STRUCTURE, INTER-ANNUAL VARIABILITY, AND LONG-TERM CHANGE IN ZOOPLANKTON COMMUNITIES OF THE CHUKCHI SEA

By

Elizaveta A. Ershova

A Dissertation Sumitted in Partial Fulfillment of the Requirements
for the Degree of

Doctor of Philosophy
in
Marine Biology

University of Alaska Fairbanks
August 2016

APPROVED:
Dr. Russell Hopcroft, Committee Chair
Dr. Ksenia Kosobokova, Committee Co-Chair
Dr. Rolf Gradinger, Committee Member
Dr. Ken Coyle, Committee Member
Dr. Peter Winsor, Committee Member
Dr. Sarah Hardy, Program Head
Marine Science and Limnology
Dr. Bradley Moran, Dean
School of Fisheries and Ocean Sciences
Dr. John Eichelberger
Dean of the Graduate School

Abstract

The Chukchi Sea is a complex transition zone between the Pacific and Arctic Oceans that has been experiencing dramatic change in recent decades due to shifting sea ice cover and increasing temperatures. We examine summer mesozooplankton communities of the Chukchi Sea in Alaskan and Russian waters during summers 2004, 2009, 2010 and 2012 within the scope of the RUSALCA (Russian-American Long Term Census of the Arctic) program. Community structure was highly variable between the study years, but was overall tightly correlated to water mass properties, with bottom temperature being the most significant factor influencing communities. Zooplankton biomass was dominated by the large copepod *Calanus glacialis*, while abundance was dominated by small shelf species of copepods, such as *Pseudocalanus* spp. and *Oithona similis*. The "cold" summers of 2009-2012 had nearly twice the biomass and abundance of zooplankton compared to the oceanographically "warm" summer of 2004. We discuss the implications of the inter-annual variability of planktonic communities within the Chukchi Sea, and the possible effects of longer-term climate change.

We then look at distribution and population structure of an ecologically important species complex within the zooplankton, *Pseudocalanus* spp, and evaluate the implications of a warming climate for this group of copepods. While numerically dominating the communities, *Pseudocalanus* spp. has been historically understudied at the species level due to very subtle morphological differences between the species. Our approach used a combination of microscopic identification as well as a novel species-specific PCR identification method to discriminate between the four species found in the Chukchi Sea. Our results suggest that shifting oceanographic patterns and climate warming will have unequal impact on this group of organisms, arising from species-specific life histories and tolerance to environmental conditions.

These recent observations on zooplankton are then placed into a historical context through comparison to data collected throughout the past half-century (1946-2012).

Despite significant challenges associated with the highly variable spatial coverage and methodology of the available datasets, significant trends were detected. In addition to high levels of inter-annual variability, we demonstrate significant increases in zooplankton biomass and abundance in recent years compared to historical studies, as well as shifting distribution ranges for several key species. This signal was most pronounced within the copepods, particularly *Calanus glacialis*, which appears to be indirectly benefiting from warming of the region. While summer zooplankton communities of the Chukchi Sea have been primarily Bering-Pacific in character for as long as our records exist, continuing warming and ice loss are increasing the influence of Bering-Pacific fauna within the Chukchi region.

In memory of Sofia Leontievna Byzova

Table of Contents

List of Figures

List of Tables

Acknowledgements

I would like to express my sincere gratitude to my co-supervisors Drs. Russell Hopcroft and Ksenia Kosobokova (co-authors on all three manuscripts) for their knowledge, support and continous guidance throughout my Ph.D study. I would also like to thank the rest of my dissertation committee: Dr. Rolf Gradinger, Dr. Peter Winsor and Dr. Ken Coyle for their insightful ideas, critiques and encouragement in times of doubt and struggle.

My sincere thanks also goes to Kathy Crane of NOAA whose enthusiasm was the backbone of the RUSALCA program, through which most of my work has been done. I would also like to thank Bob Pickart, Maria Pisareva and Terry Whitledge for sharing CTD and chlorophyll data, as well as the rest of the scientists and crew of RUSALCA and R/V "Professor Khromov".

My gratitude also goes to Jenn Questel (co-author on Chapter 2) for helping me master molecular techniques and providing me with COI sequences necessary to develop species-specific primers, as well as Ian Herriot and the DNA Core Lab for providing access to laboratory space and equipment and guidance with molecular techniques. I would also like to thank my co-authors on Chapter 3: Kohei Matsuno, R. John Nelson, Atsushi Yamaguchi, Lisa Eisner for providing their datasets to include in the time-series analysis. Additionally, I sincerely thank Elena Markhaseva and the Zoological Institute of the Russian Academy of Sciences for providing access to some of the older datasets on zooplankton. I also thank Arny Blanchard for help with statistical analysis, as well as the anonymous reviewers on all published manuscripts.

I thank the members of the UAF Zooplankton Lab: Cheryl Hopcroft, Imme Rutzen, Caitlin Smoot and Faith Stemmler for their help and support. I also sincerely thank my fellow (present and former) UAF graduate students, especially Jonathan and Charlotte Whitefield, Alexandra Ravelo, Kim Powell, Raphaelle Descoteaux, Dmitry Brazhnikov, Martin Schuster, Till Baumann, Jess Pretty and Ann Zinnkann for the moral support,

stimulating discussions, sleepless nights working together, and for all the great memories we have made in the last six years.

I would also like to thank my friends and family both near and far away, particularly: my parents and sisters, my running "family" in Fairbanks, Evdokiya Gasumyan and Daria Shipilina. Finally, I especially thank Andrey Bushuev for being a constant source of support, encouragement, and motivation throughout the years and a source of light when all else seemed dark.

This work was primarily funded by NOAA through the RUSALCA (Russian American-Long Term Census of the Arctic) program; additional funding was provided by the Center for Global Change Student Grant and the Robert Byrd Award.

1 Introduction

Zooplankton are critical components of the world oceans, providing an essential link from the ocean's dominant primary producers to the upper levels of the food web. Monitoring zooplankton communities provides us with critical insight on the state of the pelagic ecosystem, as well as the implications for consumers, such as fish, birds, mammals and humans. Most planktonic species are characterized by short generation times and react very rapidly to shifts in the physical environment compared to organisms in other marine and terrestrial habitats. Additionally, since plankton drift passively with currents, distinct planktonic communities and individual species can serve as useful markers of currents and water mass types. Thus, plankton are ideal first sentinels of climate change, suggesting the importance of zooplankton community surveys to document on-going climate-related ecosystem shifts (Richardson, 2008).

Although the effects of climate change are globally evident, within the Arctic Ocean climate-related changes have been among the most apparent (IPCC, 2013). As the multiyear ice pack rapidly disappears, all organisms and biological processes that directly or indirectly rely on sea ice are affected. At present, considerable debate exists as to whether these changes will lead to a more or less productive Arctic (Arrigo and van Dijken, 2015; Lee et al., 2012). The Pacific Arctic Region (PAR) has been experiencing dramatic rates of change in recent decades, even when compared to adjacent regions of the Arctic Ocean. The mean average temperature of water flowing through the Bering Strait region has increased 1°C in just the past decade (Luchin and Panteleev, 2014; Woodgate et al., 2010) and the sea ice extent is at historical lows (Wood et al., 2015). As the seasonal ice cover continues to contract and weather patterns shift, a "new normal" climate may be emerging for the Pacific Arctic region (Wood et al., 2015). The complex oceanography of the region, which shapes the biological communities, may also be altered. Monitoring planktonic communities of this region is essential to understand and quantify the changes that are occurring.

This dissertation focuses on zooplankton communities within the Chukchi Sea, which is an important transition zone between the Pacific and the Arctic Oceans. Although likely similar to other Arctic shelf seas during winter, during the summer months the Chukchi Sea becomes a flow-through system, composed of a complex mixture of northward flowing water masses from the Pacific Ocean through the Bering Strait. These water masses bring in vast quantities of fresh water, nutrients and biomass into the Chukchi Sea, which may be deposited on the shelf or even carried out to the Arctic Basin (Grebmeier and Harvey, 2006). During the ice-free season, production on the Chukchi Sea shelf can be exceedingly high, and surpass that of all other Arctic shelf seas (Grebmeier and Maslowski, 2014; Kosobokova and Pertsova, 2012). For these reasons, the Chukchi Sea plays a critical role in the overall heat, energy and biomass budget of the Arctic Ocean.

Relatively little research has been done historically within the Chukchi Sea compared to more accessible regions of the Arctic, due to its remoteness and extensive ice cover, which prevented access by all but large ice-breaking vessels. Nevertheless, a significant number of isolated studies have been done within Chukchi Sea, dating back to the beginning of the last century. Zooplankton researchers from the Soviet Union conducted these earliest studies, and despite being largely quantitative in nature, they noted the strong relationships between zooplankton distribution and oceanography (i.e. Virketis, 1952). Unfortunately, very few of these Soviet studies ended up published in western literature, and many were never made publically available. In the second half of the century, a number of sampling programs emerged in the US, shedding light on the distribution and composition of zooplankton in the US sector of the Chukchi Sea (Johnson, 1953; Wing, 1974). In the 1980's, the Inner Shelf Transfer and Recycling (ISHTAR) Program was launched. This program spanned a number of consecutive years and covered a broad area within the Southern Chukchi, allowing for the first estimates of inter-annual variability and biomass contribution of the region (Springer et al., 1989) . However, the majority of these studies remained isolated in their spatial coverage and methodology, which prevents a broad synthesis of the biology of the region. Additionally, with the exceptions of the 1970 “Mayak” expedition (Pavshtiks, 1984) and the 1988 joint US-USSR Bering

& Chukchi Seas expedition (BERPAC) all of the historical studies have been limited to either one side the political border. As a result, very little contemporary information exists from the Russian side of the Chukchi Sea.

In recent years, efforts within the US sector of the Chukchi Sea region have intensified, driven in part by prospects of oil and gas exploration, as well as increasing interest in effects of climate change. The Russian-American Long Term Census of the Arctic (RUSALCA) program, launched in 2004, was the first modern attempt to address the knowledge gap resulting from studying just one side of the geo-political border and to establish a long-term interdisciplinary monitoring program in the entire central/western Chukchi Sea region. The initial expedition in August 2004 covered a broad region from the Bering Strait to Wrangel Island, and provided a much-needed baseline study, describing the distribution of zooplankton communities over both political sides of the Chukchi Sea during that year (Hopcroft et al., 2010).

Chapter 2 expanded on this initial effort by examining zooplankton communities during three additional RUSALCA sampling years (2009, 2010, 2012). The physical oceanography and distribution of water masses in the region was significantly different during each of the study years; additionally, the summer of 2004 was oceanographically much warmer than the subsequent cruises. This provided the opportunity to assess how variations in climate and oceanography are reflected in the zooplankton communities within the Chukchi Sea. Zooplankton data obtained during the 4 RUSALCA years was used to quantitatively describe the distinct planktonic communities within the Chukchi Sea. Their connections to water mass distribution and physical parameters were also illuminated, and an assessment of inter-annual variability observed in this region and the possible implications of longer-term climate change was provided. This manuscript was published in *Polar Biology* journal (Ershova et al., 2015a) and co-authored by Russell Hopcroft and Ksenia Kosobokova. While E.E. is the primary author on this manuscript in all regards, R.H. and K.K. designed the sampling program in 2004, as well as collected and processed the 2004 data and provided insightful comments and edits during preparation of the manuscript.

The biology of individual key species is often overlooked in ecosystem research, however is essential for understanding the large-scale picture. *Chapter 3* focused closely one of the more important genera within the Chukchi zooplankton communities, the copepod genus *Pseudocalanus*. Four species of this genus are found in the Pacific Arctic (Frost, 1989; Questel et al., 2016); however, despite their essential role in the ecosystem, very little research has been done on the species-specific aspects of their biology and ecology, with most studies grouping them as *Pseudocalanus* spp. Much of the confusion surrounding *Pseudocalanus* results from the morphological ambiguity of the species, with differences between species being very indistinct, particularly at juvenile stages. I developed a molecular identification method (species-specific PCR), which allowed for relatively rapid and inexpensive routine identification of the four species that we observe in the region. This method was then used to describe the species-specific distribution and relative contribution of these species in the Chukchi Sea during three RUSALCA years. Additionally, to assess their relative contribution to secondary production, as well as reproductive potential in the Arctic environment, we examined the reproductive rates of the co-occurring species, both in *in-situ* (Hopcroft and Kosobokova, 2010) and in laboratory controlled environments. Incubating reproducing females at different temperatures allowed assessment of their relative responses to the range of the temperatures that we observe in this region, as well as making inferences about their relative success under climate change scenarios. This chapter has been submitted for publication to the *Journal of Plankton Research.* It was co-authored by Jennifer Questel, Russell Hopcroft and Ksenia Kosobokova. E.E. is the primary author in all regards. J.Q. contributed by providing her sequences for creation of the species-specific primers and helping to design the PCR protocol. R.H. and K.K. contributed by designing and carrying out the *in-situ* egg production experiments in 2004, as well as providing comments on revising the text and figures during manuscript preparation.

Moving beyond the scope of the RUSALCA program, in *Chapter 4* I used historical data on zooplankton to describe long-term patterns and trends in the Chukchi Sea, associated with changes in climate that we observed in the region. This effort included incorporating all available historical datasets on zooplankton collected within the Chukchi Sea, dating as far back as the 1940's, as well as a number of modern sampling efforts, including the four RUSALCA expeditions described in *Chapter 2*. Many of the older datasets analyzed have not been publically available prior to this work, or were buried in Russian literature. This synthesis was a challenging endeavor due to the irregular nature of the data: inconsistent methods of collections and processing, variable spatial and seasonal coverage and very different taxonomic resolution. "Standardizing" the data inevitably led to the loss of much resolution. However, despite these challenges, and the inherent faultiness of such a patchy dataset, I was able to show consistent patterns of change within the Chukchi Sea zooplankton communities over the last seven decades. This manuscript has been published in *Oceanography* journal as part of the special synthesis issue on RUSALCA (Ershova et al., 2015b) and co-authored by Russell Hopcroft, Ksenia Kosobokova, Kohei Matsuno, R. John Nelson, Atsushi Yamaguchi, and Lisa Eisner. E.E. was the primary author; K.N. and R.H. contributed by providing guidance and constructive criticism during the writing process; K.M., R.J.N., A.Y. and L.E. contributed by providing their datasets to use in the analysis.

The final concluding section of the dissertation summarizes the main findings from the three preceding chapters, as well some overarching conclusions. The limitations of this project are considered and future directions of research are suggested to further expand our knowledge of the marine pelagic ecosystems of this region.

1.1 References

Arrigo, K. R. and van Dijken, G. L. (2015). Continued increases in Arctic Ocean primary production. *Prog. Oceanogr.*, 136:60–70.

Ershova, E. A., Hopcroft, R. R., and Kosobokova, K. (2015a). Inter-annual variability of summer mesozooplankton communities of the western Chukchi Sea: 2004-2012. *Polar Biol.*, 38(9):1461–1481.

Ershova, E. A., Hopcroft, R. R., Kosobokova, K., Matsuno, K., Nelson, R. J., Yamaguchi, A., and Eisner, L. B. (2015b). Long-Term Changes in Summer Zooplankton Communities of the Western Chukchi Sea, 1945-2012. *Oceanography*, 28(3):100–115.

Frost, B. (1989). A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can. J. Zool.*, 67(3):525–551.

Grebmeier, J. M. and Harvey, R. H. (2006). The Western Arctic Shelf-Basin Interactions (SBI) project: An overview. *Deep Sea Res. II*, 52(24-26):3109–3115.

Grebmeier, M. J. and Maslowski, W., editors (2014). *The Pacific Arctic Region - Ecosystem Status and Trends in a Rapidly Changing Environment.* Springer.

Hopcroft, R. R. and Kosobokova, K. (2010). Distribution and egg production of *Pseudocalanus* species in the Chukchi Sea. *Deep Sea Res. II*, 57(1):49–56.

Hopcroft, R. R., Kosobokova, K., and Pinchuk, A. I. (2010). Zooplankton community patterns in the Chukchi Sea during summer 2004. *Deep Sea Res. II*, 57(1):27–39.

IPCC (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Johnson, M. W. (1953). Studies on plankton of the Bering and Chukchi seas and adjacent area. *Proceedings of the seventh Pacific Science Congress of the Pacific Science Association; held at Auckland and Christchurch, New Zealand*, pages 580–500.

Kosobokova, K. and Pertsova, N. M. (2012). Zooplankton Belogo morja: struktura, dinamika i ekologija soobshestv. In Lisitsyn, A. P., editor, *Sistema Belogo Morja: Prirodnaja Sreda Vodosbora Belogo Morja*, pages 640–675. Nauchnyj mir, Moscow.

Lee, S. H., Joo, H. M., Liu, Z., Chen, J., and He, J. (2012). Phytoplankton productivity in newly opened waters of the Western Arctic Ocean. *Deep Sea Res. II*, 81:18–27.

Luchin, V. and Panteleev, G. (2014). Thermal regimes in the Chukchi Sea from 1941 to 2008. *Deep Sea Res. II*, 109:14–26.

Pavshtiks, E. A. (1984). Zooplankton of the Chukchi Sea as indices of water origins. *Trudy Arkticheskogo i Antarkticheskogo Nauchno-Issledovatel'skogo Instituta*, 368:140–153.

Questel, J., Blanco-Bercial, L., Hopcroft, R. R., and Bucklin, A. (2016). Phylogeography and connectivity of the *Pseudocalanus* (Copepoda: Calanoida) species complex in the eastern North Pacific and the Pacific Arctic Region. *J. Plankton Res.*, 38(3):610–623.

Richardson, A. (2008). In hot water: zooplankton and climate change. *ICES J. Mar. Sci.*, 65(3):279–295.

Springer, A., McRoy, C., and Turco, K. (1989). The paradox of pelagic food webs in the northern Bering Sea - II. Zooplankton communities. *Cont. Shelf Res.*, 9(4):359–386.

Virketis, M. (1952). Zooplankton of the Chukchi Sea and Bering Strait . In Brodsky, K. A., editor, *The far North-east of the USSR. 2. Fauna and Flora of the Chukchi Sea*, pages 323–335. Izdatelstvo Akademy Nauk SSSR, Moscow.

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, Seattle.

Wood, K. R., Bond, N. A., Danielson, S. L., Overland, J. E., Salo, S. A., Stabeno, P., and Whitefield, J. (2015). A decade of environmental change in the Pacific Arctic region. *Prog. Oceanogr.*, 136:12–31.

Woodgate, R. A., Weingartner, T. J., and Lindsay, R. (2010). The 2007 Bering Strait oceanic heat flux and anomalous Arctic sea-ice retreat. *Geophys. Res. Lett.*, 37(1):L01602.

2 Inter-annual variability of summer mesozooplankton communities of the western Chukchi Sea: 2004 – 2012[1]

2.1 Abstract

The Chukchi Sea shelf is a complex transition zone between the Pacific and Arctic Oceans, on which climate variation may have a profound impact. We examined summer zooplankton community structure of the western Chukchi Sea in Alaskan and Russian waters during 2004, 2009, 2010 and 2012 within the ongoing Russian-American Long-term Census of the Arctic program. The four study years were very different both in water mass properties and in zooplankton community structure. A "warm" year with an early ice retreat and highest water temperatures occurred in 2004, whereas the years 2009–2012 were "cold" with a later-than-average ice retreat and colder average water temperatures during the sampling period. The extent and prominence of different water masses (Bering Sea–Anadyr Water, Alaska Coastal Current, Siberian Coastal Current, Resident Chukchi Water) within the Chukchi Sea varied between years, which was in turn reflected within the zooplankton communities. Community structure was highly correlated with water mass properties, with bottom temperature being the most significant factor influencing communities. The "cold" summers of 2009–2012 had nearly twice the biomass and abundance of zooplankton compared with the "warm" summer of 2004. Biomass was dominated by the large copepod *Calanus glacialis* believed to originate from the Bering Sea, and abundance was dominated by small shelf species of copepods, such as *Pseudocalanus* spp., *Acartia* spp. and *Oithona similis*. We discuss the implications of the inter-annual variability of planktonic communities within the Chukchi Sea and the possible effects of longer-term climate change.

---

[1] Published as E. A. Ershova, R. R. Hopcroft, K. N. Kosobokova (2015) Inter-annual variability of summer mesozooplankton communities of the western Chukchi Sea: 2004–2012. *Polar Biology* 38(9):1461-1481. DOI:10.1007/s00300-015-1709-9

2.2 Introduction

The Chukchi Sea is a marginal Arctic sea that serves as the transitional zone between the Pacific and Arctic Oceans. While sharing many common features with other Arctic shelf seas, it differs by being an inflow system, with most of the water masses arriving directly from the Pacific Ocean via the Bering Sea (Carmack and Wassmann, 2006). Unlike its Atlantic equivalent, the Barents Sea, it has a wide, shallow (<50 m deep) shelf with a very gentle slope that stretches all the way to the Arctic shelf break, which in combination with other factors creates a very different ecosystem. Also, unlike the Barents Sea, where incoming warm Atlantic water discourages extensive ice formation, the Chukchi region remains completely ice-covered during the winter, while waters entering through Bering Strait have near-freezing temperatures (Hunt et al., 2013).

The amount of Pacific water entering the Chukchi Sea annually is estimated at ~1 – 1.2 Sv (Woodgate et al., 2012) with the strongest flow occurring during the summer months (Coachman et al., 1975; Woodgate et al., 2012). Several distinct water masses compose the Chukchi Seawater during the summer, named for the currents that carry them. The Alaska Coastal Current (Alaska Coastal Water, ACW) brings in seasonally warmer (up to 12°C), reduced-salinity (< 31) coastal water from the southeastern Bering Sea shelf along the coast of Alaska (Springer et al., 1984). Anadyr Water (AW), which originates on the continental slope of the Bering Sea (Coachman et al., 1975), is a flow of nutrient-rich, cold (0 – 10°C) and saline (32.3 – 33.3) oceanic water. A water type with intermediate properties that originates on the Bering Sea shelf (BSW) separates the two water masses; it mixes with AW to form Bering Shelf – Anadyr Water (BSAW) (Coachman et al., 1975). Together, these water masses carry with them large quantities of nutrients, phytoplankton and zooplankton and make the Chukchi Sea one of the most productive regions of the Arctic (Grebmeier and Maslowski, 2014). The annual primary production of the Chukchi region is estimated to be ~42 Tg C year^{-1}, or almost 15% of all primary production in the Arctic Ocean (Sakshaug, 2004).

The significant reduction in sea ice thickness, extent and timing of coverage that has been recorded across the entire Arctic in recent decades has been most pronounced in its Pacific sector (IPCC, 2013). The Chukchi Sea pelagic ecosystem, which is finely tuned to the seasonal ice formation and retreat, is now experiencing a dramatic change with shifting sea ice cover. Models and some observations suggest an average increase in primary production, mainly driven by the increased area of open water, across the entire Arctic with greatest change in the Chukchi/Bering Sea area (Arrigo and van Dijken, 2011). Alternately, others believe that nutrient limitation will ultimately restrain primary productivity in the Arctic, with little or no increase in annual production (Lee et al., 2012). Some studies suggest that the Arctic planktonic communities are nearing a threshold favoring a regime shift (a.k.a. tipping point) (Duarte et al., 2012). Shifts from diatom-dominated to picoplankton-dominated communities, driven by ocean warming and sea ice reduction, have already been recorded for several regions in the central Arctic Ocean, and some studies suggest that such a regime shift may occur within the foreseeable future (Arrigo and van Dijken, 2011; Li et al., 2009; Tremblay et al., 2012). A protracted ice-free summer period within the Chukchi region could potentially benefit advected Pacific zooplankton species, permitting them to play a larger role in the summer planktonic communities and facilitate a northward shift of their ranges, likely at the expense of “resident” Arctic species.

A number of studies focusing on zooplankton communities of the Chukchi region have been done sporadically beginning with the middle of the twentieth century (for a review, see Hopcroft et al., 2010). These efforts have recently intensified, fueled by interest in both climate change and the extraction of oil and gas reserves (e.g., Questel et al., 2013). Notably, most historical and contemporary studies have focused on smaller-scale areas and have been spatially limited to either Russian or US waters, but for several decades, sampling has been confined to US waters (e.g., Eisner et al., 2012; Lane et al., 2008; Matsuno et al., 2011; Springer et al., 1989). The Russian-American Long-Term Census of the Arctic (RUSALCA) program, established in 2004, is a unique attempt to investigate a much wider territory — from the Bering Strait to north of Wrangel Island on both sides of the political border — over a long-term time period (Hopcroft et al., 2010).

In this study, we describe the summer zooplankton communities of the western Chukchi Sea, illuminating the poorly described Russian section. We examine the inter-annual variability within the plankton communities, which are strongly shaped by physical drivers (e.g., Eisner et al., 2012; Hopcroft et al., 2010). This effort contributes solid snapshots for monitoring climate-related change within the region, placing them into perspective with past, ongoing and future surveys. Such observations will enable us to better discriminate systematic environmental change from the natural year-to-year variability.

2.3 Methods

Three 3-week interdisciplinary cruises with emphasis on ecosystem components have been carried out within the framework of the RUSALCA program: August 4–25, 2004, September 4–27, 2009 and September 2–24, 2012. Plankton was also collected on a shorter oceanographic expedition August 1–11 2010 (Fig. 2.1). The initial sampling area in 2004 included 34 stations that sampled the Chukchi Sea on both sides of the US–Russian border from the Bering Strait northward to Herald Canyon (Hopcroft et al., 2010). The expeditions in 2009–2012 repeated sampling of the transects established in 2004. During 2009, many additional sections in the East Siberian Sea and surrounding Wrangel Island were also sampled, for a total of 60 stations. In 2012, due to poor weather conditions and sea ice, only 25 stations were sampled. In 2010, only the two southern study lines were occupied, plus an additional short transect in the East Siberian Sea, for a total of 16 stations.

Zooplankton samples were collected using vertically hauled 150 μm double-ring nets of 60 cm mouth diameters, sampling entire water column to within 3–5 meters of the ocean floor. While we recognize that the system often consists of different water masses overlaying each other, collecting stratified samples was not logistically possible. Total volume of water through the nets was measured using General Oceanics or Ocean

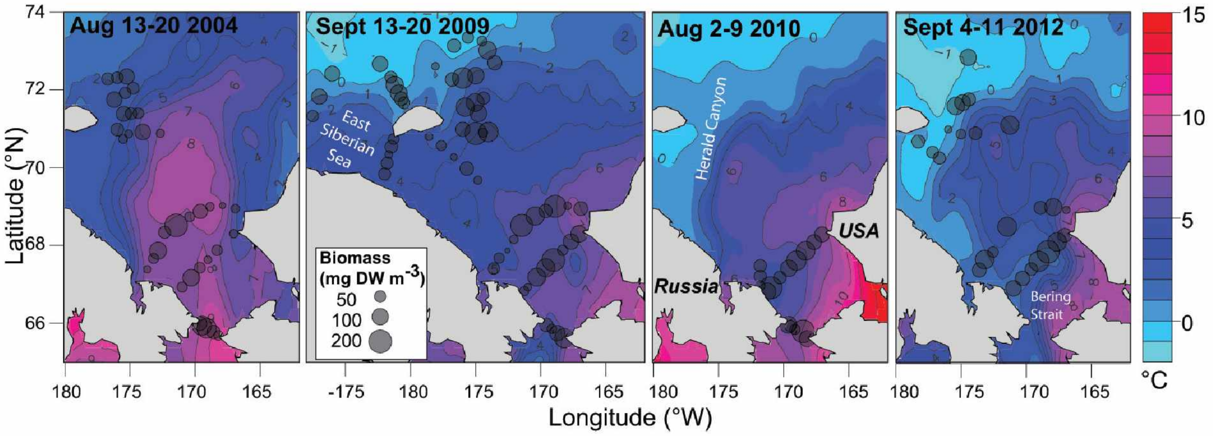

Figure 2.1: Locations of sampling stations and holozooplankton biomass (estimated from the 150-μm vertical ring net) overlain on sea surface temperatures (SST, °C) averaged over a mid-cruise 7-day interval

Test flow meters, which were positioned at the mouth of each net and rigged not to spin during descent. Additionally, larger and rarer taxa were collected in 2009 and 2012 with obliquely towed flow-metered 505 μm Bongo nets, sampling at 2 knots (1 m s^{-1}) to a depth near the bottom. Samples were collected during both the day and night. Upon retrieval, one of the samples from each net was preserved in 95 % molecular-grade ethanol, while the other 150-μm sample was preserved in 10 % formalin, and the 505-μm sample was live-sorted immediately for fragile gelatinous organisms on a light table prior to formalin preservation.

Fresh gelatinous specimens were keyed to species and measured, and then ctenophores were discarded, as they are known to quickly disintegrate in preservatives. The large (5 cm) specimens were weighed using a scale; the weight of the smaller individuals was predicted from taxa-specific weight–length relationships of the same or similar species (Table 2.1). To reduce the inflated importance of cnidarians and ctenophores resulting from their low carbon content, we normalized their biomass through division by 4 (Kosobokova and Hopcroft, 2010), in order to make their dry-weight (DW) more comparable with that of crustacean zooplankton (i.e., typically carbon is 10 % of dry-weight in gelatinous species vs. 40 % in crustaceans), while retaining the units of biomass most common in zooplankton literature (Båmstedt, 1986; Larson, 1986).

Table 2.1: Length–weight relationship of gelatinous zooplankton species; *DW* dry-weight, *TL* total length, *BD* bell diameter

Species	Regression equation	Units	Source
Bolinopsis infundibulum	$DW = 0.062TL^{2.34}$	mm mg	Kasuya et al. (2000)
Mertensia ovum	$DW = 0.104TL^{2.12}$	mm mg	Percy (1989)
Beroe ovata	$DW = 0.018TL^{2.69}$	mm mg	Kremer et al. (1986)
Cyanea capillata	$DW = 0.006BD^{2.721}$	cm g	Bailey et al. (1995)
Aeginura grimaldii (morphologically similar to *Aeginopsis laurentii*)	$DW = 5.04BD^{1.12}$	mm mg	Bailey et al. (1995)
Hydrozoan jellyfish	$DW = 0.00194TL^{3.05}$	mm mg	Matthews and Hestad (1977)

At each station, oceanographic data were collected with a Seabird 911 + CTD equipped with an oxygen sensor, transmissometer and fluorometer (Pickart et al., 2010; Pisareva et al., 2015), with all data binned into 1-m intervals during post-processing. Chlorophyll samples were collected by Niskin bottles on the CTD rosette every 5 m from the surface to bottom, filtered at low pressure onto GF/F filters and analyzed fluorometrically (Lee et al., 2007).

The formalin-preserved samples were processed in the laboratory to determine community composition, abundance and biomass. The entire samples were scanned for large and uncommon species, which were identified and measured. The remainder of the sample was then split using a Folsom splitter such that there were about 100 individuals of the most common species in the terminal split. Increasingly larger splits were scanned for rarer taxa; a minimum of 400 individuals were examined from each sample, with 500–600 typically identified. All organisms were measured using a computer-assisted measurement system (ZoopBiom software, Roff and Hopcroft, 1986), and the dry-weight (DW) of each specimen was predicted from a length–weight regression relationship known for the same species, or a morphologically similar organism (Hopcroft et al., 2010). Copepods were staged and keyed to species; juveniles within some genera (such as *Pseudocalanus* spp. and *Acartia* spp.), which are morphologically undistinguishable, were grouped together.

The species complex *Calanus glacialis/marshallae*, which is also undistinguishable morphologically, was considered to be *C. glacialis* within our region (Nelson et al., 2009). Meroplankton was grouped to the macrotaxa or to the family level (in the case of shrimp larvae). Copepod nauplii were counted only in 2009, 2010 and 2012. Here and hereafter, the copepods *C. glacialis*, *Neocalanus* spp., *Metridia* spp. and *Eucalanus bungii* are referred to as "large copepods"; all other copepods are considered "small copepods". Only the 150-μm net samples are discussed in detail in this paper; however, the 505-μm net samples were included in the overall species lists with biomass values from the 505-μm nets only presented for the live-sorted gelatinous organisms.

Water masses were separated by cluster analysis using Euclidean distances on the normalized temperature and salinity values. Surface (averaged for 0–10 m), bottom (averaged for 10 m above sea floor), and midwater layers (10–10 m above sea floor) at each station were examined separately to partially account for the complex-stratified oceanography of the region and to determine where multiple water types may be present at a single location. The resulting groups (surface and bottom only) were plotted on a T–S diagram for quantitative separation and on a map of the study area. Increasing the surface and bottom depth intervals to 15–20 m thickness resulted in an identical separation of clusters, but slightly lower correlations to biological data. The midwater layer was not included in analysis because it was highly auto-correlated to the bottom and surface layers. High-resolution satellite SST data were extracted from the NOAA website at http://www.esrl.noaa.gov/psd/. The R packages "maps", "mapplots" and "ggplot2" were used to create figures and plots (Becker and Wilks, 2013; Gerritsen, 2013; Wickham, 2009).

Differences in total abundance and biomass, as well as abundance and biomass of taxonomic groups and individual species between years, were examined using ANOVA with station location as a blocking factor. Significant interactions between years were established using the Tukey's HSD test. Due to different spatial coverage during the 4 years, only the southern Chukchi domain (three southern transects) was included in this analysis. Full domain community patterns were explored using the "vegan" package in R (Oksanen et al., 2015). Both the abundance and biomass datasets were examined independently for the stations pooled from all years. The datasets were power-transformed (fourth root), and the Bray–Curtis similarity index was calculated for all stations for each year. All taxonomic categories that contributed at least 3 % after transformation to any sample were included in the analysis; categories that were employed only during some of the years (e.g., copepod nauplii, crab megalopa) were excluded from analysis. Hierarchical cluster analysis using average linkage was carried out, and qualitative separation of groups was established by overall similarity (30–35 %), the SIMPROF routine (significance at $\alpha = 0.05$) (Clarke and Gorley, 2005) and subjective biological interpretation. These resulting groups were super-imposed on 2D and 3D plots of nonparametric multidimensional-scaled (nMDS) datasets and spatial plots of the study area. The correspondence between zooplankton community patterns and physical data were explored using the BIOENV routine (Clarke and Ainsworth, 1993), which establishes correlations between these two data matrices. The significance of these correlations was established using Mantel's test of associations (Mantel, 1967).

2.4 Results

2.4.1 Water masses

August 2004 was the warmest sampling period, with an average sea surface temperature (SST) across the sampled domain of 6.3 °C and with water as warm as 8 °C entering the Herald Canyon region (Fig. 2.1). The coldest temperatures were observed in September 2012, averaging only 3.4 °C, nearly three degrees colder than 2004. The warm waters of the Alaska Coastal Current (ACW), and the resultant temperature gradient across the shelf, were most pronounced in 2010 and 2012, while in 2009, the surface water temperatures were the most uniform.

Cluster analysis of surface and bottom water properties (Temperature and Salinity) within each year splits them into 11 distinct groups; these were subsequently grouped

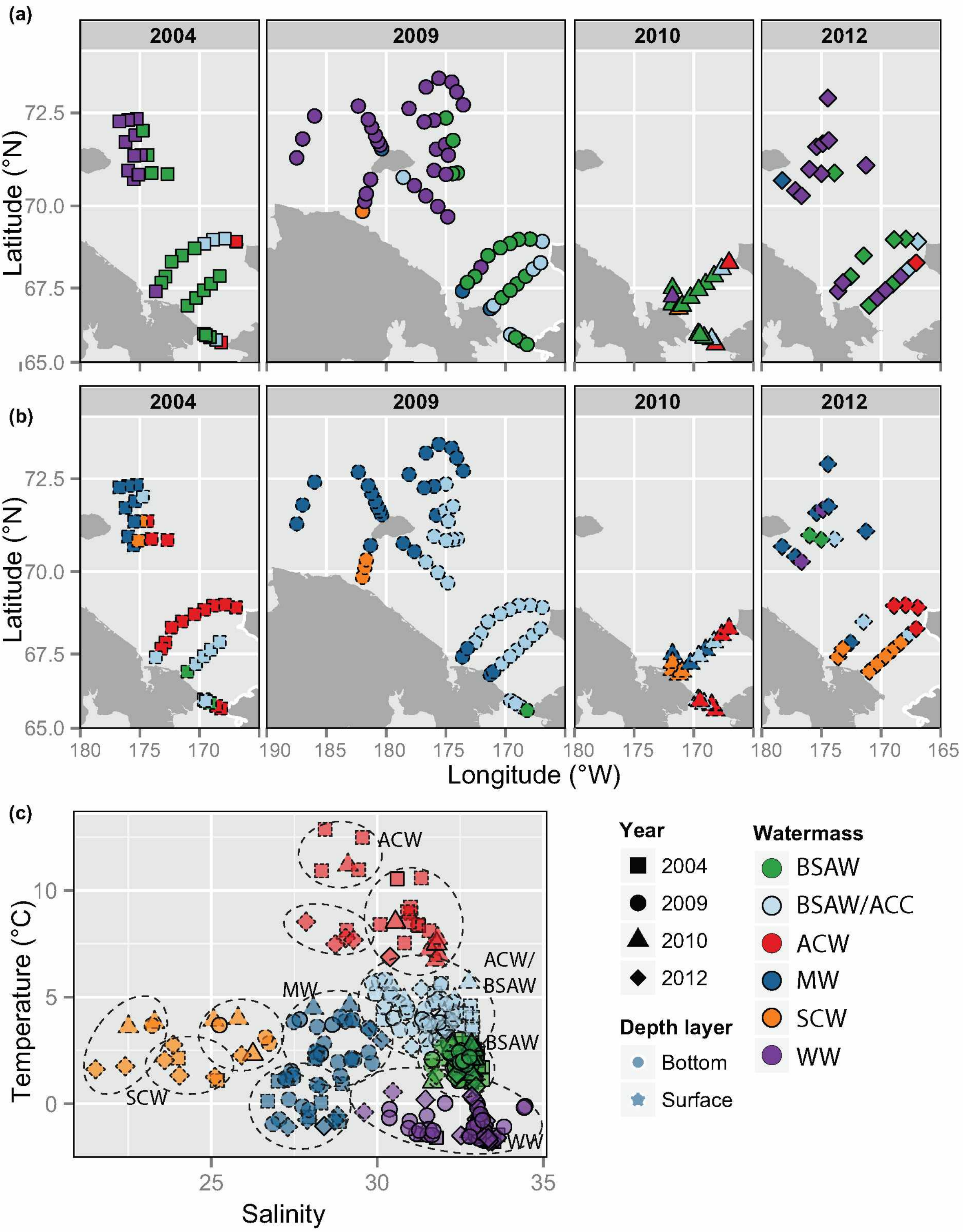

Figure 2.2: Cluster analysis of depth-integrated temperature/ salinity observations in the Chukchi Sea, (a) bottom waters, (b) surface waters, (c) temperature– salinity plot. Dashed line boundaries indicate individual clusters; each cluster has been assigned a water mass type.Water mass abbreviations: BSAW, Bering Sea–Anadyr Water; ACW, Alaska Coastal Water; SCW, Siberian Coastal Water; MW, melt water; WW, winter water

into six water types, as recognized by the literature characterizations (i.e. Eisner et al., 2012) (Fig. 2.2). While this approach is an oversimplification, particularly within the surface waters, which are influenced by melting, mixing and radiative forcing, it provides us with a broad-scale picture of the physical environment within our study. The fresh and warm Alaska Coastal Water (ACW, red) was the most recognizable assemblage, which includes three cluster groups: extremely warm low-salinity water, present only in 2004 and at one station in 2010; colder low-salinity water present only in 2012 (and one station in 2004, which was most likely an outlier); and colder higher-salinity water visible in all years except 2009. ACW waters were most pronounced in 2004, when they were found in surface waters across the entire offshore section of the southern Chukchi, and even as far north as eastern Herald Canyon. The higher-salinity and colder Bering Sea–Anadyr Water (BSAW, green) was present in bottom waters throughout the southern Chukchi and as far north as 72 °N in Herald Canyon in 2004 and 2009. An intermediate water type, most likely a mixture of ACW and BSAW (BSAW/ACW, light blue) (Pisareva et al., 2015), was found within the surface waters of the southern Chukchi during all years, particularly in 2009, when it reached far north into the Herald Canyon. Resident Chukchi Winter Water (WW, purple) was the dominating bottom water type in western Herald Canyon and was typically overlain by BSW/BSAW or lower-salinity melt water (dark blue). The surface waters of the northernmost stations (in 2009) and the stations surrounding Wrangel Island (in 2004 and 2012) also contained a very cold, low-salinity water type most likely resulting from ice melt (melt water, dark blue). The very low-salinity (<27), cold waters of the Siberian Coastal current (SCW, orange) were visible along the Siberian coast in 2009 and 2010 and farther offshore in 2012.

