0.01
<i>Oncaea borealis</i>	64.9	0.10	<i>Obelia</i> sp.	0.4	<0.01
<i>Pseudocalanus juvenile</i>	1604.6	4.51	<i>Polyorchis</i> sp.	<0.1	0.02
<i>Pseudocalanus minutus</i>	71.7	0.89	<i>Halitholus yoldia-arcticae</i>	<0.1	0.02
<i>Pseudocalanus acuspes</i>	38.6	0.51	<i>Tiaropsis multicirrata</i>	Observed	
<i>Pseudocalanus newmani</i>	92.8	0.55	<i>Plotocnide borealis</i>	Observed	
Copepod total	3104	30.05	<i>Ptychogena lacteal</i>	<0.1	0.08
Larvaceans			<i>Rathkea octopunctata</i>	11.6	0.02
<i>Oikopleura vanhoeffeni</i>	255.9	4.12	<i>Sarsia tubulosa</i>	<0.1	0.02
<i>Fritillaria borealis</i>	84.7	0.01	Ostracods		
Cladocerans			<i>Polychaetes</i>		
<i>Evadne nordmani</i>	11.3	0.040	<i>Tomopteris</i> sp.	<0.1	0.01
<i>Podon leuckarti</i>	14.5	0.069	Meroplankton		
Euphausiids			Barnacle Cypris	226.7	
<i>Euphausiid Nauplii</i>	2.6	<0.01	Barnacle Nauplii	1008.9	
<i>Euphausiid calyptopis</i>	0.2	<0.01	Bivalvia larvae	148.3	
<i>Thysanoessa juvenile</i>	3.3	0.65	Crab Megalops	0.2	
<i>Thysanoessa inermis</i>	0.1	0.44	Crab Zoea	<0.1	
<i>Thysanoessa raschii</i>	<0.1	0.08	Decapod Zoea	0.3	
<i>Thysanoessa longipes</i>	Observed		Echinodermata larvae	795.1	
			Fish larvae	0.2	
			Shrimp Mysid stage	Observed	
			Polychaeta larvae	81.9	
			Paguriid Zoea	0.3	
			Other total	2658	11.9

Observed material was noticed during the study, but not in the subsamples analyzed.

strongest peaks at approximately 0.4–1.6 mm, 3–3.5 mm followed and 7.5–8.5 mm.

For non-copepod groups, considerable populations of larvaceans, particularly the large arctic *O. vanhoeffeni*, were observed throughout the sampling area (Table 2). *Oikopleura* (followed *Oithona* within the holozooplankton) rivaled the most important copepod species in terms of average biomass contribution, and exceeded the biomass of dominant copepod species at some of the Herald Valley stations (Fig. 3). The chaetognath *Parasagitta elegans* also contributed significantly to community biomass, with much lower contribution by the deeper water species *Eukrohnia hamata*. Abundances of the three *Thysanoessa* species of euphausiids, as well as the hyperiid amphipods, were low and variable, but ichthyoplankton samples from a concurrently towed 505 µm-mesh Bongo net (Norcross et al., 2009, plus unpublished) suggested our catches generally reflected their absolute abundances. Within the study area there was also a notable diversity of both small and large scyphozoans, hydromedusae and ctenophores. More than a dozen species were encountered in the samples, but only the hydromedusae *Aglantha digitale* and *Rathkea octopunctata* were common, with only *A. digitale* contributing significantly to community biomass. Finally, pelagic larvae of benthic organisms were also exceptionally common throughout the sampling region, exceeding the abundance of holozooplankton

at some stations where they were concentrated. Although meroplankton biomass could not be accurately estimated, it appears to have been considerable at some stations based on their abundance (Fig. 2).

Multivariate analysis of the data revealed similar overall patterns across stations within the data, regardless of the severity of the transformation (i.e. square root, fourth root, log+1), but the fourth root transformation (Fig. 5) produced fewer and more spatially contiguous clusters. For abundance, seven station groups were significant, with these forming four major hierarchical clusters and one unique station (station 67) at a Bray–Curtis similarity of ~70% (Fig. 5A). Two-dimensional ordination of the MDS space confirmed the appropriateness of these groupings (Fig. 5B), 0.15 in 2 dimensions. Spatially, these major clusters present (1) group A–B along the Alaska Coastal Current (ACC), (2) group G that extends from the middle of Bering Strait northward beside the ACC and joining the southeastern boundary of Herald Valley, (3) group D on the Western side of Bering Strait that encompasses much of the southern Chukchi Sea, and (4) group F that encompasses most of Herald Valley (Fig. 5C). The clustering of station 11 into group F appears anomalous. Minor group E shares closest similarity with group F.

Biomass revealed surprisingly similar patterns given that it emphasizes a different suite of species: again, four major

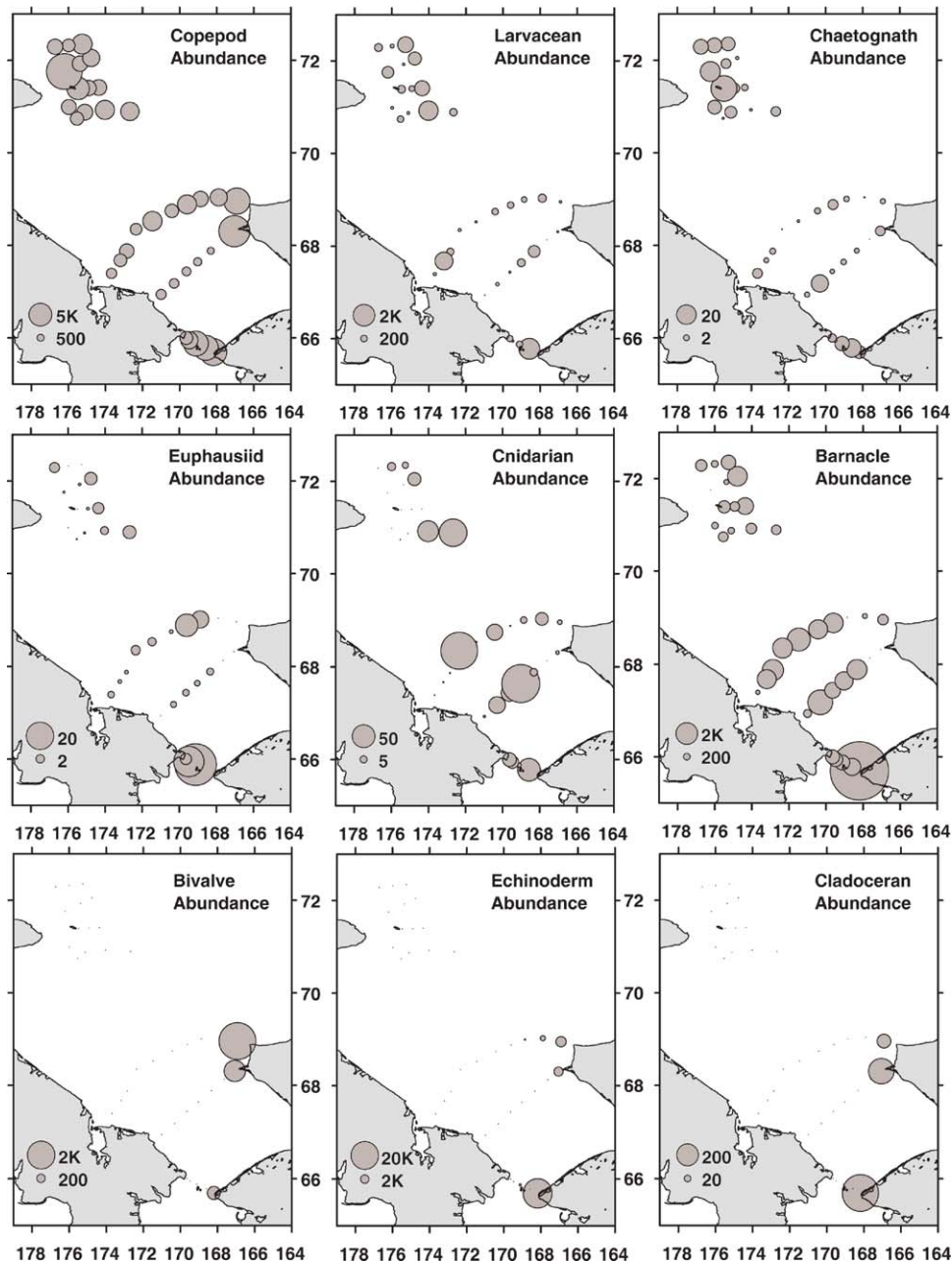


Fig. 2. Abundance (ind. m^{-3}) of major taxonomic planktonic groups in the Chukchi Sea, August 2004. Longitude is in $^{\circ}\text{N}$, latitude is in $^{\circ}\text{W}$.

hierarchical clusters, plus two unique stations (stations 27 and 67) are suggested at a Bray–Curtis similarity of $\sim 65\text{--}70\%$ (Fig. 6A). Similarly, two-dimensional ordination of the MDS space confirmed the appropriateness of these grouping (Fig. 6B); however, the 2D stress value of 0.15 showed limited improvement (to 0.11) when using 3 dimensions. Spatially, these major clusters resemble those of abundance, except that group F extends more northward along the eastern side of Herald Valley (Fig. 6C).