2.4.2 Zooplankton taxa

Total holozooplankton abundance estimated by the 150-μm nets varied across a wide range: from 400 individuals (ind) m^{-3} to 25,000 ind m^{-3}. Abundance averaged ∼3000 ± 2500 ind m^{-3} in 2004 and 2012; in 2009 and 2010, it was almost three times higher, averaging ∼ 8000 ± 6500 ind m^{-3}, mainly due to the extremely high abundance of small

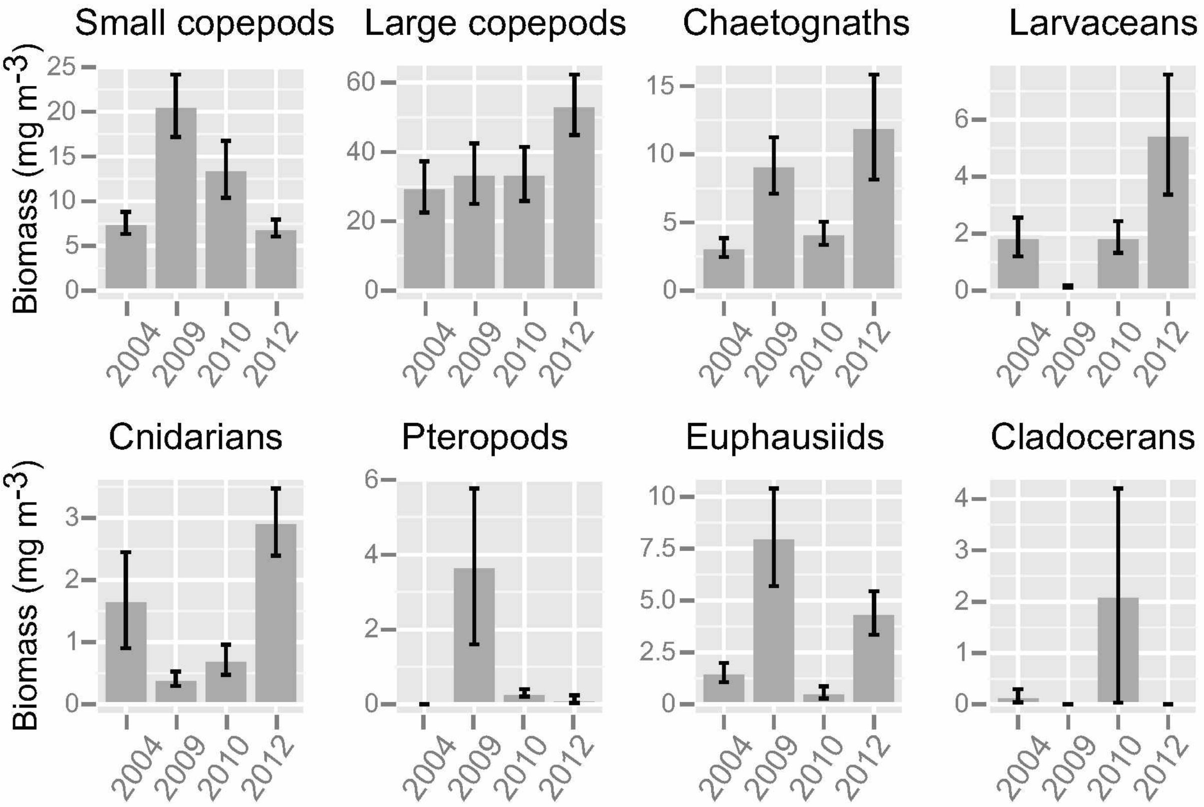

Figure 2.3: Inter-annual variability in mean biomass (mg DW m^{-3}) of major zooplankton groups across the Southern Chukchi Sea (southern 3 sampling sections), black bars - standard error

copepods during those 2 years (copepod nauplii are excluded from all counts). The total holozooplankton biomass varied by almost two orders of magnitude across the studied domain during the four study years, with the minimum observation being around 8 mg dry-weight (DW) m^{-3} and the maximum 360 mg DW m^{-3} (Fig. 2.1). The lowest biomass (averaged across the entire domain) was observed in 2004, averaging 44 ± 31 mg DW m^{-3} (here and henceforth values are mean ± SD); biomass was somewhat higher in 2010, averaging 63 ± 35 mg DW m^{-3}. During 2009 and 2012 years, the observed biomass was relatively similar, averaging ~75 ± 40 mg DW m^{-3}. Across the southern Chukchi domain, which was common for all four cruises, difference in overall biomass was significant, with lower values observed in 2004 than in 2009 and 2012 (ANOVA, $p < 0.05$, Tukey's HSD); abundance was significantly higher in 2009 than in 2004 and 2012 (Table 2.3).

A total of 82 unique taxa from 13 taxonomic groups were encountered during the four study years (Table 2.2). The majority of these were advected subarctic Pacific

Table 2.2: Species encountered during RUSALCA 2004–2012 cruises in the Chukchi Sea; Species marked in bold were estimated using the 505-μm net; *obs*, species were observed during the cruise, but not noted (or counted) within the samples; "–", species not observed; "+" < 0.01; NA, no data available; ^{a}, Biomass standardized through division by 4; ^{b}, Arctic species

	Abundance (ind m-3)				Biomass (mg DW m-3)			
	2004	2009	2010	2012	2004	2009	2010	2012
Amphipoda								
Gammaridae	0.05	0.06	+	0.4	0.14	0.11	+	0.13
Apherusa glacialis^b	–	obs	–	0.02	–	obs	–	0.06
Monoculodes sp.	–	obs	–	obs	–	obs	–	obs
Hyperiidae	–	0.1	–	0.01	–	+	–	+
Hyperoche sp.	–	0.14	+	0.03	–	0.2	+	0.05
Themisto libellula	0.03	0.05	0.2	0.05	+	1.4	4.8	0.48
T. pacifica/abyssorum	0.04	0.01	0.01	0.03	0.07	0.02	+	0.07
Hyperia galba	–	–	–	+	–	–	–	+
Scina borealis	–	–	–	+	–	–	–	+
Sum	0.12	0.36	0.21	0.14	0.2	1.73	4.81	0.66
Appendicularia								
Fritillaria borealis	85.09	308.5	1470.3	2.61	0.01	0.03	0.11	+
Oikopleura vanhoeffeni	256.6	27.95	375.1	63.64	4.12	0.14	1.76	5.34
Sum	341.69	336.45	1845.4	66.26	4.13	0.17	1.88	5.34
Chaetognatha								
Eukrohnia hamata	0.43	+	8.68	–	0.34	0.05	0.23	–
Parasagitta elegans	5.69	109.16	40.52	23.72	4.77	17.15	3.97	11.22
Sum	6.12	109.17	49.19	23.72	5.11	17.2	4.2	11.22
Cladocera								
Evadne nordmanni	11.35	–	196.85	–	0.04	–	1.55	–
Podon leuckarti	14.51	–	103.85	0.25	0.06	–	0.57	+
Sum	25.85	–	300.7	0.25	0.1	–	2.12	+
Copepoda								
Acartia hudsonica	2.52	14.19	7.28	11.26	0.01	0.05	0.04	0.04
Acartia longiremis	199.43	67.12	507.2	101.67	0.41	0.14	0.72	0.16
Acartia tumida	+	0.36	–	–	+	+	–	–
Calanus glacialis	35.67	144.72	78.67	263.73	6.7	24.55	14.14	35.03
Calanus hyperboreus^b	–	0.08	–	–	–	0.06	–	–
Centropages abdominalis	190.23	78.24	135.91	64.31	0.5	0.48	0.53	0.27
Epilabidocera amphitrites	–	0.01	0.2	0.02	–	+	0.03	+
Chiridius obtusifrons	–	0.04	–	+	–	+	–	+
Aetideidae	–	0.01	0.19	+	–	+	+	+
Eucalanus bungii	14.62	7.8	146.64	3.02	1.33	0.43	3.37	0.3
Paraeuchaeta glacialis^b	+	+	–	+	+	0.01	–	+
Eurytemora herdmani	5.69	16.95	1.09	22.26	0.03	0.1	0.01	0.09
E. pacifica	+	0.07	–	–	+	+	–	–
Jaschnovia brevis^b	–	0.05	–	0.32	–	+	–	0.01
J. tolli^b	0.32	–	–	–	0.01	–	–	–
Mesocalanus tenuicornis	+	–	–	–	+	–	–	–
Metridia longa^b	–	1.36	–	–	–	0.28	–	–
M. pacifica	39.75	71.6	367.48	11.29	1.41	1.81	10.01	0.15
Microcalanus pygmaeus	8.18	2.17	32.09	1.88	0.01	+	0.05	+
Neocalanus cristatus	0.94	0.06	0.27	0.75	6.38	0.36	1.75	5.19
N. flemingeri	7.09	2.4	7.84	2.59	4.5	0.28	4.21	1.46
N. plumchrus	2.1	0.29	0.23	0.11	1.42	0.22	0.14	0.07
Pseudocalanus acuspes^b	38.55	78.72	34.5	31.79	0.51	0.77	0.41	0.34

Table 2.2 – **continued from previous page**

	Abundance (ind m-3)				Biomass (mg DW m-3)			
	2004	2009	2010	2012	2004	2009	2010	2012
P. mimus	–	3.24	26.22	1.72	–	0.03	0.25	0.01
P. minutus[b]	71.81	8.21	46.33	9.8	0.89	0.11	0.84	0.17
P. newmani	92.8	141.23	41.66	22.59	0.55	0.72	0.23	0.12
Pseudocalanus spp.	1606.62	4150.74	1739.67	1655.06	4.51	9.45	4.61	4.3
Scolecitrichidae	–	0.3	–	0.05	–	0.01	–	+
Spinocalanus sp.	–	0.03	–	–	–	+	–	–
Tortanus discaudatus	–	0.06	–	0.02	–	+	–	+
Harpacticus sp.	–	7.24	6.24	0.03	–	0.03	0.02	+
Microsetella norvegica[b]	19.26	59.72	550.89	14.94	0.09	0.42	2.92	0.09
Oithona similis	701.95	2471.66	1721.77	490.42	0.77	3.37	2.65	0.66
Triconia borealis	65.02	12.96	87.71	6.85	0.1	0.02	0.29	0.01
Calanoid nauplii	NA	618.91	1119.95	289.55	NA	0.43	1.27	0.25
Sum	5106.56	9969.49	8670.02	5018.02	30.14	44.16	48.49	48.73
Ostracoda								
Boroecia sp.[b]	0.01	0.03	–	–	+	+	–	–
Polychaeta								
Tomopteris sp.	+	+	–	+	0.01	+	–	+
Ctenophora (505 μm net)								
Beroe abyssicola	**NA**	**-**	**NA**	**+**	**NA**	**-**	**NA**	**0.04**[a]
Beroe cucumis	**NA**	**+**	**obs**	**0.01**	**NA**	**0.05**[a]	**obs**	**1.71**[a]
Mertensia ovum	**obs**	**0.06**	**obs**	**0.31**	**obs**	**0.82**[a]	**obs**	**1.56**[a]
Bolinopsis infundibulum	**obs**	**+**	**obs**	**0.01**	**obs**	**0.60**[a]	**obs**	**0.37**[a]
Sum	**NA**	**0.06**	**NA**	**0.33**	**NA**	**1.48**	**NA**	**3.67**
Decapoda and other crustacea								
Cumacea	–	0.13	–	–	–	0.21	–	–
Hippolytidae	–	0.31	0.23	0.1	–	0.02	0.21	0.1
Eualus gaimardii	–	0.05	–	0.03	–	0.06	–	0.02
Pandalidae	–	0.02	–	0.03	–	0.03	–	0.34
Sum	0	0.5	0.23	0.16	0	0.31	0.21	0.45
Euphausiidae								
Thysanoessa inermis	0.14	0.02	–	0.13	0.44	0.19	–	0.6
T. raschii	0.03	0.34	0.05	0.36	0.08	2.89	0.46	1.81
Thysanoessa juveniles	6.12	5.09	63.13	9.14	0.66	1.55	0.12	3.85
Sum	6.3	5.46	63.17	9.62	1.17	4.63	0.58	6.27
Cnidaria								
Aeginopsis laurentii[b]	–	4.89	–	0.31	–	0.48[a]	–	0.07[a]
Aglantha digitale	5.35	5.63	44.76	1.89	0.95[a]	0.20[a]	0.51[a]	2.00[a]
Aurelia aurita	–	+	–	–	–	0.01[a]	–	–
Eumedusa birulai[b]	–	0.02	0.1	+	–	0.05[a]	0.01[a]	0.01[a]
Euphysa flammea	0.06	0.01	–	–	0.08[a]	+	–	–
Melicertum octocostatum[b]	0.01	0.01	–	0.09	0.01[a]	0.02[a]	–	0.01[a]
Obelia longissima[b]	0.4	0.16	2.49	0.03	+	0.01[a]	0.13	+
Catablema/Halitholis [b]	+	0.01	+	0.12	0.02[a]	0.03[a]	0.01[a]	0.64[a]
Plotocnide borealis[b]	–	0.4	–	0.29	–	+	–	0.01[a]
Polyorchis penicillatus	+	–	–	–	0.02[a]	–	–	–
Rathkea octopunctata[b]	11.6	0.12	15.56	0.06	0.02[a]	+	0.03[a]	+
Sarsia tubulosa	+	0.06	–	+	0.02[a]	0.15[a]	–	+
Dimophyes arctica[b]	–	+	–	–	–	+	–	–
Bougainvillia superciliaris[b]	–	–	0.01	–	–	–	0.01	–
Sum (150 μm)	17.43	11.31	62.92	2.8	1.2	0.95	0.69	2.74
Cnidaria (505 μm)								
Cyanea capillata	**NA**	**+**	**NA**	**0.02**[a]	**NA**	**0.10**[a]	**NA**	**1.96**[a]
Mitrocomella polydiademata	**NA**	–	**NA**	**+**	**NA**	–	**NA**	**0.80**[a]

Table 2.2 – continued from previous page

	Abundance (ind m-3)				Biomass (mg DW m-3)			
	2004	2009	2010	2012	2004	2009	2010	2012
Catablema vesicarium / Halitholis cirratus	**NA**	**+**	**NA**	**0.04**[a]	**NA**	**0.01**[a]	**NA**	**0.07**[a]
Sarsia tubulosa	**NA**	**0.01**[a]	**NA**	**+**	**NA**	**0.02**[a]	**NA**	**0.01**[a]
Eumedusa (=Calycopsis) birulai	**NA**	**+**	**NA**	**+**	**NA**	**+**	**NA**	**+**
Chrysaora melanaster	**NA**	**–**	**obs**	**+**	**NA**	**–**	**obs**	**1.16**[a]
Aeginopsis laurentii[b]	**NA**	**1.40**[a]	**NA**	**0.09**[a]	**NA**	**0.15**[a]	**NA**	**0.18**[a]
Aglantha digitale	**NA**	**0.75**[a]	**NA**	**0.38**[a]	**NA**	**0.04**[a]	**NA**	**0.11**[a]
Sum (505 μm)	**NA**	**2.16**	**NA**	**0.53**	**NA**	**0.32**	**NA**	**4.29**
Meroplankton								
Bipinnaria	–	0.32	12.5	1	–	+	0.02	+
Echinodermata larvae	795.56	46.03	1437.76	19.38	0.37	0.05	0.29	+
Bivalvia larvae	148.31	217.77	1730.72	49.38	0.05	0.12	2.72	0.02
Cirripeda larvae	1235.55	102.68	1181.63	39.57	5.28	1.49	2.03	0.58
Decapoda zoea	0.31	0.04	0.08	0.24	0.21	0.04	+	0.02
Fish larvae	0.2	+	0.1	0.01	0.88	0.25	0.02	0.51
Actinula (anenome larvae)	0.24	0.16	–	0.3	0.3	0.13	–	0.06
Pagurus zoea	0.32	0.6	0.52	0.28	0.11	0.09	+	+
Polychaete larvae	81.85	70.28	642.19	3.56	0.81	0.37	2.31	0.05
Pilidium (nemertine larvae)	–	–	3.12	–	–	–	+	–
Sum	2262.35	437.89	5008.63	113.74	8.01	2.49	7.4	1.29
Mysidae								
Mysis oculata	+	0.02	–	0.01	0.04	0.02	–	0.01
Neomysis awatschensis	–	obs	–	–	–	obs	–	–
Pteropoda								
Clione limacina	–	0.22	0.42	0.15	–	0.03	0.04	0.42
Limacina helicina	–	101.94	76.97	0.45	–	1.45	0.27	+
Sum	0	102.16	77.39	0.6	0	1.48	0.31	0.43

species, which are shared with the Bering Sea. However, a number of species, including the majority of the observed hydrozoan jellyfish and some copepods (marked by asterisks in Table 2.2), are generally not found south of the northern Bering Sea/Chukchi region and can therefore be considered resident Arctic species. Copepods dominated both community biomass and abundance (Table 2.2; Fig. 2.3) — large copepods, mainly *Calanus glacialis* (Fig. 2.4), dominated the biomass at most locations, while small copepods dominated the abundance. Other large copepods, such as *Metridia pacifica*, *Eucalanus bungii* and *Neocalanus* spp., were present mainly in Bering Sea waters, with numbers declining to the north and toward the Siberian coast (Figs. 2.4; 2.7). Small copepods, such as *Pseudocalanus* spp., *Oithona similis* and *Acartia* spp. were common throughout the study region, but were particularly abundant near the coasts (Figs. 2.8; 2.9; 2.6). Study year 2009 stood out by significantly higher (2–3 times) average abundance of small copepods:

juvenile *Pseudocalanus* spp. and *O. similis* (Fig. 2.3; Table 2.3). Warm-water euryhaline copepods, such as *Eurytemora herdmani* and *Centropages abdominalis* (not shown), were generally only found in Alaska coastal waters; in 2009, however, these species were found throughout the southern Chukchi domain (Fig. 2.5). The pelagic harpacticoid copepod *Microsetella norvegica* was a prominent member of zooplankton communities in the Herald Canyon region and around Wrangel Island and was mostly absent from Bering Sea and Alaskan waters (Fig. 2.5). The presence of a number of Arctic taxa in 2009 (i.e., *Calanus hyperboreus*, *Metridia longa*, *Chiridius obtusifrons*) was largely due to the extended sampling region during that year.

A number of other non-copepod groups were also of high importance. Hydrozoan jellyfish, such as *Aeginopsis laurentii* and *Halitholis cirratus*, was common within waters around Wrangel Island and along the Siberian coast; *A. laurentii* was particularly abundant in 2009 (Fig. 2.8) and *H. cirratus* in 2012 (not shown). *Aglantha digitale*, on the other hand, was widespread throughout the study region during all years, particularly in waters influenced by Alaska Coastal Water, and was especially abundant in 2010 (Fig. 2.8). Other groups contributed variably across the area and between the studied years. Pteropods (*Limacina helicina* and *Clione limacina*) were extremely numerate in 2009 and 2010, especially near the Alaskan coast, but were rare in 2012 and completely absent in 2004 (Table 2.2; Fig. 2.7). Similarly, cladocerans were completely absent from the zooplankton in 2009. The larvacean *Oikopleura vanhoeffeni* (Fig. 2.7) was an important contributor in terms of abundance in 2004 (particularly in the Herald Canyon region) and in 2010 (Table 2.2). Despite much lower overall numbers in 2012, the much larger size of the individuals resulted in an exceptionally high biomass of this species during that year (significantly higher than in all other years) (Table 2.3). It is noteworthy that in 2009, the biomass and abundance of larvaceans were extremely low. The predatory chaetognath *Parasagitta elegans* (Fig. 2.7) was present at all sampling locations; its abundance (and biomass) was highest in 2009, especially in Herald Valley and around Wrangel Island. Cirripeda larvae were also common during all years throughout the studied region and were particularly abundant during the two summer surveys (2004 and 2010) (Fig. 2.7).

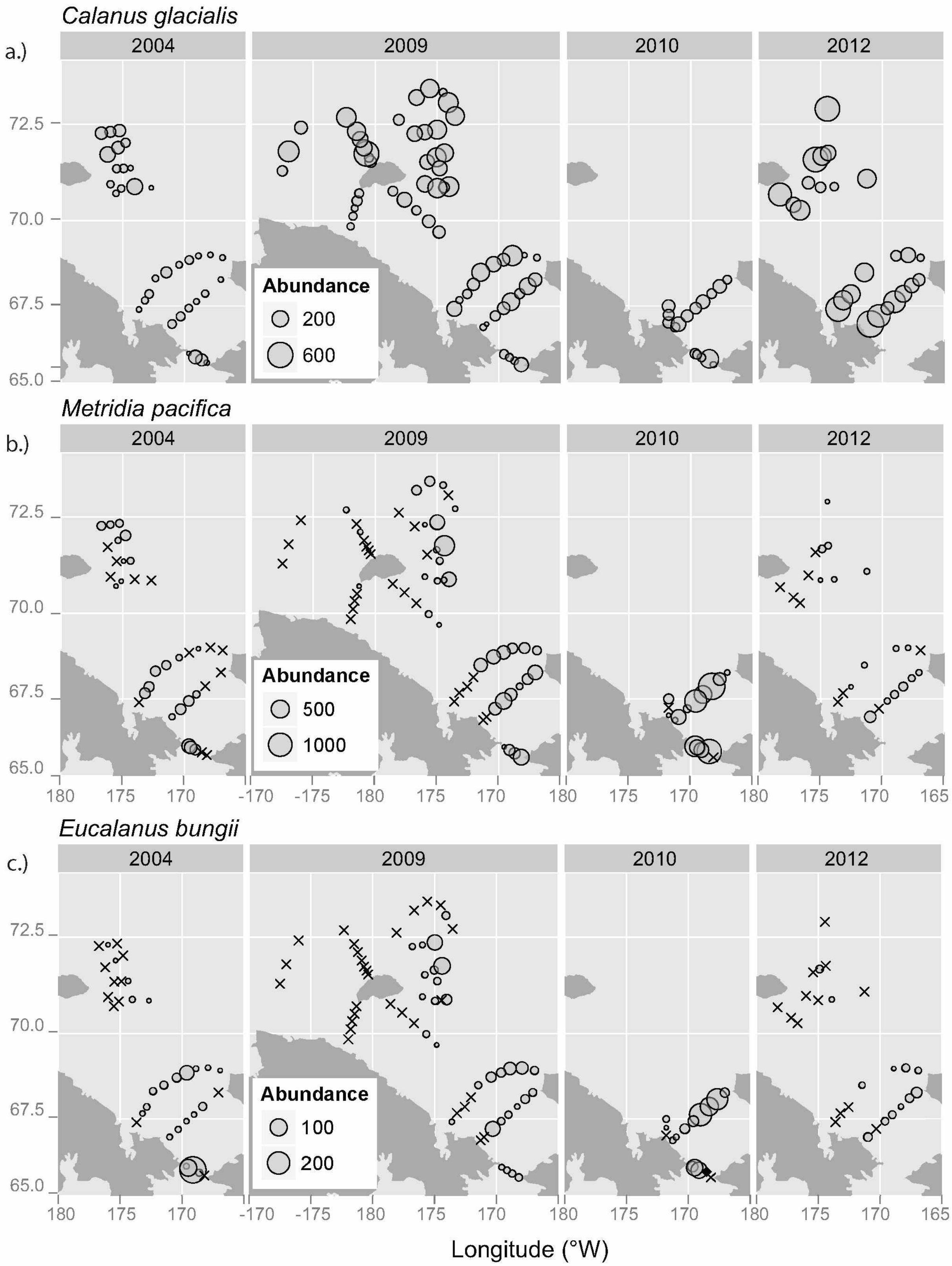

Figure 2.4: Abundance of large copepods (ind m^{-3}) across the Southern Chukchi Sea; cross symbol species absent at this location

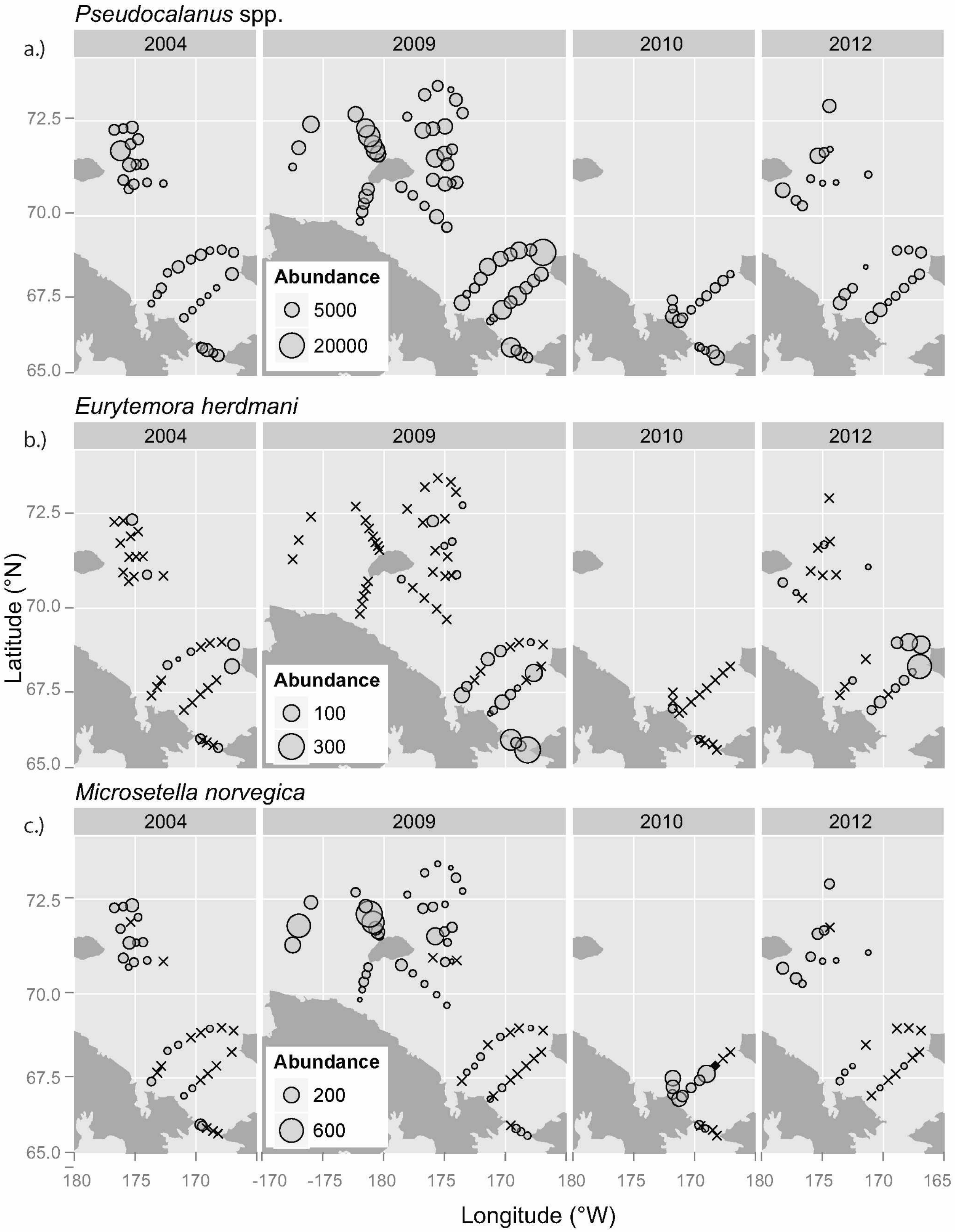

Figure 2.5: Abundance of small copepods (ind m^{-3}) across the Southern Chukchi Sea; cross symbol species absent at this location

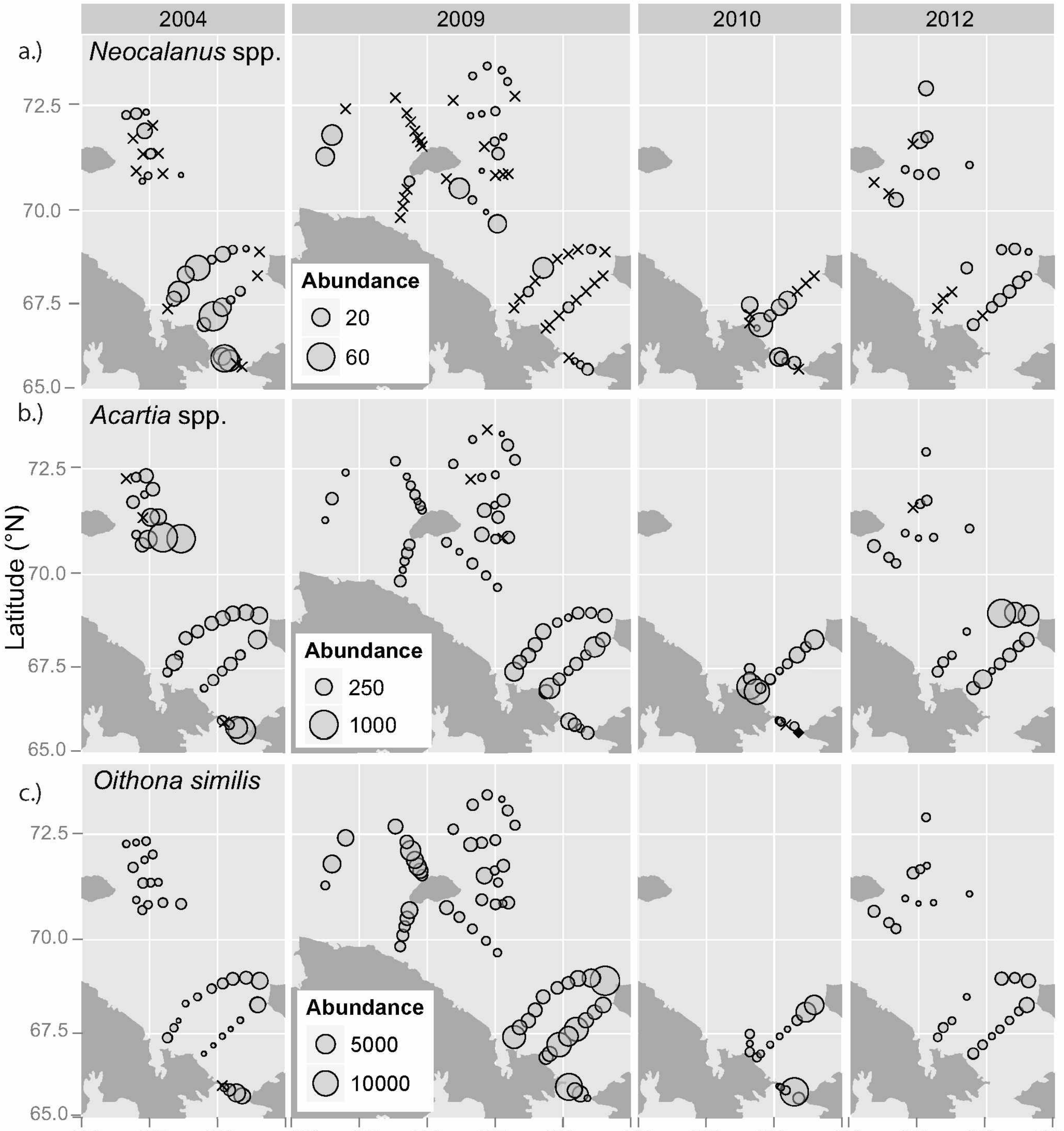

Figure 2.6: Abundance of copepods (ind m^{-3}) across the Southern Chukchi Sea; cross symbol species absent at this location

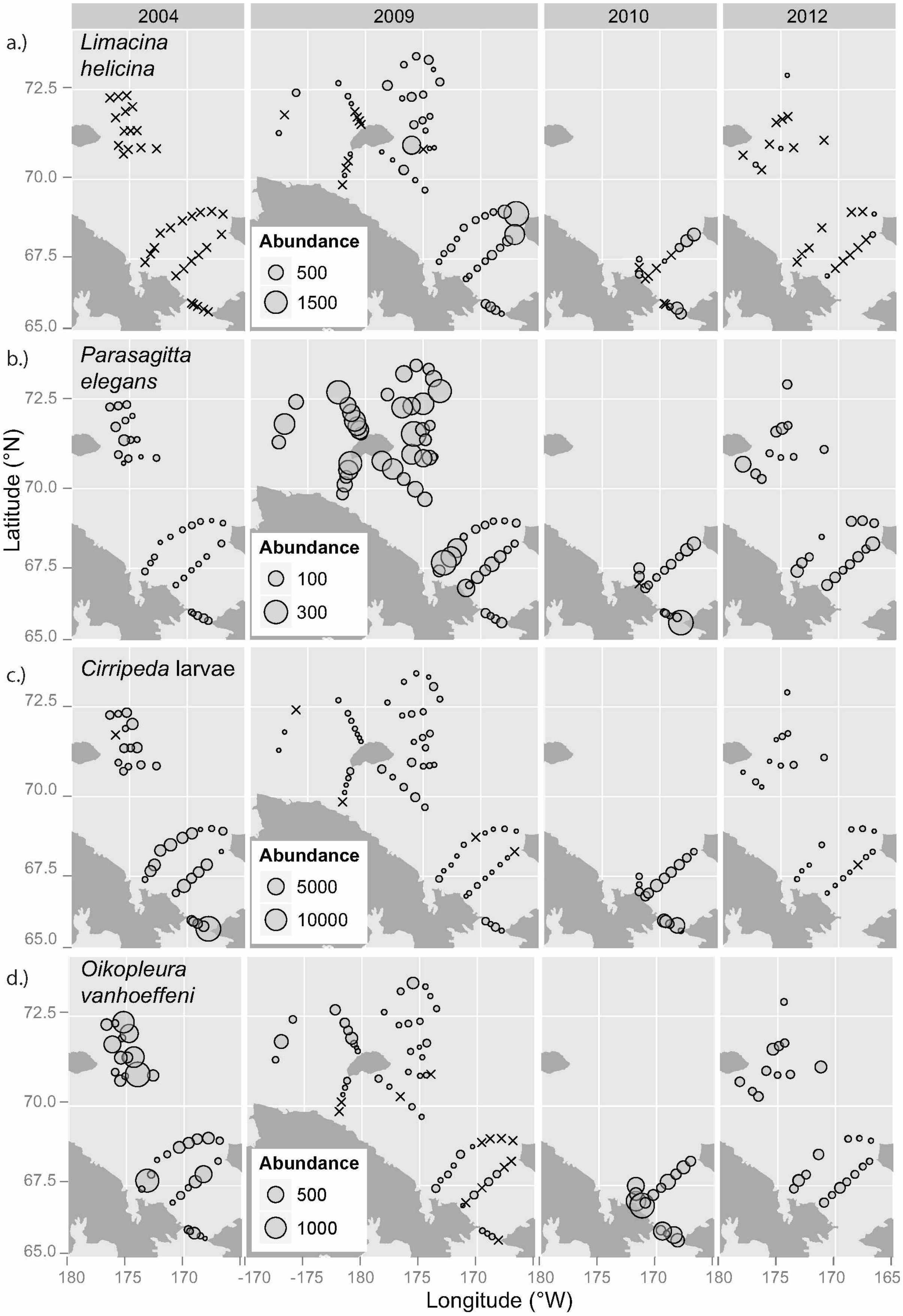

Figure 2.7: Abundance of other taxa (ind m^{-3}) across the Southern Chukchi Sea; cross symbol species absent at this location

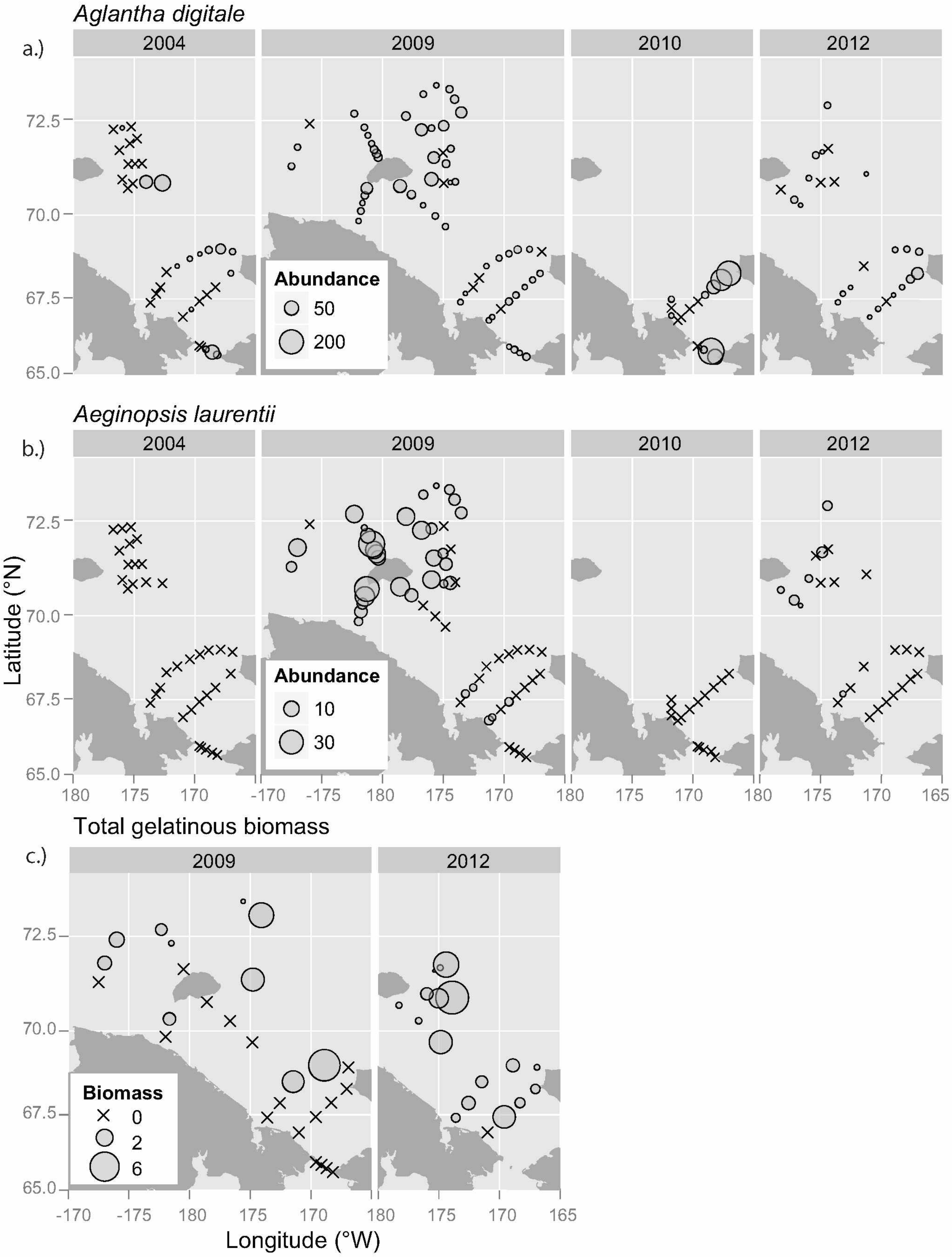

Figure 2.8: (a), (b) Abundance of gelatinous species (ind m^{-3}) across the Southern Chukchi Sea; cross symbol species absent at this location; (c) total biomass (mg DW m^{-3}) of gelatinous plankton in the Chukchi Sea as estimated by 505-μm nets

Table 2.3: One–way ANOVA results for the southern Chukchi Sea domain during all years for (a) total holozooplankton (b) taxonomic groups (c) individual copepod species; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. Significant interactions ($p < 0.05$) via Tukey HSD test; bold italic indicates significance at $p = 0.1$ level

	Abundance (ind m-3)					Significant interactions	Biomass (DW m-3)					Significant interactions
	2004	2009	2010	2012	p		2004	2009	2010	2012	p	
(a) Total	3295.6	10605.1	7944.5	3218.8	***	2009 > 2004, 2012	46.1	78.5	62	86.2	*	2004 < 2009, 2012
(b)												
Large copepods	116.2	237.6	601.3	287.5	**	2010 > 2004, 2009	29.9	33.7	33.7	53.6	NS	none
Small copepods	2823.1	9672.8	4938.6	2825.2	***	2009 > 2004, 2010, 2012	7.6	20.7	13.6	7	***	2009 > 2012, 2004
Chaetognaths	4.2	58.5	49.2	26	NS	none	3.2	9.2	4.2	12	*	2012 > 2004
Larvaceans	277.3	432.3	1845.4	60.4	***	2010 > 2004, 2009, 2012	1.9	0.1	1.9	5.5	**	2012 > 2004, 2009, 2010
Cnidarians	22.5	1.8	68.3	3.9	***	2010 > 2004, 2009, 2012	1.7	0.4	0.7	2.9	*	2012 > 2009, 2010
Euphausiids	9.2	5.7	63.2	14	*	2010 > 2004, 2009	1.5	8.1	0.6	4.4	**	2009 > 2004, 2010
Pteropods	0	196.2	77.4	0.8	*	2009 > 2004	0	3.7	0.3	0.1	NS	none
Cladocerans	43.1	0	300.7	0.6	NS	none	0.2	0	2.1	0	NS	none
Amphipods	0.1	0.2	0.2	0.3	NS	none	0.1	2.6	4.8	0.6	NS	none
Decapods	0	0	0.2	0.1	NS	none	0	0	0.2	0.1	*	2010 > 2004, 2009
(c)												
Calanus glacialis	20.9	98.6	78.7	270.3	***	2012 > 2004, 2009, 2010	5.7	27.8	14.1	44.7	**	2012 > 2004, 2010; 2009 > 2004
Metridia pacifica	55.3	126.1	367.5	9.9	***	2010 > 2004, 2009, 2012	2.3	4.5	10	0.1	**	2010 > 2004, 2012
Neocalanus flemingeri	10.7	1.3	7.8	1.6	*	2004 > 2009, 2012	6.8	0.4	4.2	1.1	**	2004 > 2009, 2012
Pseudocalanus spp.	1356.3	5103.1	1888.4	1756.3	**	2009 > 2004, 2010, 2012	5.2	13.5	6.3	5	**	2009 > 2004, 2010, 2012
Oithona similis	946.6	4154.5	1721.8	665.2	***	2009 > 2004, 2010, 2012	1	5.3	2.6	0.9	***	2009 > 2004, 2010, 2012
Eurytemora herdmani	7.4	42.6	1.1	42	*	2009 > 2004, 2010	0	0.2	0	0.2	**	2009 > 2004, 2010

As with copepods, the presence of a number of Arctic jellyfish species in 2009 was largely due to the extended sampling region during that year.

When properly accounted for (in 2009 and 2012), ctenophores and large jellyfish were important contributors to the community biomass, resulting in a 2–10 % average increase in the biomass estimated by preserved samples. At several stations, particularly in 2012, the normalized biomass of large gelatinous taxa was over 40 mg DW m^{-3} and exceeded copepod biomass (Fig. 2.8). The ctenophore *Mertensia ovum* (Fig. 2.8) was the most abundant species, particularly in 2012, when it occurred at nearly every station and contributed an average of 2 mg DW m^{-3} to the overall holozooplankton biomass (and up to 10 mg DW m^{-3}). In 2009, we only encountered *M. ovum* above 69 °N, but its average contribution to biomass across the entire area was nevertheless high at 0.8 mg DW m^{-3}. The ctenophores *Bolinopsis infundibulum* and *Beroe cucumis* (not shown) were less common, occurring at 15–25 % of the stations sampled, but due to their large size and weight, their average contribution to biomass is also substantial during both years (Table 2.2). The large scyphomedusan *Cyanea capillata* was also common in 2012, with smaller individuals (up to 20 cm) occurring throughout the collections and contributing an average of 2 mg DW m^{-3} to the biomass (Table 2.2); in 2009, we only observed this jellyfish at three stations.

2.4.3 Community structure

Twelve station groups were identified by cluster analysis for all years (Fig. 2.9a). The nMDS ordination largely reinforces (Fig. 2.9c) the results of cluster analysis, with improvement in stress from 0.21 to 0.14 when increasing from two to three dimensions. Generally, the stations separate by year, with several exceptions. Specifically, the Chukchi communities in 2009 clustered together with the Chukchi/SCW stations in 2012; the ACW-influenced communities in 2012 were grouped together with most of the stations of the southern Chukchi in 2009. Overall, 2004 was more similar to 2010, and 2009 to 2012, and it is notable that the former two cruises took place in August, and the other

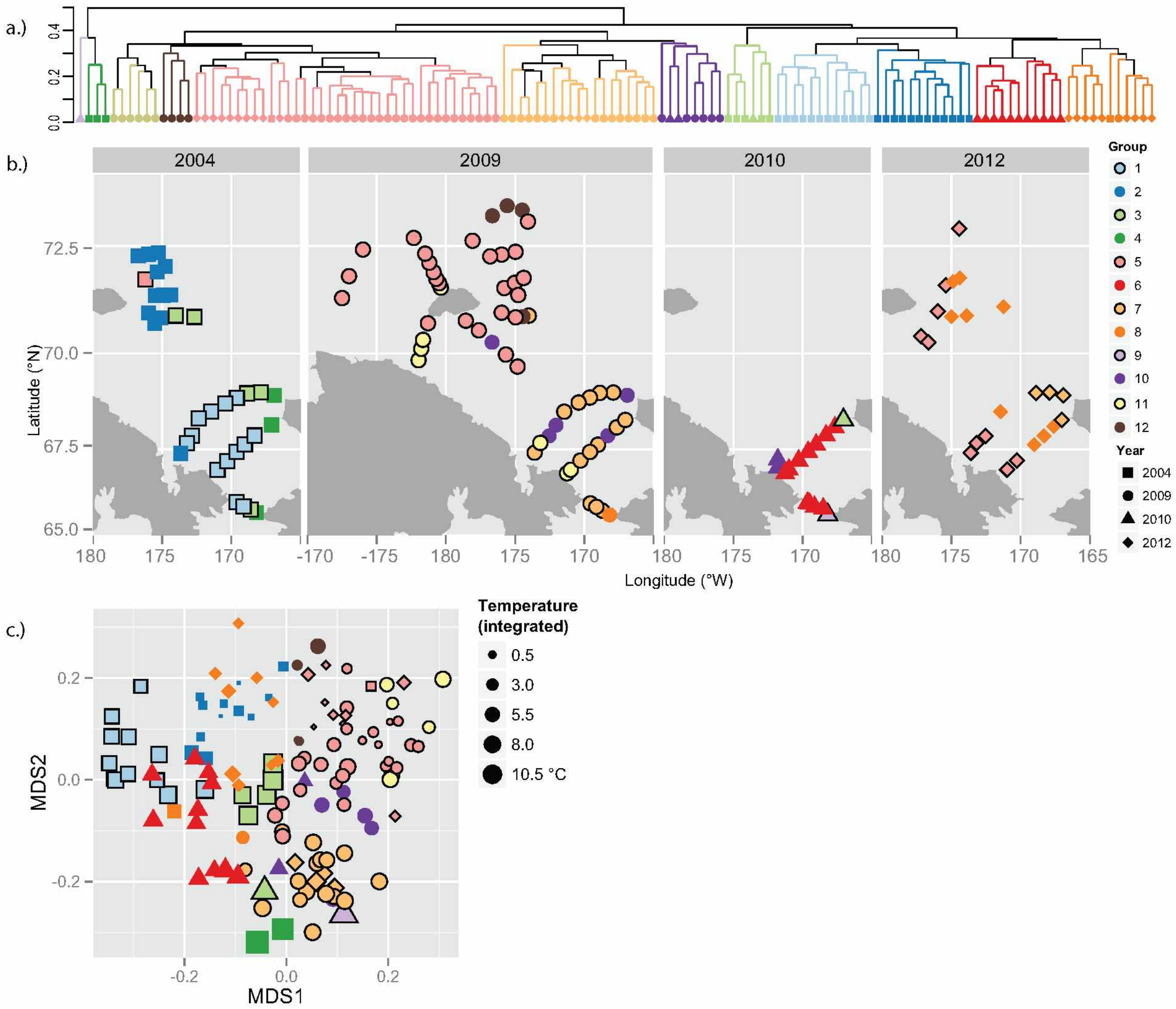

Figure 2.9: Zooplankton abundance. (a), (b) Cluster analysis and (c) nMDS ordination plot (first two axes) for combined 2004, 2009, 2010 and 2012 stations in the Chukchi Sea. Bottom temperature overlaying nMDS plot indicates strong relationship with community structure. Solid colors connect clusters that were significant at $\alpha = 0.05$ level; same colors indicate 35 % similarity

two in September. A strong cross-shelf (east to west) gradient in community structure of the southern Chukchi was evident in 2004, 2010 and 2012, with an ACW-influenced community along the Alaskan coast being replaced by Bering Sea communities farther offshore and by Siberian coastal/Chukchi communities closer to the Siberian Coast. In 2009, there was no distinct separation of communities across the southern Chukchi using either biomass or abundance, with several stations (dark purple) being most similar to the Siberian communities in 2010. Stations on the east edge of Herald Canyon were generally characterized by Bering Sea/Chukchi communities, yet the western stations were more similar to the SCW stations.

In terms of species composition (Fig. 2.10), the ACW communities were the most recognizable assemblage, characterized by the presence of several of warmer-water euryhaline taxa: the cladocerans *Evadne nordmanni* and *Podon leuckarti*; the copepods *Pseudocalanus newmani*, *Acartia hudsonica*, *Centropages abdominalis* and *Epilabidocera longipedata*. The Bering Sea communities were dominated by shelf species, such as the copepods *Pseudocalanus* spp., *Oithona similis*, *Acartia* spp., cirriped larvae as well as the more oceanic copepods *Calanus glacialis*, *Metridia pacifica*, *Neocalanus* spp., and *Euclanus bungii*. The communities associated with the Chukchi Winter Waters, while sharing a large number of advected Pacific species with the Bering Sea communities, were characterized by a lower overall biomass of copepods, particularly *C. glacialis*, and by the increased presence of Arctic taxa, such as several hydrozoan jellyfish species, as well as the copepod *Microsetella norvegica*. Several other Arctic and ice-associated species, such as the copepods *Metridia longa* and *Jaschnovia* spp., and the amphipod *Apherusa glacialis* also occurred within these communities. The SCW assemblages (2009 and 2010) were similar to the Chukchi communities, but with a reduced presence of Pacific taxa. Large copepods were nearly absent from these communities, with biomass dominated by small copepods and adult euphausiids. Interestingly, in 2010, these communities contained a number of entrained warm-water neritic species, such as the copepods *P. newmani* and *C. abdominalis*, while in 2009, they were nearly absent. While the copepod *C. glacialis* was present in all communities during all years, the distribution of developmental stage of this species reveals patterns suggesting multiple origins (Fig. 2.11). Within BSAW, the *C. glacialis* population consisted mainly of C5 copepodites, while within the resident Chukchi/Siberian Coastal Waters, subadult C5's were scarce or absent, and the population consisted mainly of young C1–C4 copepodites. Younger copepodites also dominated within the ACW *C. glacialis* populations.

We found the community structure within each year to be strongly correlated with environmental parameters via the BIOENV routine. Bottom temperature was the most important variable during most years (with the exception of 2012, when surface temperature was the highest-correlated variable) (Table 2.4 — as also apparent from the nMDS

Table 2.4: Pearson's correlations between environmental variables and transformed abundance data in the Chukchi Sea. All results presented are significant at $\alpha = 0.05$ level. Best correlations highlighted in **bold**. *T* temperature, *S* salinity, *btm* bottom layer, *surf* surface layer, *dist* distance from Bering Strait, *Depth* station depth

	2004	q	2009	q	2010	q	2012	q
1	S.btm	0.5690	dist	0.4653	T.btm	0.6985	**T.surf**	**0.5570**
2	**T.btm, S.btm**	**0.6454**	T.btm, dist	0.5435	Depth, T.btm	0.7370	T.surf, T.btm	0.5468
3	T.btm, S.btm, T.surf	0.6287	**T.btm, S.btm, dist**	**0.5933**	**T.btm, Depth, T.surf**	**0.7599**	T.surf, T.btm, S.surf	0.5406

temperature overlay, Fig. 2.9c). Other variables that improved the model included bottom salinity, surface temperature and salinity, station depth, and distance from Bering Strait (Table 4). Using biomass and abundance matrices produced very similar results. Including more than three parameters or other variables (Fluorescence, Chlorophyll, Oxygen) produced no significant (<3 %) improvement in correlations. Bottom temperature also had a strong inverse relationship to prosome length in several copepod species, such as *C. glacialis*, *M. pacifica*, *Pseudocalanus acuspes* and *P. newmani* ($r^2 = 0.36$, 0.28, 0.35, 0.25, respectively) (Fig. 2.12).

2.5 Discussion

While the relationship between zooplankton communities and water masses within this region has been well documented by studies beginning as early as the 1930 s (e.g., Kulikov, 1992; Pavshtiks, 1984; Stepanova, 1937), no prior study has encompassed as many different water masses (ACW, BSAW, SCW, WW) within a single survey. Furthermore, repeated sampling over several years allowed us to observe the spatial variability of these relationships and their spatial manifestations. Within our study, four broad community types were identified: Alaska Coastal, Bering Sea (Pacific), Chukchi/Arctic and Siberian Coastal in broad agreement with study by Hopcroft et al. (2010) based on only 2004 data. Within these assemblages, the Alaska Coastal communities were the most identifiable, marked by the presence of a number of warm-water euryhaline taxa. In two of the study years (2004 and 2010), a marked boundary in both the physical properties and zooplank-

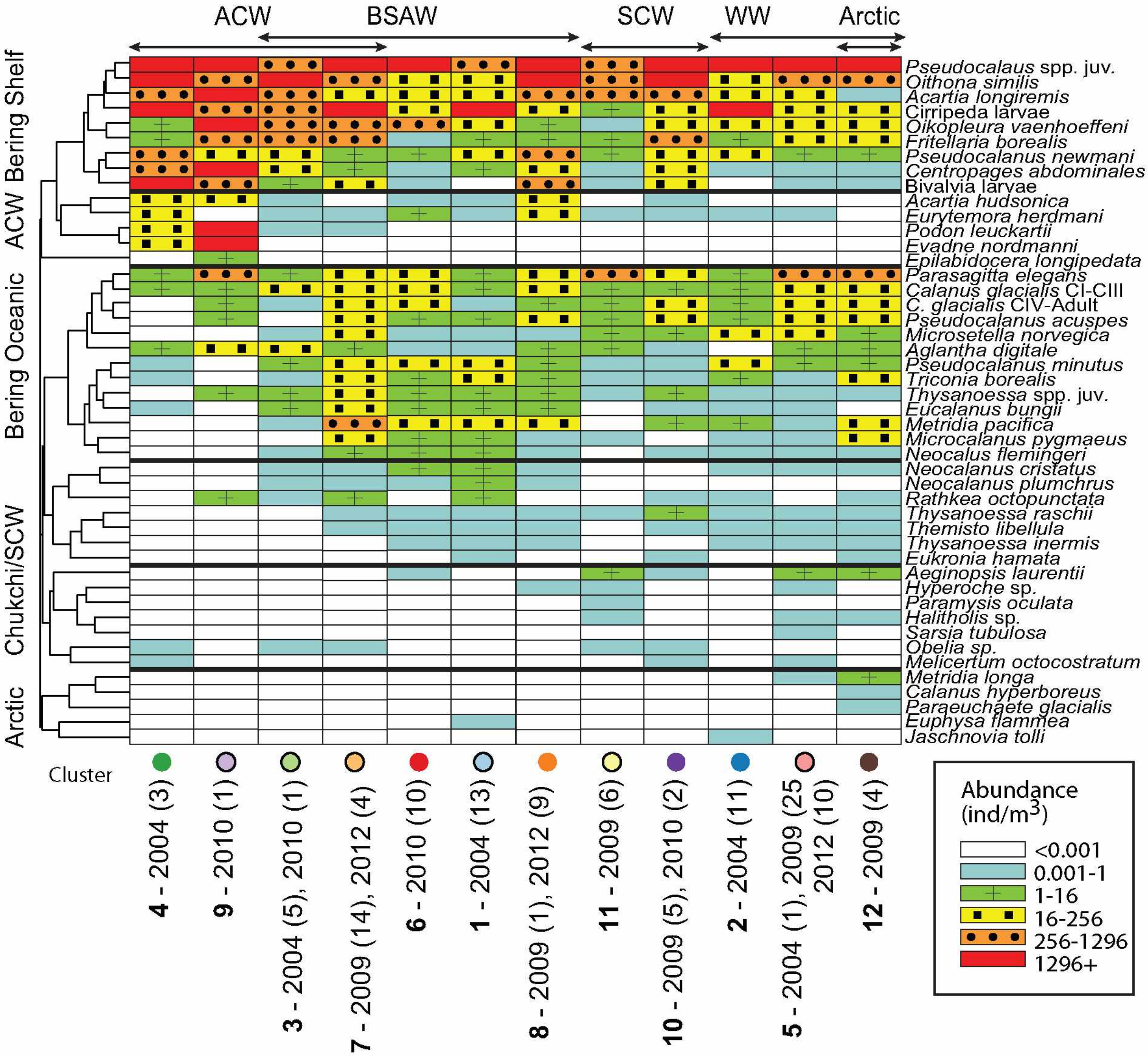

Figure 2.10: Results of cluster analysis of species composition (columns) and stations (rows) in the Chukchi Sea. Text labels along axes indicate correspondence to water mass types; column names indicate cluster number (as defined in Fig. 2.9). Numbers in parentheses indicate number of stations per cluster and years observed

ton communities separated these communities from adjacent BSAW waters; in 2012, this boundary was weaker, and in 2009, it was nearly absent, with species characteristic of the ACW found in diluted numbers across the entire southern Chukchi shelf. The boundary between Bering Sea oceanic and shelf communities, as described by Springer et al. (1989) and Hopcroft et al. (2010) for 2004, was variable and often obscured by mixing and layering of water masses of different origins. As a result, shelf and oceanic Bering water properties and communities were grouped into a broad BSAW category, which carries both oceanic and shelf zooplankton species in varying proportions, presumably as

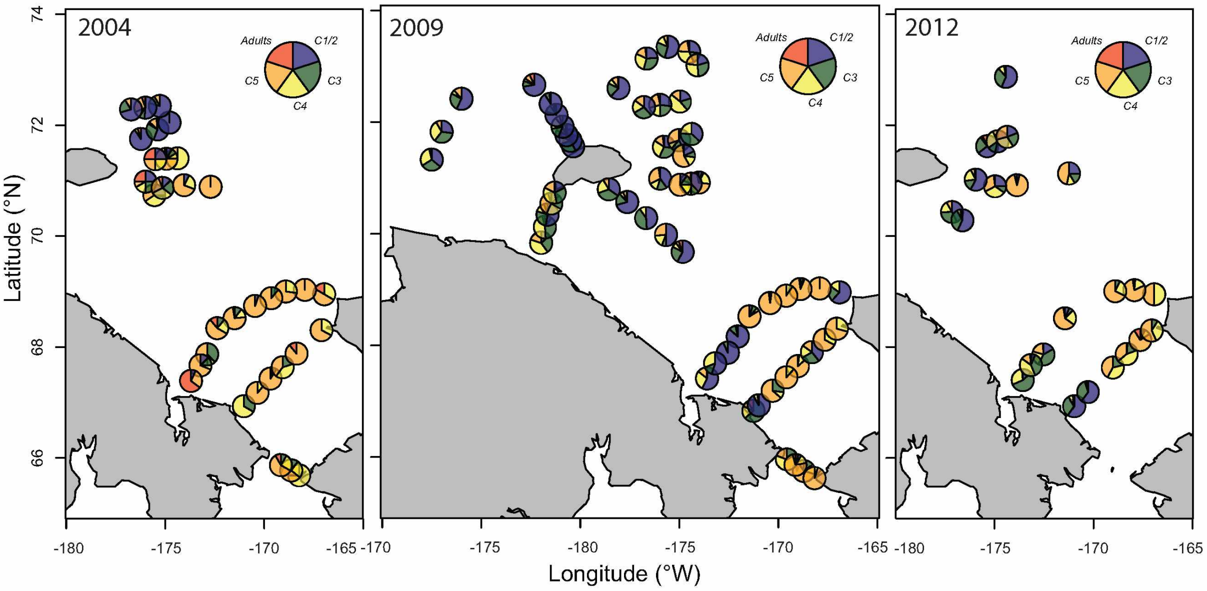

Figure 2.11: Distribution of developmental stages of *Calanus glacialis* in the Chukchi Sea during 2004, 2009 and 2012 cruises

influenced by corresponding water masses.

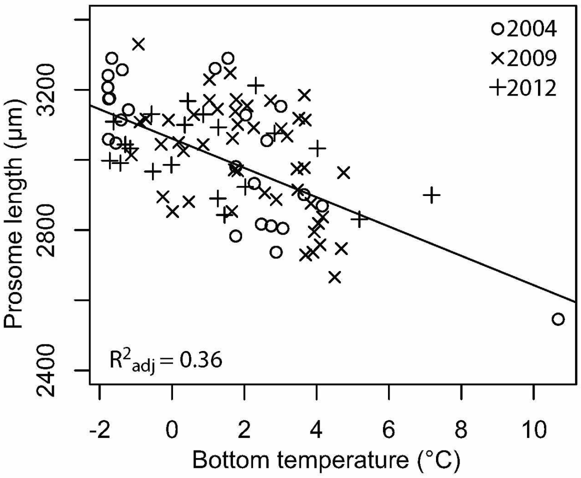

Figure 2.12: Prosome length of C5 *Calanus glacialis* versus bottom temperature across all Chukchi Sea stations in 2004, 2009 and 2012

An important transitional zone between Pacific and Arctic communities was formed in Herald Canyon. Most of the plankton observed on the eastern side of the canyon was strongly influenced by Bering Sea communities, with more resident Chukchi and Siberian coastal groups appearing to the west, accepting that our methodology weakens the intensity of some patterns when two water masses co-occur at a single station. The northward boundary, where Arctic zooplankton communities begin to replace Pacific communities, was visible in the deeper northernmost stations in 2009. Siberian coastal communities were characterized by lower biomass compared with the adjoining Chukchi Sea and were similar to those found in other shallow river-influenced Arctic seas, dominated by small neritic copepods (*Pseudocalanus* spp., *O.*

similis, *M. norvegica*), hydrozoan jellyfish, and chaetognaths (Pavshtiks, 1994).

The very low numbers of the copepod *C. glacialis* in the SCW and resident Chukchi communities strongly suggest that most of the *C. glacialis* population in the shallow Chukchi Sea was advected from the Bering Sea rather than the Arctic basins, and thus was not composed of resident individuals. This point is further reinforced by the distribution of copepodite stages of *C. glacialis* (Fig. 2.11), suggesting that during all the years, there were at least two distinct populations with different timing of life historiesacross the Chukchi Sea. A Pacific population presumably advected from the Bering Sea shelf and dominated by late copepodite stages IV–V was the main contributor to community biomass within the offshore section of the Southern Chukchi and the eastern side of Herald Canyon. In contrast, a resident Arctic population, composed of mainly early stages copepodite stages I-III and some adults, was found in the WW and SCW. This observation is consistent with results of population genetics, which also show two distinct haplotypes present in the Pacific Arctic: a Bering Sea haplotype which follows the Bering Sea water into the Chukchi Sea and a resident lineage, which is found throughout the marginal Arctic seas (Nelson et al., 2009). The latter may also sometimes be carried into the southern Chukchi by the SCW and even into the northern Bering Sea during occasional wind-driven current reversals.

The heightened presence of adult euphausiids in the East Siberian waters during 2009 and 2010 is also noteworthy. Surveys of marine mammals along the Chukotka coast show that this area may be an important feeding area for bowhead whales, which are known to actively prey upon euphausiids (Moore et al., 1995, 2010). Euphausiids are also active swimmers that are able to successfully avoid plankton nets; their increased presence in net tows may indicate reduced fitness in the cold and freshened waters of the Siberian Coastal Current.

While the primary members of the zooplankton communities remained the same between years, there was strong variability between years on the absolute and relative contribution to the communities by different taxa. For example, larvaceans, which were a very prominent component of the system in 2004 and 2012 (up to 40 % of total biomass at some stations), were nearly absent in 2009. Concurrent surveys in the northeastern Chukchi in 2009 also indicated extremely low larvacean abundance in that area (Questel et al., 2013) compared with 2012 (Hopcroft et al., 2014). Moreover, while our average abundance of *Oikopleura vanhoeffeni* in 2004 was two times higher than that of 2012, the biomass was significantly higher in 2012, due to the much larger sizes of the animals encountered. Most likely, this is the result of the combined effect of overall lower water temperature observed during 2012 (whereby slower growth at lower temperature results in larger body size) and later timing of that cruise (thus encountering individuals at a later stage of their life cycle).

Abundance of other taxa, such as pteropods (completely absent in 2004), hydrozoan medusae and other gelatinous species, also showed very strong variability in contribution to communities during the different study years. Such year-to-year shifts from crustacean-dominated communities to communities with a higher contribution of gelatinous taxa may have important implications for the higher trophic levels. Jellyfish are predators of both zooplankton and fish larvae and can be detrimental to fish populations, which in turn are exploited by marine mammals (Brodeur et al., 2008, 2002). Since very few higher trophic levels can prey on gelatinous plankton, it also often represents a trophic “dead end” in the pelagic system.

The biomass and abundance values (42–80 mg DW m^{-3}, 3000–8000 ind m^{-3}) we observed within our study during the 4 years are comparable to estimates obtained by other historical and contemporary studies, some of which overlap our study in temporal and spatial coverage.The survey with the most comparable cross-shelf coverage ISHTAR (Springer et al., 1989) reported an average biomass of $\sim$2–5 g DW m^{-2} ($\sim$40–100 mg DW m^{-3}) for the northern Bering Sea/southern Chukchi region, which is close to the range that we observed in our work, although our study uses different methods to arrive at biomass estimates. Older surveys, while imperfectly comparable due to different sampling techniques, generally report both biomass and abundance values within a similar range (see review in Hopcroft et al., 2010). The most recent estimates for the Eastern Chukchi (Matsuno et al., 2011)are also comparable, averaging 28–36 g WW m^{-2} (assuming DW to be ∼10–15 % of WW). Interestingly, concurrent work in the northeastern Chukchi (Questel et al., 2013) found much lower overall biomass (∼16 mg DW m^{-3}) from 150-μm nets in 2009 than we observed within our study, while the same study in 2010 reports much higher abundance and biomass values than were recorded by us during the same time period (101 mg DW m^{-3}/16,000 ind m^{-3}). The observed communities in 2012, however, are directly comparable, with similar biomass (66 mg DW m^{-3}) and an exceptionally high contribution of *C. glacialis* (Hopcroft et al., 2014). These observed differences may indicate that different processes are responsible for shaping zooplankton communities in the east and west Chukchi regions. Compared to other Arctic shelf systems, the biomass values observed in the Chukchi sea (2–5 g DW m^{-2}) are higher than that in most other regions, with the exception of the much deeper Barents Sea inflow system; biomass with the Barents Sea is reported to be 1–10 g DW m^{-2}, with estimates usually closer to the upper range (5–10 g DW m^{-2}) (Hunt et al., 2013). Biomass of summer zooplankton within the non-inflow shelf systems, such as the Laptev, Kara and White seas, is significantly lower, being of the order of ∼1–2 mg DW m^{-2} (Kosobokova and Pertsova, 2012).

It is important to note that while our results are presented as “snapshots”, the Chukchi Sea is a highly dynamic system, where detectable seasonal change may occur over only a few weeks (Questel et al., 2013). It is not uncommon for wind activity to slow down or even reverse currents (Weingartner et al., 1999), as we observed during the 2009 cruise (Pisareva et al., 2015). Fronts of different water masses may also advance seasonally (Weingartner et al., 2013), replacing the community type present at a specific geographic location. These processes, which may have occurred on smaller timescales than the duration of the cruises, may have obscured the patterns observed. Nevertheless, the strong relationships between environmental factors and community structure during all years indicate that communities are very strongly structured by physical processes within the water column.

Inter-annual comparisons were also confounded by the slightly different seasonality of the cruises, including different timings relative to the spring breakup. The study years 2004 and 2010 both were sampled in early August, with the zooplankton communities observed during those years markedly different from those observed in 2009 and 2012 when sampling occurred in September. For example, meroplankton abundance was an order of magnitude higher in the two summer surveys; many meroplankton groups are only found in the plankton over a period of days or weeks before settling out to the benthos. Relatively large changes in community structure can occur over such timescales (Questel et al., 2013). Trophic interactions within the zooplankton communities may also play a large role in seasonal successions. The extremely high biomass of the chaetognath *Parasagitta elegans* observed in both September cruises (2009 and 2012), which at some stations exceeded the biomass of its prey, may indicate the transition of zooplankton communities from summer to autumn, when copepod production slows down, but the higher trophic levels are still capitalizing on the abundant food.

Indices of climate variability, such as the Pacific decadal oscillation (PDO), provide us with an opportunity to observe the effect that longer-term climate change may have on an ecosystem. PDO-related anomalies have been studied extensively within the Bering Sea, with zooplankton and fish communities visibly responding to changes in temperature and ice cover (Hunt et al., 2011). Namely, colder years with later ice retreat seem to benefit the shelf populations of large copepod *C. glacialis*, while abundances of small copepods and cnidarians decrease during cold years (Eisner et al., 2014). The Chukchi Sea's thermal regimes should reflect the conditions observed in the same years in the Bering Sea, as well as the shifts in zooplankton communities (Coyle et al., 2011; Eisner et al., 2014). Our 2004 survey was the only "warm" (positive PDO) year during our study period; it was also the year with the lowest observed biomass in the Chukchi Sea. The coldest year, 2012, was also the year with the highest biomass of advected *C. glacialis* across the Chukchi Sea, as also observed to the Northeast (Hopcroft et al., 2014). We did not observe a decrease in the numbers of small copepod species in 2009–2012, as was observed for the same period in the Bering Sea (Eisner et al., 2014); on the contrary, 2009 stands out by an almost twofold increase in small copepod abundance. This is indicative of the fact that the faster-growing small copepod populations may be more responsive to local conditions than to processes upstream.

While warm years such as 2004 may be examined as somewhat representative of what will happen to zooplankton communities as climate warms and sea ice retreats, for any permanent shift to occur within the plankton communities, such conditions must be maintained. The extent of variability observed within our study and other studies in the Chukchi (e.g. Hopcroft et al., 2014; Questel et al., 2013) indicates that the system is highly flexible and responsive to year-to-year shifts in climatic forcing. While a longer warm-water summer period, as observed in 2004, may provide an opportunity for boreal Pacific species to play an increased role in summer communities within the Chukchi Sea, during the winter and spring, the Northern Bering Sea remains at least partially ice-covered, and waters entering and within the Chukchi Sea during the winter have near-freezing temperatures. Thus, advected species are unlikely to survive the winter and establish permanent populations with the Chukchi (Wassmann et al., 2015). This is in contrast to the North Atlantic inflow system of the Barents Sea, where year-round above-freezing conditions may allow for permanent range expansion of southern species with warming water temperatures (Hunt et al., 2013; Kwasniewski et al., 2012).

Small copepods, such as *Pseudocalanus* spp. and *Oithona similis*, may play a proportionately larger role in a warmer Chukchi, although other local factors such as food availability may be more important in determining their ultimate success. Although a prolonged ice-free period may increase primary production and potentially benefit some zooplankton groups and higher trophic levels, a decrease and/or mismatch in sea ice algae production may affect Arctic species that are tuned to the spring ice algae bloom. Furthermore, an overall increase in productivity may be accompanied by a shift to smaller phytoplankton species (Arrigo and van Dijken, 2011), which may cycle more production within the microbial loop and be detrimental to herbivorous species that specialize on large phytoplankton cells. Since body size is inversely related to temperature (Hop et al.,

2006) (and as observed for several species within our study, Fig. 2.12), a downward shift in zooplankton size distribution even within species would be expected. Smaller zooplankton may be less effectively preyed upon by vertebrate predators, with significant consequences to many higher trophic levels (e.g., Kwasniewski et al., 2012).

2.6 Conclusions

The structure, biomass and productivity of zooplankton communities within the Chukchi Sea clearly reflect variations in physical properties of the water column, as well asseasonal differences and intensity of downstream productivity and Pacific water transport. While our results are snapshots of an extremely dynamic system, broad patterns are nevertheless emergent and together with other concurrent studies and historical data may be used to infer the fate of the pelagic communities both upstream and downstream of the studied region. Here, we establish spatial and inter-annual variability of summer plankton communities across a broad area within the Chukchi Sea, which is strongly shaped by different water masses. Future surveys, including those during "warm" years, should seek to capture more of the seasonal and inter-annual dynamics of the system and their responses to progressive climatic forcing.