Pronounced changes in temperature and salinity occurred across the transect lines (Fig. 7; for Herald Valley see Pickart et al., 2009). The temperature and salinity data formed five distinct clusters, warm fresh Alaska Coastal Current Water, cool salty Bering Sea Water, a transitional group between them, cold salty Bering Winter Water, and a small cluster of cold fresh Resident

Chukchi Water (Fig. 8A). A CTD cast was not available for Station 17, but we assumed it would be very similar to the nearby and downstream Station 18 for subsequent analysis. The distribution of these clusters matches almost exactly that revealed by zooplankton community analysis (Fig. 8B). The community assemblages were statistically correlated with various combinations of the environmental variables of temperature, salinity and/or density, with maximum similar Spearman's correlations of 0.78 for several 2- and 3-variable models (Table 3), demonstrating that it is physical properties of the water masses to which the assemblages are associated. There was no marked improvement in using environmental parameters within narrower layers as compared to over the upper 50 m, although layered models produced more combinations of higher correlation owing to the larger number of variables (and

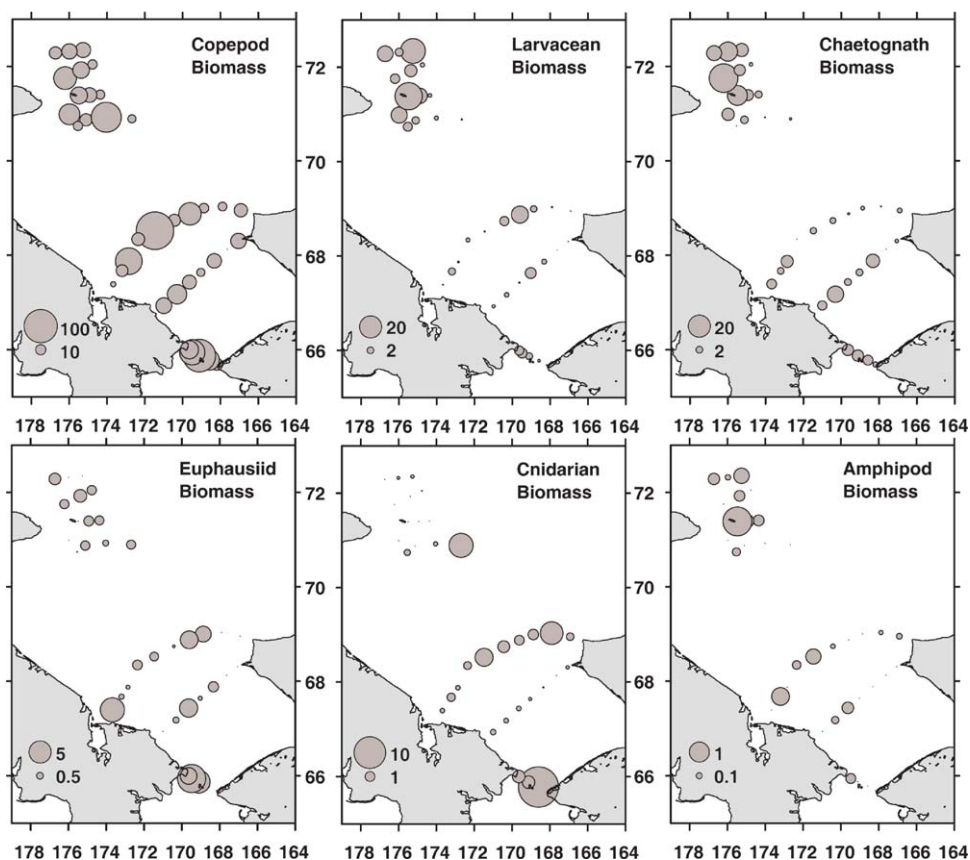


Fig. 3. Biomass (mg m^{-3}) of major holozooplankton groups in the Chukchi Sea, August 2004. Longitude is in $^{\circ}\text{W}$, latitude is in $^{\circ}\text{N}$.

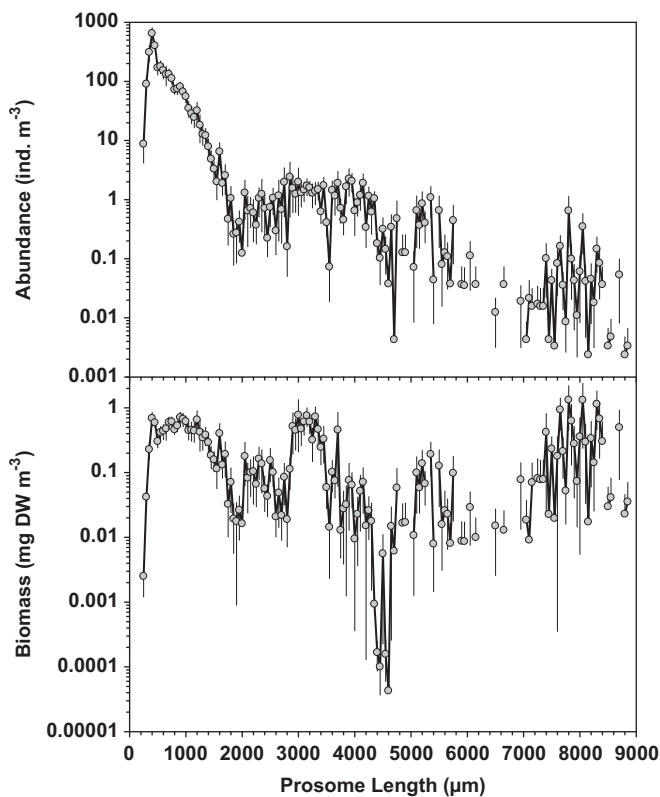


Fig. 4. Size spectra of copepod community in the Chukchi Sea, August 2004, in terms of abundance and biomass, based on $150\mu\text{m}$ mesh nets. All size bins are $50\mu\text{m}$ wide. Data represent the average over the 3 southern transects, with associated standard errors.

correlations within the layered variable set). The inclusion of chlorophyll, oxygen concentration, transmissivity or fluorescence—alone or in combination—only lowered the strength of the correlations.

Arrangement of the zooplankton abundances based on the independent clustering of stations and species provides an insightful summary of the underlying patterns (Fig. 9). Firstly, there is a group of generally abundant and relatively neritic/shelf species broadly distributed across all station groups. The ACC water is characterized most distinctly by a group of neritic, low-salinity tolerant zooplankton species, the absence of the more oceanic Bering Sea species, and the reduction of Bering Sea shelf species. The Bering Sea Water is characterized by the presence of most species, except for those unique to the ACC. The transitional stations are intermediate between these. The Winter Water is similar to the Bering Sea Water, but lacks (or has reduced abundances) of the more oceanic Bering Sea species, particularly those with annual life cycles. The Resident Chukchi water shows further reductions of Bering Sea oceanic fauna.

4. Discussion

4.1. Species composition

The Chukchi Sea displays a similar level of diversity, and high biomass compared to the adjoining East Siberian (Jaschnov, 1940; Pavshchik, 1994) and Beaufort (e.g. Horner, 1981) Seas, but less diversity than is present in the deep vertically structured basins (e.g. Kosobokova and Hirche, 2000; Kosobokova and Hopcroft, 2009). It is also notable that with the exception of the few cases of *C. glacialis* and *Jaschnovia tolli*, all copepod species observed in this

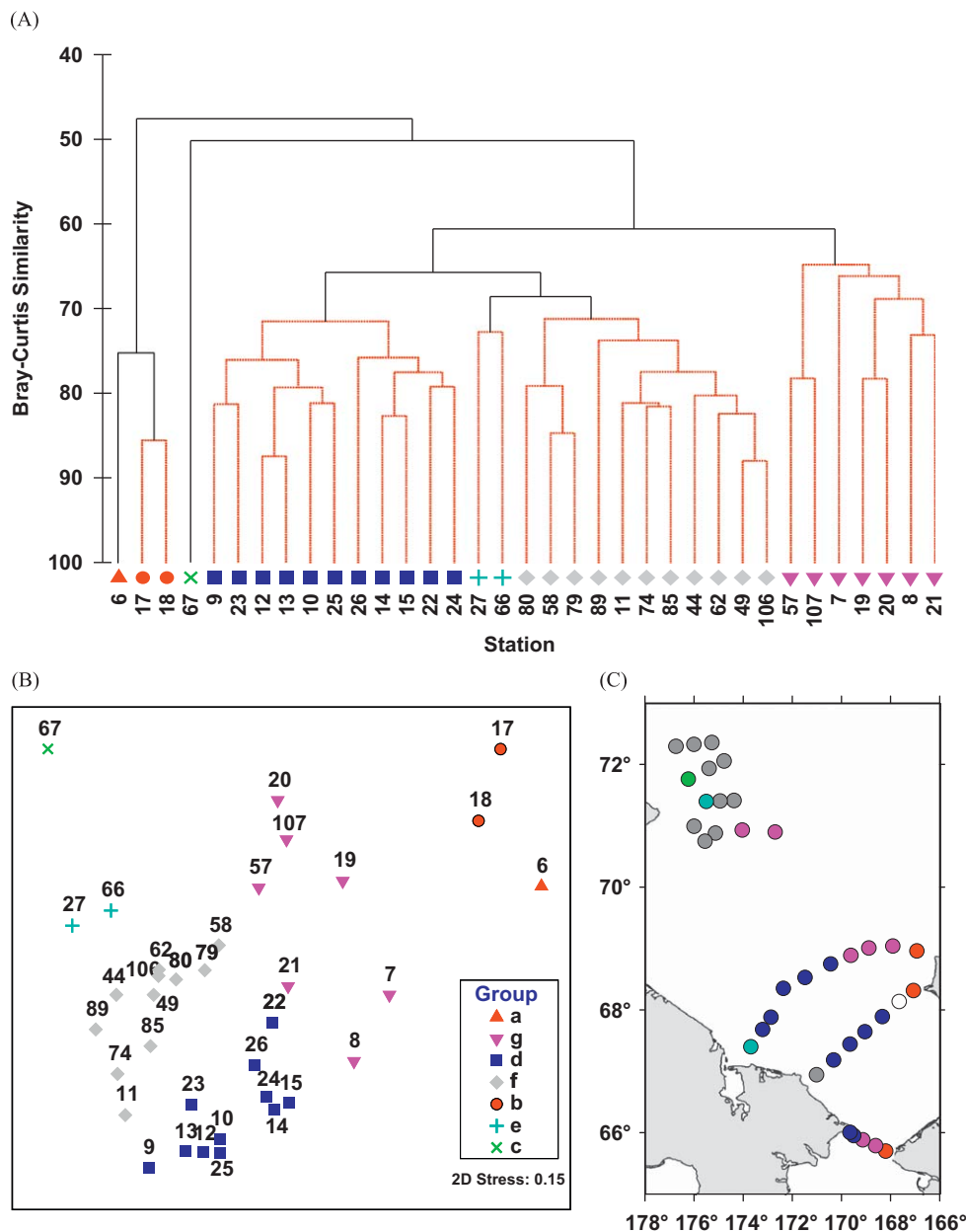


Fig. 5. (A) Station similarity as determined by hierarchical clustering of fourth root-transformed zooplankton abundance. Red lines connect stations that are not statistically unique ($P < 0.05$). (B) Multidimensional scaling of zooplankton community abundances. (C) Spatial distribution of zooplankton clusters in the Chukchi Sea, August 2004. Color-code is shared. Data missing for unfilled symbol.

study were common to the subarctic Pacific Ocean and/or the Bering Sea rather than to the Arctic (Brodsky, 1950, 1957). Nonetheless, the species composition is generally similar to that observed during the summer ice-free period in this region when similar-sized collecting meshes are employed (e.g. Springer et al., 1989; Kulikov, 1992), or allowances are made for differences in mesh size (e.g. Wing, 1974; English and Horner, 1977). Interestingly, our estimate of 42 mg DW m^{-3} ($\sim 2.1 \text{ g DW m}^{-2}$), overlaps the broad range of older biomass estimates for the region, $\sim 2 \text{ g DW m}^{-2}$ for herbivorous zooplankton in summer north and south of Bering Strait (Springer et al., 1989), $2.5\text{--}5.5 \text{ g DW m}^{-2}$ on the US side of the Chukchi sea or 1.3 spanning both sides of the Chukchi (Turco, 1992a, b). Furthermore, 14.8 g WW m^{-2} (Kulikov, 1992) and 356 mg WW m^{-3} (14.2 g WW m^{-2} —Pavshits, 1984) for all meso-zooplankton spanning the Chukchi Sea is also close if we assume DW is 10–15% of WW (Wiebe et al., 1975). Our observations also overlap the range of more recent observations ($3\text{--}58 \text{ mg DW m}^{-3}$)

to the northeast near the shelf (Lane et al., 2008; Llinas et al., 2009), and are surprisingly similar to values for the upper 50 m (42 mg DW m^{-3}) further into the adjoining basin (Kosobokova and Hopcroft, 2009).

In terms of composition, the species observed in this study have in general been reported previously for this region, but not consistently within single publications. Changes in mesh size between studies (e.g. $505 \mu\text{m}$ mesh used in ISHTAR—Springer et al., 1989; Turco, 1992a, b) greatly complicates quantitative comparison of community composition between studies, except for the largest species. Comparison between previous studies is also hampered to various extents by both changes in taxonomic resolution, taxonomic proficiency, and taxonomy itself, which warrant review. Presuming that copepods should be the best identified group, historically *Pseudocalanus* adults in this region have seldom been separated to species (e.g. Cooney, 1977; Springer et al., 1989) or regarded as only *P. minutus* (e.g. Pavshits,

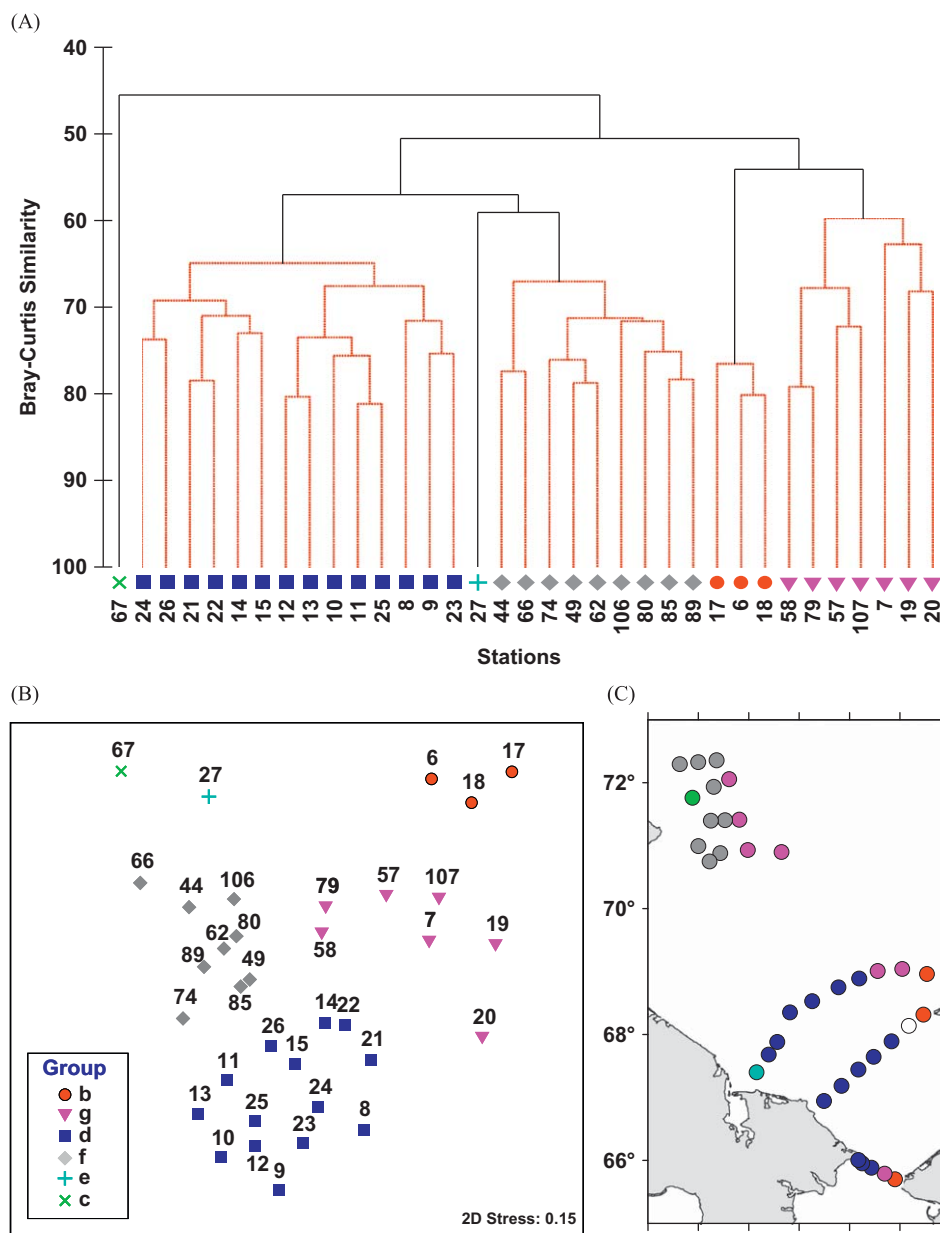


Fig. 6. (A) Station similarity as determined by hierarchical clustering of zooplankton biomass. Red lines connect stations that are not statistically unique ($P < 0.05$). (B) Multidimensional scaling of zooplankton community biomasses. (C) Spatial distribution of zooplankton clusters in the Chukchi Sea, August 2004. Color-code is shared. Data missing for unfilled symbol.