2.7 References

Arrigo KR, van Dijken GL (2011) Secular trends in Arctic Ocean net primary production. J Geophys Res 116:1–15

Bailey TG, Youngbluth MJ, Owen GP (1995) Chemical composition and metabolic rates of gelatinous zooplankton from midwater and benthic boundary layer environments off Cape Hatteras, North Carooina, USA. Mar Ecol Prog Ser 122:121–134

Båmstedt U (1986) Chemical composition and energy content. In Corner EDS, O'Hara SCM (eds.) The biological chemistry of marine copepods, pp. 1–58. Oxford University Press, Oxford

Becker RA, Wilks AR (2013) maps: Draw Geographical Maps. R package version 2.3

Brodeur R, Decker M, Ciannelli L, Purcell JE, Bond N, Stabeno P, Acuna E, Hunt G Jr (2008) Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. Prog Oceanogr 77:103–111

Brodeur RD, Sugisaki H, Hunt GL Jr (2002) Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. Mar Ecol Prog Ser 233:89–103

Carmack E, Wassmann P (2006) Food webs and physical–biological coupling on pan-Arctic shelves: unifying concepts and comprehensive perspectives. Prog Oceanogr 71:446–477

Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. Mar Ecol Prog Ser 92:205–219

Clarke KR, Gorley RN (2005) PRIMER: Getting started with v6. PRIMER-E Ltd: Plymouth

Coachman LK, Aagaard K, Tripp RB (1975) Bering Strait: The Regional Physical Oceanography. University of Washington Press

Coyle KO, Eisner LB, Mueter F, Pinchuk AI, Janout MA, Cieciel KD, Farley EV, Andrews AG (2011) Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the oscillating control hypothesis. Fisheries Oceanography 20:139–156

Duarte CM, Agustí S, Wassmann P, Arrieta JM, Alcaraz M, Coello A, Marbà N, Hendriks IE, Holding J, García-Zarandona I, Kritzberg E, Vaqué D (2012) Tipping elements in the Arctic marine ecosystem. AMBIO 41:44–55

Eisner LB, Hillgruber N, Martinson E, Maselko J (2012) Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi seas. Polar Biol 36:87–113

Eisner LB, Napp JM, Mier KL, Pinchuk AI, Andrews AG III (2014) Climate-mediated changes in zooplankton community structure for the eastern Bering Sea. Deep Sea Res II 109:157–171

Gerritsen H (2013) mapplots: Data visualisation on maps. R package version 1.4

Grebmeier MJ, Maslowski W (eds.) (2014) The Pacific Arctic Region - Ecosystem Status and Trends in a Rapidly Changing Environment. Springer

Hop H, Falk-Petersen S, Svendsen H, Kwasniewski S, Pavlov V, Pavlova O, Søreide JE (2006) Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. Prog Oceanogr 71:182–231

Hopcroft RR, Hariharan P, Questel J, Lamb J, Lessard E, Foy M, Clarke-Hopcroft C (2014) Oceanographic assessment of the planktonic communities in the northeastern Chukchi Sea. Report for Survey year 2012. Chukchi Sea Environmental Program p. 19

Hopcroft RR, Kosobokova K, Pinchuk AI (2010) Zooplankton community patterns in the Chukchi Sea during summer 2004. Deep Sea Res II 57:27–39

Hunt G Jr, Coyle KO, Eisner LB, Farley EV, Heintz RA, Mueter F, Napp JM, Overland J, Ressler PH, Salo S, Stabeno P (2011) Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES J Mar Sci 68:1230–1243

Hunt GL Jr, Blanchard AL, Boveng P, Dalpadado P, Drinkwater KF, Eisner LB, Hopcroft RR, Kovacs KM, Norcross BL, Renaud P (2013) The Barents and Chukchi Seas: Comparison of two Arctic shelf ecosystems. J Marine Syst 109:43–68

IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

Kasuya T, Ishimaru T, Murano M (2000) Metabolic characteristics of the lobate ctenophore Bolinopsis mikado (Moser). Plankton Biol Ecol 47:114–121

Kosobokova K, Hopcroft RR (2010) Diversity and vertical distribution of mesozooplankton in the Arctic's Canada Basin. Deep Sea Res II 57:96–110

Kosobokova K, Pertsova NM (2012) Zooplankton Belogo morja: struktura, dinamika i ekologija soobshestv. In Lisitsyn AP (ed.) Sistema Belogo Morja: Prirodnaja Sreda Vodosbora Belogo Morja, pp. 640–675. Nauchnyj mir, Moscow

Kremer P, Canino MF, Gilmer RW (1986) Metabolism of epipelagic tropical ctenophores. Mar Biol 90:403–412

Kulikov AS (1992) Characteristics of zooplankton communities. In Nagel, A P (eds.) Results of the Third Joint US–USSR Bering and Chukchi Seas expedition (BERPAC), Summer 1988, p. 161. US Fish and Wildlife Service, Washington

Kwasniewski S, Gluchowska M, Walkusz W, Karnovsky NJ, Jakubas D, Wojczulanis-Jakubas K, Harding AM, Goszczko I, Cisek M, Beszczynska-Möller A (2012) Interannual changes in zooplankton on the West Spitsbergen Shelf in relation to hydrography and their consequences for the diet of planktivorous seabirds. ICES J Mar Sci 69:890–901

Lane PV, Llinás L, Smith SL, Pilz D (2008) Zooplankton distribution in the western Arctic during summer 2002: hydrographic habitats and implications for food chain dynamics. J Marine Syst 70:97–133

Larson RJ (1986) Seasonal changes in the standing stocks, growth rates, and production rates of gelatinous predators in Saanich Inlet, British Columbia. Mar Ecol Prog Ser 33:89–98

Lee S, Whitledge T, Kang S (2007) Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. Cont Shelf Res 27:2231–2249

Lee SH, Joo HM, Liu Z, Chen J, He J (2012) Phytoplankton productivity in newly opened waters of the Western Arctic Ocean. Deep Sea Res II 81:18–27

Li WKW, McLaughlin FA, Lovejoy C, Carmack EC (2009) Smallest algae thrive as the Arctic Ocean freshens. Science 326:539

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Res 27:209–220

Matsuno K, Yamaguchi A, Hirawake T, Imai I (2011) Year-to-year changes of the mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and 2007, 2008. Polar Biol 34:1349–1360

Matthews JBL, Hestad L (1977) Ecological studies on the deep-water pelagic community of Korsfjorden, western Norway. Sarsia 63:57–63

Moore SE, George JC, Coyle KO, Weingartner TJ (1995) Bowhead Whales Along the Chukotka Coast in Autumn. Arctic 48:155–160

Moore SE, George JC, Sheffield G, Bacon J, Ashjian C (2010) Bowhead whale distribution and feeding near Barrow, Alaska, in late summer 2005–06. Arctic 63:195–205

Nelson RJ, Carmack EC, McLaughlin FA, Cooper GA (2009) Penetration of Pacific zooplankton into the western Arctic Ocean tracked with molecular population genetics. Mar Ecol Prog Ser 381:129–138

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, OHara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2015) vegan: Community Ecology Package. R package version 23-1

Pavshtiks AE (1994) Composition and quantitative distribution of the zooplankton in the East Siberian Sea. In Ekosistemy, flora i fauna Chaunskoi guby Vostochno- Sibirskogo morya., pp. 17–47. Zoological Institute RAS, St. Petersburg

Pavshtiks EA (1984) Zooplankton of the Chukchi Sea as indices of water origins. Trudy Arkticheskogo i Antarkticheskogo Nauchno-Issledovatel'skogo Instituta 368:140–153

Percy JA (1989) Abundance, biomass, and size frequency distribution of an arctic ctenophore, Mertensia ovum (Fabricius) from Frobisher Bay, Canada. Sarsia 74:95–105

Pickart R, Pratt L, Torres D, Whitledge T, Proshutinsky A, Aagaard K, Agnew T, Moore G, Dail H (2010) Evolution and dynamics of the flow through Herald Canyon in the western Chukchi Sea. Deep Sea Res II 57:5–26

Pisareva MN, Pickart R, Torres D, Moore GWK (2015) Flow of Pacific water in the western Chukchi sea: results from the 2009 RUSALCA expedition. Deep Sea Res I 105:53–73

Questel JM, Clarke C, Hopcroft RR (2013) Seasonal and interannual variation in the planktonic communities of the northeastern Chukchi Sea during the summer and early fall. Cont Shelf Res 67:23–41

Roff J, Hopcroft RR (1986) High precision microcomputer based measuring system for ecological research. Can J Fish Aquat Sci 43:2044–2048

Sakshaug E (2004) Primary and Secondary Production in the Arctic Seas. pp. 57–81. Springer Berlin Heidelberg, Berlin, Heidelberg

Springer A, McRoy C, Turco K (1989) The paradox of pelagic food webs in the northern Bering Sea - II. Zooplankton communities. Cont Shelf Res 9:359–386

Springer AM, Roseneau DG, Murphy EC, Springer MI (1984) Environmental Controls of Marine Food Webs: Food Habits of Seabirds in the Eastern Chukchi Sea. Can J Fish Aquat Sci 41:1202–1215

Stepanova VS (1937) Biological indicators of currents in the northern Bering and southern Chukchi Seas. Issledovanija Morei SSSR 25:175–216

Tremblay JÉE, Robert D, Varela DE, Lovejoy C, Darnis G, Nelson RJ, Sastri AR (2012) Current state and trends in Canadian Arctic marine ecosystems: I. Primary production. Clim Change 115:161–178

Wassmann P, Kosobokova K, Slagstad D, Drinkwater KF, Hopcroft RR, Moore SE, Ellingsen I, Nelson RJ, Carmack E, Popova E, Berge J (2015) The contiguous domains of Arctic Ocean advection: Trails of life and death. Prog Oceanogr 139:42–65

Weingartner TJ, Danielson S, Sasaki Y, Pavlov V, Kulakov M (1999) The Siberian Coastal Current: A wind- and buoyancy-forced Arctic coastal current. J Geophys Res 104:29697–29713

Weingartner TJ, Dobbins E, Danielson S, Winsor P, Potter R, Statscewich H (2013) Hydrographic variability over the northeastern Chukchi Sea shelf in summer-fall 2008–2010. Cont Shelf Res 67:5–22

Wickham H (2009) ggplot2: Elegant Graphics for Data Analysis. Springer Science

Woodgate RA, Weingartner TJ, Lindsay R (2012) Observed increases in Bering Strait oceanic fluxes from the Pacific to the Arctic from 2001 to 2011 and their impacts on the Arctic Ocean water column. Geophys Res Lett 39:L24603

3 Population structure and production of four sibling species of *Pseudocalanus* spp. in the Chukchi Sea[1]

3.1 Abstract

Copepods of the genus *Pseudocalanus* are important members of zooplankton communities in temperate and polar shelf regions, but few studies have focused on their species-specific biology due to the very subtle morphological differences between the species. We assess the distribution, population structure and production of four co-occurring species of *Pseudocalanus* across the Chukchi Sea during 2004, 2009 and 2012. Our approach used a combination of microscopic identification and species-specific PCR to discriminate between the species. Currently the arctic *P. acuspes* dominates the genus (50-90%), with the relative distribution of species closely linked to water mass distribution and variations in physical properties, making *Pseudocalanus* important indicators of water mass origin. Although the temperate *P. newmani* had a significant presence throughout the Chukchi Sea, its stage distribution suggests that they recruit poorly in cold waters. Direct temperature-manipulation experiments further suggest that the reproductive activity of the two temperate species is inhibited at low temperatures, while the arctic *P. acuspes* exhibits reduced fitness and lower reproductive capacity when temperatures are increased to 10°C. Our results suggest that shifting oceanographic patterns and climate warming will have unequal impact on this genus, arising from species-specific differences in life histories and tolerance to environmental conditions.

3.2 Introduction

The Chukchi Sea shares many features with other shallow Arctic Shelf seas, including ice-cover throughout a large portion of the year. However, in the summer months (June-September) it is dominated by advective processes and becomes largely Pacific in character. The unique hydrography of the Chukchi Sea, as well as its role as both an Arctic

---

[1] Submitted to *Journal of Plankton Research* as E. A. Ershova, J. Questel, K. N. Kosobokova, R. R. Hopcroft. Population structure and production of four sibling species of *Pseudocalanus* spp. in the Chukchi Sea.

and seasonally sub-arctic habitat, result in unique patterns within the zooplankton communities (Eisner *et al.*, 2012; Ershova *et al.*, 2015a; Hopcroft *et al.*, 2010; Questel *et al.*, 2013). Copepods of the genus *Pseudocalanus* are common members of planktonic ecosystems of the Chukchi Sea, as they are in temperate, sub-polar and polar seas throughout the northern hemisphere. Despite a comparatively small body size, their extremely high abundance together with high production rates (Hopcroft and Kosobokova, 2010; Liu and Hopcroft, 2008) make them one of the most important components of shelf zooplankton communities. Within the Chukchi Sea, *Pseudocalanus* spp. can contribute up to 50-90% of mesozooplankton abundance and 10-15% of zooplankton biomass (Ershova *et al.*, 2015a). Five of the seven species of this genus are reported from the Pacific Arctic region. *Pseudocalanus acuspes* and *P. minutus* are circumpolar species, shared with all Arctic and sub-Arctic shelf seas; they are also common in the northern Bering Sea, which is oceanographically similar to the Chukchi Sea. *Pseudocalanus newmani* and *P. mimus*, on the other hand, are temperate species that are common throughout the North Pacific and are considered expatriates in the Arctic. While some studies have also reported *P. major* in the Chukchi Sea (i.e. Matsuno *et al.*, 2011) its occurrence has never been confirmed by taxonomists or other research groups with more intensive efforts in the region; even if present, this species likely plays a miniscule role in the overall community.

Closely related species can often share a very similar morphology, but differ substantially in their biology, thus playing distinctive roles within an ecosystem. There are numerous examples among high-latitude planktonic copepods, including *Pseudocalanus* spp., of congeneric species exhibiting distinct behavior and life history and contributing unequally to secondary production (e.g. Conover, 1988; Miller and Clemons, 1988; Renz *et al.*, 2008). Studies on species-specific biology of high-latitude organisms become particularly important in light of the rapid climate-related changes in their environment, which may shift conditions to favor some species while being detrimental to their close relatives. With longer ice-free seasons (Wood *et al.*, 2015), increasing water temperatures (Luchin and Panteleev, 2014) and observed shifts in phytoplankton communities (Arrigo and van Dijken, 2011), the Chukchi Sea is adapting to a "new normal" climate

(Wood *et al.*, 2015), forcing changes in the pelagic system (Ershova *et al.*, 2015b). One expectation of climate related change is that there will be shifting prominence of closely related species. As Chukchi Sea conditions become more "boreal" for longer periods of the season cycle, the advected warm-water species, such as *P. newmani* and *P. mimus*, may have an opportunity to play an increased role in their communities. This may occur at the expense of the "resident" arctic *P. acuspes* and *P. minutus*, whose life history is thought to be closely linked to seasonal ice retreat and ice-associated production.

Despite the wide distribution and the foundational role of *Pseudocalanus* spp. in pelagic ecosystems, comparatively little is known about their species-specific biology and ecology. Species-specific studies are generally hampered by very subtle morphological differences between the species, particularly at juvenile stages, when they become virtually indistinguishable (Frost, 1989). Molecular studies on this genus suggest that even adults are systematically misidentified (Aarbakke *et al.*, 2011; Bucklin *et al.*, 2015). The mitochondrial cytochrome oxidase I (COI) gene is a commonly-used barcoding tool to identify cryptic species. In recent years multiple molecular protocols were developed using COI to discriminate between several co-existing *Pseudocalanus* species, shedding some light on their distribution, abundance, and population genetics (Aarbakke *et al.*, 2014, 2011; Bucklin *et al.*, 2015). However, with the exception of a handful of studies published within the last year (Bailey *et al.*, 2015; Cleary *et al.*, 2015; Questel *et al.*, 2016), most of this research has been restricted to the Atlantic sector (Aarbakke *et al.*, 2014; Bucklin *et al.*, 2001, 2015; Grabbert *et al.*, 2010), while the majority of researchers still only focus on adult females, which may poorly represent the entire species population.

In this work, we examined species-specific aspects of *Pseudocalanus* spp. in the Chukchi Sea during summers of 2004, 2009 and 2012 within the framework of the Russian-American Long Term Census of the Arctic (RUSALCA) program. The present study is the first to examine the species-specific distribution, population structure, and production of all four *Pseudocalanus* spp. in the Pacific Arctic using a species-specific polymerase chain reaction (ssPCR) to discriminate between species.

3.3 Methods

3.3.1 Physical environment

Three expeditions occurred within the RUSALCA framework: August 4-25, 2004, September 4-27, 2009 and September 2-24, 2012 (Fig. 3.1). The thermal characteristics of the region, distribution and properties of the water masses and overall patterns in zooplankton communities in the Chukchi Sea during the three expeditions are described in detail elsewhere (Ershova *et al.*, 2015b; Pickart *et al.*, 2010; Pisareva *et al.*, 2015a,b). Overall, 2004 was the warmest of the three study years, with an average surface temperature (SST) of 6.3°C over the sampled stations, and with surface waters as warm as 10-12°C present along the Alaska Coast and the entrance of the Herald Valley region. The years 2009 and 2012 were markedly colder, with the coldest SST observed in September 2012, averaging only 3.4°C. The warm and fresh water of the Alaska Coastal Current (Alaska Coastal Water, ACW) was constrained to the eastern shelf in 2012, resulting in a strong temperature gradient from east to west. In 2004 this water mass type also occupied the surface waters of a number of stations in the southwestern Chukchi (Fig. 3.1). During the 2009 expedition the ACW was diverted by northerly winds onto the western shelf region and into Herald Valley (Pisareva *et al.*, 2015b). Bering Sea Anadyr Water, characterized by colder temperatures and oceanic salinity, was found on stations through the central Chukchi and on the eastern side of Herald Canyon. Cold and fresh Siberian Coastal Water (SCW) was present in 2009 and 2012 near the coast of Siberia and around Wrangell Island. Cold and saline resident Chukchi Winter Water (WW), usually overlain by ice Melt Water (MW) was constrained to the northern Chukchi region in 2004 and 2009; in 2012 it was also observed in the southern sampling domain at the stations approaching the Siberian coast (Pisareva *et al.*, 2015a) (Fig. 3.1).

3.3.2 Plankton collection and processing

Zooplankton samples were collected using 150-μm double ring nets of 60cm mouth diameter. The nets were hauled vertically over the entire water column from within 3-5

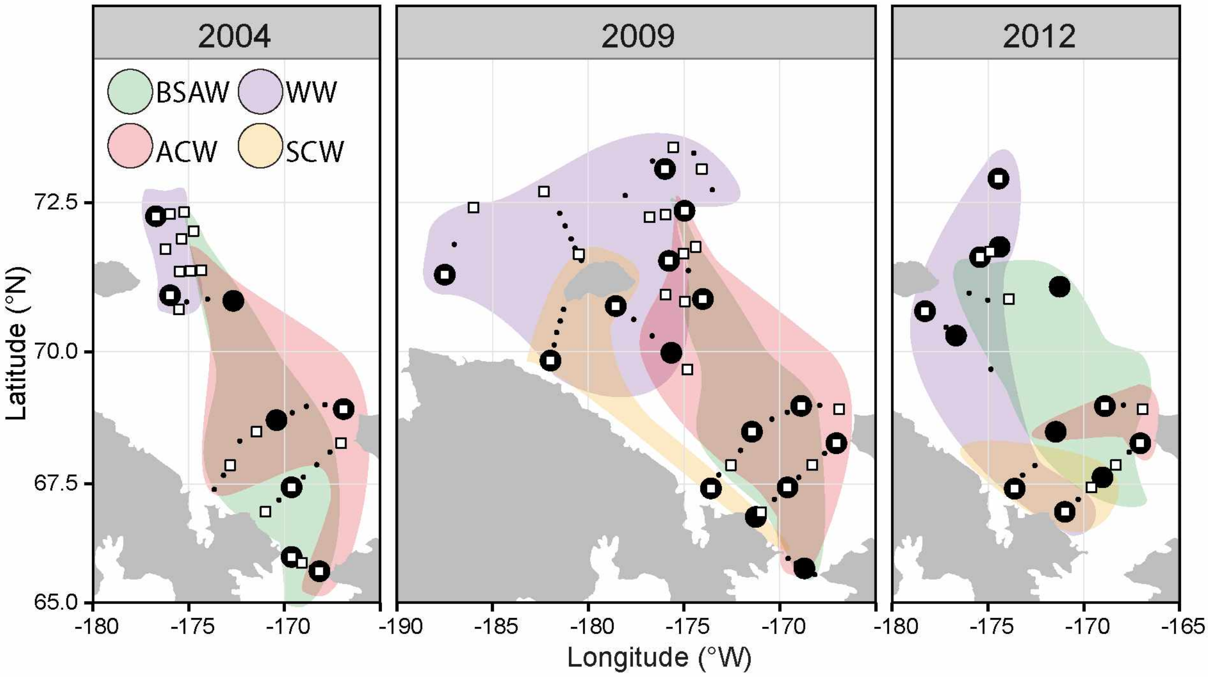

Figure 3.1: Map of Chukchi Sea region with station locations in 2004, 2009 and 2012. Small black dots indicate stations where quantitative zooplankton samples and CTD data were collected; large black dots indicate stations where molecular identification of Pseudocalanus spp. was obtained; white squares indicate stations where egg production experiments were carried out. Color overlays indicate water mass types present at the stations (based on Pisareva *et al.*, 2015a): BSAW – Bering Sea Anadyr Water; ACW – Alaska Coastal Water; WW – Winter Water; SCW – Siberian Coastal Water

meters of the seafloor to the surface. The average depth over the entire sampling area was 40-50m. The total volume of water filtered through the nets was measured using General Oceanics or Sea-gear flow meters, which were positioned at the mouth of each net, and rigged not to spin during descent. Upon retrieval, one of the samples was preserved in 10% formalin and the other in 95% molecular-grade ethanol.

The formalin preserved samples were processed in the laboratory to determine community composition, abundance and biomass (see Ershova *et al.*, 2015a). *Pseudocalanus* spp. adult females were identified to the species level; all juveniles and adult males were simply classified as *Pseudocalanus* spp. All individuals were separated into copepodite stages (C1-C5/AF/AM) and measured using a computer measurement system (ZoopBiom software, Roff and Hopcroft, 1986). Typically, a minimum of 80-100 individuals were enumerated per station. The dry weight (DW) of each organism was predicted from a length-weight regression relationship for this genus (Liu and Hopcroft, 2008). Total abundance and biomass were calculated by scaling the subsample counts of each copepodite stage with the total volume filtered by each net. *Pseudocalanus* nauplii were excluded from analysis because they are generally extruded by 150-μm nets.

Oceanographic data was collected at each station with a Seabird 911+ CTD equipped with an oxygen sensor, transmissometer and fluorometer (e.g. Pickart *et al.*, 2010), with all physical data binned into 1-m intervals during post processing. Due to the frequent layering of distinct water masses at a single location, surface (averaged for 0-10m), bottom (averaged for 10m above sea floor), and mid-water temperature (10m-10m above sea floor) and salinity values at each station were examined as separate variables. Chlorophyll *a* samples were collected by Niskin bottles on the CTD rosette every 5 m from the surface to bottom, filtered at low pressure onto GF/F filters, and analyzed fluorometrically (Lee *et al.*, 2007; Yun *et al.*, 2016, 2014). Mean mixed-layer as well as maximum chlorophyll values were used in the analysis.

3.3.3 ssPCR identification

Species-specific primers were designed for each of the 4 species of *Pseudocalanus* spp. using 710-base pair (b.p.) cytochrome oxidase I (COI) consensus sequences obtained from Questel *et al.* (2016). The forward primer was common for each species (PseudoF, 5'-TTCGAATAGAGYTAGGHMVAGY-3') (Questel *et al.*, 2016); the reverse primers were selected from different sites along the COI gene at regions that were conserved within a species, yet allowed enough sequence variability between them (a minimum difference of 2 b.p.). Primers were selected using CodonCode Aligner (www.codoncode.com/aligner) and were examined for annealing temperature compatibility and primer dimer formation using online tools from Fisher Scientific. The species-specific primers were as follows, with numbers in the primer names indicating the location along the consensus sequence.

- acuspes238R; 5'-AGAGGAGGGTATACAGTTCACC-3'
- newmani522R; 5'-CACCCCCACCAACATCRTAG-3'

- minutus398R; 5'-CGCAAACARAGGTATTTGGTCT-3'
- mimus93R; 5'-ACYAGCCAGTTACCAAAACCC-3'

The resulting amplification products for each species were of different lengths and were thus distinguishable using gel electrophoresis (Fig. 3.2).

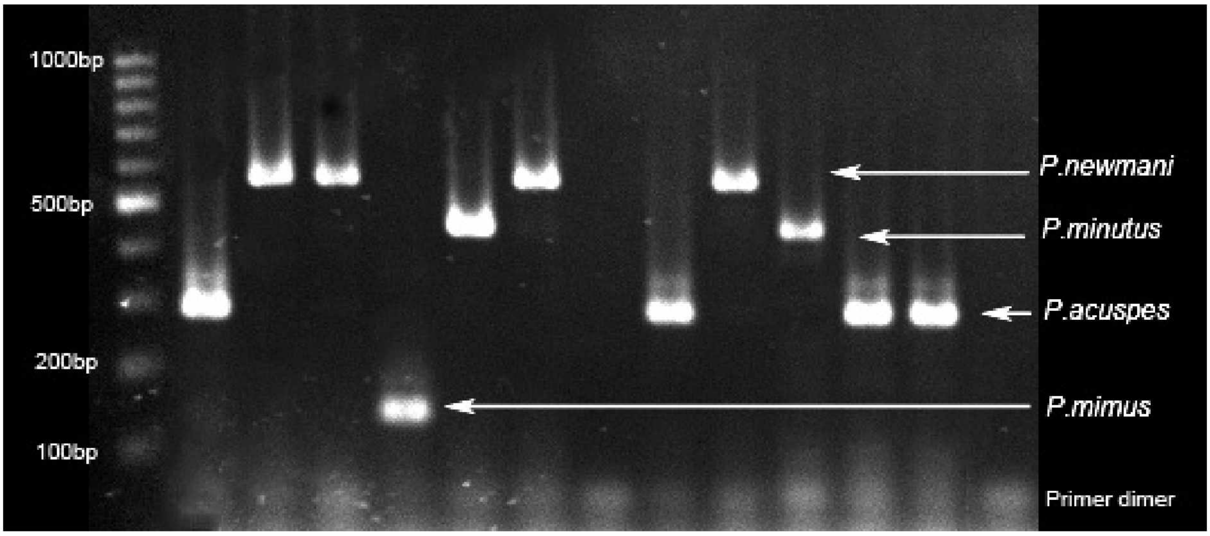

Figure 3.2: Example of species-specific sPCR results with all four species of *Pseudocalanus* spp. present

Species-specific abundance and population structure was examined at 27 stations (Fig. 3.1). Stations were selected to represent the different water mass and community types that we observed during the 3 study years (Ershova *et al.*, 2015a). Between 100-200 individuals of *Pseudocalanus* spp. were randomly selected from each station for molecular identification, with a minimum of 15 and typically 20-30 individuals of each copepodite stage selected per station. Insufficient numbers of adult males occurred within most samples to reach such thresholds. The stage, sex (for C5's and adults) and prosome length of each individual was recorded. To evaluate the accuracy of routine visual identifications, of adult females were keyed to species based on prosome length and head shape (Frost, 1989). The copepods were soaked in distilled water for 20-30 minutes, and then transferred to individual wells on a 96-well plate, containing 16μl of distilled water. The plates were microwaved for 2 minutes to remove any remnants of ethanol. PCR master mix, including a mix of the 5 primers, was added to bring the total reaction volume to 25 μl.

No DNA extractions were done, and the PCR reactions were run with intact copepods in tubes, (Grabbert *et al.*, 2010). The amplification protocol was: 94 °C (40 sec); 60 °C (40sec); 69 °C (50 sec) for 35 cycles. The amplified DNA was electrophoresed on a 2% agarose gel, soaked in ethidium bromide solution and visualized under UV light. One negative and four positive controls for each species, confirmed by sequencing, were run with each 96-well plate. After confirming the morphological and morphometric differences between adult females of different species by obtaining results on ∼300 females, for expediency we only ran PCR on those females that had ambiguous characteristics. The abundance of each species at each station was calculated by overlaying the relative contribution of each species and stage from molecular identification onto the quantitative data obtained from the formalin-preserved samples.

3.3.4 Egg production experiments

Pseudocalanus spp. are sac-spawners that carry egg-clutches attached to their first abdominal segment until hatching. We measured egg production rates at 20 stations in 2004, 28 stations in 2009 and 12 stations in 2012 (Fig. 3.1) using established methods (Hopcroft and Kosobokova, 2010). For each experiment, 50-120 *Pseudocalanus* spp. females were placed individually into 70 mL polystyrene culture flasks containing 50-μm filtered seawater collected at the same station, then incubated at temperatures close (within 1-2°C) to ambient for 48 hours. Females were monitored every 24 hours for newly produced egg clutches; all reproducing individuals were removed and preserved individually. The remaining females were preserved together at the end of each experiment.

In the laboratory, preserved females were identified to species and the eggs were counted from each clutch. Prosome length of each female was measured, and its dry weight was estimated from length. Eggs were assumed to have a constant weight within each species, as predicted from mean diameters known for each species in this habitat (Hopcroft and Kosobokova, 2010). Egg production rate (EPR) was calculated for each species as the total number of eggs produced per day by all the females of that species in the experiment; EPR was averaged over 2 days. To standardize egg production to female size, we calculated specific egg production (SEP) for each species, dividing the weight of the produced eggs (assuming 0.14 pg C μm^{-3}; Kiørboe and Sabatini, 1994) by the female's mean body weight for each female within each experiment. Production rates were adjusted for temperature by standardizing SEP to 0°C using a Q_{10} value of 1.43 for in-situ sac-spawning adult copepods (Hirst and Bunker, 2003).

3.3.5 Secondary production

Secondary production was calculated as $P_i = g_i \times B_i$, where P_i was the production (μg DW m^{-3} day^{-1}), g_i was the growth rate and B_i was the biomass (μg DW $^{-3}$) of copepodite stage i. Growth rate (g_i) for copepodite stages C1-C5 was calculated at each station as $g_i = log(W_i + 1/W_i)/D_i$, where W was the mean dry weight (μg) obtained from length-weight regression relationship, and D was the developmental time in days from i to $i+1$ for this group of species (Liu and Hopcroft, 2008), adjusted for temperature using a Q_{10} of 2.6 for food-satiated sac-spawing juveniles (Hirst and Bunker, 2003). While other estimates for developmental times of different species of *Pseudocalanus* exist in literature, those selected best reflect the conditions and species composition of the Pacific Arctic. For adult females, g_i = SEP obtained at each station (or neighboring stations when experiments were not carried out at a location). Overall production for each species at each station was obtained by summing the production for each stage. This overall production estimate excludes production by naupliar stages, which can be significant during recruitment pulses (Renz *et al.*, 2007).

3.3.6 Temperature-controlled egg production experiments

We conducted temperature-controlled egg production experiments to assess the responses of the different species of *Pseudocalanus* using collections from the Gulf of Alaska in mid-September 2013 and from the northeast Chukchi Sea in early October 2013. A minimum of 60-90 females from each location were placed into 500 mL flasks (20-30 females per flask) containing filtered seawater and a food mixture and incubated at temperatures of

0, 3, 7, and 10°C. The food mixture consisted of frozen cultures of *Pavlova* spp. and *Isochrysis galbana*, and a live culture of *Thalassiosira weissflogii* (cultured at 20°C in F/2 medium on a 12 hour light/dark cycle). They were provided at a cell count ratio of 5:5:1, with a final phytoplankton concentration of $\sim$0.4 μg C mL^{-1} that is considered to be above the limiting food concentration for *Pseudocalanus* (Corkett and McLaren, 1978).

After allowing the females to acclimatize to the new conditions ($\sim$5-7 days), they were transferred to individual 70 mL flasks containing filtered sea-water and the phytoplankton mixture and incubated for an additional 7-10 days. The flasks were mixed by inversion 2-3 times a day to keep the algal cells suspended; every 72 hours the water was replaced with fresh seawater and food mixture. Females were examined twice a day for new clutches; once a female produced a clutch she was removed from the experiment. Prior to female preservation in 4% formalin, some egg clutches were gently removed with a probe. These eggs were counted and left to hatch in 10 mL of filtered seawater at the temperatures that they were produced. Eggs were monitored every 12 hours for hatching with the number of successfully hatched nauplii, stillborn nauplii and unhatched eggs recorded. At the conclusion of the experiment all remaining females were preserved in formalin.

Processing of females and egg clutches in the laboratory was similar to that described in the previous section. Egg production rates were calculated from the average number of eggs produced by all the living females in the experiment per day; rates were obtained for each 2-day period of the experiment. SEP rates were adjusted to temperature using a Q_{10} of 2.6 for food-satiated sac-spawing juveniles (Hirst and Bunker, 2003).

3.3.7 Statistical analysis

All statistical analyses were carried out in R. Differences in abundances, population structure (mean developmental stage) and egg production rates between years and species were compared using two-way ANOVA, with station-region used as a blocking factor. Significant interactions ($p < 0.05$) between categories were examined using the Tukey

HSD test. Mean stage of each species at each station was calculated when a minimum of 10 individuals of this species was identified at the station. For this reason, we do not show population structure of *P. mimus*, as there were very few stations where this criterion was met. The relationship of species abundances, size distributions and egg production rates to physical parameters were examined using multiple linear regression, with the best model selected using AIC (Akaike Information Criterion).

The distribution patterns of *Pseudocalanus* species complex were explored using cluster analysis and non-parametric multi-dimensional scaling (nMDS) using the R package "vegan" (Oksanen *et al.*, 2013). We investigated abundance matrices for pooled stages of 4 species (4 categories), as well as for each species divided into 3 groups: "early juveniles" (C1-C3), "sub-adults" (C4-C5) and "adults" (adult females and males) (i.e. 12 categories). As most researchers consider adult female abundances representative of the entire sub-adult population, we also investigated the patterns observed if only adult female abundances were employed (4 categories). Abundances were log-transformed and the Bray–Curtis similarity index was calculated for all stations during each year. Hierarchical cluster analysis using average linkage was carried out and qualitative separation of groups was established by overall similarity (∼65-70%). These resulting groups were superimposed on 2D plots of (nMDS) plots and spatial plots of study area. The relationships to physical factors were explored by establishing correlations to species abundances and environmental factors to the nMDS ordination, and via the BIOENV routine (Clarke and Ainsworth, 1993), which establishes the best set of correlations between two data matrices sharing samples or variables. Significance of these correlations was established using a permutation test (n=10000) at $p < 0.05$.

3.4 Results

3.4.1 Molecular identification

A total of 4300 individuals were identified using ssPCR. Failure rate (the number of individuals that failed to produce a distinct band) ranged from 0 to 50% per station,

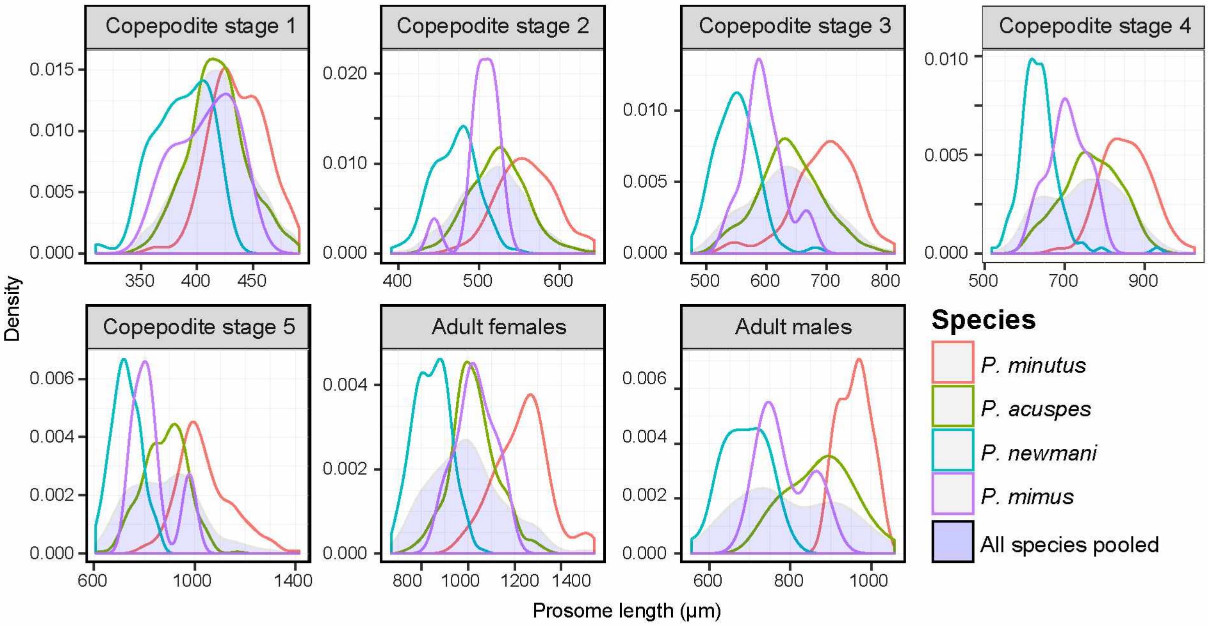

Figure 3.3: Density distribution of size frequencies for all developmental stages (C1-Adults) of 4 species of *Pseudocalanus* spp. in the Chukchi Sea. Shaded curve represents the density plot for each stage with all species pooled

and was highest in the oldest (2004) samples. Some reactions resulted in double banding (bright *P. acuspes* and faint *P. mimus* bands); sequencing these individuals always confirmed that they belong to *P. acuspes*. All four species of *Pseudocalanus* were identified successfully using this method. The results of molecular identification revealed that within adult females approximately 95% of *P. minutus* and 90% of *P. acuspes* and *P. newmani* were identified correctly based on morphology only. Within the misidentified individuals, small *P. minutus* were usually mistaken for *P. mimus*, and small *P. acuspes* and large *P. newmani* were confused where their size ranges overlap (Fig. 3.3). Of the 12 *P. mimus* females that were identified using ssPCR, only 5 were identified correctly using morphology only, the remaining 7 were mistakenly identified as *P. minutus* or *P. acuspes*.

The estimated probability function (Fig. 3.3) revealed that each species, with the exception of *P. mimus*, has a distinct size mode at each stage. However, the size classes overlapped significantly, particularly between *P. acuspes* and *P. newmani*, and increasingly so at younger stages. Pooling the species at each stage produced an indistinctly bi-modal distribution for the older individuals (C4 to adults); however at younger stages

Table 3.1: Abundance (ind m^{-3}), biomass (mg DW m^{-3}) and overall contribution (%) of 4 species of *Pseudocalanus* spp. in the Chukchi Sea in 2004, 2009 and 2012

	2004	2009	2012	*p*-value	Significant interactions
P. acuspes					
Mean abundance	630	1998	1784	0.05	2009 > 2004
Mean biomass	1.6	5.1	4.7		
% Total abundance	51	64.4	87		
P. minutus					
Mean abundance	232	372	171	0.15	none
Mean biomass	0.7	1.2	0.6		
% Total abundance	18.8	12	8.3		
P. newmani					
Mean abundance	295	714	92	0.01	2009 > 2012
Mean biomass	0.8	2.7	0.3		
% Total abundance	23.9	23	4.5		
P. mimus					
Mean abundance	79	15	3	0.01	2004 > 2009, 2012
Mean biomass	0.2	0.1	<0.1		
% Total abundance	6.4	0.3	0.2		
Total abundance	1236	3099	2050	0.03	2009 > 2004
Total biomass	3.3	9.1	5.6		

it resulted in a near-normal distribution without any distinct peaks.

3.4.2 Abundance and distribution

Pseudocalanus acuspes had highest abundance and biomass during the 3 years, composing 50-90% of all *Pseudocalanus* in the region (Fig. 3.4, Table 3.1). Mean abundance and biomass of *P. acuspes* was over three times higher in 2009 and 2012 than in 2004 ($p < 0.05$). Despite the similar values observed for this species in 2009 and 2012, *P. acuspes* played a much larger role relative to other species in 2012, composing nearly 90% of the *Pseudocalanus* population. On the other hand, abundance and biomass of *P. newmani* were highest in 2009 and drastically lower in 2012 ($p < 0.05$), accounting on average for only 4% of the *Pseudocalanus* observed during 2012 (Fig. 3.4, Table 3.1). Although overall occurrence of this species was lower in 2004 than in 2009 (NS), its relative contribution to abundance and biomass of *Pseudocalanus* was comparable. There were no significant differences between years in abundance of *P. minutus*; however, in 2004 its proportional contribution was ~2 times greater than in 2009 or 2012. *P. mimus* was the rarest of all species during all 3 years, but showed a significantly higher presence in 2004 than in 2009 and 2012 (Fig. 3.4, Table 3.1).