1984; Turco, 1992a,b) prior to the revision of the genus (Frost, 1989), despite their prominence and their species-affiliation with different water masses (this study, see Hopcroft and Kosobokova (2009) for more detail on *Pseudocalanus* distribution). In terms of the biomass dominants, earlier studies either predate or fail to distinguish the subarctic *C. marshallae* (Frost, 1974) from the closely related *C. glacialis* (e.g. Pavshitskiy, 1984; Kulikov, 1992), and even today routine morphological separation is difficult (Llinás, 2007; Lane et al., 2008). Similarly, many studies predate the separation of *Neocalanus plumchrus* into *N. plumchrus* and *N. flemingeri* (Miller, 1988). Several misidentifications are notable, for example, records of *M. pacifica* identified as *M. lucens* (Cooney, 1977; several cruises in Turco, 1992a,b). Three species of *Acartia* appear to be present in the study area, with *A. longiremis* dominant and lesser numbers contributed by *A. hudsonica*, which has been frequently misidentified as *A. clausi* (e.g. Cooney, 1977; Neimark, 1979; Kulikov, 1992). Although we can verify the

presence of *A. tumida*, the existence of *A. bifilosa* (Neimark, 1979) within the region cannot yet be verified. Finally, we verify the existence of at least two species of *Eurytemora*, *E. hermandi* (dominant) and *E. pacifica* (rare), but did not observe *E. americana* (i.e. Neimark, 1979). It is notable that the average size-spectrum of the copepod community was relatively flat compared to the California Current (Hopcroft et al., 2001), and more like the spectra observed in the Arctic Basins (Hopcroft et al., 2005), but lacks the depressed region between ~600 and 2000 μm observed in the Canada Basin due to the contribution of *Pseudocalanus* and other small- to medium-sized calanoids.

Other holoplanktonic crustacean groups, such as euphausiids and cladocerans, present less of a taxonomic challenge and are generally accurately reported in previous works, although sometimes not to the species level. Non-crustacean groups have been recorded with variable resolution and proficiency in previous studies. There were considerable populations of larvaceans,

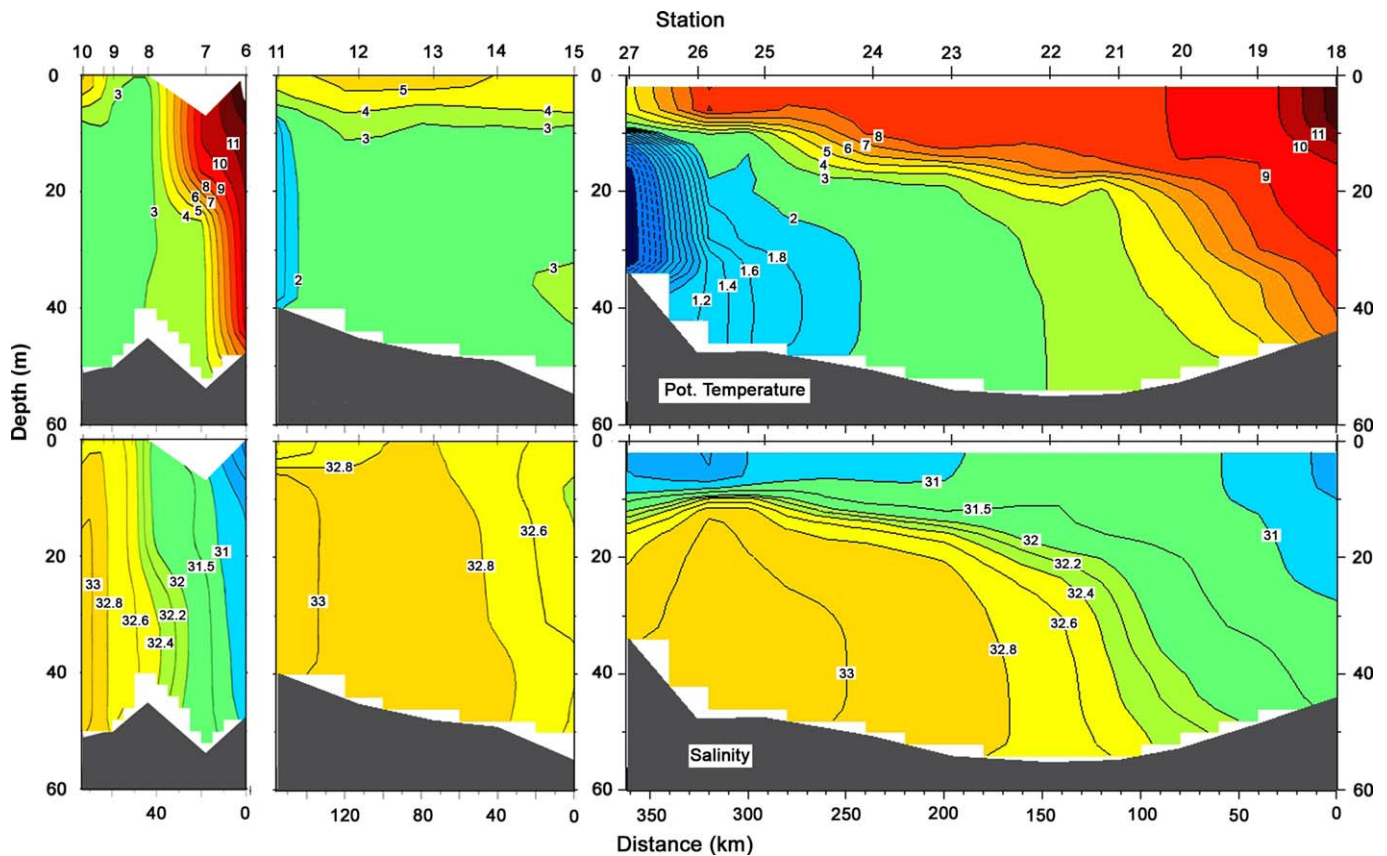


Fig. 7. Temperature (above) and salinity (below) sections along the three lower transect lines (Fig. 1) in the Chukchi Sea, August 2004. The viewer is looking north, with southern most transect on the left.

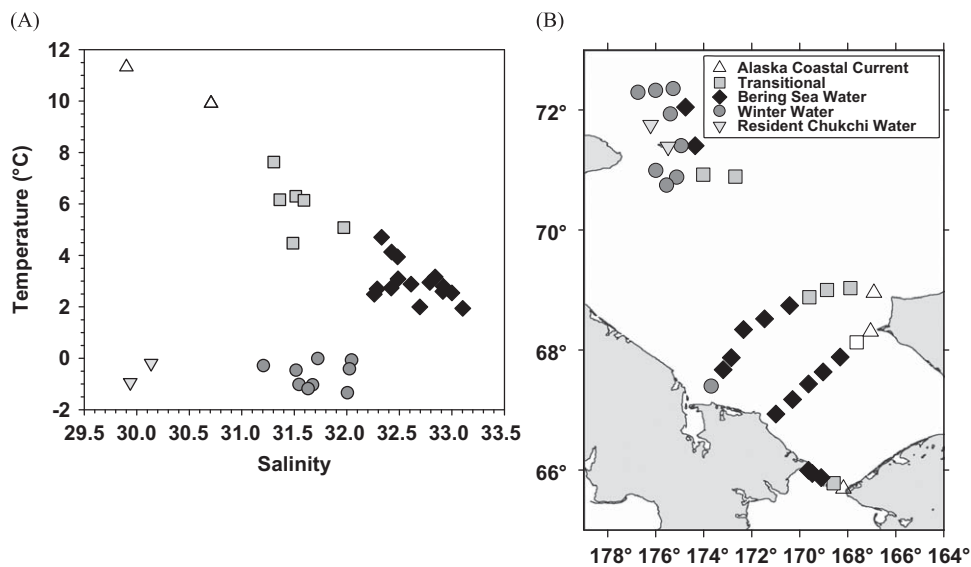


Fig. 8. (A) Water masses present in the Chukchi Sea study area, August 2004, as determined using mean values for the station (to a maximum of 50 m). (B) Distribution of water masses over the Chukchi Sea, August 2004, based on T-S properties from averages over the upper 50 m of the water column. Data is missing for unfilled square symbol.

particularly the large arctic *O. vanhoeffeni* throughout the sampling area, that have been reported in high numbers (e.g. Kulikov, 1992; Lane et al., 2008) and/or high biomass by other studies (Springer et al., 1989), consistent with reports from the

northern Bering Sea (Shiga et al., 1998). Larvaceans are increasingly implicated as key players in polar systems (e.g. Acuna et al., 1999; Hopcroft et al., 2005; Deibel et al., 2005) due to their high grazing and growth rates. At times, the biomass of larvaceans in

Table 3
Environmental variables correlated to the observed community structure as revealed by the BEST analysis, for temperature (T), salinity (S), density (ρ), oxygen (O), turbidity (Tu), in situ fluorescence (Fl), and extracted chlorophyll (Chl).

No. of variables	Best variable combinations using 0–50 m layer (Spearman Rank Correlation)			
2	<i>T, ρ</i> (0.75)			
3	<i>T, ρ, S</i> (0.75)	<i>T, ρ, O</i> (0.69)	<i>T, ρ, Fl</i> (0.67)	
4	<i>T, ρ, S, O</i> (0.71)	<i>T, ρ, S, Fl</i> (0.71)	<i>T, ρ, S, Chl</i> (0.68)	<i>T, ρ, S, Tu</i> (0.67)
5	<i>T, ρ, S, O, Fl</i> (0.69)	<i>T, ρ, S, Tu, Fl</i> (0.66)	<i>T, ρ, S, O, Chl</i> (0.65)	<i>T, ρ, S, O, Tu</i> (0.65)
Best variable combinations using multiple depth layers (Spearman Rank Correlation)				
2	<i>T_{10–50}, $\rho_{0–50}$</i> (0.78)			
3	<i>S_{10–50}, $\rho_{0–50}, T_{10–50}$</i> (0.77)	<i>$\rho_{10–50}, \rho_{0–50}, T_{10–50}$</i> (0.77)	<i>S_{0–50}, T_{10–50}, $\rho_{10–50}$}</i> (0.77)	<i>S_{0–50}, $\rho_{0–50}, T_{10–50}$}</i> (0.77)
4	<i>S_{0–50}, $\rho_{0–50}, T_{10–50}, \rho_{10–50}$}</i> (0.77)	<i>T_{0–50}, $\rho_{0–50}, T_{10–50}, S_{10–50}$}</i> (0.77)	<i>$\rho_{0–50}, T_{10–50}, S_{10–50}, \rho_{10–50}$</i> (0.77)	<i>T_{0–50}, $\rho_{0–50}, S_{0–50}, \rho_{10–50}$}</i> (0.76)
5	<i>T_{0–50}, $\rho_{0–50}, S_{0–50}, T_{10–50}, \rho_{10–50}$}</i> (0.77)	<i>T_{0–50}, $\rho_{0–50}, T_{10–50}, S_{10–50}, \rho_{10–50}$}</i> (0.77)	<i>T_{0–50}, $\rho_{0–50}, T_{10–50}, S_{10–50}, Tu_{0–10}$}</i> (0.77)	<i>T_{0–50}, $\rho_{0–50}, S_{0–50}, T_{10–50}, S_{10–50}$}</i> (0.76)

Subscripts indicate the layer (in m) over which the variable has been constructed.

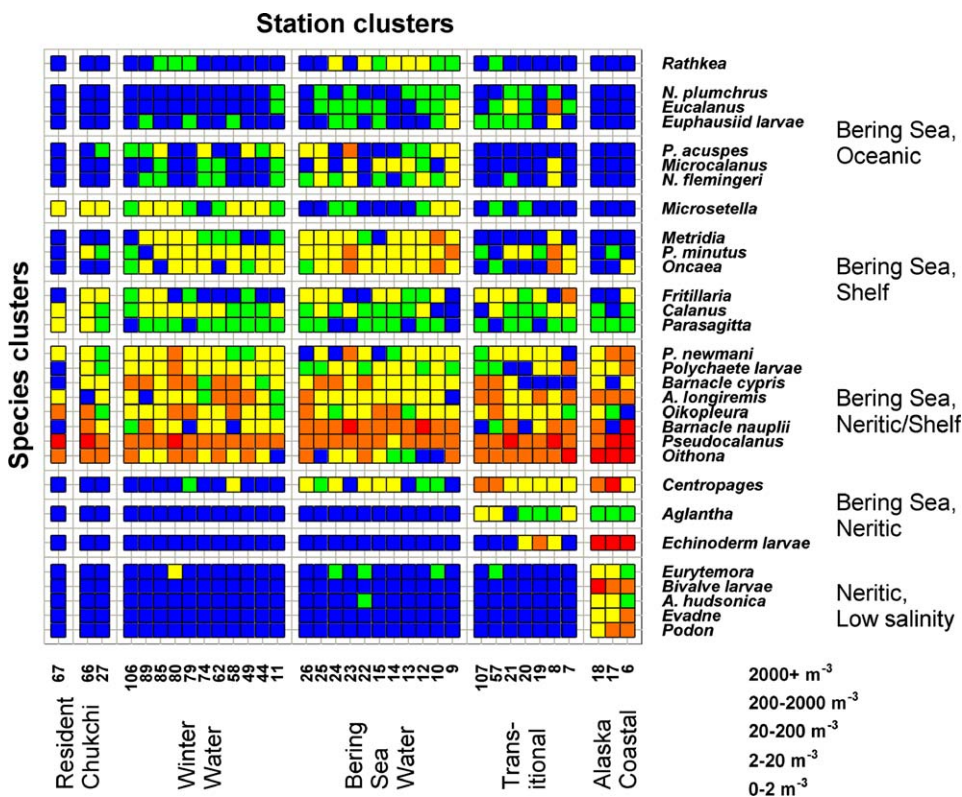


Fig. 9. Zooplankton abundance (ind. m^{-3}), clustered by species and stations in the Chukchi Sea, August 2004, with corresponding water masses and faunal affinities noted.

2004 rivaled that of the copepods, particularly at the ice-edge stations in Herald Canyon, where some of the highest reported abundances for *O. vanhoeffeni* were observed.

The dominant predators in terms of abundance and biomass were the chaetognaths, mostly *P. elegans*, consistent with other studies from the region (e.g. Cooney, 1977; Neimark, 1979; Springer et al., 1989; Kulikov 1992; Lane et al., 2008). There was

considerable diversity of both small and large gelatinous organisms: scypho- and hydromedusae, and ctenophores that are often overlooked: more than a dozen species were encountered in 2004, with *A. digitale* and *Rathkea octopunctata* being most common. All studies confirm the numerical dominance of *Aglantha* within the hydromedusae (e.g. Cooney, 1977; Neimark, 1979; Springer et al., 1989; Kulikov, 1992), while the composition and relative

contribution of other species varies greatly between these studies. Several species of amphipods formed a relatively minor predatory/omnivorous group, as did several forms of larval decapods.

Finally, suspension-feeding meroplanktonic larvae of benthic organisms were exceptionally common throughout the sampling region in 2004. High abundance of meroplankton is typical of summer-time data in this region (e.g. Cooney, 1977; Neimark, 1979; Springer et al., 1989; Kulikov, 1992), and improved knowledge of their abundance and distribution is relevant to understanding recruitment to the rich benthic communities in this region (Iken et al., 2009). Relationships between the size and weight for meroplanktonic groups need to be established to more fully appreciate their role in this region; based on the observed abundances, their biomass and impact as grazers could be significant.

4.2. Community patterns

The spatial distribution of the zooplankton communities in the Chukchi Sea is shown to be strongly tied to the different water masses, a conclusion reached by several previous studies in this region. Such patterns were first recognized by Russian researchers as early as the 1930s (Stepanova, 1937a,b), and are to a large extent a continuation of patterns observed in the northern Bering Sea (see review by Coyle et al., 1996). These patterns were reiterated by later Russian studies (e.g. Pavshits, 1984) that identified at least three water types in the region. Although the first years of the ISHTAR program were restricted to sampling in US waters, oceanic Anadyr waters, continental shelf and low-saline nearshore waters were all recognized (Springer et al., 1989). Cross-basin studies by the BERPAC program also identified three zooplankton clusters within the Chukchi Sea, but failed to articulate their species assemblages or associate them with specific water masses (Kulikov, 1992). Concurrent sampling for ichthyoplankton within this program revealed a remarkably similar grouping of stations as were identified here, and also coupled their groups to water masses (Norcross et al., 2010).