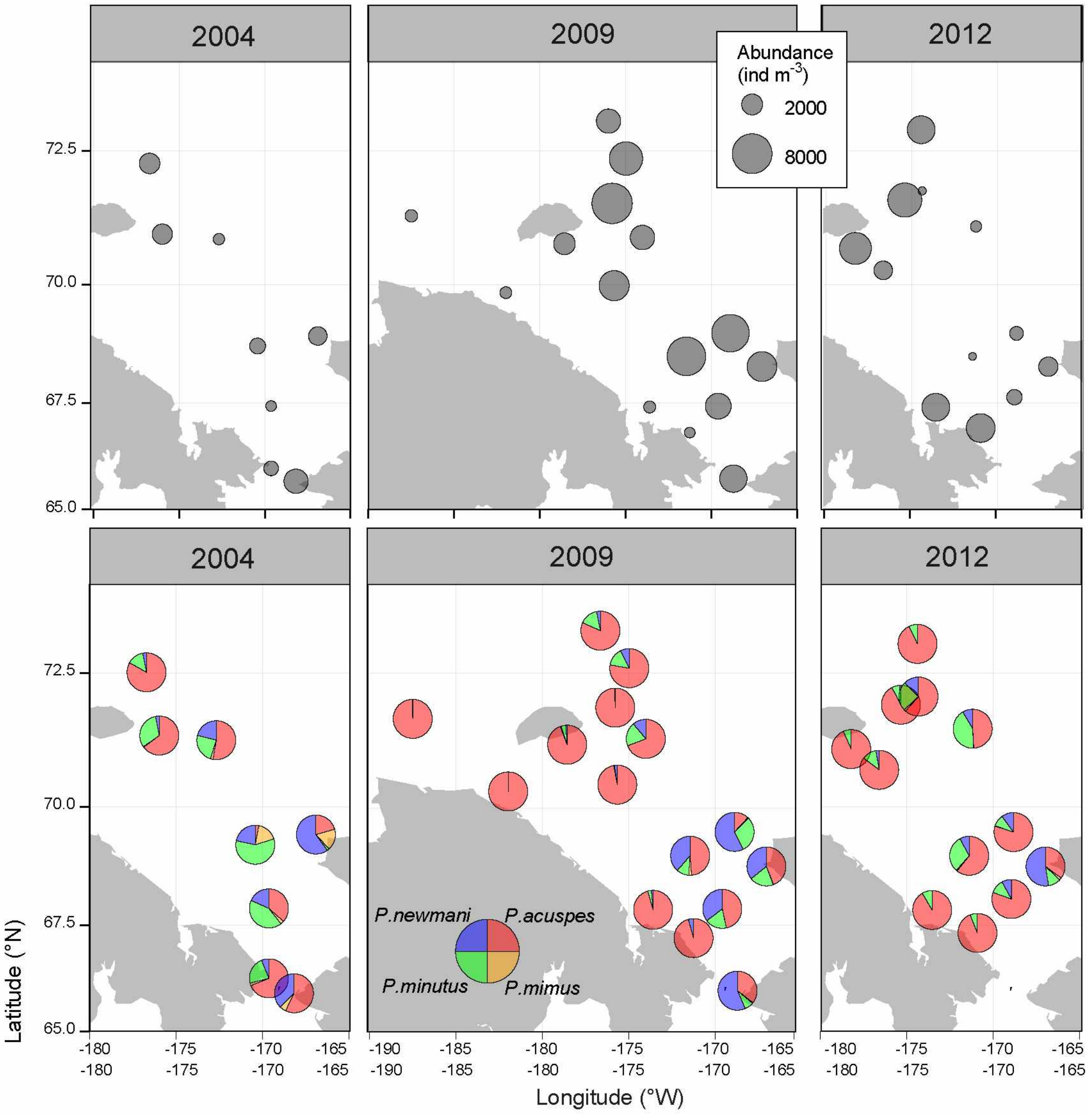

Figure 3.4: *Pseudocalanus* spp. abundance (ind m^{-3}) (a) and relative contribution of species at each station (b) for four species of *Pseudocalanus* spp. in 2004, 2009 and 2012

3.4.3 Species-specific population structure

No spatial or inter-annual differences in population structure were observed for the *P. acuspes* population, which generally consisted of all developmental stages, with the mean stage being 2.9-3.1 (Fig. 3.5). Adults rarely exceeded 10% of the population. On the other hand, the mean stage of the *P. newmani* population was significantly higher than

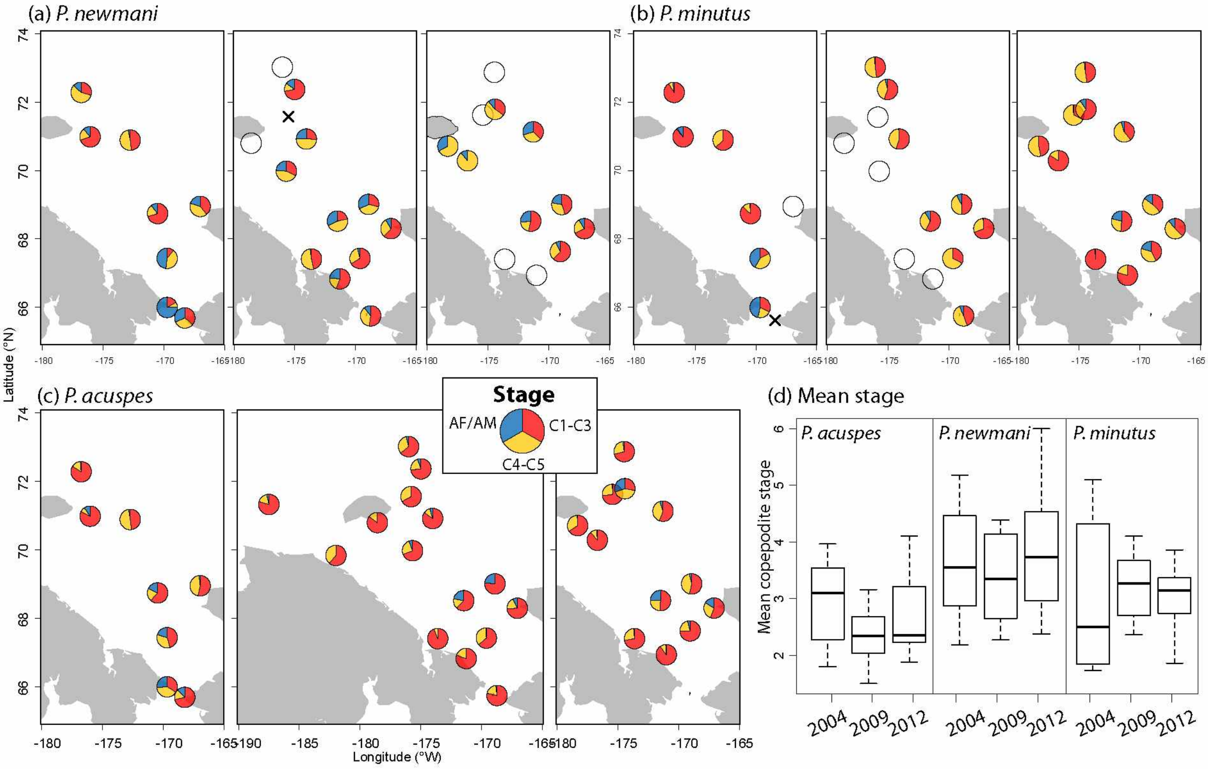

Figure 3.5: Relative contribution of early stage juveniles (C1-C3), late stage juveniles (C4-C5), and adults (AF/AM) for three *Pseudocalanus* species in the Chukchi Sea in summer during (a) 2004, (b) 2009 and (c) 2012; (d) shows median stage of each species per cruise

that of *P. acuspes* during all 3 years, especially in 2004 and 2012, when it was 3.8-4.0. No significant differences in stage distribution were observed between the years. The *P. minutus* population was heavily skewed towards later-stage juveniles (C4-C5's) in 2009 and 2012; in 2004 there was a sharp contrast between the southern stations, which were dominated by adults and later-stage juveniles, and the northern stations, which were almost entirely composed of early stages. The stations near the Siberian coast in 2009 and 2012 were notable in their almost complete absence of adults and later stages for both *P. acuspes* and *P. minutus* (Fig. 3.5).

3.4.4 Community structure and relationship to physical factors

Abundances of *P. newmani* and *P. mimus* showed a high positive correlation to temperature and salinity, with surface measurements producing the strongest relationship ($p < 0.01$, $r^2 = 0.46$ and 0.65, respectively). Abundance of *P. minutus* correlated with bottom

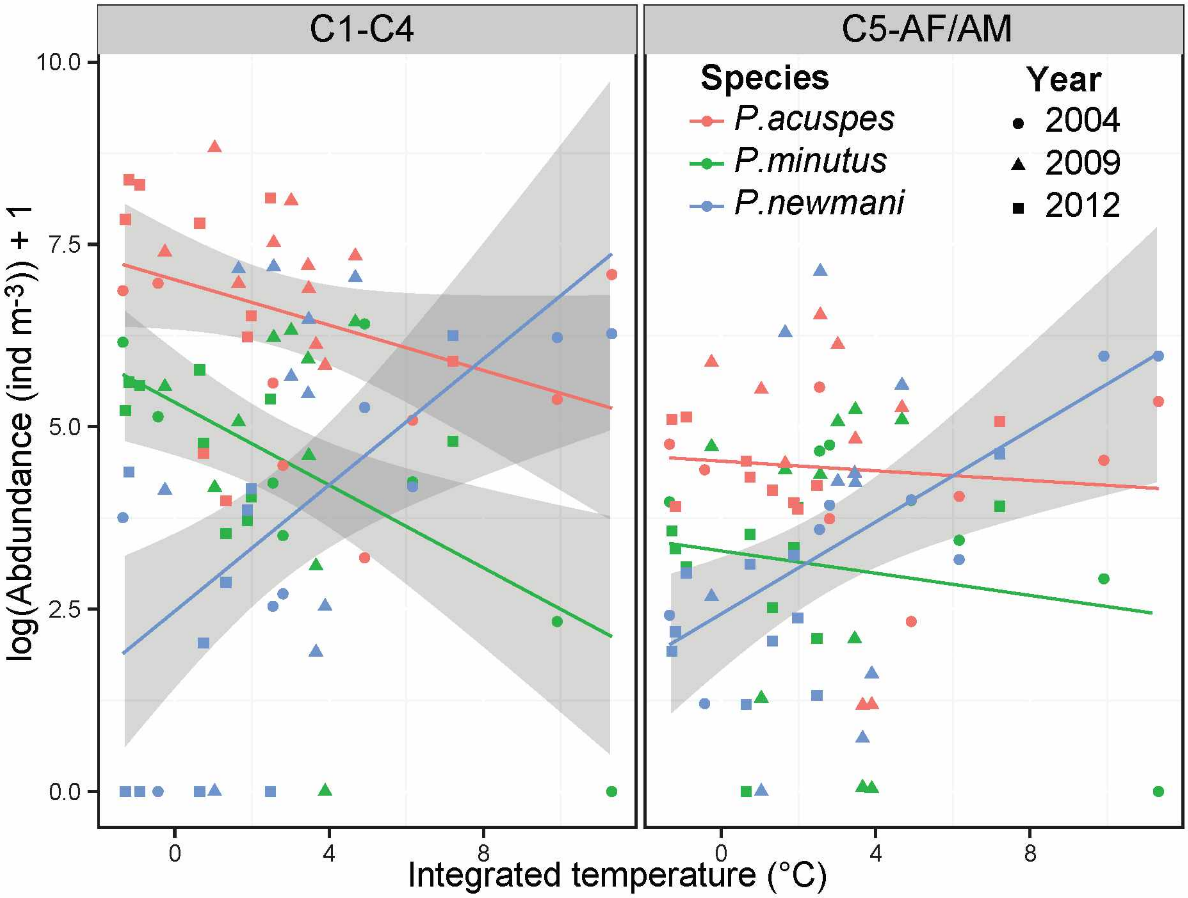

Figure 3.6: Abundance of younger (C1-C4) (a) and older (C5-adults) (b) of *Pseudocalanus acuspes*, *P. minutus* and *P. newmani* plotted vs. temperature. Different symbols indicate stations sampled during different years. Trendlines insignificant for for *P. minutus* and *P.acuspes* in (b)

salinity ($p < 0.01$, $r^2 = 0.35$), the relationship to temperature was statistically insignificant. When these environmental factors were incorporated into the multiple regression model with year as a categorical variable, differences in abundance between years became insignificant (with the exception of *P. mimus*, where 2004 >2009). In contrast, overall abundance of *P. acuspes*, while significantly different between years, was not significantly correlated to physical factors. The results were somewhat different when population structure was taken into account. Abundance of young copepodites (C1-C4) of *P. acuspes* showed a significant relationship to both temperature and salinity (p $<$ 0.05, $r^2 =$ 0.25), with higher abundances occurring at lower temperatures and higher salinities; but no such relationship was observed for adults plus sub-adults of this species (Fig. 3.6). While overall abundance of *P. minutus* was not significantly related to temperature, juveniles of this species (C1-C4) correlated negatively to bottom temperature, as well as bottom salinity; separating population into adults/sub-adults and juveniles resulted in an increased r^2 of 0.42 for the juveniles. Incorporating copepodite data did not improve the models for *P. newmani* or *P. mimus*.

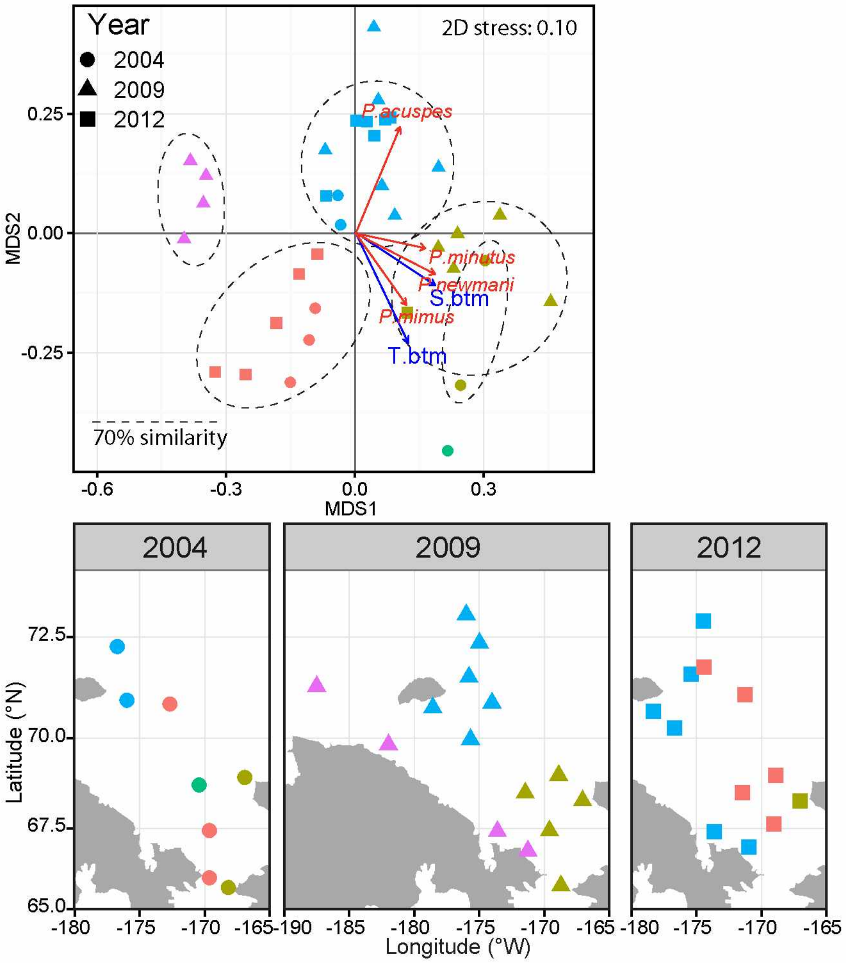

Figure 3.7: Multivariate analysis of log-transformed abundance of 4 species of *Pseudocalanus* in the Chukchi Sea in 2004, 2009 and 2012; (a) nMDS plot with vectors indicating correlations of species and variables to axes; colors represent station groupings at 65% similarity; dotted line indicates clusters at 70% similarity; (b) station clusters overlaid on map of study area

When relative abundances of species were examined together (each species split into 3 categories: juveniles C1-C3, C4-C5 and Adults (C6), the stations clustered into 5 distinct groups (with one outlier), with most groups containing stations from all 3 years. This separation was confirmed by nMDS ordination (2D stress = 0.1) (Fig. 3.7). Among the four species, abundance of *P. acuspes* was strongly and significantly correlated with MDS Axis 1, while *P. newmani* and *P. minutus* were driving Axis 2. Axis 2 was strongly driven by bottom temperature ($r = 0.88$, $p < 0.05$), while bottom salinity was the main factor driving Axis 1 ($r = 0.85$, $p < 0.05$). The groups identified by cluster analysis and nMDS corresponded exactly to the water mass types present at these stations (Fig. 3.1), confirming that the relative abundance of *Pseudocalanus* species was shaped by physical parameters and water mass distribution. The BIOENV routine predicted that the relative *Pseudocalanus* distribution was best correlated to all four variables, resulting in a Spearman's correlation of 0.48. Using overall species abundance (4 categories) produced similar, but slightly less robust results. On the other hand, when only adult female abundance was used and the copepodite stages were grouped as *Pseudocalanus* spp., no spatial structure or correlation to physical variables was observed.

3.4.5 Size structure

Since size is one of the main features routinely used to identify *Pseudocalanus* spp., we examined the distribution of size variability and its relationship to physical parameters (Fig. 3.8). In *P. acuspes* and *P. newmani*, prosome length of each stage correlated negatively to water temperature (p < 0.01, $r^2 = 0.25$-0.6), except for C1 and C2 of *P. newmani* where the number of observations was low. In *P. minutus*, the relationship was significant only for C2; no relationship could be established for C1 or older stages (C3-adults). No relationships were observed to salinity or chlorophyll for any species.

3.4.6 Egg-production rates

Daily specific egg production rates (SEP) (Fig. 3.9) were significantly higher for *P. acuspes* in 2004, when they averaged 15%, than in 2009 and 2012, when they were 8-9% (ANOVA, $p < 0.05$). For *P. newmani*, production rates were significantly higher in 2004 (14%) than in 2009 (7%); the differences between 2004 and 2012 (9%) were insignificant. Insufficient observations were obtained for *P. minutus* in 2009 and 2012 to compare their production between years. No significant differences in production rates were found between species; *P. newmani* displayed comparable SEP values to *P. acuspes* and *P. minutus* at all stations where they co-occurred.

SEP of *P. newmani* showed a strong positive correlation to log-transformed chlorophyll-*a* ($p < 0.001$, r^2=0.43); a weaker relationship was observed for *P. acuspes* ($p < 0.01$, $r^2 = 0.31$) and *P. minutus* ($p < 0.05$, $r^2 = 0.19$) (Fig. 3.10). Standardization of SEP

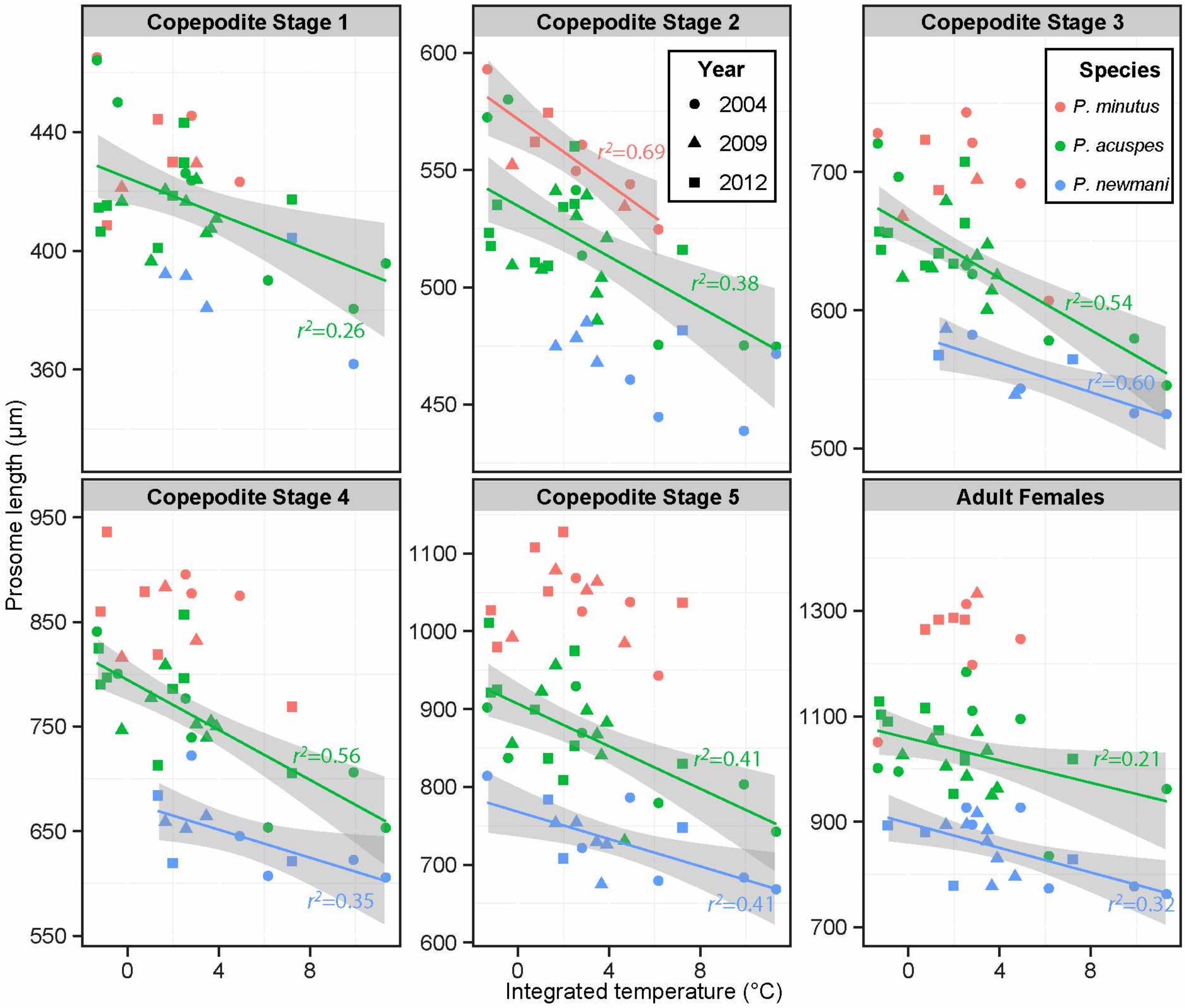

Figure 3.8: Prosome length vs. integrated temperature for all developmental stages of *P. acuspes*, *P. minutus* and *P. newmani* (pooled data for all years). Each point represents the mean size at a station where at least 5 individuals of this species and stage were observed. Lines show linear trends with 95% confidence interval. Only significant trends are shown

to 0°C using a Q_{10} value of 1.43 (Hirst and Bunker, 2003) improved the model for *P. newmani* ($r^2 = 0.48$); however, no significant improvement was observed for *P. acuspes*. For *P. minutus*, standardizing the SEP values to temperature made the relationship to chlorophyll non-significant; on the contrary, SEP values of this species showed a slight negative relationship to temperature (including temperature in the model improved r^2 to 0.21). The differences in production rates between years for *P. acuspes* and *P. newmani* remained significant even after accounting for chlorophyll and temperature.

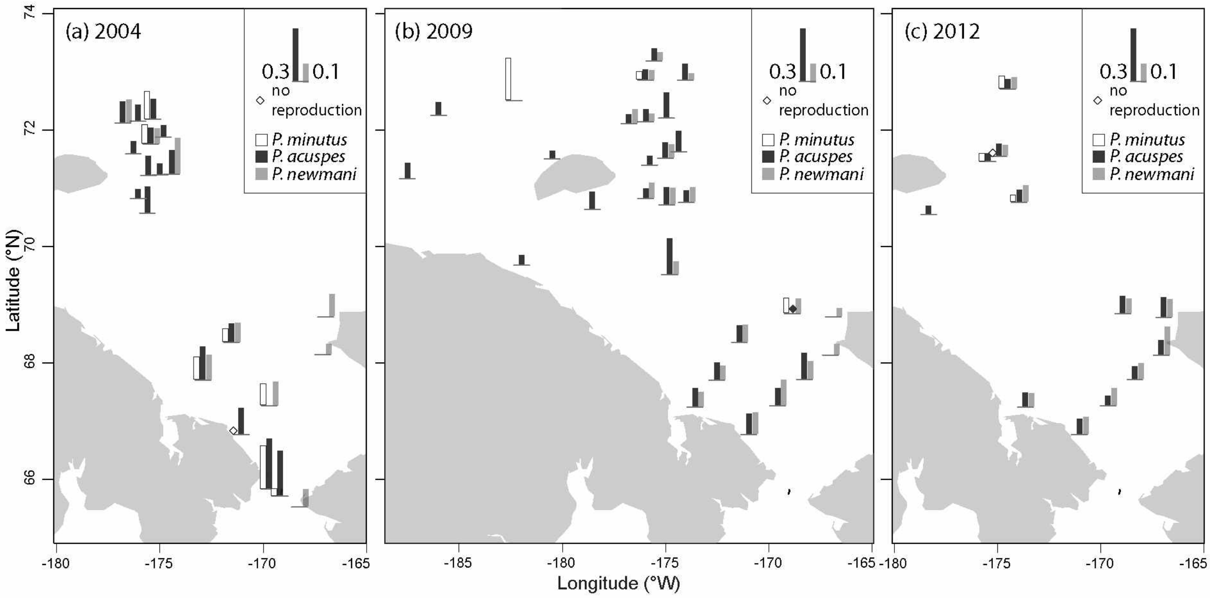

Figure 3.9: Daily specific egg production (SEP) of *P. acuspes*, *P. minutus* and *P. newmani* in the Chukchi Sea in 2004, 2009 and 2012. Diamonds represent at SEP of 0; empty bars indicate no experimental data for this species at this location

3.4.7 Temperature-controlled egg production experiments

Within the Chukchi Sea, the females were mainly identified as *P. acuspes* and *P. newmani*, with insufficient *P. minutus* obtained to estimate egg production rates. Clutch size for *P. acuspes* was significantly lower (by ~5 eggs) at 10°C than at 0 and 3°C ($p < 0.01$). No significant differences in clutch size were observed for *P. newmani*. Average Q_{10}-adjusted SEP of *P. acuspes* remained fairly constant at 0-7°C; but was slightly lower at 10°C, mainly due to smaller clutches produced by females. In contrast, SEP of *P. newmani* was lowest at 0°C, and highest at 3°C, with a small decrease in production observed at the highest temperatures (Table 3.2). Hatching success rates were variable within both *P. acuspes* and *P. newmani*, ranging from ~70-100%. Significantly lower hatching rates were observed for *P. newmani* at 0°C (Table 3.2), but no significant differences were observed between the other temperatures or for *P. acuspes*.

The females obtained from the Gulf of Alaska belonged primarily to *P. mimus*, with a smaller presence of *P. newmani*. Reproduction of *P. mimus* was extremely low at the coldest temperatures (0 and 3°C); at 0°C females nearly ceased reproducing. *P. newmani* exhibited lower reproduction rates at 0°C than individuals of this species collected in

Table 3.2: (a) Daily specific egg production (%) of *Pseudocalanus* spp. in the Chukchi Sea and Gulf of Alaska at 0, 3, 7 and 10°C (Q_{10}-corrected to 5°C); mean ± sd, (number of females); and (b) Hatching success rate (%) of *P. acuspes* and *P. newmani* in the Chukchi Sea at 0, 3, 7 and 10°C ; mean ± sd, (number of clutches)

(a)

	0°C	3°C	7°C	10°C	*p*-value	Significant interactions
Chukchi Sea						
P. acuspes	14±4	15±4	14±2	10±1	NS	none
	(38)	(30)	(31)	(29)		
P. newmani	6±2	13±3	12±1	12±2	< 0.01	0 < 3, 7, 10°C
	(53)	(39)	(42)	(46)		
Gulf of Alaska						
P. newmani	3±0	10±2	11±1	14±1	< 0.01	0 < 3, 7, 10°C; 10 > 3, 7°C
	(26)	(21)	(22)	(18)		
P. mimus	0±0	5±1	10±1	10±1	< 0.01	0 < 3, 7, 10°C; 3 < 7, 10°C
	(36)	(50)	(41)	(31)		

(b)

	0°C	3°C	7°C	10°C	*p*-value	Significant interactions
P. acuspes	77±23	72±24	90±10	91±7	NS	none
	(8)	(8)	(14)	(7)		
P. newmani	60±22	72±28	88±12	89±11	< 0.01	0, 3 < 7, 10°C
	(9)	(23)	(24)	(35)		

the Chukchi Sea; however, rates were higher than those observed for *P. mimus*. At 3 and 7°C, reproductive rates of *P. newmani* from the Gulf of Alaska were comparable to those obtained for *P. newmani* and *P. acuspes* from the Chukchi Sea, with highest rates observed at 10°C (Table 3.2).

3.4.8 Secondary production

Table 3.3: Secondary production, P (mg DW m^{-3} day^{-1}) and productivity, P/B (Production/Biomass) for three species of *Pseudocalanus* in 2004, 2009 and 2012, mean value (25%-75% quartiles)

	P. acuspes		*P. newmani*		*P. minutus*	
Year	P	P/B	P	P/B	P	P/B
2004	0.09 (0.03-0.16)	0.061	0.06 (0.01-0.09)	0.075	0.04 (0.01-0.06)	0.057
2009	0.17 (0.07-0.31)	0.031	0.10 (0.003-0.1)	0.037	0.03 (0.01-0.05)	0.027
2012	0.13 (0.05-0.21)	0.025	0.01 (0.003-0.01)	0.040	0.02 (0.01-0.02)	0.033

Total secondary production by *Pseudocalanus* spp. was estimated to be about 1.3 times higher in 2009 than in 2004 and 2012, however differences were not statistically

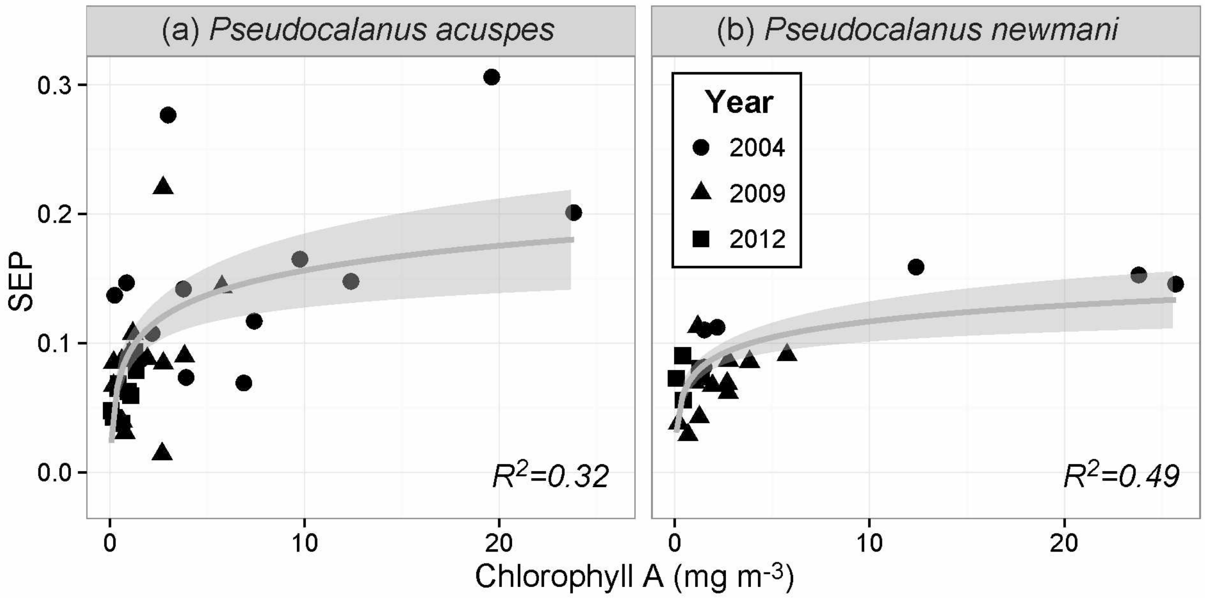

Figure 3.10: Daily specific egg production (SEP) in relation to maximum in-situ chlorophyll for (a) *P. acuspes* and (b) *P. newmani*

significant (Table 3.3). It is notable that although the biomass of *Pseudocalanus* spp. in 2012 was almost double that of 2004, production was nearly equal due to warmer temperatures and significantly higher daily production rates (ANOVA, Tukey HSD Test, $p < 0.05$) observed in 2004 (Table 3.3). Similarly, differences in secondary production observed between 2009 and 2004 were much less pronounced than the differences in abundance or biomass. Of the three species, contribution to secondary production was highest by *P. acuspes* during all three expeditions (ANOVA, Tukey HSD Test, $p < 0.05$). On the other hand, *P. newmani* had significantly higher daily production rate than the other two species (ANOVA, Tukey HSD Test, $p < 0.05$) during all three study years.

3.5 Discussion

This study is the first to detail species-specific production and distribution of four species of *Pseudocalanus* in the Pacific Arctic using a molecular method to discriminate between species. While other studies have implemented ssPCR to distinguish between two co-occurring species of *Pseudocalanus* (Aarbakke *et al.*, 2011; Bucklin *et al.*, 2015), this is the first to provide a method to discriminate between all 4 sympatric species found in the Pacific Arctic. Our results confirm their morphological ambiguity and the high variability in body size at all developmental stages, making size alone a poor predictor of species identity.

All four species were found within the Chukchi Sea; all but *P. mimus* were important contributors to zooplankton abundance and biomass. The arctic *P. acuspes* was the dominant *Pseudocalanus* species during all years and at most stations in terms of abundance, biomass, and production. However, abundance of its younger stages declined in warmer waters, and its reproductive output was slightly reduced at 10°C compared to lower temperatures, suggesting that this species could be negatively affected by warming of the region. The temperate *P. newmani* was present at nearly every station sampled and was more abundant in 2009, than 2004, despite the colder temperatures observed during 2009. Its reproductive activity was also comparable to that of *P. acuspes* and *P. minutus* at all but the lowest temperatures, and overall daily production rates were highest among the three species. Despite its southern origin, *P. newmani* seems to be well-adapted to the Chukchi environment in the summer months. The temperate *P. mimus*, on the other hand was practically absent from the communities in all years but 2004. This species is common in the Gulf of Alaska and the outer domain of the Bering Sea (Bailey *et al.*, 2015; Napp *et al.*, 2005), where they are the dominant species of *Pseudocalanus*. Their near absence in the Chukchi, and by inference, in the rest of the Pacific Arctic during most years suggests they have a lower tolerance for cold temperatures; this is also inferred by their elevated presence in the oceanographically-warmer summer of 2004 and by the extremely low reproductive rates observed for this species in the Gulf of Alaska at 0 and 3°C.

Even when data on seasonal dynamics of a species are not available, examining the developmental stage composition of a copepod population can provide important insight into the life history of a species. A continuously reproducing and growing population will be expected to have a lower mean stage than a population whose recruitment is paused or inhibited, due to the latter being dominated by longer-living later stages and adults. Although the production of the temperate *P. newmani* is comparable to that of *P. acuspes* and *P. minutus*, the prevalence of older copepodite stages of *P. newmani* suggests that recruitment may be arrested compared to the two Arctic species. This is further reinforced by the higher egg mortality of this species observed at 0°C temperatures that are typical for the Arctic environment. Additionally, our study emphasizes the importance of incorporating all life stages of a species into ecosystem studies, rather than just the adults. Distribution and abundance of adult females – the only *Pseudocalanus* developmental stage identified to species in most zooplankton community studies – failed to reveal the same strong patterns of association to water masses that we observed for the entire population (Fig. 3.7). The same species may also respond differently to environmental factors over the course of its life cycle. Varying tolerance over different ontogenetic stages to changing temperatures, salinity and CO_2 levels has been observed for several groups of marine crustaceans (Byrne, 2011; Miller *et al.*, 2013). The negative correlations to temperature that we observed for earlier stage juveniles of *P. acuspes* and *P. minutus*, but not adults and sub-adults, suggest that the earlier stages may be more vulnerable to climate-related increases in temperature.

The egg production rates that we observed in our study, particularly during the two colder years (2009 and 2012), are in the lower range or significantly lower than most those observed at lower latitudes for *Pseudocalanus* spp. in the North Pacific (Halsband-Lenk *et al.*, 2005; Lee *et al.*, 2003; Napp *et al.*, 2005). On the other hand, spring-time estimates of *Pseudocalanus* spp. reproduction in the southeastern Bering Sea (Vidal and Smith, 1986) report SEP rates of around 4-5.5%, which is substantially lower than we observed in Chukchi Sea in the summer at comparable temperatures. Egg production rates and daily production rates in 2009 and 2012 were similar to values obtained for *P. acuspes* in the Baltic Sea at substantially higher temperatures but lower salinity (Renz *et al.*, 2007), where SEP of females was 1-13% and maximum daily production rates were estimated to be around 3% $\text{day}^{-}1$. It should be noted that our estimates of production are snapshots in time, and assume consistent isochronal development across all species present, which is likely not the case. A study on the life cycles and population dynamics of temperate *P. elongatus* and arctic *P. acuspes* in the North Sea has shown that these two species differ dramatically in their life history, with the faster growing *P. elongatus* completing up to 4-5 generations per year, and the larger and slower growing *P. acuspes* never exceeding 1-2 generations (Renz *et al.*, 2008). This resulted in an almost 8-fold lower secondary production by *P. elongatus* despite comparable abundance values (Renz *et al.*, 2008). The smaller-bodied *P. newmani* may also have faster developmental times than *P. acuspes* and *P. minutus*, as has been demonstrated for some populations of *P. newmani* off the coast of Japan (Lee *et al.*, 2003), which suggests a likely underestimation of production rates for this species. Alternatively, if the advected population of *P. newmani* experiences arrested development in the Arctic environment, as their population structure suggests, then our production estimates may be too high.

Closely related and morphologically similar co-occurring species can nevertheless differ significantly in their biology and life history. Within the North Pacific system, the ecologically important *Neocalanus plumchrus* and *N. flemingeri*, which were only recently separated into two species (Miller and Clemons, 1988) are a notable example. Later studies demonstrated that these two species differ significantly in their reproductive strategy and life history, capacity to store lipids, and vertical habitat (Saito and Tsuda, 2000; Tsuda *et al.*, 1999). Few studies have focused on species-specific life history of *Pseudocalanus*, although the example of P. elongatus and *P. acuspes* in the North Sea (Renz *et al.*, 2008), show that the differences between species may be dramatic. Recent findings further suggest that different species of *Pseudocalanus* may have different feeding strategies, with *P. acuspes* diet consisting significantly of heterotrophic flagellates, and *P. minutus* and *P. newmani* feeding predominately on pelagic diatoms (Cleary *et al.*, 2015). The much stronger relationship of reproductive activity to in situ chlorophyll concentrations for *P. newmani* compared to *P. acuspes* supports these observations. *P. acuspes* and *P. minutus* are also believed to depend on sea-ice production (Conover *et al.*, 1986; Runge and Ingram, 1991); the common occurrence of these species in the Bering Sea (Bailey *et al.*, 2015) is likely a direct consequence of the Arctic-like ice dynamics that occur in that region. *Pseudocalanus* acuspes and *P. minutus* are also generally much larger in size, and richer in lipids, than their temperate counterparts (McLaren *et al.*, 1989), which has direct implications for higher trophic levels which rely upon these organisms as a food source.

Distribution of *Pseudocalanus* spp. in the Chukchi Sea is closely related to oceanography and water mass distribution, making them important indicator organisms of water mass types, as well as potential markers of climate-related change in the communities. Patterns of *Pseudocalanus* distribution (Fig. 3.7) are remarkably similar to those observed for the entire zooplankton community (Ershova *et al.*, 2015a), as well as the water mass types present at these stations (Fig. 3.1). It is notable that despite strong inter-annual variability, the stations grouped by water mass types, rather than by year. Nevertheless, the overall distribution, abundance and production patterns of *Pseudocalanus* spp. were markedly different during the oceanographically warm summer of 2004 from the colder summers of 2009 and 2012. Daily productivity of *Pseudocalanus*, driven by higher temperatures and a favorable food environment, was highest during 2004, despite the lowest overall abundances observed during that year. However, not all inter-annual differences observed can be attributed simply to thermal conditions. For example, despite ∼50% of the variability in *P. newmani* abundance being accounted for by temperature and salinity – with higher abundances observed at warmer temperatures – this species was most abundant during 2009 rather than the warmer 2004. It is likely that the spreading of the Alaska Coastal Current over the western Chukchi shelf and into Herald Valley during the time of the 2009 expedition (Pisareva *et al.*, 2015b) resulted in the increased presence of this species. The lower abundances of *Pseudocalanus* spp. observed during 2004 may reflect a number of different factors, such as a higher mortality due to predation or lower abundances and recruitment in the Bering Sea during that year. Alternatively, 2004 may simply reflect an earlier seasonal state, since the 2004 expedition occurred in August, while the years 2009 and 2012 were sampled in September. *Pseudocalanus* respond very rapidly to the surrounding environment, as seen from their instantaneously increased reproductive rates associated with higher food availability, as well as the strong relationship of body size to water temperature. Overall, temperature appears to be the main factor influencing *Pseudocalanus* spp. production and distribution (Liu and Hopcroft, 2008; McLaren and Corkett, 1978). This is manifested through direct effects, such as temperature-dependent growth and reproduction, as well as indirectly, through temperature controlled sex ratios (Lee *et al.*, 2003), growth inhibition through temperatures outside of the species' preferred thermal range (Klein Breteler *et al.*, 1995; Lee *et al.*, 2003), and effects on the overall pelagic ecosystem.