The species assemblages observed in this study are most clearly demarcated by the euryhaline nearshore cladocerans (i.e. *Podon* and *Evadne*), *A. hudsonica*, *Eurytemora* species and selected meroplankton that denote the Alaska Coastal Current (ACC). These species have been shown to be particularly abundant in the nearshore waters, while the oceanic assemblage is absent from such waters (Cooney, 1977; Neimark, 1979; Springer et al., 1989). Earlier Russian studies have failed to detect the ACC community because they lacked stations sufficiently close to the American shore to sample ACC waters. Most other community groups appear to be less rigid, and more transitional, involving more subtle changes in absolute and relative abundances. The strong contribution of oceanic subarctic Pacific expatriates to the community biomass was noted in the earliest studies in the region (i.e. Stepanova, 1937a,b) and remains a consistent feature of all subsequent summer studies. Not surprisingly, there is a transition zone between these coastal waters and the adjoining Bering Sea waters. What is interesting is that although physical oceanographers have debated the pathways of water across the Chukchi shelf (see Pickart et al., 2009), we demonstrate that the zooplankton community shows some traces of even ACC communities along the eastern edge of Herald Valley.

The cold Bering Sea Winter Waters encountered through much of the Herald Valley (Pickart et al., 2009), and possibly present also at Stations 27 and 11 along the Siberian Coast, is characterized to a large degree by the absence of the large-bodied Pacific expatriates. These expatriates are not present because this water was likely formed on the Bering Sea Shelf during winter

(Weingartner, pers. comm.) when these species have undertaken the ontogenetic vertical migration to depth in their life cycle (Miller and Clemons, 1988; Mackas and Tsuda, 1999), and so are absent from these waters. Only a few stations appeared to reflect Resident Chukchi Water with its more Arctic assemblage of species, and such a community would be expected to be encountered moving eastward into Long Strait south of Wrangel Island, or moving more northward (e.g. Pavshits, 1984, 1994). Ultimately, as one moves northward we would anticipate transition into water masses of a strictly Arctic Ocean origin with their unique assemblage of predominantly oceanic species (e.g. Pavshits, 1994; Ashjian et al., 2003; Hopcroft et al., 2005; Lane et al., 2008), but such regions were not encompassed by this expedition.

5. Conclusions and outlook

In terms of mechanisms, planktonic communities of the Chukchi Sea are likely to undergo climate-related changes both through shifts in the absolute transport rate and penetration of Pacific species into the Arctic, and by environmental changes that affect their survival. It has been estimated that 1.8 million metric tons of Bering Sea zooplankton are carried into the Chukchi Sea annually (Springer et al., 1989). These zooplankton, along with the entrained phytoplankton communities, are responsible for the high productivity of the Chukchi Sea in comparison to adjoining regions of the Arctic Ocean (e.g. Plourde et al., 2005; Lane et al., 2008). In the summer of 2004 one would characterize the southern Chukchi zooplankton fauna as primarily Pacific in character, and these Pacific species were carried far northward through the Herald Valley. Other Pacific species have been observed as far as the Chukchi Plateau (Ashjian et al., 2003), and at very low numbers within the adjoining basins (Hopcroft et al., 2005; Kosobokova and Hopcroft, 2009). Given the range of variability in the literature, and the lack of comparable sampling methods and stations, there is no indication summer zooplankton biomass in this region has changed systematically over the past few decades, although changes have been documented to occur closer to the shelf break (Lane et al., 2008).

Future increases in transport would, however, carry more Pacific zooplankton through Bering Strait with even further penetration into the Arctic. In contrast, a reduction in transport of Bering Sea water would not only decrease the overall biomass and productivity of the Chukchi Sea, but give it a more Arctic Ocean faunal character. Thus, changes in the transport rates ultimately affect the species composition of this region, as well as the absolute zooplankton biomass distributed throughout the Chukchi Sea, and such shifts would also result in changes in the size structure of zooplankton communities. As indicated by both species composition and size spectra, the southern Chukchi Sea already has much greater contribution from, and importance of, smaller-bodied species/stages than observed in the Arctic Basins (e.g. Hopcroft et al., 2005). This pattern could become common across the entire Chukchi Sea. Most higher trophic levels select their prey based on size; thus, the consequences of size-structure shifts could be even more important than changes in zooplankton biomass (Richardson and Schoeman, 2004; Lane et al., 2008).

As with most long-term observations, the challenge will be detecting systematic change from the year-to-year variability already noted in this region (e.g. Springer et al., 1989; Turco, 1992a,b; Pavshits, 1994), understanding how rate processes respond to temperature, and recognizing the importance of water mass origin in defining the observed community structure. A more systematic, spatially distributed and regularly repeated, international sampling program in the region will be essential to

address this need given the Chukchi Sea's oceanographic complexity. Emerging molecular tools may further aid in our ability to separate problematic species (e.g. Llinás, 2007; Lane et al. 2008; Bucklin et al., 2009) and even populations within them (Nelson et al., 2009). In addition to the regular addition of new data, the challenge to build predictive models for the future will be greatly aided by the rescue of older data, and larger effort should be expended on consolidating past knowledge than is the current practice.

Acknowledgments

We thank NOAA's John Calder and Kathy Crane for their vision and perseverance in making the RUSALCA program a reality. We also thank Marshall Swartz, Mark Dennett, and Robert Pickart for providing physical oceanographic data and Terry Whitedge for providing chlorophyll values. Three anonymous reviewers provided valuable comments toward improvement of this work. This research was partially funded by NOAA's Office of Ocean Exploration, NOAA's Arctic Research Office, and the Cooperative Institute for Arctic Research (CIFAR) through NOAA Cooperative Agreement NA17RJ1224 with the University of Alaska. The work of K.N.K. was also supported by Russian Foundation for Basic Research, Grant no. 06-05-65187. This research is a contribution to the Arctic Ocean Biodiversity (ArcOD) project of the Census of Marine Life.