The on-going reduction in sea ice extent and timing of coverage in the Arctic Ocean has been particularly pronounced within the Pacific sector (IPCC, 2013; Wood *et al.*, 2015). As the ice free summer becomes longer, and waters become warmer within the Chukchi Sea region, we expect to observe a shift in the biological communities. A significant increase in overall zooplankton biomass has already been observed over the past century (Ershova *et al.*, 2015b), and several Pacific species within the fish communities (Wassmann *et al.*, 2015) may have extended their ranges northward. Since life cycles of *P. acuspes* and *P. minutus* may be highly dependent on sea ice algae production, reduction in winter ice extent in the Bering Sea may result in a range contraction of these species, decreasing their advected biomass into the Chukchi Sea. Furthermore, a longer ice-free summer in the Chukchi may continue to negatively impact these two arctic species, which may be stressed by the increasing temperatures, while benefiting the advected Pacific species. On the other hand, at present *P. acuspes* successfully inhabits many temperate seas in the north Atlantic and does not appear to be particularly stressed by temperatures up to 13°C in some locations (Ershova *et al.*, 2016). The reduced ability of *P. newmani* and *P. mimus* to accumulate and store lipids (Aarbakke *et al.*, 2011; Bucklin *et al.*, 2015; McLaren *et al.*, 1989) will likely prevent them from establishing self-sustaining populations in the Arctic due to seasonal ice-cover and limited primary production during the winter months, thus restricting them to the summer months. Most likely, a combination of abiotic, biotic, and oceanographic factors will determine who will be the "winners" and "losers" in the Chukchi Sea under climate change scenarios.

3.6 Conclusions

The distribution of the four species of *Pseudocalanus* in the Chukchi Sea is tightly linked to water mass distribution and thermal regimes in the region, making this assemblage important markers of water mass origin, as well as potential sentinels of climate change. The contribution and northward penetration of the two temperate species, *P. newmani* and *P. mimus*, is expected to increase with warming temperatures and increasing inflow from the Pacific during the summer months, although it is unlikely that they will establish self-sustaining populations in the Arctic. Shifting oceanographic and climate patterns may have unequal impacts on the different species, as determined by their individual life histories and tolerance to environmental conditions. Studying species-specific biology of closely related species, such as *Pseudocalanus* spp. may provide researchers with important insights on ecosystem shifts under climate change scenarios.

3.7 References

Aarbakke, O. N. S., Bucklin, A., Halsband, C. and Norrbin, F. (2014) Comparative phylogeography and demographic history of five sibling species of *Pseudocalanus* (Copepoda: Calanoida) in the North Atlantic Ocean. *J. Exp. Mar. Biol. Ecol.*, **461**, 479–488.

Aarbakke, O. N. S., Bucklin, A., Halsband-Lenk, C. and Norrbin, F. (2011) Discovery of *Pseudocalanus moultoni* (Frost, 1989) in Northeast Atlantic waters based on mitochondrial COI sequence variation. *J. Plankton Res.*, **33**, 1487–1495.

Arrigo, K. R. and van Dijken, G. L. (2011) Secular trends in Arctic Ocean net primary production. *J. Geophys. Res.*, **116**, 1–15.

Bailey, J., Durbin, E. G. and Rynearson, T. (2015) Species composition and abundance of copepods in the morphologically cryptic genus *Pseudocalanus* in the Bering Sea. *Deep Sea Res. II.*

Bucklin, A., Guarnieri, M., McGillicuddy, D. and Sean Hill, R. (2001) Spring evolution of *Pseudocalanus* spp. abundance on Georges Bank based on molecular discrimination of *P. moultoni* and *P. newmani*. *Deep Sea Res. II*, **48**, 589–608.

Bucklin, A., McGillicuddy, D. J. J., Wiebe, P. H. and Davis, C. S. (2015) Habitat usage by the cryptic copepods *Pseudocalanus moultoni* and *P. newmani* on Georges Bank (Northwest Atlantic). *Cont. Shelf Res.*, **111**, 83–94.

Byrne, M. (2011) Impact of Ocean Warming and Ocean Acidification on Marine Invertebrate Life History Stages: Vulnerabilities and Potential for Persistence in a Changing Ocean. *Oceanogr. Mar. Biol.*, **49**, 1–42.

Clarke, K. R. and Ainsworth, M. (1993) A method of linking multivariate community structure to environmental variables. *Mar. Ecol. Prog. Ser.*, **92**, 205–219.

Cleary, A. C., Durbin, E. G. and Rynearson, T. A. (2015) Feeding by *Pseudocalanus* copepods in the Bering Sea: Trophic linkages and a potential mechanism of niche partitioning. *Deep Sea Res. II.*

Conover, R. (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia*, **167**, 127–142.

Conover, R., Herman, A. W., Prinsenberg, S. J. and Harris, L. R. (1986) Distribution of and Feeding by the Copepod *Pseudocalanus* Under Fast Ice During the Arctic Spring. *Science*, **232**, 1245–1247.

Corkett, C. J. and McLaren, I. A. (1978) The biology of *Pseudocalanus*. *Adv. Mar. Biol.*, **15**, 1–231.

Eisner, L. B., Hillgruber, N., Martinson, E. and Maselko, J. (2012) Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi seas. *Polar Biol.*, **36**, 87–113.

Ershova, E. A., Hopcroft, R. R. and Kosobokova, K. (2015a) Inter-annual variability of summer mesozooplankton communities of the western Chukchi Sea: 2004-2012. *Polar Biol.*, **38**, 1461–1481.

Ershova, E. A., Hopcroft, R. R., Kosobokova, K., Matsuno, K., Nelson, R. J., Yamaguchi, A. and Eisner, L. B. (2015b) Long-Term Changes in Summer Zooplankton Communities of the Western Chukchi Sea, 1945-2012. *Oceanography*, **28**, 100–115.

Ershova, E. A., Kosobokova, K. N. and V, V. O. (2016) Changes in the egg production rates of two species of *Pseudocalanus* in relation to temperature in the White Sea. *Oceanology*, **56**, 592–598.

Frost, B. (1989) A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can. J. Zool.*, **67**, 525–551.

Grabbert, S., Renz, J., Hirche, H.-J. and Bucklin, A. (2010) Species-specific PCR discrimination of species of the calanoid copepod *Pseudocalanus*, *P. acuspes* and *P. elongatus*, in the Baltic and North Seas. *Hydrobiologia*, **652**, 289–297.

Halsband-Lenk, C., Pierson, J. and Leising, A. (2005) Reproduction of *Pseudocalanus newmani* (Copepoda: Calanoida) is deleteriously affected by diatom blooms – A field study. *Prog. Oceanogr.*, **67**, 332–348.

Hirst, A. G. and Bunker, A. J. (2003) Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. *Limnol. Oceanogr.*, **48**, 1988–2010.

Hopcroft, R. R. and Kosobokova, K. (2010) Distribution and egg production of *Pseudocalanus* species in the Chukchi Sea. *Deep Sea Res. II*, **57**, 49–56.

Hopcroft, R. R., Kosobokova, K. and Pinchuk, A. I. (2010) Zooplankton community patterns in the Chukchi Sea during summer 2004. *Deep Sea Res. II*, **57**, 27–39.

IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Kiørboe, T. and Sabatini, M. (1994) Reproductive and life cycle strategies in egg-carrying cyclopoid and free-spawning calanoid copepods. *J. Plankton Res.*, **16**, 1353–1366.

Klein Breteler, W., Gonzalez, S. and Schogt, N. (1995) Development of *Pseudocalanus elongatus* (Copepoda, Calanoida) cultured at different temperature and food conditions. *Mar. Ecol. Prog. Ser.*, **119**, 99–99.

Lee, H., Ban, S., Ikeda, T. and Matsuishi, T. (2003) Effect of temperature on development, growth and reproduction in the marine copepod *Pseudocalanus newmani* at satiating food condition. *J. Plankton Res.*, **25**, 261–271.

Lee, S., Whitledge, T. and Kang, S. (2007) Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. *Cont. Shelf Res.*, **27**, 2231–2249.

Liu, H. and Hopcroft, R. R. (2008) Growth and development of *Pseudocalanus* spp. in the northern Gulf of Alaska. *J. Plankton Res.*, **30**, 923–935.

Luchin, V. and Panteleev, G. (2014) Thermal regimes in the Chukchi Sea from 1941 to 2008. *Deep Sea Res. II*, **109**, 14–26.

Matsuno, K., Yamaguchi, A., Hirawake, T. and Imai, I. (2011) Year-to-year changes of the mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and 2007, 2008. *Polar Biol.*, **34**, 1349–1360.

McLaren, I. A. and Corkett, C. J. (1978) Unusual genetic variation in body size, development times, oil storage, and survivorship in the marine copepod *Pseudocalanus*. *Biol. Bull.*, **155**, 347–359.

McLaren, I. A., Sévigny, J. M. and Corkett, C. J. (1989) Temperature-dependent development in *Pseudocalanus* species. *Can. J. Zool.*, **67**, 559–564.

Miller, C. B. and Clemons, M. J. (1988) Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. *Prog. Oceanogr.*, **20**, 293–313.

Miller, N. A., Paganini, A. W. and Stillman, J. H. (2013) Differential thermal tolerance and energetic trajectories during ontogeny in porcelain crabs, genus *Petrolisthes*. *J. Therm. Biol.*, **38**, 79–85.

Napp, J. M., Hopcroft, R. R., Baier, C. T. and Clarke, C. (2005) Distribution and species-specific egg production of *Pseudocalanus* in the Gulf of Alaska. *J. Plankton Res.*, **27**, 415–426.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., OHara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. and Wagner, H. (2013) vegan: Community Ecology Package. R package version 2.0-9.

Pickart, R., Pratt, L., Torres, D., Whitledge, T., Proshutinsky, A., Aagaard, K., Agnew, T., Moore, G. and Dail, H. (2010) Evolution and dynamics of the flow through Herald Canyon in the western Chukchi Sea. *Deep Sea Res. II*, **57**, 5–26.

Pisareva, M., Pickart, R., Iken, K., Ershova, E., Grebmeier, J., Cooper, L., Bluhm, B., Nobre, C., Hopcroft, R. R., Hu, H., Wang, J., Ashjian, C., Kosobokova, K. and Whitledge, T. (2015a) The Relationship Between Patterns of Benthic Fauna and Zooplankton in the Chukchi Sea and Physical Forcing. *Oceanography*, **28**, 68–83.

Pisareva, M. N., Pickart, R., Torres, D. and Moore, G. W. K. (2015b) Flow of Pacific water in the western Chukchi sea: results from the 2009 RUSALCA expedition. *Deep Sea Res. I*, **105**, 53–73.

Questel, J., Blanco-Bercial, L., Hopcroft, R. R. and Bucklin, A. (2016) Phylogeography and connectivity of the *Pseudocalanus* (Copepoda: Calanoida) species complex in the eastern North Pacific and the Pacific Arctic Region. *J. Plankton Res.*, **38**, 610–623.

Questel, J. M., Clarke, C. and Hopcroft, R. R. (2013) Seasonal and interannual variation in the planktonic communities of the northeastern Chukchi Sea during the summer and early fall. *Cont. Shelf Res.*, **67**, 23–41.

Renz, J., Mengedoht, D. and Hirche, H.-J. (2008) Reproduction, growth and secondary production of *Pseudocalanus elongatus* Boeck (Copepoda, Calanoida) in the southern North Sea. *J. Plankton Res.*, **30**, 511–528.

Renz, J., Peters, J. and Hirche, H.-J. (2007) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: II. Reproduction, growth and secondary production. *Mar. Biol.*, **151**, 515–527.

Roff, J. and Hopcroft, R. R. (1986) High precision microcomputer based measuring system for ecological research. *Can. J. Fish. Aquat. Sci.*, **43**, 2044–2048.

Runge, J. and Ingram, R. G. (1991) Under-ice feeding and diel migration by the planktonic copepods *Calanus glacialis* and *Pseudocalanus minutus* in relation to the ice algal production cycle in southeastern Hudson Bay, Canada. *Mar. Biol.*, **108**, 217–225.

Saito, H. and Tsuda, A. (2000) Egg production and early development of the subarctic copepods *Neocalanus cristatus*, *N. plumchrus* and *N. flemingeri*. *Deep Sea Res. I*, **47**, 2141–2158.

Tsuda, A., Saito, H. and Kasai, H. (1999) Life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* (Calanoida: Copepoda) in the western subarctic Pacific. *Mar. Biol.*, **135**, 533–544.

Vidal, J. and Smith, S. L. (1986) Biomass, growth, and development of populations of herbivorous zooplankton in the southeastern Bering Sea during spring. *Deep Sea Res. I*, **33**, 523–556.

Wassmann, P., Kosobokova, K., Slagstad, D., Drinkwater, K. F., Hopcroft, R. R., Moore, S. E., Ellingsen, I., Nelson, R. J., Carmack, E., Popova, E. and Berge, J. (2015) The contiguous domains of Arctic Ocean advection: Trails of life and death. *Prog. Oceanogr.*, **139**, 42–65.

Wood, K. R., Bond, N. A., Danielson, S. L., Overland, J. E., Salo, S. A., Stabeno, P. and Whitefield, J. (2015) A decade of environmental change in the Pacific Arctic region. *Prog. Oceanogr.*, **136**, 12–31.

Yun, M. S., Whitledge, T., Stockwell, D., Son, S. H., Lee, J. H., Park, J. W., Lee, D. B., Park, J. and Lee, S. (2016) Primary production in the Chukchi Sea with potential effects of freshwater content. *Biogeosciences*, **13**, 737–749.

Yun, M. S., Whitledge, T. E., Kong, M. and Lee, S. H. (2014) Low primary production in the Chukchi Sea shelf, 2009. *Cont. Shelf Res.*, **76**, 1–11.

4 Long-term changes in summer zooplankton communities of the western Chukchi Sea, 1945-2012[1]

4.1 Abstract

The Chukchi Sea pelagic ecosystem, which is finely tuned to the seasonal ice formation and retreat, has been experiencing dramatic oceanographic change related to shifting sea ice cover and increasing temperatures over the last decades. We examine historical datasets on zooplankton communities in the central Chukchi Sea during the time period spanning 1946-2012. Analysis is confounded by differences between years in terms of spatial coverage, seasonal variability, and methodology; nonetheless, trends remain detectable when a sufficient number of study years are compiled. In addition to high levels of inter-annual variability, we demonstrate significant increases in zooplankton biomass and abundance in recent years compared to historical studies, as well as shifting distribution ranges for several key species. This signal is most pronounced within the copepods, particularly *Calanus glacialis*, which appears to be indirectly benefiting from warming of the region. While summer zooplankton communities of the Chukchi Sea have been primarily Bering-Pacific in character for as long as our records exist, continuing warming and ice loss are increasing the influence of Bering-Pacific fauna within the Chukchi region.

4.2 Introduction

The Chukchi Sea is an important transition zone between the Pacific and Arctic Oceans, being a significant source of heat, fresh water, and organic carbon for the latter. The Pacific water entering the Bering Strait is rich in nutrients, phytoplankton and zooplankton and is responsible for the exceptionally high productivity of the Chukchi Sea compared to other Arctic shelf seas (Kosobokova and Pertsova, 2012). This environment is changing rapidly as manifested by sea ice concentrations consistently below the long-term mean for the last decade (Wood et al., 2015), a longer ice-free summer period, and above-average

---

[1] Published as E. A. Ershova, R. R. Hopcroft, K. N. Kosobokova, K. Matsuno, R. J. Nelson, A. Yamaguchi, L. Eisner (2015) Long-term changes in summer zooplankton communities of the western Chukchi Sea, 1945-2012. *Oceanography* 28(3):100–115, DOI:10.5670/oceanog.2015.60

sea surface temperatures during most months. The environmental conditions within the region are presumed to propagate to the marine biological communities within this region, although proof of such change is so far elusive.

Planktonic communities in particular may serve as useful “beacons of climate change” (Richardson, 2008) due to their relatively short life cycles, rapid response in growth rates to changing temperatures, and dependence on ocean currents for dispersal. These attributes make them 2-3 times more responsive to climate-related changes than terrestrial communities (Richardson, 2008). A growing body of literature for many regions of the Arctic demonstrates the close relationship of zooplankton community structure to water column properties and water mass distribution (summarized in Wassmann et al., 2015). This relationship is particularly pronounced within the Chukchi Sea, where several incoming Pacific water masses of different origin carry distinct planktonic communities (Eisner et al., 2012; Hopcroft et al., 2010), that dilute or displace the resident Arctic shelf communities. With the higher frequency of warmer summer temperatures during recent years and a longer ice-free period, one would expect that Pacific species will be transported farther north into the Arctic and will remain in the plankton for longer periods of time, potentially competing for resources with resident Arctic species. A longer summer period and warmer waters may also lead to phenological shifts in plankton life history as has been reported for many plankton groups in various parts of the world (Richardson, 2008). Many Arctic and sub-Arctic species have life cycles that are finely tuned to the ice break up and seasonal phytoplankton blooms. An earlier ice retreat would potentially be damaging to these species and provide a competitive edge to organisms that are more opportunistic in their life history traits.

Unfortunately, historical time-series for pelagic communities do not exist within the Chukchi Sea. A number of sporadic, spatially isolated and methodologically inconsistent surveys have been conducted throughout the past century, beginning with the 1940’s, but many remain unpublished and buried in national journals and institutional reports. Most of these studies were confined to one of the two sides of a strongly enforced political border, with most early work done in Russian waters and the more recent studies being restricted to US waters. Sampling efforts have intensified significantly in the past 2 decades, fueled by interest both in climate change and the development of natural resources, but only recently have coordinated time-series begun to emerge (Grebmeier, 2012).

In the current work we present an outline and analysis of the modern and historical data available on zooplankton communities in the central and western Chukchi Sea region; examine the extent of variability within the communities; and explore some underlying mechanisms that may be responsible for driving these patterns. A central hypothesis is that within the earlier sampling years (1946-1976), the plankton communities of the Chukchi Sea are overall less "Pacific" in character and are more typical of Arctic shelf seas. Secondarily, we also anticipate phenological shifts have occurred in key species as a direct result of warmer temperatures and an earlier ice retreat. There are many challenges involved in such an attempt, the greatest being the highly variable spatial coverage and methodology of the historical and contemporary data. Documenting temporal or climatological trends is further complicated by the lengthy time gaps within the historical data, with several decades lacking any observations. Recent work done within the Chukchi Sea has repeatedly shown that planktonic communities exhibit an extremely high level of variability – spatially, seasonally and inter-annually (Ershova et al., 2015; Matsuno et al., 2011; Questel et al., 2013). Thus, one of the central challenges when examining a time series, such the one analyzed in this study, will be discerning natural variability vs. climate-mediated long-term change.

4.3 Methods

4.3.1 Description of datasets

We accumulated reports and publications on expeditions to the Chukchi during the 1900s and obtained later datasets directly from colleagues to build an extensive compilation of zooplankton studies conducted in the Central and Western Chukchi, along with matching physical oceanographic data, when available (Supplementary table 4.S1, Figure 4.1). We

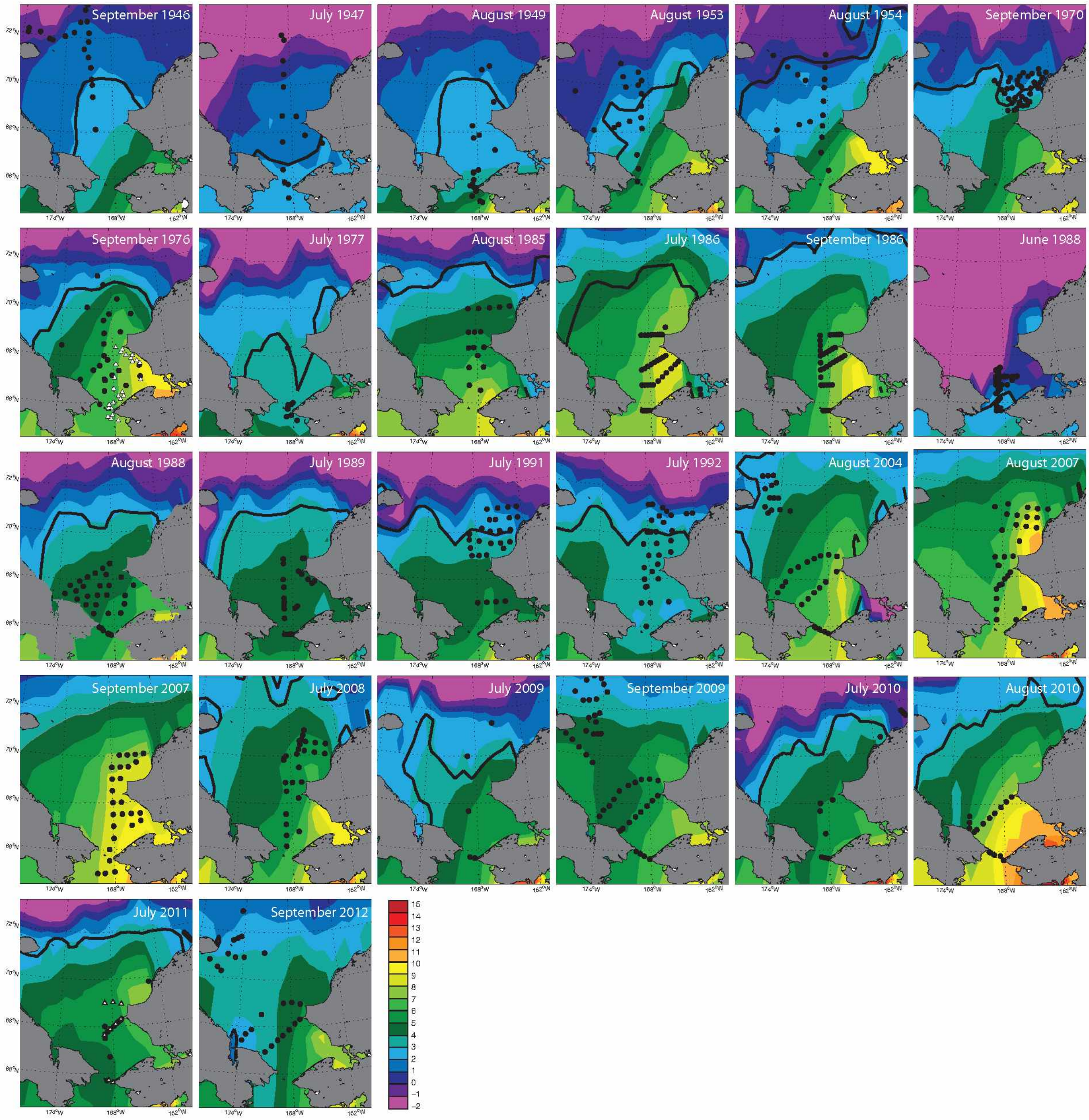

Figure 4.1: Monthly mean sea surface temperature in the Chukchi Sea during sampling years. The black line shows sea ice extent, and black dots indicate zooplankton stations sampled. The white triangles on the 1976 and 2011 maps indicate concurrent expeditions

have intentionally excluded studies that were confined to the shelf break (i.e. the Shelf Basin Interaction (SBI) program Grebmeier and Harvey, 2006, the Burton Island expedition, etc.) to avoid encompassing the distinct Arctic Basin communities (e.g/ Kosobokova and Hopcroft, 2010). Our compilation incorporated 28 expeditions reaching as far back as 1946 (on the Russian icebreaker "Severnyj Poljus"), and as recent as September 2012 (Russian Long-Term Census of the Arctic, RUSALCA). Most of the recovered datasets were spatially confined to either the US or Russian waters, with the notable exceptions of the 1976 expedition on RV "Mayak" (Pavshtiks, 1984), the 1988 BERPAC (Joint US-USSR Bering-Pacific Expedition) (Kulikov, 1992) survey and 4 RUSALCA expeditions (2004-2012) (Ershova et al., 2015). Overall, spatial coverage was highly variable between cruises, with several expeditions covering the entire Chukchi domain from the Bering Strait to 72°N and beyond, while other were confined to only the Southern Chukchi region or a small localized sampling region (i.e. WEBSEC 70, TT221). Most of the sampling efforts took place in the mid-summer months (July-August), however, several expeditions occurred in September, and one (TT221) took place in June, which is oceanographically early spring within the Chukchi Sea region. With the exception of September 1946, most sampling occurred when the areas was accessible by non-icebreaking vessels with ice cover less than 50 %.

4.3.2 Environmental data

Physical data (temperature and salinity) was compiled for most datasets (see Table 4.1) from cruise reports, the US National Ocean Data Center (NODC) or directly supplied by colleagues. Historical sea surface temperature and sea ice data were obtained from the Met Office Hadley Centre (http://www.metoffice.gov.uk/hadobs/hadisst/); modern SST data were obtained from NOAA at http://www.esrl.noaa.gov/psd/. Sea ice extent was defined as less than 15 % ice cover. Due to the frequent two-layer nature of water masses within this region, average surface (0-10 m) and bottom (10 m layer above bottom) temperature and salinity were calculated for each station. Bottom and surface waters at each station were then categorized into water mass types using cluster analysis, as well as subjective interpretation using literature values. Cluster analysis was performed using Euclidean distances of normalized values using the R library vegan (Oksanen et al., 2015). This method of water mass identification is approximate and may be somewhat inaccurate (particularly for the surface waters), but it provides a useful broad-scale approximation of the water masses present in the area historically.

4.3.3 Climatic indices

Within the North Pacific, variations in atmospheric indices such as the Pacific Decadal Oscillation (PDO) and Arctic Oscillation (AO) influence conditions in the marine environment as well as the biological communities that inhabit it (Hare and Mantua, 2000; Mantua et al., 1997). To examine the potential relationship of these indices to plankton variability in the Chukchi Sea, we obtained a 6-month average of each index for the winter months prior to each sampling year (November-April). Mean monthly values were obtained from the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) (http://research.jisao.washington.edu/pdo/) and the NOAA National Centers for Environmental Information (https://www.ncdc.noaa.gov/teleconnections/ao/).

4.3.4 Standarization and subsetting of biological data

The zooplankton data was highly variable in quality, with taxonomic resolution being vastly different (see Supplementary Table 4.S1). Many studies identified only the copepods to species or genus level, and grouped all remaining organisms into broad taxonomic categories (i.e. “Amphipods”, “Cnidaria”). High-resolution data (with 50+ taxonomic categories identified) was only available within the 2004-2012 RUSALCA expeditions, the “Dyson” 2007 expedition, the 2009-2011 “Laurier” expeditions, and the 1946 “Severnyj Poljus” expedition. Taxonomy was aligned using the Arctic Register of Marine species (Sirenko et al., 2015), and World Register of Marine Species (WoRMS Editorial Board, 2015) to establish synonyms and remove suspicious identifications. The species complex *Calanus glacialis*/*Calanus marshallae*, which is often indistinguishable morphologically, was considered to be primarily *C. glacialis* based on results from molecular analysis (e.g.

Nelson et al., 2009, John Nelson, pers. com.) and therefore simply referred to as *C. glacialis* within this analysis. The group "Large copepods" included *Calanus glacialis*, *Metridia* spp., *Neocalanus* spp., and *Eucalanus bungii*; the other copepod species were grouped into "Small copepods". While our dataset covers a span of nearly 7 decades, it inherently represents a patchy time-series, with large decadal gaps in the sampling years (1955-1970, 1992-2004).

The most complex problem in comparing zooplankton datasets was accounting for differences in the sampling gear used to obtain the samples, with the pore size of the mesh and mouth opening of the nets being of greatest concern. The type of sampling gear used to collect plankton samples is known to greatly influence the biomass, abundance and composition in the resulting data (Skjoldal et al., 2013). Most American studies historically employed coarse 500-μm nets (0.5 to 1m mouth diameter), while Russians used Juday nets (~170-μm, 0.37m mouth diameter) or Nansen nets (333-μm, 0.7m mouth diameter). The 500-μm nets under-sample the small organisms, such as small copepods and meroplankton, that generally constitute >90 % of total abundance within this region, while the 170-μm Juday nets may under-represent the larger, rarer and faster swimming species. Abundance values were always converted to ind m^{-3}. It is notable that average abundances reported for each expedition highlight that the coarse-mesh nets report an abundance of ~100-400 ind m^{-3}, while the fine mesh nets provide a value closer to ~1500-9000 m^{-3} (Supplementary Table 4.S1). For this reason, we only directly compare abundances of the large, widespread copepods, which are generally common enough to be well-represented by the fine mesh nets, but large enough for most stages to be captured by coarser nets. These large copepods are also the least likely to be misidentified. Species characteristic for the Alaska Coastal Water (ACW) communities were defined as coastal neritic species present in the Alaska Coastal Current in the Gulf of Alaska, and absent or very rarely observed elsewhere in the Chukchi Sea (Coyle et al., 1996; Ershova et al., 2015). While the list of these species is substantial, only those species large enough to be sampled adequately by the more commonly used coarser mesh nets (333μm and 500μm) were included to create the distribution maps for this community type.

While biomass estimates within this habitat are reported to be similar (i.e. within a factor of 1.5-2) across the range of the mesh sizes (150-500 μm) considered in this study (Questel et al. 2013), the methods for calculating zooplankton biomass varied during each expedition: most commonly, studies measured wet weight (WW) of the total sample (displacement volume); others measured WW of individual groups; some used linear measurements to predict dry weight (DW) or WW from length-weight regressions. We converted all available biomass values to mg DW m^{-3} using existing equations converting WW to DW for different groups of organisms (Kiørboe, 2013). When biomass data was not available, we used averaged biomass for each taxonomic category from published data (Ershova et al., 2015), which was then multiplied by the abundance values. Average yearly biomass was calculated for the sampling region south of 71°N and east of -180°W to maximize comparability between cruises.

We established temporal trends of overall biomass and abundance of key species using linear mixed effects models. Relationships of biomass and abundance to variations in the physical environment (temperature, salinity, water mass type, bottom depth, atmospheric indices) were also explored using mixed modeling. Fixed factors in the models included year, month, water temperature, salinity, bottom depth, water mass type present at each stations and mean AO and PDO signals for each year (6 month winter average); the random factors included station location (averaged to a 1°by 1°grid). We also included the gear used (net type) as a blocking factor. Abundance and biomass values were log transformed to account for unequal variance. Mixed modeling was performed in R using the lme4 (Bates et al., 2015) and nlme (Pinheiro et al., 2015) libraries. Significance was defined as $p < 0.05$. The data were examined for spatial correlation using R package geoR (Ribeiro and Diggle, 2015) and autocorrelation between years and was found to meet the assumptions of independence over space and time. The best model was selected using AIC (Akaike Information Criterion) using the R package bbmle (Bolker and Team, 2014). Multiple comparisons were estimated using the R library lmerTest (Kuznetsova et al., 2015). The relationships between zooplankton community structure and physical data for each dataset were explored using the BIOENV routine (Clarke and Ainsworth,

1993) from the R library vegan (Oksanen et al., 2015). This method establishes the best subset of environmental variables, so that the Euclidean distances of scaled environmental variables have the maximum correlation with the Bray–Curtis dissimilarity index of the community abundance data for each station (Oksanen et al., 2015). Community matrices contained log-transformed abundance of all species that contributed at least 3 % to transformed abundance. Ambiguous species and broad taxonomic categories were excluded from the analysis. The environmental matrix included normalized temperature and salinity for the bottom and surface 10 m layers. The significance of these correlations was established using Mantel's test of associations (Mantel, 1967).

4.4 Results

4.4.1 Physical environment

Overall, temperature and ice conditions during the sampling periods were variable, with colder conditions observed during the earlier sampling years (Figure 4.1). The ice edge during the period of sampling extended to at least 70°N during all years prior to 1992. The sea surface temperature also averaged less than 0-2°C at these latitudes. September 1986 was the warmest year of the pre-2000's sampling time period, with surface water temperatures of the sampling region averaging 7°C and the sea ice edge being north of 72°N in the eastern Chukchi. June 1988 was the coldest sampling period, with near-freezing temperatures and most of the Chukchi Sea still completely ice covered. This dataset reflects oceanographic spring, rather than summer conditions in the Chukchi. The climatic indices (PDO and AO) for the examined time span are shown in Supplementary Figure 4.S1.

The strong east-to-west gradient in SST across the Chukchi Sea shelf, associated with the Alaska Coastal Current, is visible during some of the sampling periods, while in others the warm surface water is smeared across the entire Chukchi domain (2004, 2007), or weakly pronounced (2009, July 1986, 1991). The datasets collected in the 2000's are variable in terms of sea surface temperatures, but the sea ice extent was always observed

Table 4.1: Summary of Chukchi Sea water mass characteristics concurrent with zooplankton sampling

Water Mass	Temperature	Salinity
Alaska Coastal Water (ACW)	>5	26-32
Bering Sea/Anadyr Water (BSAW)	0-5	31-33
Melt Water (MW)	<2.5	26-30
Siberian Coastal Water (SCW)	0-5	20-27
Winter Water (WW)	<0	31-33
MW/SCW	2.5-6	26-29
ACW/BSAW	2.5-10	29-32.5

much farther north (north of the plotted sampling region in 2004, 2007, 2009 and 2010). 2004, 2007 and 2010 stand out as particularly warm years, with SST in the Southern Chukchi region exceeding 10-12°C.

4.4.2 Description of water masses

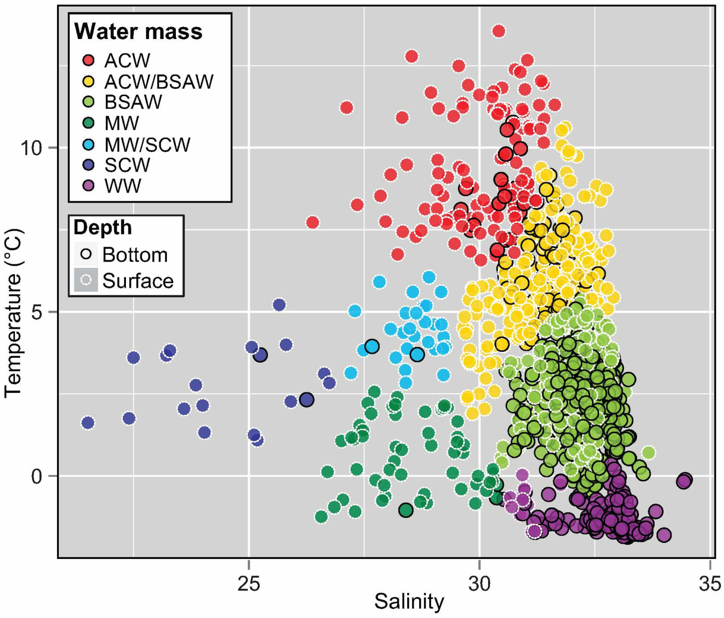

Figure 4.2: Temperature-salinity plot of water masses sampled concurrent with zooplankton collections in the Chukchi Sea, 1946–2012 (top/bottom 10 m properties). ACW = Alaska Coastal Water. BSAW = Bering Sea/Anadyr Water. MW = Melt Water. SCW = Siberian Coastal Water. WW = Winter Water

Five broad water mass types were identified as previously described in literature (Alaska Coastal Water (ACW), Bering Sea/Anadyr Water (BSAW), Winter Water (WW), Melt Water (MW), Siberian Coastal Water (SCW)) (i.e. Eisner et al., 2012; Pickart et al., 2010; Pisareva et al., 2015), as well as two water types with intermediate properties (BSAW/ACW, MW/SCW) (Figure 4.2, Table 4.1). It is notable that our characterization of BSAW is based on its typical summer proper-

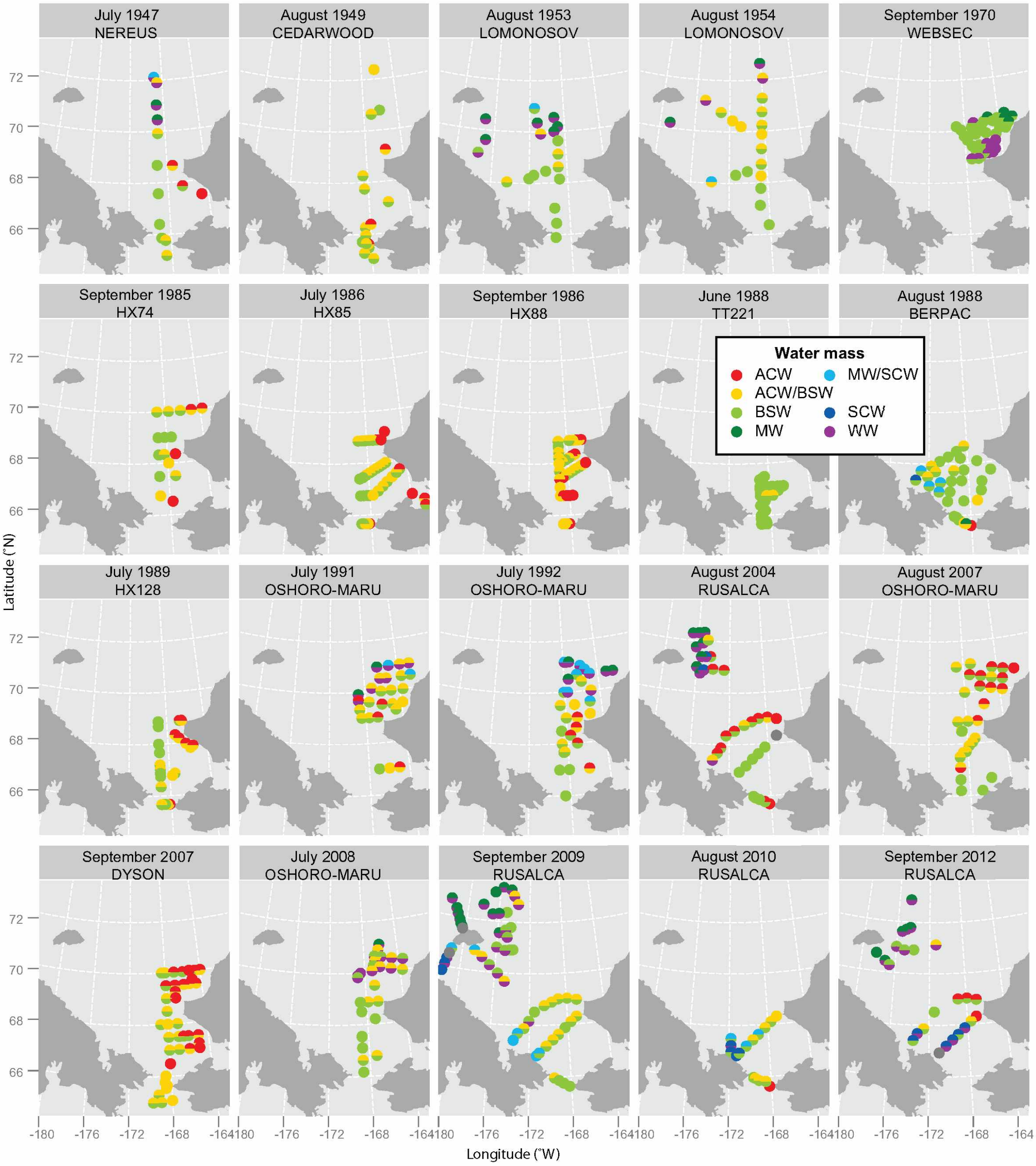

Figure 4.3: Distribution of water masses sampled in the Chukchi Sea, 1946–2012. Upper color on each symbol represents surface water type (top 10 m average), and lower color represents bottom water type (bottom 10 m average). ACW = Alaska Coastal Water. BSAW = Bering Sea/Anadyr Water. MW = Melt Water. SCW = Siberian Coastal Water. WW = Winter Water

ties, such that the seasonal timing of warming in the Bering Sea will strongly influence our ability to recognize this water type in the Chukchi Sea.