References

- ACIA, 2004. Impacts of a Warming Arctic. Arctic Climate Impact Assessment. Cambridge University Press, Cambridge 139 pp.
- Acuna, J.L., Deibel, D., Bochdansky, A.B., Hatfield, E., 1999. In situ ingestion rates of appendicularian tunicates in the Northeast Water Polynya (NE Greenland). *Marine Ecology Progress Series* 186, 149–160.
- Ashjian, C.J., Campbell, R.G., Welch, H.E., Butler, M., Keuren, D.V., 2003. Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. *Deep-Sea Research I* 50, 1235–1261.
- Auel, H., Werner, I., 2003. Feeding, respiration and life history of the hyperiid amphipod *Themisto libellula* in the Arctic marginal ice zone of the Greenland Sea. *Journal of Experimental Marine Biology and Ecology* 296, 183–197.
- Båmstedt, U., 1986. Chemical composition and energy content. In: Corner, E.D.S., O'Hara, S.C.M. (Eds.), *The Biological Chemistry of Marine Copepods*. Clarendon Press, Oxford, pp. 1–58.
- Bogorov, V.G., 1939. The characteristics of seasonal phenomena in the plankton of the Arctic seas and their significance for ice forecastings. *Zoological Journal* 18 (5) (in Russian).
- Brodsky, K.A., 1950. Copepods (Calanoida) of the far-eastern seas of the USSR and the polar basin. Leningrad Institute of the Academy of Sciences of the USSR, Leningrad (in Russian).
- Brodsky, K.A., 1957. The copepod fauna (Calanoida) and zoogeographic zonation of the North Pacific and adjacent waters. *Izvestiya Akademii Nauk SSSR, Leningrad* [in Russian].
- Bucklin, A., 2000. Methods for population genetic analysis of zooplankton. In: Harris, R.P., Weibe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds.), *ICES Zooplankton Methodology Manual*. Academic Press, London, pp. 533–570.
- Bucklin, A., Hopcroft, R.R., Kosobokova, K.N., Nigro, L.M., Ortman, B.D., Jennings, R.M., Sweetman, C.J., 2009. DNA barcoding of Arctic Ocean holozooplankton for species identification and recognition. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2009.08.05].
- Carmack, E., Barber, D., Christensen, J., Macdonald, R., Rudels, B., Sakshaug, E., 2006. Climate variability and physical forcing of the food webs and the carbon budget on panarctic shelves. *Progress in Oceanography* 71, 145–181.
- Clarke, K.R., Warwick, R.M., 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, second ed. PRIMER-E, Plymouth.
- Cooney, R.T., 1977. Zooplankton and micronekton studies in the Bering-Chukchi/Beaufort Seas. NOAA OCSEP Annual Report 10, pp. 275–363.
- Coyle, K.O., Chavtur, V.G., Pinchuk, A.I., 1996. Zooplankton of the Bering Sea: a review of Russian-language literature. In: Mathisen, A.O., Coyle, K.O. (Eds.), *Ecology of the Bering Sea: A Review of the Russian Literature*. Alaska Seagrant College Program, Fairbanks, pp. 97–133.
- Coyle, K.O., Bluhm, B.A., Konar, B., Blanchard, A., Highsmith, R.C., 2007. Amphipod prey of grey whales in the northern Bering Sea: changes in biomass and distribution. *Deep-Sea Research II* 54, 2906–2918.
- Deibel, D., 1986. Feeding mechanism and house of the appendicularian *Oikopleura vanhoefeni*. *Marine Biology* 93, 429–436.
- Deibel, D., Daly, K.L., 2007. Zooplankton processes in Arctic and Antarctic polynyas. In: Smith Jr., W.O., Barber, D.G. (Eds.), *Arctic and Antarctic Polynyas*. Elsevier, Amsterdam, pp. 271–322.
- Deibel, D., Saunders, P.A., Acuña, J.L., Bochdansky, A.B., Shiga, N., Rivkin, R.B., 2005. The role of appendicularian tunicates in the biogenic carbon cycle of three Arctic polynyas. In: Gorsky, G., Youngbluth, M.J., Deibel, D. (Eds.), *Response of Marine Ecosystems to Global Change: Ecological Impact of Appendicularians*. Gordon and Breach, Paris, pp. 327–356.
- English, T.S., 1966. Net plankton volumes in the Chukchi Sea. In: Wilimovsky, N.J., Wolfe, J.N. (Eds.), *Environment of the Cape Thompson Region, Alaska*. US Atomic Energy Commission, Washington, pp. 809–915.
- English, T.S., Horner, R., 1977. Beaufort Sea plankton studies. NOAA OCSEAP Annual Report 9, pp. 275–627.
- Feder, H.M., Jewett, S.C., Blanchard, A., 2005. Southeastern Chukchi Sea (Alaska) epibenthos. *Polar Biology* 28, 402–421.
- Feder, H.M., Jewett, S.C., Blanchard, A.L., 2007. Southeastern Chukchi Sea (Alaska) macrobenthos. *Polar Biology* 30, 261–275.
- Fenaux, R., 1976. Premieres donnees specifiques sur les rapports poids/taille chez les Appendiculaires en Mediterranee. Rapport et Process-Verbaux Réunions. Conseil International pour l'Exploration de la Mer 23, 67–69.
- Frost, B.W., 1974. *Calanus marshallae*, a new species of calanoid copepod closely allied to the sibling species *C. finmarchicus* and *C. glacialis*. *Marine Biology* 26, 77–99.
- Frost, B.W., 1989. A taxonomy of the marine calanoid genus *Pseudocalanus*. *Canadian Journal of Zoology* 67, 525–551.
- Fukuchi, M., Sasaki, H., Hattori, H., Matsuda, O., Tanimura, A., Handa, N., McRoy, C.P., 1993. Temporal variability of particulate flux in the northern Bering Sea. *Continental Shelf Research* 13, 693–704.
- Grebmeier, J.M., Barry, J.P., 1991. The influence of oceanographic processes on pelagic-benthic coupling in polar regions: a benthic perspective. *Journal of Marine Systems* 2, 495–518.
- Grebmeier, J.M., Harvey, H.R., 2005. The Western Arctic Shelf-Basin Interactions (SBI) project: an overview. *Deep-Sea Research II* 52, 3109–3576.
- Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006a. Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. *Progress in Oceanography* 71, 331–361.
- Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., McNutt, S.L., 2006b. A major ecosystem shift in the northern Bering Sea. *Science* 311, 1461–1464.
- Grebmeier, J.M., Smith Jr., W.O., Conover, R.J., 1995. Biological processes on Arctic continental shelves: ice-ocean-biotic interactions. In: Smith Jr., W.O., Grebmeier, J.M. (Eds.), *Arctic Oceanography: Marginal ice Zones and Continental Shelves*. American Geophysical Union, Washington, pp. 231–261.
- Hansen, B.W., Nielsen, T.G., Levinsen, H., 1999. Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. III. Mesozooplankton. *Aquatic Microbial Ecology* 16, 233–249.
- Hirche, H.-J., Hagen, W., Mumm, N., Richter, C., 1994. The Northeast Water Polynya, Greenland Sea. III. Meso- and macrozooplankton distribution and production of dominant herbivorous copepods during spring. *Polar Biology* 14, 491–503.
- Hopcroft, R.R., Clarke, C., Chavez, F.P., 2002. Copepod communities in Monterey Bay during the 1997 to 1999 El Niño and La Niña. *Progress in Oceanography* 54, 251–263.
- Hopcroft, R.R., Clarke, C., Nelson, R.J., Raskoff, K.A., 2005. Zooplankton Communities of the Arctic's Canada Basin: the contribution by smaller taxa. *Polar Biology* 28, 197–206.
- Hopcroft, R.R., Kosobokova, K.N., 2009. Distribution and production of *Pseudocalanus* species in the Chukchi Sea. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2009.08.004].
- Hopcroft, R.R., Roff, J.C., Chavez, F.P., 2001. Size paradigms in copepod communities: a re-examination. *Hydrobiologia* 453/454, 133–141.
- Hopcroft, R.R., Roff, J.C., Lombard, D., 1998. Production of tropical copepods in the nearshore waters off Kingston, Jamaica: the importance of small species. *Marine Biology* 130, 593–604.
- Horner, R., 1981. Beaufort Sea plankton studies. NOAA Outer Continental Shelf Environmental Program, Final Report 13, 65–314.
- Ikeda, T., Shiga, N., 1999. Production, metabolism and production/biomass (P/B) ratio of *Themisto japonica* (Crustacea: Amphipoda) in Toyama Bay, southern Japan Sea. *Journal of Plankton Research* 21, 299–308.
- Iken, K., Bluhm, B., Dunton, K., 2009. Do differing water mass properties affect benthic food web structure in the southern Chukchi sea? *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2009.08.007].
- Jaschnov, V., 1940. *Plankton productivity of the northern seas of the USSR*. Moscovskoe Obshchestvo Ispytatelei Prirody Press, Moscow (in Russian).
- Johnson, M.W., 1934. The production and distribution of zooplankton in the surface waters of the Bering Sea and Bering Strait, Part II. Report of the oceanographic cruise US Coast Guard Cutter *Chelan*—1934, pp. 45–82.
- Johnson, M.W., 1953. Studies on the plankton of the Bering and Chukchi Seas and adjacent areas. In: Proceedings of the 7th Pacific Science Congress (1949), vol. 4, Zoology, pp. 480–500.
- Johnson, M.W., 1956. The plankton of the Beaufort and Chukchi Sea areas of the Arctic and its relation to hydrography. Arctic Institute of North America, Montreal.
- Johnson, M.W., 1958. Observations on inshore plankton collected during the summer 1957 at Point Barrow, Alaska. *Journal of Marine Research* 17, 272–281.

- Kobari, T., Shinada, A., Tsuda, A., 2003. Functional roles of interzonal migrating mesozooplankton in the western subarctic Pacific. *Progress in Oceanography* 57, 279–298.
- Kosobokova, K., Hirche, H.-J., 2000. Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. *Deep-Sea Research I* 47, 2029–2060.
- Kosobokova, K.N., Hopcroft, R.R., 2009. Diversity and vertical distribution of mesozooplankton in the Arctic's Canada Basin. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2009.08.009].
- Kulikov, A.S., 1992. Characteristics of zooplankton communities. In: Nagel, P.A. (Ed.), Results of the Third Joint US–USSR Bering and Chukchi Seas expedition (BERPAC), Summer 1988. US Fish and Wildlife Service, Washington, pp. 161.
- Lane, P.V.Z., Llinás, L., Smith, S.L., Pilz, D., 2008. Zooplankton distribution in the western Arctic during summer 2002: hydrographic habitats and implications for food chain dynamics. *Journal of Marine Research* 70, 97–133.
- Lee, S.H., Whitledge, T.E., Kang, S.-H., 2007. Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. *Continental Shelf Research* 27, 2231–2249.
- Liu, H., Hopcroft, R.R., 2006a. Growth and development of *Metridia pacifica* (Copepoda: Calanoida) in the northern Gulf of Alaska. *Journal of Plankton Research* 28, 769–781.
- Liu, H., Hopcroft, R.R., 2006b. Growth and development of *Neocalanus flemingeri/plumchrus* in the northern Gulf of Alaska: validation of the artificial cohort method in cold waters. *Journal of Plankton Research* 28, 87–101.
- Liu, H., Hopcroft, R.R., 2007. A comparison of seasonal growth and development of the copepods *Calanus marshallae* and *C. pacificus* in the northern Gulf of Alaska. *Journal of Plankton Research* 29, 569–581.
- Liu, H., Hopcroft, R.R., 2008. Growth and development of *Pseudocalanus* spp. in the northern Gulf of Alaska. *Journal of Plankton Research* 30, 923–935.
- Llinás, L., 2007. Distribution, reproduction, and transport of zooplankton in the western Arctic. Ph.D. Dissertation, University of Miami, Coral Gables, Florida.
- Llinás, L., Pickart, R.S., Mathis, J.T., Smith, S., 2009. Zooplankton inside an Arctic Ocean cold-core eddy: Probable origin and fate. *Deep-Sea Research II*, 56, 1290–1304.
- Mackas, D.L., Tsuda, A., 1999. Mesozooplankton in the eastern and western subarctic Pacific: community structure, seasonal life histories, and interannual variability. *Progress in Oceanography* 43, 335–363.
- Matthews, J.B.L., Hestad, L., 1977. Ecological studies on the deep-water pelagic community of Korsfjorden, Western Norway. Length/weight relationships for some macroplanktonic organisms. *Sarsia* 63, 57–63.
- Middlebrook, K., Roff, J.C., 1986. Comparison of methods for estimating annual productivity of the copepods *Acartia hudsonica* and *Eurytemora herdmani* in Passamaquoddy Bay, New Brunswick. *Canadian Journal of Fisheries and Aquatic Sciences* 43, 656–664.
- Miller, C.B., Clemons, M.J., 1988. Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. *Progress in Oceanography*, 20, 293–313.
- Mumm, N., 1991. On the summerly distribution of mesozooplankton in the Nansen Basin, Arctic Ocean. *Reports on Polar Research* 92, 1–173 (in German).
- Neimark, B.S., 1979. Zooplankton ecology of Norton Sound, Alaska. M.Sc. Thesis, University of Alaska, Fairbanks.
- Nelson, R.J., Carmack, E.C., McLaughlin, F.A., Cooper, G.A., 2009. Penetration of Pacific zooplankton into the western Arctic Ocean tracked with molecular population genetics. *Marine Ecology Progress Series* 381, 129–138.
- Norcross, B.L., Holladay, B.A., Busby, M.S., Mier, K.L., 2009. Frontal structure in the Chukchi Sea determines small demersal and larval fish communities. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2009.08.006].
- Pavshitski, E.A., 1984. Zooplankton of the Chukchi Sea as indices of water origins. *Trudy Arkticheskogo i Antarkticheskogo Nauchno-Issledovatel'skogo Instituta* 368, 140–153 (in Russian).
- Pavshitski, E.A., 1994. Composition and quantitative distribution of the zooplankton in the East Siberian Sea. *Ekosistemy, flora i fauna Chaunskoi guby Vostochno-Sibirskogo morya*. Zoological Institute RAS, St.-Petersburg, pp. 17–47 (in Russian).
- Pickart, R.S., Pratt, L.J., Torres, D.J., Whitledge, T.E., Proshutinsky, A.Y., Aagaard, K., Agnew, T.A., Moore, G.W.K., Dail, H.J., 2009. Evolution and dynamics of the flow through Herald Canyon in the western Chukchi Sea. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2009.08.002].
- Pinchuk, A.I., Hopcroft, R.R., 2007. Seasonal variations in the growth rate of euphausiids (*Thysanoessa inermis*, *T. spinifera*, and *Euphausia pacifica*) from the northern Gulf of Alaska. *Marine Biology* 151, 257–269.
- Plourde, S., Campbell, R.G., Ashjian, C.J., Stockwell, D.A., 2005. Seasonal and regional patterns in egg production of *Calanus glacialis/marshallae* in the Chukchi and Beaufort Seas during spring and summer, 2002. *Deep-Sea Research II* 52, 3411–3426.
- Richardson, A.J., Schoeman, D.S., 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305, 1609–1612.
- Roff, J.C., Hopcroft, R.R., 1986. High precision microcomputer based measuring system for ecological research. *Canadian Journal of Fisheries and Aquatic Sciences* 43, 2044–2048.
- Sabatini, M., Kiørboe, T., 1994. Egg production, growth and development of the cyclopoid *Oithona similis*. *Journal of Plankton Research* 16, 1329–1351.
- Shiga, N., Takagi, S., Nishiuchi, K., 1998. Interannual variation and vertical distribution of appendicularians in the south of St. Lawrence Island, northern Bering Sea shelf, in summer. *Memoirs of the Faculty of Fisheries, Hokkaido University* 45, 48–51.
- Smith, S.L., Schnack-Schiel, S.B., 1990. Polar zooplankton. In: Smith Jr., W.O. (Ed.), *Polar Oceanography, Part B: Chemistry, Biology, and Geology*. Academic Press, San Diego, pp. 527–598.
- Springer, A.M., McRoy, C.P., Turco, K.R., 1989. The paradox of pelagic food webs in the northern Bering Sea-II. Zooplankton communities. *Continental Shelf Research* 9, 359–386.
- Stepanova, V.S., 1937. Biological indicators of currents in the northern Bering and southern Chukchi Seas. *Issledovanija Morei SSSR* 25, 175–216 (in Russian).
- Stepanova, V.S., 1937. Distribution of Bering Sea water in the Chukchi Sea (from data of the analysis of zooplankton from a cruise on the icebreaker Krasin in 1935). *Trudy Arkticheskogo Nauchno-Issledovatel'skogo Instituta* 82, 113–143 (in Russian).
- Thibault, D., Head, E.J.H., Wheeler, P.A., 1999. Mesozooplankton in the Arctic Ocean in summer. *Deep-Sea Research I* 46, 1391–1415.
- Tsyban, A.V., 1999. The BERPAC project: development and overview of ecological investigations in the Bering and Chukchi Seas. In: Loughlin, T.R., Ohtani, K. (Eds.), *Dynamics of the Bering Sea*. Alaska Sea Grant College Program, Fairbanks, pp. 713–731.
- Turco, K., 1992a. Zooplankton taxa, abundance and biomass data. ISHTAR Data Report No. 6, Part 1 (1985–1987). Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska, 620 pp.
- Turco, K., 1992b. Zooplankton taxa, abundance and biomass data. ISHTAR Data Report No. 6, Part 2 (1988–1989). Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska, 620 pp.
- Unstad, K.H., Tande, K.S., 1991. Depth distribution of *Calanus finmarchicus* and *C. glacialis* to environmental conditions in the Barents Sea. In: Sakshaug, E., Hopkins, C.C.E., Øritsland, N.A. (Eds.), *Proceedings of the Pro Mare Symposium on Polar Marine Ecology*. *Polar Research* 10, 409–420.
- Uye, S., 1982. Length–weight relationships of important zooplankton from the Inland Sea of Japan. *Journal of the Oceanographical Society of Japan* 38, 149–158.
- Virketis, M., 1952. Zooplankton of the Chukchi Sea and Bering Strait. In: Brodsky, K.A. (Ed.), *The far North-east of the USSR. 2. Fauna and Flora of the Chukchi Sea*. Izdatelstvo Akademii Nauk SSSR, Moscow, pp. 323–335 (in Russian).
- Webber, M.K., Roff, J.C., 1995. Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. *Marine Biology* 123, 481–495.
- Weingartner, T.J., Aagaard, K., Woodgate, R.A., Danielson, S.L., Sasaki, Y., Cavalieri, D., 2005. Circulation on the North Central Chukchi Sea Shelf. *Deep-Sea Research II* 52, 3150–3174.
- Weingartner, T.J., Cavalieri, D.J., Aagaard, K., Sasaki, Y., 1998. Circulation, dense water formation, and outflow on the northeast Chukchi shelf. *Journal of Geophysical Research* C 103, 7647–7661.
- Wing, B.L., 1974. Kinds and abundances of zooplankton collected by the USCG icebreaker *Glacier* in the eastern Chukchi Sea, September–October 1970. Technical Report SSRF-679, National Marine Fisheries Service, Seattle, p. 18.
- Wiebe, P.H., Boyd, S., Cox, J.L., 1975. Relationships between zooplankton displacement volume, wet weight, dry weight, and carbon. *Fisheries Bulletin* 73, 777–786.
- Wishner, K.F., Gelfman, C., Gowing, M.M., Outram, D.M., Rapien, M., Williams, R.L., 2008. Vertical zonation and distributions of calanoid copepods through the lower oxycline of the Arabian Sea oxygen minimum zone. *Progress in Oceanography* 78, 163–191.