Overall, water mass distribution follows similar patterns from the oldest to the most recent study years (Figure 4.3). The warm and fresh ACW is the spatially most variable water mass among expeditions. During some years, ACW is found across almost the entire southern Chukchi domain (as observed in RUSALCA 2009); in others – it is completely absent, or limited to 1-2 coastal stations. During some years the ACW reached as far north as 71-72°N (e.g. during RUSALCA). Several Russian datasets fail to capture the ACW completely, because they sampled too far from the Alaskan coast. The colder and salty BSAW was present during every sampling year within the southern and central Chukchi Sea, and was found as far north as 70-71°N during most study years. BSAW was frequently found underlying the warmer and fresher ACW.

The very cold and salty WW, which forms in the fall and winter months as brine is expelled during sea ice formation, was found in the bottom waters north of 70°N during colder years and north of 72°N during the warmer years. Winter waters were generally overlaid by MW or advected Pacific water (ACW or BSAW). Fresh and cold SCW was only visible in datasets approaching close to the Russian coast, and only during some expeditions (SEVERNYJ POLJUS 1946; LOMONOSOV 1953; BERPAC 1988; RUSALCA 2009-2012). In September 2012 this water type was found in the central Chukchi, well away from the Siberian coast; it is possible that this water is in fact ice melt water, rather than belonging to the SCW.

4.4.3 Physics shaping planktonic communities

Within each individual year, bottom temperature was most commonly the strongest factor shaping community structure, although in some years this was surface temperature (Table 4.2). Including salinity improved the model in several instances. Salinity was the most important factor during 1949, both cruises in 1986, and June 1988. The relationship between physical properties of the water column and community structure was generally

Table 4.2: Pearson correlations (ρ) of variables determined via BIOENV analysis relating species abundance and physical parameters. T.surf/S.surf = surface temperature/salinity. T.btm/S.btm = bottom temperature/salinity

Cruise/Ship	Year	Month	Env. parameters (ρ)
"NEREUS"	1947	July	T.btm, 0.56
"CEDARWOOD"	1949	August	S.surf, 0.498
"LOMONOSOV"	1953	August	T.surf, 0.2
"LOMONOSOV"	1954	August	T.btm, 0.25
HX74	1985	Aug-Sept	T.btm, S.btm, 0.41
HX85	1986	July	S.surf, S.btm, 0.66
HX88	1986	Aug-Sept	S.btm, 0.45
BERPAC	1988	August	T.btm, 0.45
TT221	1988	June	S.surf, 0.43
HX128	1989	July	T.btm, 0.38
"OSHORO-MARU"	1991	July	T.btm, 0.34
"OSHORO-MARU"	1992	July	T.btm, 0.39
RUSALCA	2004	August	T.btm, S. btm, 0.65
"OSHORO-MARU"	2007	August	T.surf, S.btm, 0.48
"OSHORO-MARU"	2008	July	T.surf, S.surf, 0.28
RUSALCA	2009	September	T.btm, S. btm, 0.6
RUSALCA	2010	August	T.btm, 0.7
RUSALCA	2012	September	T.surf, 0.55

very pronounced, with Spearman's correlations being 0.4-0.7.

4.4.4 Annual biomass

Average yearly biomass in the southern Chukchi domain (south of 71°N and east of 180°W) ranged from 10 to 140 mg DW m^{-3} (average for all years ~65 mg DW m^{-3}); with variability between stations within some years spanning 4 orders of magnitude (0.5-700 mg DW m^{-3}) (Supplementary Table 4.S2). Substantially lower biomass (< 50 mg DW m^{-3}) was observed during most of the earlier study years (pre-1980), with the notable exception of 1954, when the biomass, driven by the high presence of large copepods, was significantly above average on several stations (overall mean 85 mg DW m^{-3}). Notably, this was also a year with warmer summer temperatures and a reduced ice extent compared to other years of that time period (Figure 4.1). During the later sampling years (1991-2012) the observed biomass was relatively similar, averaging 50-100 mg DW m^{-3}. The best fitting mixed model as determined by AIC included Year, Month, Water mass and

PDO/AO index. When examined over the entire southern sampling region, the increase in biomass observed over the seven decades was highly significant ($p < 0.01$) (Figure 4.4), with an average increase of 10 mg DW m^{-3} per decade. Stations containing BSAW or BSAW/ACW had significantly higher biomass (by an average of 20-30 mg DW m^{-3}) than stations containing other water mass types. Stations containing SCW had the lowest biomass of all water masses (Supplementary Table 4.S2). Mean PDO signal accounted significantly ($p < 0.05$) for some additional variability in biomass, with higher biomass observed during the cold-phase PDO years. The years sampled earlier in the summer (July) had significantly higher biomass than those sampled in August-October; the only spring cruise (TT221 in 1988) had substantially lower biomass than when sampled in August that same year (Supplementary Table 4.S2).

Given the strong association between water masses and planktonic communities, as well as the substantial differences in biomass between water masses, we will structure subsequent biological characterization around the water mass types.

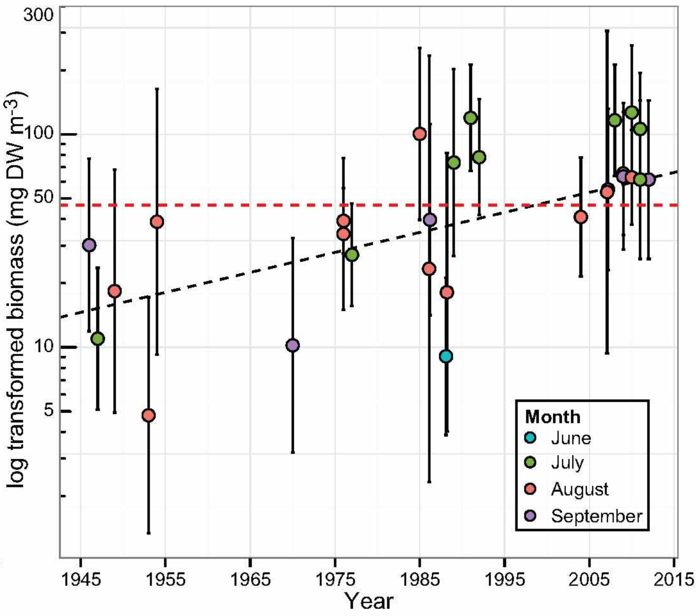

Figure 4.4: Mean log-transformed biomass vs. year sampled in the Chukchi Sea. Each symbol represents one cruise; bars represent 95% confidence interval. Black dashed line indicates fitted linear trend over averaged data. Red dashed line indicates long-term mean

4.4.5 Alaska Coastal (ACW) Communities

Alaska Coastal Waters stations were defined as those that contained ACW at least in the surface layer. While this definition introduces a certain degree of noise due to the nature of depth-integrated plankton data in a vertically layered physical

Table 4.3: List of mesozooplankton species characteristic for the Alaska Coastal Waters

Species	Typical body length (μm) (all stages)	Included in distribution map (Figure 4.6)
Evadne nordmanni	500-1200	yes
Podon leuckarti	150-1200	yes
Acartia hudsonica	250-1000	no
Eurytemora spp.	300-1000	no
Centropages abdominales	400-1400	yes
Pseudocalanus newmani	300-1000	no
Epilabidocera longipedata	2000-4000	yes
Tortanus discaudatus	1000-3000	yes

environment, it allows us to broadly compare these communities between years. Typically, communities inhabiting ACW were dominated by small copepods (*Pseudocalanus* spp., *Acartia* spp., *Oithona* spp.), meroplankton (mostly barnacle and bivalve larvae) and cladocerans, which were common during some years and nearly absent in others (Figure 4.5). Large, heavy Pacific copepods were absent or scarce within these communities; as a result, total biomass was generally lower than observed in Bering Sea waters (Supplementary Table 4.S2). Other taxa (chaetognaths, larvaceans) were present variably. The communities identified in ACW waters within the study year 2012 (RUSALCA) stood out by an unusually high biomass of large copepods and a near absence of meroplankton. The elevated biomass of large copepods is likely a consequence of the presence of significant volumes of BSAW very close to the Alaskan coast and the layering of ACW and BSAW. The absence of meroplankton, on the other hand, could be due to the late timing of the cruise and the abnormally cold temperatures that were observed during that year.

Overall, the distribution of species characteristic for ACW (Table 4.3, Supplementary Figure 4.S2) corresponds closely to the stations where ACW was present, although one of the species (*Centropages abdominalis*), while most common in ACW, was also present in smaller numbers in other water masses. Similar to water mass distribution, the distribution of ACW-specific taxa is highly variable year to year; during some years these organisms are localized to a few stations near the Alaskan coast while in others they are found throughout the entire Chukchi domain.

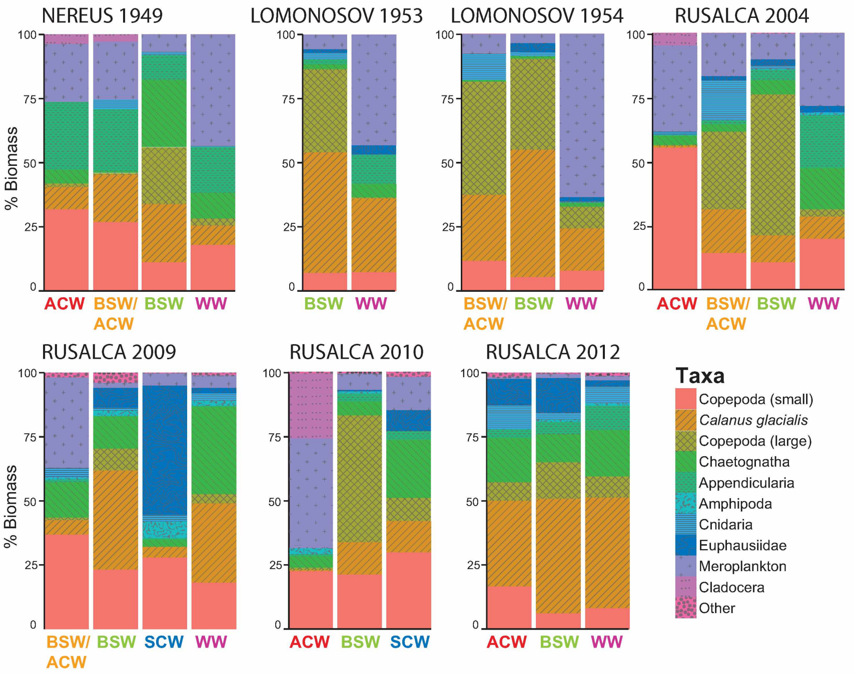

Figure 4.5: Relative contribution to biomass of different taxonomic groups in the Chukchi Sea during several of the study years (only years sampled by 100–200 μm mesh nets reported due to undersampling of smaller taxa by coarser nets)

Some species, such as the hydrozoan jellyfish *Aglantha digitale* were largely confined to the ACW during most years, although in some years they occurred across the entire Chukchi domain (Supplementary Figure 4.S3). September 1970 (WEBSEC) stood out among all the sampling years by A. digitale dominating the plankton communities both in absolute numbers and biomass, exceeding even the copepods. Data from others years contain very few cases of this species or no records at all (which could be due to sampling or identification bias – in some datasets all jellyfish were grouped into a broad “Cnidaria” category).

4.4.6 Bering Sea (BSAW) Communities

BSAW and BSAW/ACW were the most common water masses observed during each year sampled, and contained the highest zooplankton biomass (Supplementary table 4.S2). These waters were dominated by large Pacific copepods (Figure 4.5), which typically composed 50-80 % of the total biomass. Of the four most important large copepod taxa, *Calanus glacialis* and *Metridia pacifica* are shelf species, while *Neocalanus* spp., and *Eucalanus bungii* are more characteristic of oceanic Anadyr waters. The abundance of *M. pacifica*, *E. bungii* and *Neocalanus* spp. within BSAW was extremely variable, spanning up to three orders of magnitude within a single expedition, as well as year

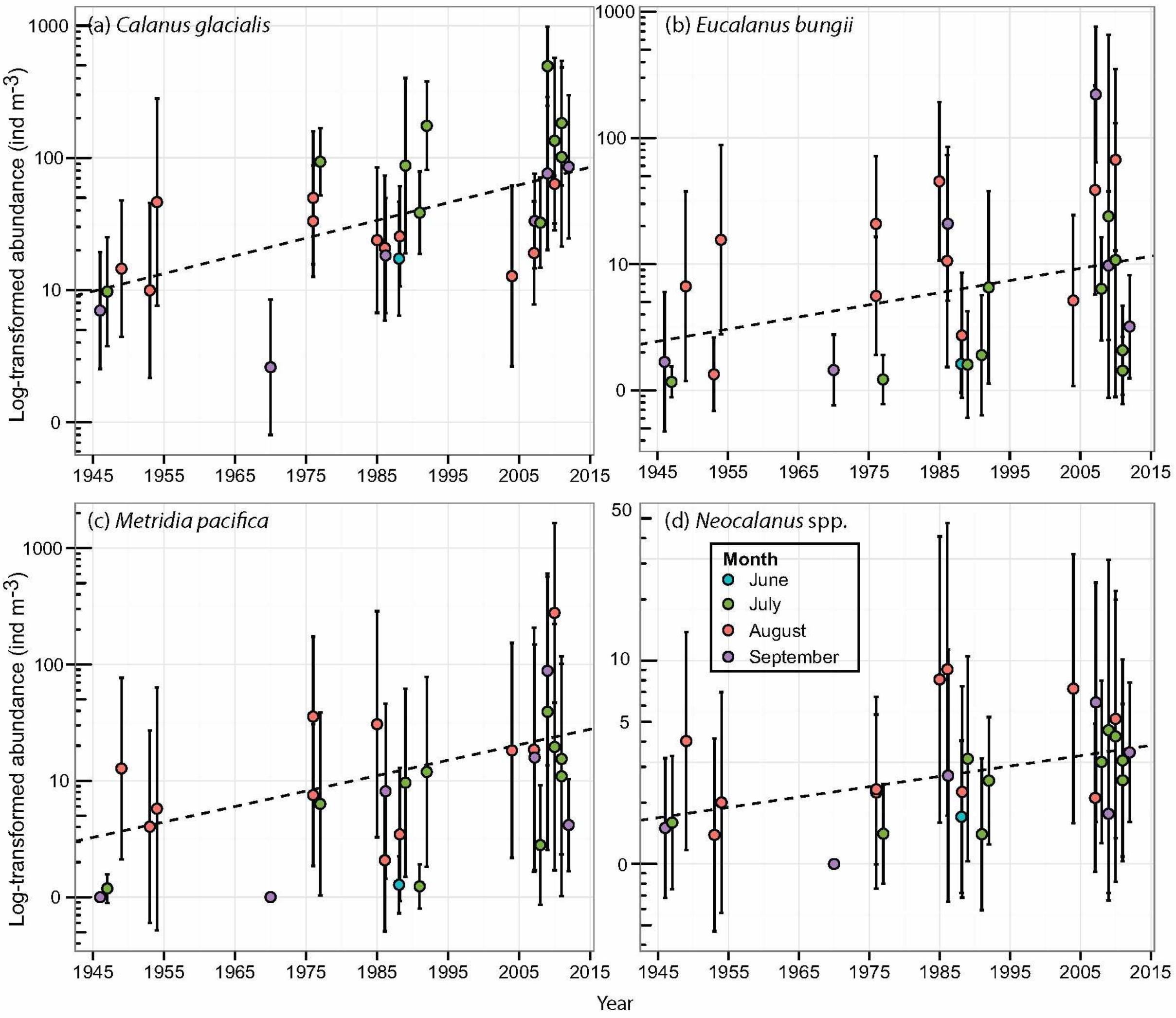

Figure 4.6: Interannual variability of Pacific copepod species abundance in the Chukchi Sea during 1946–2012. Each symbol represents one cruise; bars indicate 95% confidence interval. Dashed line shows fitted linear trend over averaged data

to year (Figure 4.6). Generally, the distribution of these species follows the pathway of the BSAW, with decreasing abundances to the north and to the west (Figure 4.7). The timing of each expedition played a critical role in the abundances observed as the advection of these species is closely linked to their life cycles in the Bering Sea. For example, in 1986 and 1988, *Metridia pacifica* was nearly absent in the plankton in the earlier months (July and June), but was highly abundant just 2 months later (September and August). The best fitting mixed model describing of all three species as determined by AIC included Year, Month and Bottom temperature (Supplementary Tables 4.S3-4.S6). There is a slight but significant ($p < 0.01$) trend of increasing abundance of all three species in Bering Sea waters over the study period. Abundances of these copepods, especially *Eucalanus bungii*, also correlated positively ($p < 0.01$) to water temperature observed during each cruise (Figure 4.8). Both surface and bottom water temperatures were significant factors, with the best model containing bottom temperature. There was no correlation of abundance to salinity or station depth, and the inclusion of the AO- or PDO-index for each year did not improve the model for any of the species.

Calanus glacialis was the most important contributor to biomass during every cruise sampled (Figure 4.5) with the exception of September 1970 (when biomass was dominated by the hydrozoan jellyfish *Aglantha digitale*). Abundance of *Calanus glacialis* was typically less variable than the Pacific oceanic species, with the standard deviation within each cruise generally spanning only a single order of magnitude (Figure 4.6). The factors for the best fitting mixed model describing *C. glacialis* abundance included Year, Month and PDO/AO. There is a significant ($p < 0.01$) trend of increasing average abundance of this species in the Chukchi Sea within Bering Sea waters ($\sim$10 ind m^{-3} / decade). The inclusion of temperature or salinity as a factor in the model did not account for any additional variability between years; however, a significant relationship ($p < 0.01$) between *C. glacialis* abundance and PDO/AO signal (6-month winter average) (Figure 4.9) was observed in BSAW waters, with higher abundances during the lower-PDO years and the higher AO years.

4.4.7 Resident Chukchi (WW) Communities

Winter water communities were defined as those stations containing WW in at least the bottom layer. These waters are typified by "resident" Chukchi communities composed of species that can overwinter and/or reproduce beneath the winter sea ice. These species are shared with other Arctic shelf seas, but are not generally found in Bering Sea waters (Ershova et al., 2015). These assemblages have a much lower contribution of copepods to overall biomass (generally < 50 %), and a high biomass of gelatinous taxa, such as chaetognaths and larvaceans (Figure 4.5). During the summer months a very high contribution of meroplankton (mainly barnacle larvae) was also observed; in contrast,

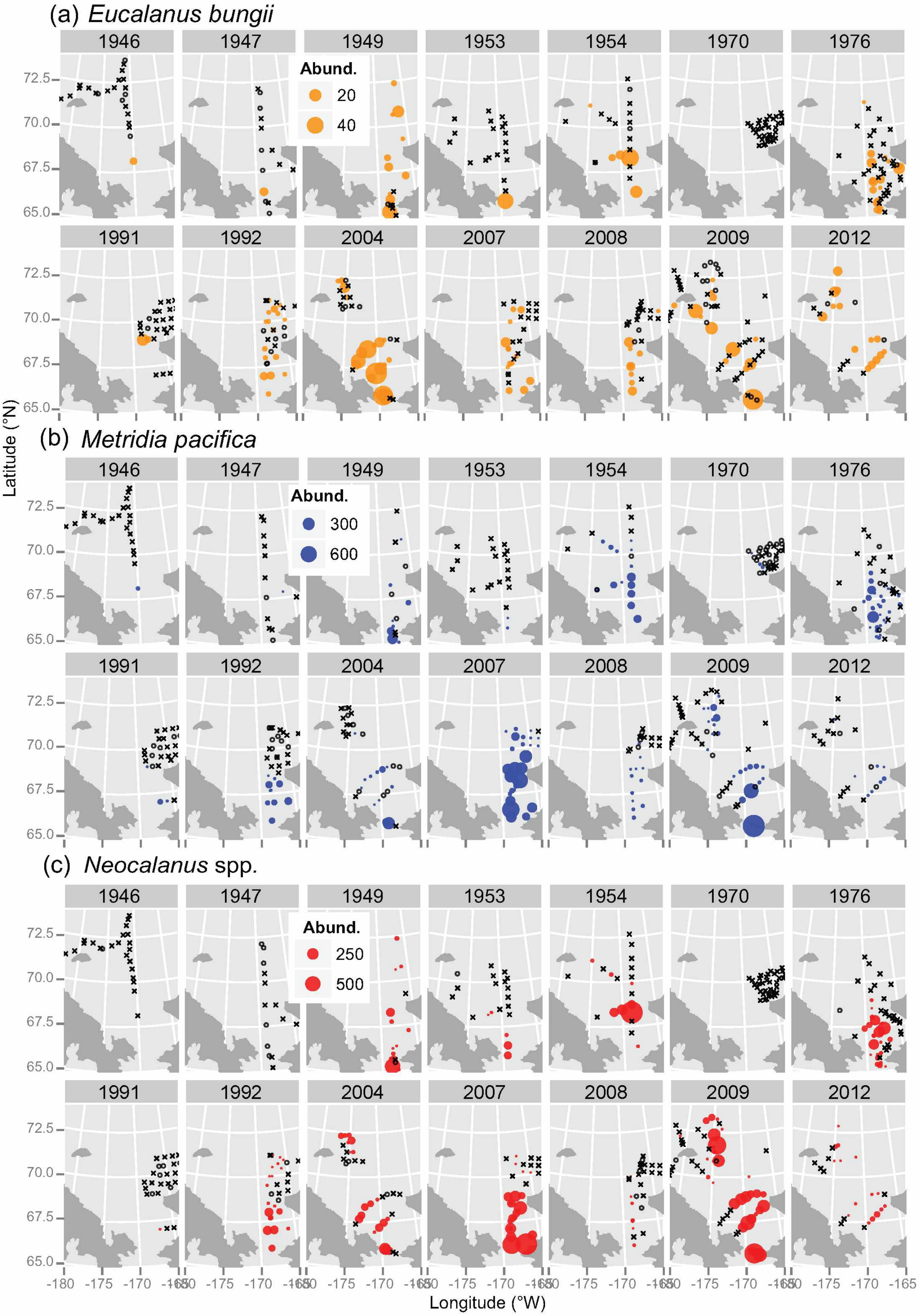

Figure 4.7: Abundance (ind m^{-3}) of (a) *Eucalanus bungii*, (b) *Metridia pacifica*, and (c) *Neocalanus* spp. in the Chukchi Sea during 1946–2012. ○ = stations where taxon was present (< 1 ind m^{-3}). × = stations where taxon was not found

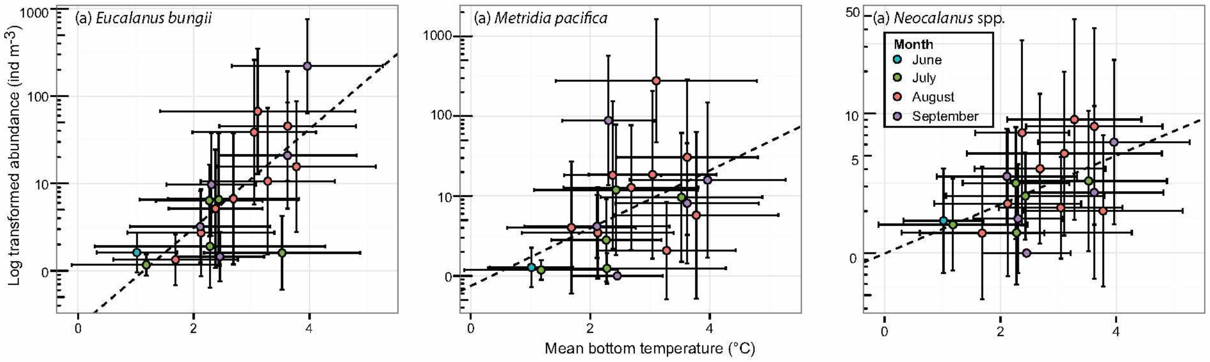

Figure 4.8: Relationship of mean abundance of (a) *Eucalanus bungii*, (b) *Metridia pacifica*, and (c) *Neocalanus* spp. to mean temperature in BSAW (each symbol represents one cruise) in the Chukchi Sea during 1946–2012. Bars indicate standard deviation (not on log scale). Dashed line indicates fitted linear trend over averaged data

during the two September cruises meroplankton was nearly absent. Some of the shelf Arctic species characteristic for these communities include a number of "Arctic" copepod species (e.g. *Microcalanus pygmaeus*, *Metridia longa*); ice-associated taxa, such as the copepod *Jaschnovia brevis* and the amphipod *Apherusa glacialis*, as well as a number of hydrozoan jellyfish that have a benthic polyp stage and are therefore limited in their spatial distribution (e.g. *Halitholis cirratus*, *Catablema visicarium*, *Plotocnide borealis*, *Aeginopsis laurentii*).

Large Bering Sea copepods are scarce within these communities, although they are present in small numbers, particularly during the recent sampling years. Average abundance north of 70°N and east of 175°W for *Eucalanus bungii*, *Neocalanus* spp. and *M. pacifica* suggest a limited trend of increasing abundance during the later years (Figure 4.10) (significant for *Neocalanus* spp., $p < 0.001$; non-significant ($p = 0.2$) for *M. pacifica* and *E. bungii*). While Chukchi Winter Waters contain a significant presence of *Calanus glacialis* (Figure 4.5), the developmental stage distribution (Figure 4.11) suggest that they belong to a different population than the one carried into the Chukchi with Bering Sea waters (see below).

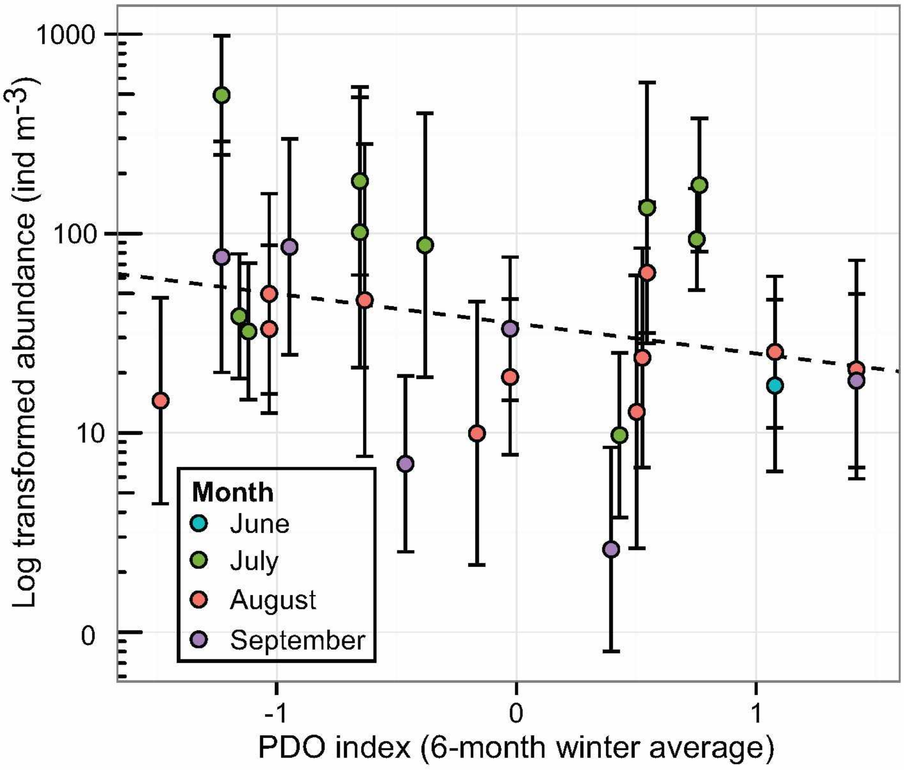

Figure 4.9: Relationship of mean abundance of *Calanus glacialis* to the Pacific Decadal Oscillation (PDO) signal (six-month winter average) in the Chukchi Sea during 1946–2012. Bars indicate 95% confidence interval

4.4.8 *Calanus glacialis* stage distribution and shifting phenology

Stage distribution of *C. glacialis* is a good indicator of the overall seasonal state of the zooplankton community. Fall communities are mainly dominated by 5th stage copepodites (C5), while earlier in the summer the community is typically composed of C3-C4 stages. There is a strong significant relationship of mean developmental stage to surface temperature ($p < 0.01$, $r^2 = 0.4$), and the communities sampled during the "warm" summers of 1954, 1992 and 2004 (July/August) are as far along in their development as those sampled over a month later during the "cold" years 2009 and 2012. This implies that yearly variability in seasonal succession can be quite significant, which further confounds year-to-year comparisons of communities. It is notable that our stage data also suggests there are likely two or more distinct populations present in the area (Figure 4.11). Bering Sea waters during late summer generally contain mostly late-stage copepodites (C4-C5's), while the *C. glacialis* population within resident Chukchi waters (WW) is composed of

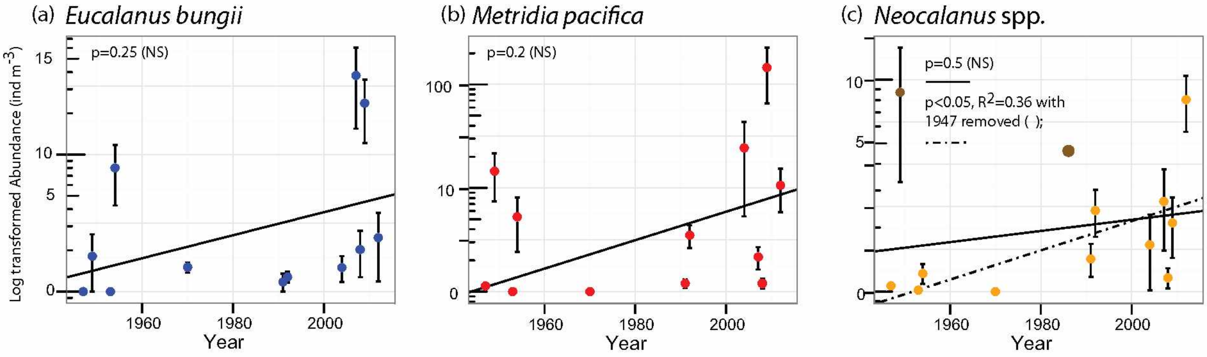

Figure 4.10: Mean abundances of (a) *Eucalanus bungii*, (b) *Metridia pacifica*, and (c) *Neocalanus* spp. in the Chukchi Sea north of 70 °N and east of 175 °W. Bars indicate 95 % confidence interval. Solid lines indicate fitted linear trend. Dotted line in (c) indicates fitted trend with one outlier removed

young C1-C3 stages. Since these populations likely respond differently to environmental factors, more elaborate patterns are probably obscured in regions where these populations overlap. The "young" state of the Chukchi C. glacialis community of around Wrangel Island in September 1946 (mean stage 1.6) compared to 2004, 2009 and 2012 during the same time of year (mean stage 2.2-2.7) is suggestive of a shift in phenology; however, data from one early year is insufficient to reach any definite conclusions.

4.5 Discussion

4.5.1 Community structure and inter-annual variability

Our results represent the first quantitative examination of the changes that have occurred in pelagic communities in the Chukchi Sea over a 70-year period. While overall water mass distribution patterns remained similar over the study years, the degree of penetration of these water masses may have changed, with either higher volumes of Bering Sea water entering the Chukchi Sea during the summer months (Woodgate et al., 2012), or summer BSAW becoming identifiable sooner in the year, and therefore appearing to penetrate further. Despite strong inter-annual variability, overall community structure (proportional contribution of taxa) within each respective water mass also remained relatively similar over the examined period (Figure 4.5), with strong correlations observed between biological communities and the physical environment (Table 4.2). Although

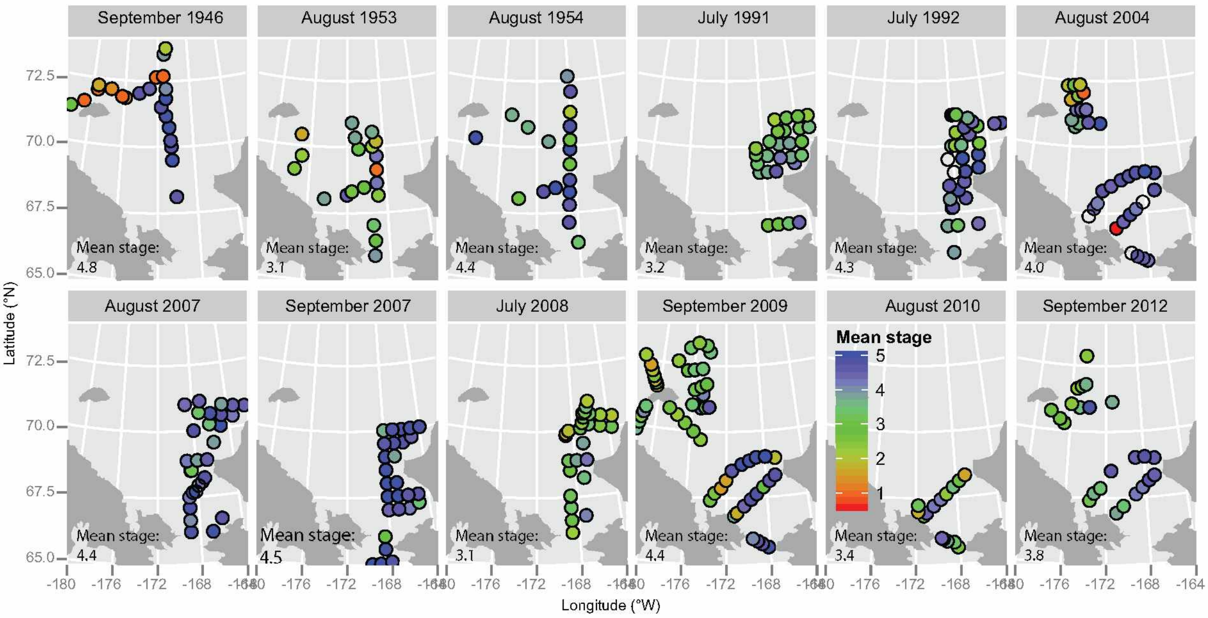

Figure 4.11: Distribution of mean copepodite stages of *Calanus glacialis* in the Chukchi Sea during 1946–2012 (copepodite data is only available for this subset of cruises)

only temperature and salinity were available as environmental factors for the historical datasets, recent studies find strong correlations only to these two variables even when a larger suite (Chlorophyll, nutrients, oxygen, etc.) is available (Questel et al., 2013). Our data demonstrate that during some years the patterns and differences between communities in different water masses are highly pronounced (i.e. 1949, 2004), while in others they are weaker or much more subtle (i.e., 2012) (Figure 4.5).

Differences between communities are often shaped by the presence or absence of rarer "indicator" species, while the most common and numerous groups are generally found across the entire sampling domain. The different taxonomic resolution as well as sampling methodology between the assembled datasets makes it difficult to establish these subtle differences, although they are apparent on a year-to-year basis. Trends are further complicated by the fact that some of the most abundant and ecologically important species (e.g. *Calanus glacialis*, *Aglantha digitale*) may have more than one population present in the area, as suggested by developmental stage distribution as well as genetic analysis (Nelson et al., 2009). The obvious trends that we observe even when most taxonomic detail is removed from the data suggest that patterns would be even stronger if consistent higher-resolution taxonomy were available. While some patterns remain visible throughout most years, the system exhibits extremely high variability in biomass, abundance and community composition. This inherent variability can easily lead one to confuse inter-annual differences with long-term change in zooplankton communities when based on only a few study years (i.e. Matsuno et al., 2011). Variable timing of the cruises also contributes to variability, since the seasonal progression within planktonic communities in this region can take place extremely rapidly (Questel et al., 2013). Our data suggest that highest biomass was present in July and then declined later in the fall; perhaps reflecting changing transport volumes of Pacific water through the Bering Strait.

4.5.2 Climatic oscillations and regime shifts

Responses of ecosystems to climate change are often not linear, but are characterized by “tipping points” that occur once a certain threshold is reached (Duarte et al., 2012). Once such a point occurs, the system shifts into a new stable state, which may remain even if the physical changes are reversed. However, due to the scarcity of time-series that span a sufficiently long period of time, it is very difficult for researchers to discern between permanent systematic change and climate-related oscillations. Abrupt changes in climatological indexes such as the PDO, NAO and AO are often associated with regime shifts in the pelagic environment, which may or may not be reversible. Within the North Pacific, such abrupt shifts, characterized by marked changes within all levels of the marine ecosystem occurred in 1977, 1989 and 2000 (Brodeur et al., 2008; Hare and Mantua, 2000). One of the most prominent changes within the plankton was the steep increase in jellyfish biomass, primarily Chrysaora melanaster, in the Bering Sea during the 1990, and then its rapid decline after 2000 (Brodeur et al., 2008). These events coincided with climatic oscillations in the Bering Sea from warmer (pre-1989) to cooler, and back to warmer (post-2000) conditions. Within some sections of the North Atlantic, the pelagic community also experienced a shift from a sub-Arctic to a more temperate type in the 1990’s; it remains unclear whether these patterns represent a permanent shift (Beaugrand et al., 2009) driven by globally warming temperatures, or are associated with shifts in the climatic indexes within the region (Greene et al., 2013).

Our results indicate a clear shift towards higher biomass and abundance of zooplankton over the time frame of 1946-2012; however, the low resolution of our data makes it unclear whether these changes are gradual (linear trend), or if there was a shift towards higher biomass sometime in the 1970-1980's. The high correlation of zooplankton biomass and abundance, particularly *Calanus glacialis*, to AO- and PDO-indices indicates that the system quickly responds to changes in the environment. The relationship between C. glacialis and climate variability is documented for the Bering Sea shelf, where sequential colder (negative PDO) years generally have much higher biomass of *C. glacialis* (Eisner et al., 2014). The patterns that we observe for this species in the Chukchi, including a negative correlation of zooplankton biomass to PDO signal, likely reflect a diluted signal of these processes in the Bering Sea. The long-term shifts in plankton biomass are also clearly reflected in the higher trophic levels. For example, a significant increase in planktivorous birds has been observed in the northeastern Chukchi since the 1970's (Gall et al., 2016).

4.5.3 Shifting biogeographical boundaries

In many regions of the world's oceans species have been shifting their geographical ranges as the climate warms and ocean currents change. One of the most pronounced examples of such a range shift in the plankton has been observed in the Northeast Atlantic using the Continuous Plankton Recorder, which has been collecting data since the 1930's. Within this region, the warm-water copepod assemblage containing Calanus helgolandicus has shifted northwards by more than 10 degrees latitude over the past 50 years and continues to move poleward at a rate of ~22km/year (Beaugrand et al., 2009). In the Arctic Ocean, similar reports include the northward shift of the Atlantic amphipod *Themisto compressa*, previously not found in Arctic waters and now observed successfully reproducing there (Kraft et al., 2013). A large number of Bering Sea fish species has also shifted their range northward over the last 2 decades (Wassmann et al., 2015).

The difference in coverage and the spatial and temporal scarcity of our data make it difficult to say conclusively the degree to which biogeographical shifts are occurring for the Chukchi zooplankton. The transit time of water flowing from the Bering Strait to the north-western Chukchi Sea (Herald Canyon) is estimated to be 4-6 months (Berline et al., 2008; Woodgate et al., 2005), and can vary significantly depending on wind conditions (Winsor and Chapman, 2004), position in the water column, and bathymetry (Berline et al., 2008). Variability in flow time will influence the composition and quantity of Pacific zooplankton reaching the shelf break of the Chukchi Sea by the end of the summer, with shorter lived species having a chance to travel farther north in favorable conditions. Additionally, an earlier onset of "summer" conditions in the Bering Sea and increased inflow of warm Pacific water (Woodgate et al., 2012) together with a longer summer ice-free period should result in advected species developing earlier in the season and carried farther north, thus playing a role in the local communities for a longer period of time. Currently, the limited stage distribution data that we have available is too scarce to say conclusively whether any phenological shifts are taking place in the resident Chukchi Sea communities or advected Bering Sea communities. However, the distribution maps for the Pacific copepods *M. pacifica* and *Neocalanus* spp. are certainly suggestive of their displacement northward. While these species were observed at a few individual stations above 70°N during the early sampling years, they are generally present at more or less every station during the 1990-2000 period (Figure 4.7), with a trend of increasing abundance at higher latitudes during the later years. Plankton surveys in the central Arctic Basin have reported a presence of these species in the high Arctic plankton communities, although they are usually found in very small numbers (e.g. Kosobokova and Hopcroft, 2010). While it is unlikely that these Pacific organisms are able to survive and reproduce in the cold and nutrient-poor waters of the Arctic, an increasing inflow of these species could have significant local impact for the plankton feeding predators within the region.

4.5.4 The fate of Chukchi Sea zooplankton

The Chukchi Sea is an advection-dominated system, with the majority of the water masses composing it arriving directly from the North Pacific via the Bering Strait. Therefore, a significant proportion of the zooplankton communities within this region are "in transit", as opposed to being produced locally. Most of the Pacific plankton transported through the Bering Strait does not make it to the deep Arctic Ocean (Wassmann et al., 2015), due to a generally shorter life span of these species and failure to reproduce in the near-freezing Arctic waters. The shock of sub-zero temperatures and scarcity of available food together with their reduced ability to store lipids are likely to contribute to mortality and make many expatriated species unlikely to survive the Arctic winter.

One of the large knowledge gaps remaining for the Chukchi region is the lack of understanding of processes that take place in the biological communities during the winter months, when the sea is completely covered with ice and water temperatures are below zero from surface to bottom. To date, no sampling efforts exist that examine the system during the peak of winter (January-March). While summer communities are largely affected by warming temperatures and a longer ice-free period, we assume that during winter the system "resets" itself and communities revert from being mainly Pacific to mainly Arctic in character. This is partially confirmed by the scarcity of Pacific species within the WW communities. The vast majority of the planktonic biomass transported into the Arctic from the North Pacific remains within the Chukchi Sea, becoming food for the local fish, bird, marine mammal and benthic communities. Bowhead whales alone are estimated to consume 1/3 of the zooplankton biomass advected through the Bering Strait (Wassmann et al., 2015). The presence of advected Pacific euphausiids on the Chukchi and Beaufort shelves (Ashjian et al., 2010; Moore et al., 2010), as well as in the Siberian Coastal current (Moore et al., 1995), can drive the seasonal migrations of whales in this area, as they composed 60-90 % percent of stomach contents in bowhead whales. Nonetheless, the Chukchi's euphausiids are considered primarily an expatriate population (Berline et al., 2008).

The majority of Bering Sea *Calanus glacialis*, which represent the bulk of biomass transported through the Bering Strait, most likely does reach far past the Chukchi shelf break. The younger *C. glacialis* found in resident Chukchi waters likely represent a distinct "local" population shared with adjacent Arctic shelf seas; alternately, they may be produced by overwintering females that were advected during the previous summer. However, the sharp boundary between the Pacific/Bering and Arctic haplotypes (Nelson et al., 2009), the absence of the Pacific haplotype within the Canada Basin, and the strong pattern observed in distribution of developmental stages (Figure 4.11) together suggest that the majority of the advected Pacific population of *C. glacialis* are unable to survive the Arctic winter and reproduce in the Arctic. Preliminary results of population genetics of this species suggest that there is a single population of this species within the Arctic Basin (Agata Weidmann, personal communication).

4.6 Summary and future directions

While our results are far from a conclusive time series, they present the first evidence of change within planktonic communities within the western Chukchi Sea over the last 70 years. A significant increase in zooplankton biomass, mostly driven by the advected copepod *Calanus glacialis*, was observed within the southern Chukchi, which likely reflects increasing inflow of biomass-rich Pacific water during the extended summer months. A trend is also observed suggesting a northward shift of Pacific species into the Chukchi Sea, which may be driven by a longer ice-free period and extended warmer summer temperatures combined with a shifting phenology favoring earlier development of species. While summer zooplankton communities of the Chukchi Sea have been primarily Pacific in character for as long as our records report, continuing warming and ice loss may further increase the influence of Pacific fauna within the Chukchi region. Our data show that the success of the key advected species is largely correlated with water temperature, so increases in abundance of these species with future warming are expected. Our findings are consistent with numerous other studies reporting climate related changes propagating from the environment to the biological communities, both within the Pacific Arctic region and in other parts of the Arctic. To become robust, future sampling efforts need to be directed towards creating a continuous time series, with consistent methods and sampling periods to better understand and predict the distribution of communities in a changing Chukchi Sea.

4.7 References

Ashjian, C., S. R. Braund, R. Campbell, and J. George. 2010. Climate Variability, Oceanography, Bowhead Whale Distribution, and Iñupiat Subsistence Whaling near Barrow, Alaska. *Arctic* 63(2):179–194.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software* 67(1):1–48.

Beaugrand, G., C. Luczak, and M. Edwards. 2009. Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Global Change Biology* 15(7):1790–1803.

Berline, L., Y. H. Spitz, C. Ashjian, R. Campbell, W. Maslowski, and S. E. Moore. 2008. Euphausiid transport in the Western Arctic Ocean. *Marine Ecology Progress Series* 360:163–178.

Bolker, B. and R. D. C. Team. 2014. Maximum likelihood estimation and analysis with the bbmle package. R package version 1.0.17 .

Brodeur, R., M. Decker, L. Ciannelli, J. E. Purcell, N. Bond, P. Stabeno, E. Acuna, and G. Hunt, Jr. 2008. Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. *Progress in Oceanography* 77(2):103–111.

Clarke, K. R. and M. Ainsworth. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* 92:205–219.

Coyle, K. O., V. G. Chavtur, and A. I. Pinchuk. 1996. Zooplankton of the Bering Sea: a review of Russian-language literature. *Ecology of the Bering Sea: a review of Russian . . .* .

Duarte, C. M., S. Agustí, P. Wassmann, J. M. Arrieta, M. Alcaraz, A. Coello, N. Marbà, I. E. Hendriks, J. Holding, I. García-Zarandona et al. 2012. Tipping Elements in the Arctic Marine Ecosystem. *AMBIO* 41(1):44–55.

Eisner, L. B., N. Hillgruber, E. Martinson, and J. Maselko. 2012. Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi seas. *Polar Biology* 36(1):87–113.

Eisner, L. B., J. M. Napp, K. L. Mier, A. I. Pinchuk, and A. G. Andrews, III. 2014. Climate-mediated changes in zooplankton community structure for the eastern Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* .

Ershova, E. A., R. R. Hopcroft, and K. Kosobokova. 2015. Inter-annual variability of summer mesozooplankton communities of the western Chukchi Sea: 2004-2012. *Polar Biology* 38(9):1461–1481.

Gall, A. E., T. C. Morgan, R. H. Day, and K. J. Kuletz. 2016. Ecological shift from piscivorous to planktivorous seabirds in the Chukchi Sea, 1975–2012. *Polar Biol.* .

Grebmeier, J. M. 2012. Shifting Patterns of Life in the Pacific Arctic and Sub-Arctic Seas. *Annual Review of Marine Science* 4(1):63–78.

Grebmeier, J. M. and R. H. Harvey. 2006. The Western Arctic Shelf-Basin Interactions (SBI) project: An overview. *Deep Sea Research Part II: Topical Studies in Oceanography* 52(24-26):3109–3115.

Greene, C. H., E. Meyer-Gutbrod, B. C. Monger, L. P. McGarry, A. J. Pershing, I. M. Belkin, P. S. Fratantoni, D. G. Mountain, R. S. Pickart, A. Proshutinsky et al. 2013. Remote climate forcing of decadal-scale regime shifts in Northwest Atlantic shelf ecosystems. *Limnology and Oceanography* 58(3):803–816.

Hare, S. R. and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47:103–145.

Hopcroft, R. R., K. Kosobokova, and A. I. Pinchuk. 2010. Zooplankton community patterns in the Chukchi Sea during summer 2004. *Deep Sea Research Part II: Topical Studies in Oceanography* 57(1):27–39.

Ingham, M. C., B. A. Rutland, P. W. Barnes, G. E. Watson, G. J. Divoky, A. S. Naidu, G. D. Sharma, B. L. Wing, and J. C. Quast. 1972. WEBSEC-70, An Ecological Survey in the Eastern Chukchi Sea, September-October 1970, Technical report, Washington, D.C.

Johnson, M. W. 1953. Studies on plankton of the Bering and Chukchi seas and adjacent area. *Proceedings of the seventh Pacific Science Congress of the Pacific Science Association; held at Auckland and Christchurch, New Zealand* pp. 580–500.

Kiørboe, T. 2013. Zooplankton body composition. *Limnology and Oceanography* 58(5):1843–1850.

Kosobokova, K. and R. R. Hopcroft. 2010. Diversity and vertical distribution of mesozooplankton in the Arctic's Canada Basin. *Deep Sea Research Part II: Topical Studies in Oceanography* 57(1):96–110.

Kosobokova, K. and N. M. Pertsova. 2012. Zooplankton Belogo morja: struktura, dinamika i ekologija soobshestv, in *Sistema Belogo Morja: Prirodnaja Sreda Vodosbora Belogo Morja*, Lisitsyn, A. P., ed., Nauchnyj mir, Moscow, pp. 640–675.

Kraft, A., E. M. Nöthig, E. Bauerfeind, and D. J. Wildish. 2013. First evidence of reproductive success in a southern invader indicates possible community shifts among Arctic zooplankton. *Marine Ecology Progress Series* 493:291–296.

Kulikov, A. S. 1992. Characteristics of zooplankton communities, in *Results of the Third Joint US–USSR Bering and Chukchi Seas expedition (BERPAC), Summer 1988*, Nagel and P. A, eds., US Fish and Wildlife Service, Washington, p. 161.

Kuznetsova, A., P. B. Brockhoff, and R. Christensen. 2015. lmerTest: Tests in linear mixed effects models. R package version 2.0-29 .

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer research* 27(2):209–220.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific Interdecadal Climate Oscillation with Impacts on Salmon Production. *Bulletin of the American Meteorological Society* 78(6):1069–1079.

Markhaseva, E. L., A. A. Golikov, T. A. Agapova, A. A. Beig, and T. N. Konina. 2005. Archives of the Arctic seas zooplankton, in *Contributions from the Zoological Institute*, Russian Academy of Sciences, St. Petersburg.

Matsuno, K., A. Yamaguchi, T. Hirawake, and I. Imai. 2011. Year-to-year changes of the mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and 2007, 2008. *Polar Biology* 34(9):1349–1360.

Moore, S. E., J. C. George, K. O. Coyle, and T. J. Weingartner. 1995. Bowhead Whales Along the Chukotka Coast in Autumn. *Arctic* 48(2):155–160.

Moore, S. E., J. C. George, G. Sheffield, J. Bacon, and C. Ashjian. 2010. Bowhead whale distribution and feeding near Barrow, Alaska, in late summer 2005–06. *Arctic* 63(2):195–205.

Nelson, R. J., E. C. Carmack, F. A. McLaughlin, and G. A. Cooper. 2009. Penetration of Pacific zooplankton into the western Arctic Ocean tracked with molecular population genetics. *Marine Ecology Progress Series* 381:129–138.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. OHara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. vegan: Community Ecology Package. R package version 2.3-1 .

Pavshtiks, E. A. 1984. Zooplankton of the Chukchi Sea as indices of water origins. . *Trudy Arkticheskogo i Antarkticheskogo Nauchno-Issledovatel'skogo Institute* 368:140–153.

Pickart, R., L. Pratt, D. Torres, T. Whitledge, A. Proshutinsky, K. Aagaard, T. Agnew, G. Moore, and H. Dail. 2010. Evolution and dynamics of the flow through Herald

Canyon in the western Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 57(1):5–26.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. C. Team. 2015. nlme: Linear and Nonlinear Mixed Effects models. R package version 3.1-121 .

Pisareva, M., R. Pickart, K. Iken, E. Ershova, J. Grebmeier, L. Cooper, B. Bluhm, C. Nobre, R. R. Hopcroft, H. Hu et al. 2015. The Relationship Between Patterns of Benthic Fauna and Zooplankton in the Chukchi Sea and Physical Forcing. *Oceanography* 28(3):68–83.

Questel, J. M., C. Clarke, and R. R. Hopcroft. 2013. Seasonal and interannual variation in the planktonic communities of the northeastern Chukchi Sea during the summer and early fall. *Continental Shelf Research* 67:23–41.

Ribeiro, P. J., Jr and P. J. Diggle. 2015. Package 'geoR'. R package version 1.7-5.2 .

Richardson, A. 2008. In hot water: zooplankton and climate change. *ICES Journal of Marine Science* 65(3):279–295.

Sirenko, B. I., C. Clarke, R. R. Hopcroft, F. Huettmann, B. A. Bluhm, and R. Gradinger (eds). 2015. The Arctic Register of Marine Species (ARMS) compiled by the Arctic Ocean Diversity (ArcOD) project, http://www. marinespecies.org/arms .

Skjoldal, H. R., P. H. Wiebe, L. Postel, T. Knutsen, S. Kaartvedt, and D. D. Sameoto. 2013. Intercomparison of zooplankton (net) sampling systems: Results from the ICES/GLOBEC sea-going workshop. *Progress in Oceanography* 108:1–42.

Springer, A., C. McRoy, and K. Turco. 1989. The paradox of pelagic food webs in the northern Bering Sea - II. Zooplankton communities. *Continental Shelf Research* 9(4):359–386.

Wassmann, P., K. Kosobokova, D. Slagstad, K. F. Drinkwater, R. R. Hopcroft, S. E. Moore, I. Ellingsen, R. J. Nelson, E. Carmack, E. Popova et al. 2015. The contiguous domains of Arctic Ocean advection: Trails of life and death. *Progress in Oceanography* 139:42–65.

Winsor, P. and D. C. Chapman. 2004. Pathways of Pacific water across the Chukchi Sea: A numerical model study. *Journal of Geophysical Research* 109(C3).

Wood, K. R., N. A. Bond, S. L. Danielson, J. E. Overland, S. A. Salo, P. Stabeno, and J. Whitefield. 2015. A decade of environmental change in the Pacific Arctic region. *Progress in Oceanography* 136:12–31.

Woodgate, R. A., K. Aagaard, J. H. Swift, K. K. Falkner, and W. M. Smethie. 2005. Pacific ventilation of the Arctic Ocean's lower halocline by upwelling and diapycnal mixing over the continental margin. *Geophysical Research Letters* 32(18):L18,609.

Woodgate, R. A., T. J. Weingartner, and R. Lindsay. 2012. Observed increases in Bering Strait oceanic fluxes from the Pacific to the Arctic from 2001 to 2011 and their impacts on the Arctic Ocean water column. *Geophysical Research Letters* 39(24):L24,603.

WoRMS Editorial Board. 2015. World Register of Marine Species, http://www.marinespecies.org at VLIZ .

4.S Supplementary materials

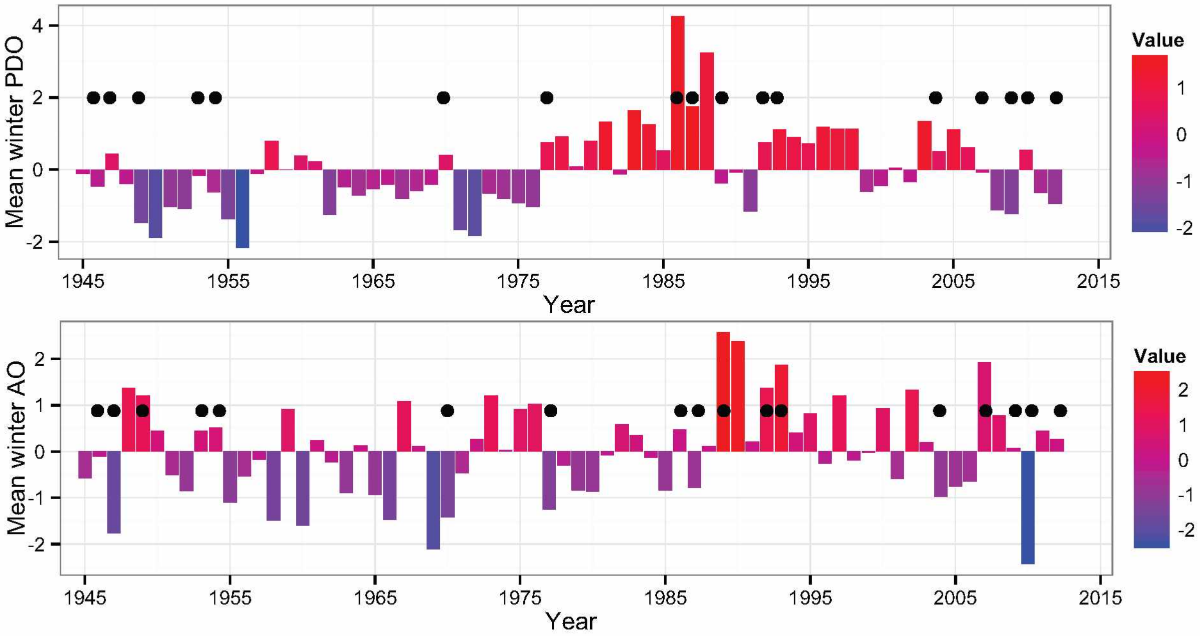

Figure 4.S1: Mean six-month winter index values for the Pacific Decadal Oscillation (PDO) and the Arctic Oscillation (AO). Black dots indicate years where zooplankton data is available

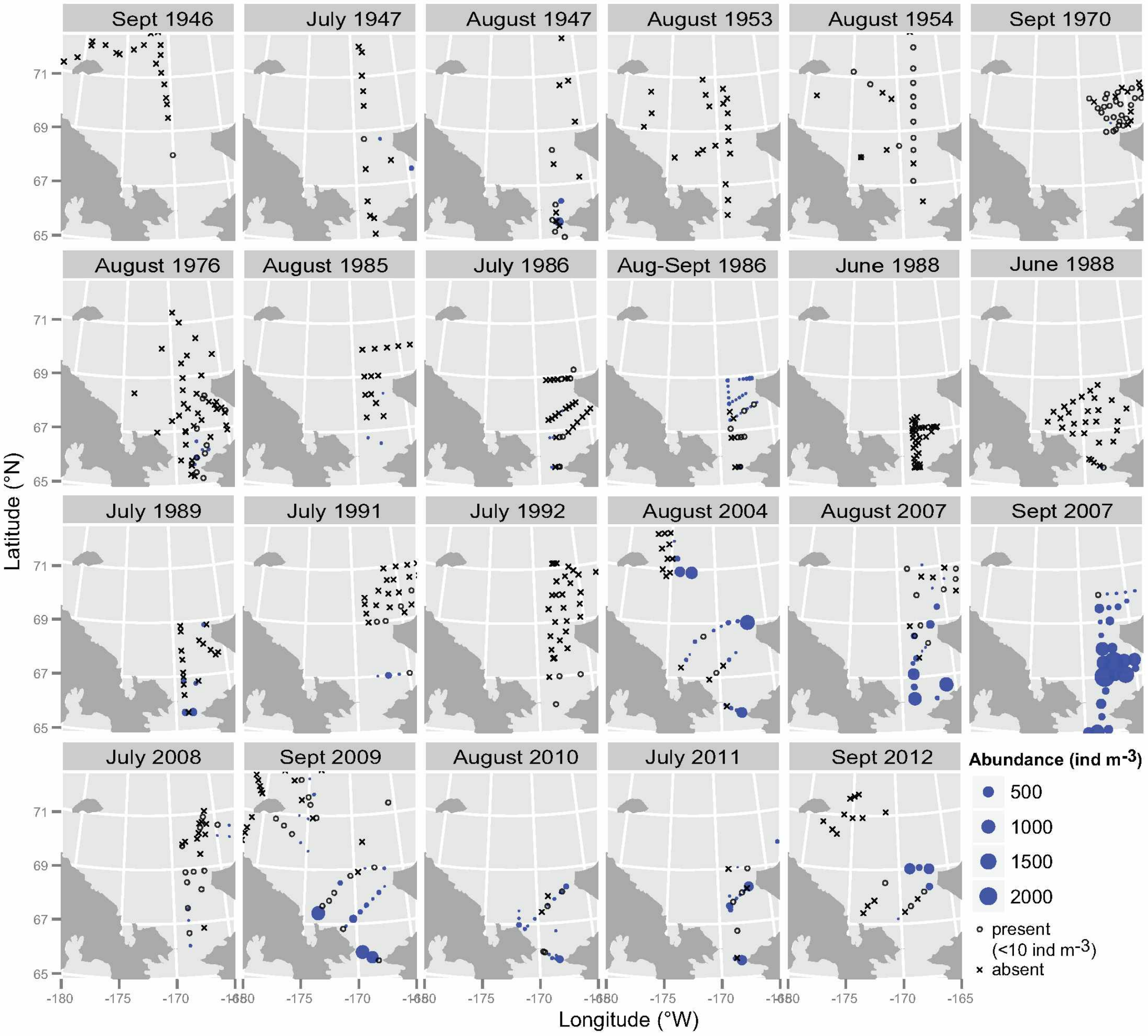

Figure 4.S2: Distribution of Alaska Coastal Water (ACW) indicator species (listed in Table 4.3) in the Chukchi Sea during 1946–2012. ○ = stations where taxon was present (< 10 ind m^{-3}). × = stations where taxon was not found

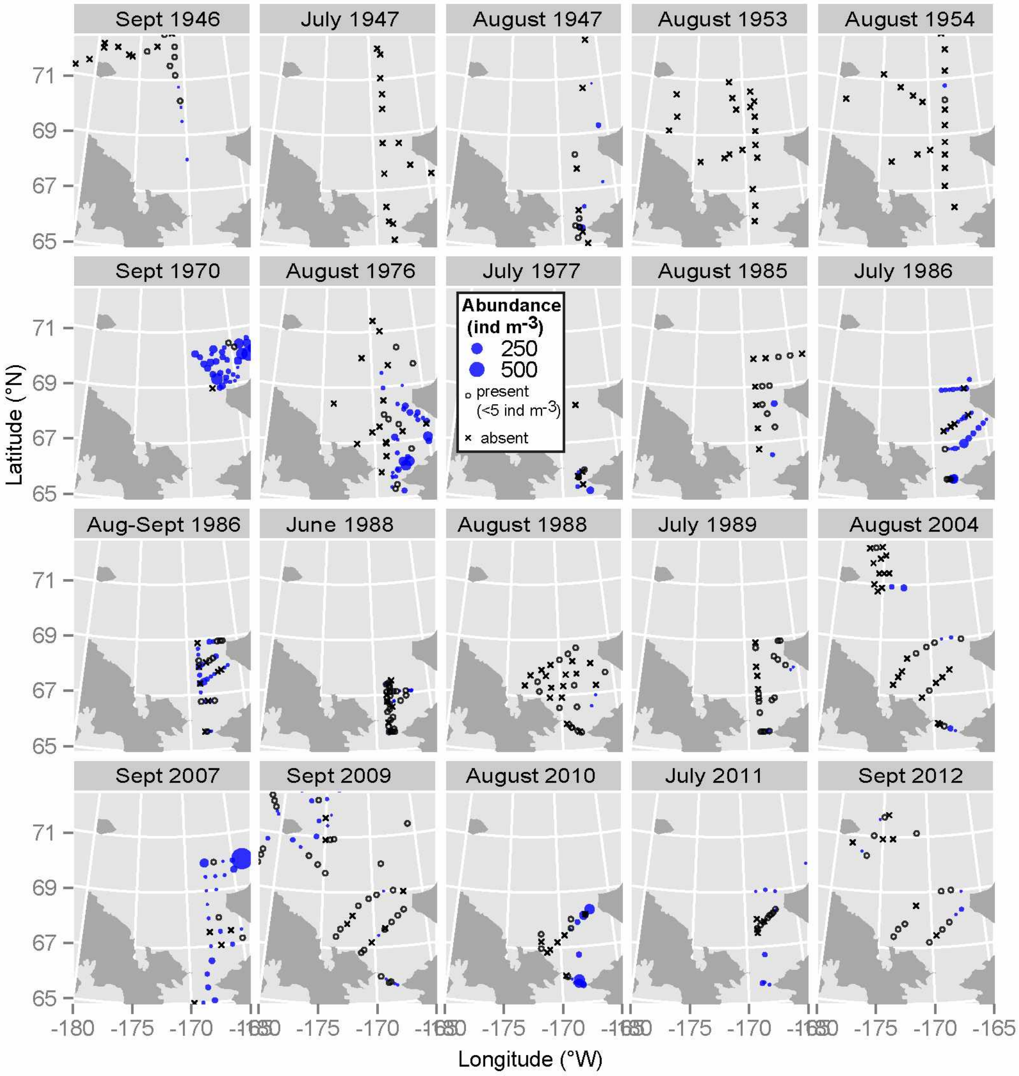

Figure 4.S3: Distribution of *Aglantha digitale* in the Chukchi Sea in 1946-2012. ○ = stations where taxon was present (< 1 ind m^{-3}). × = stations where taxon was not found

Table 4.S1: Summary of datasets used in study. Taxonomic resolution: L (low) - <30 species; M (medium) – 30-50 species; H (high) >50 species. Methods of calculating biomass: (1) Biomass from abundance data using mean weights from literature (2) Length-weight regressions (3) WW converted to DW (4) Preserved WW with correction for weight loss

EXPEDITION/ Ship	Year	Month	# of stns	Mesh size	CTD Data	Mean SST	Taxon. Resol.	Biom. Meth.	Mean biomass (mg DW m^{-3})	Mean abund. (ind m^{-3})	Published/available in
Severnyj Polyus	1946	Sept	36	167μm Juday	NO	2.16	H	1	23.7	1621	Markhaseva et al. (2005)
Nereus	1947	July	14	500μm	YES	2.14	M	1	13.5	2500	Johnson (1953)
Cedarwood	1949	August	21	~150μm	YES	2.20	H	2	28.7	1068	Unpublished
Lomonosov	1953	August	19	333μm	YES	3.27	L	3	10.35	254	Unpublished
Lomonosov	1954	August	21	333μm	YES	3.41	M	3	84.75	2986	Unpublished
WEBSEC/ CGC Glacier	1970	Sept-Oct	39	570μm	YES	3.24	M	1	17.7	114	Ingham et al. (1972)
Mayak	1976	August	25	167μm Juday	NO	4.93	L	3	46.3	4104	Pavshtiks (1984)
OSCEAP/ ”Discoverer”	1976	August	25	333μm	NO	4.93	M	1	41.6	537	Unpublished
OSCEAP/ ”Surveyor”	1977	July	7	333μm	NO	3.64	M	1	49.1	1212	Unpublished
ISHTAR HX74/ “Alpha Helix”	1985	Aug-Sept	16	505μm	YES	4.72	L	4	141.9	415	Springer et al. (1989)
ISHTAR HX85/ “Alpha Helix”	1986	July	38	505μm	YES	4.24	M	4	84.4	252	Springer et al. (1989)
ISHTAR HX88/ “Alpha Helix”	1986	Aug-Sept	38	505μm	YES	5.39	H	4	57.1	247	Springer et al. (1989)
BERPAC/ “Akademik Korolev”	1988	August	32	505μm	YES	3.92	M	4	33.1	147	Kulikov (1992)
ISHTAR TT221 / “Thomas Thompson”	1988	June	24	505μm	YES	1.5	L	4	13.4	225.5	Unpublished
ISHTAR HX128 / “Alpha Helix”	1989	July	42	505μm	YES	3.62	M	4	106.7	337	Unpublished
Oshoro-Maru	1991	July	27	333μm	YES	5.0	M	3	117.5	1616	Matsuno et al. (2011)
Oshoro-Maru	1992	July	34	333μm	YES	4.7	M	3	76.4	1110	Matsuno et al. (2011)
RUSALCA/ “Khromov”	2004	August	34	Bongo 150μm	YES	6.3	H	2	49.7	5762	Hopcroft et al. (2010)
Oshoro-Maru	2007	August	31	333μm	YES	8.9	M	3	91.7	1728	Matsuno et al. (2011)
“DYSON”	2007	Sept	25	505/150 μm	YES	9.6	H	1	175/57	64/1348	Eisner et al. (2012)
OSHORO-MARU	2008	July	28	333μm	YES	3.4	M	3	119.2	2771	Matsuno et al. (2011)
“Laurier”	2009	July	5	Bongo 150μm	NO	4.9	H	2	76.4	4061	Unpublished
RUSALCA/ “Khromov”	2009	Sept	60	Bongo 150μm	YES	3.2	H	2	72.1	8967	Ershova et al. (2015)
“Laurier”	2010	July	16	Bongo 150μm	NO	5.4	H	2	170	16313	Unpublished
RUSALCA / “Khromov”	2010	August	17	Bongo 150μm	YES	5.6	H	2	70.7	14070	Ershova et al. (2015)
“Laurier”	2011	July	23	Bongo 150μm	NO	5.5	H	2	126.6	12327	Unpublished
RUSALCA / “Khromov”	2011	July	9	Bongo 150μm	NO	5.5	H	2	98.1	2359	Unpublished
RUSALCA/ “Khromov”	2012	Sept	25	Bongo 150μm	YES	2.6	H	2	85.4	3224	Ershova et al. (2015)

Table 4.S2: (a) Summary and (b) comparisons between least squares means for factors (only significant comparisons reported) for the mixed model $log(Biomass) \sim Year + Month + PDO + Watermass + Gear + 1|Facet$

(a)	Factor	Estimate	Standard Error	DF	t-value	p-value
Intercept	-	-22.542	2.548	451	-8.847	***
Year	-	0.012	0.001	451	9.344	***
PDO index	-	-0.095	0.027	451	-3.484	**
Month	August	1.435	0.074	362.5	19.52	***
	July	1.659	0.078	366	21.23	***
	June	0.756	0.115	536.7	6.58	***
	September	1.442	0.075	391	19.33	***
Water mass (bottom/ surface)	ACW	1.182	0.078	193.2	15.19	***
	BSAW	1.487	0.048	66.3	30.72	***
	BSAW/ACW	1.431	0.052	83.8	27.6	***
	BSAW/SCW	1.452	0.156	363	9.33	***
	BSAW/WW	1.190	0.255	576.5	4.66	***
	SCW	0.778	0.171	302.4	4.56	***
	WW	1.318	0.077	275.6	17.2	***
	WW/BSAW	1.292	0.094	349.3	13.67	***
	WW/SCW	1.105	0.151	516.4	7.32	***

(b)	Factor A	Factor B	Estimate (difference)	Error	p-value
Month	August	July	-0.2	0.058	***
	August	June	0.7	0.097	***
	July	June	0.9	0.104	***
	July	September	0.2	0.060	***
	June	September	-0.7	0.100	***
Water mass (bottom/ surface)	ACW	BSAW	-0.3	0.081	***
	ACW	BSAW/ACW	-0.2	0.074	***
	ACW	SCW	0.4	0.182	*
	BSAW	SCW	0.7	0.174	***
	BSAW	WW	0.2	0.085	*

Table 4.S3: Mixed model results of *Calanus glacialis* abundance in BSAW. Best model reported as predicted by AIC (a) Results and (b) comparisons between least squares means for month (only significant comparisons reported) for the model $log(Abundance + 1) \sim Year + Month + PDO + (Gear) + 1|Facet$

(a)	Factor	Estimate	Std. Error	df	t-value	p-value
(Intercept)	-	-17.50	3.14	402.00	-5.57	***
Year	-	0.01	0.00	402.00	5.98	***
PDO index	-	-0.11	0.03	386.50	-3.30	**
Month	August	1.32	0.06	51.30	22.58	***
	July	1.60	0.08	130.40	19.26	***
	June	1.14	0.11	257.10	10.51	***
	September	1.16	0.07	81.00	17.24	***

(b)	Estimate	Std. Error	df	t-value	p-value
August - July	-0.30	0.08	396.50	-3.39	***
August - September	0.20	0.07	400.70	2.25	*
July - June	0.50	0.12	373.50	3.75	***
July - September	0.40	0.09	387.40	5.03	***

Table 4.S4: Mixed model results of *Metridia pacifica* abundance in BSAW. Best model reported as predicted by AIC (a) Results and (b) comparisons between least squares means for month (only significant comparisons reported) for the model $log(Abundance + 1) \sim Year + Month + Surface.Temp + (Gear) + 1|Facet$

(a)	Factor	Estimate	Std. Error	df	t-value	p-value
(Intercept)		-26.97	6.30	372.70	-4.28	***
Year		0.01	0.00	372.70	4.40	***
Mean Bottom Temperature		0.37	0.07	371.00	5.22	***
Month	August	1.03	0.10	117.00	10.34	***
	July	0.72	0.13	212.00	5.45	***
	June	0.07	0.18	315.00	0.40	
	September	1.05	0.12	170.00	8.97	***

(b)	Estimate	Std. Error	df	t-value	p-value
August - July	0.30	0.12	362.50	2.57	*
August - June	1.00	0.17	363.80	5.50	***
July - June	0.70	0.18	356.00	3.69	***
July - September	-0.30	0.14	363.80	-2.37	*
June - September	-1.00	0.17	367.70	-5.90	***

Table 4.S5: Mixed model results of *Eucalanus bungii* abundance in BSAW. Best mixed model reported as predicted by AIC (a) Results and (b) comparisons between least squares means for month (only significant comparisons reported) for the model $log(Abundance + 1) \sim Year + Month + Bottom.Temp + (Gear) + 1|Facet$

(a)	Factor	Estimate	Std. Error	df	t-value	p-value
(Intercept)	-	-24.65	4.74	323	-5.19	***
Year	-	0.01	0.00	323	5.10	***
Mean Bottom Temperature	-	0.46	0.06	323	7.82	***
Month	August	0.83	0.08	107.5	10.62	***
	July	0.28	0.12	220.5	1.46	*
	June	0.83	0.18	335.9	0.69	***
	September	0.95	0.10	175.5	10.06	***

(b)	Estimate	Std. Error	df	t-value	p-value
August - July	0.50	0.10	360.1	5.51	***
July - June	-0.5	0.16	368.8	-3.28	**
July - September	-0.7	0.12	361.8	-5.70	***
June - September	-0.1	0.18	372.4	-0.66	***

Table 4.S6: Mixed model results of *Neocalanus* spp. abundance in BSAW. Best model reported as predicted by AIC (a) Results and (b) comparisons between least squares means for month (only significant comparisons reported) for the model $log(Abundance + 1) \sim Year + Month + (Gear) + 1|Facet$

(a)	Factor	Estimate	Std. Error	df	t-value	p-value
(Intercept)	-	-10.24	3.62	370.8	-3.43	***
Year	-	0.01	0.00	371.4	3.53	***
Mean bottom temperature	-	0.19	0.05	368.8	3.53	***
Month	August	0.58	0.05	122.0	10.88	***
	July	0.42	0.08	204.9	6.71	***
	June	0.50	0.14	217.5	3.61	
	September	0.21	0.07	227.7	2.96	***

(b)	Estimate	Std. Error	df	t-value	p-value
August - September	0.40	0.07	364.5	5.35	***
July - September	0.30	0.13	363.1	3.56	***
June - September	0.30	0.15	312.6	2.31	*

5 Conclusions

The preceding chapters present new insights on the structure of zooplankton communities in the Chukchi Sea, as well as evidence of on-going change within these communities. I found that the zooplankton community structure in the Chukchi Sea was closely tied to physical parameters and water mass distribution. These patterns occurred for both contemporary as well as historical surveys, and were consistent with other recent studies from the region (Eisner et al., 2012; Matsuno et al., 2011; Questel et al., 2013).

In *Chapter 2*, I described the inter-annual variability in composition, biomass, and productivity of zooplankton communities within the Chukchi Sea. These communities are dominated by a relatively low diversity of copepods, euphausiids, pteropods and larvaceans, along with predatory medusae and chaetognaths. Community composition clearly reflected variations in physical properties of the water column, as well as the intensity of downstream productivity and Pacific water transport. For the four RUSALCA expedition years – 2004, 2009, 2010 and 2012 – I identified four broad zooplankton community types across a broad region of the Chukchi Sea associated with water mass types: Alaska Coastal, Bering Sea-Anadyr, Resident Chukchi and Siberian Coastal Communities. I found that although water masses shared common characteristics between years, inter-annual variability in community structure was greater than differences between water mass types. For future expeditions, more consistent seasonal timing, more consistent resampling of stations and use of depth-stratified sampling to separate the frequently-overlaid water masses would help future resolve spatial and long-term patterns.

In *Chapter 3*, I provided detailed examinations of the distribution, population structure and production of four sibling species of *Pseudocalanus* spp. in the Chukchi Sea during three RUSALCA sampling years. Since only adult females of *Pseudocalanus* are distinguishable morphologically, I developed and implemented a novel molecular method (species-specific PCR) to discriminate between the species at juvenile stages, which dominate the population. I found that the distribution of the four species of *Pseudocalanus* in the Chukchi Sea is tightly linked to oceanography and thermal regimes in the region, making this assemblage important markers of water mass origin, as well as potential indicators of climate change. My results emphasize the importance of including all developmental stages when accounting for species abundances, rather than only those of adult females. The observed spatial and inter-annual distributions of species, as well as results of direct temperature-manipulation experiments on reproduction of *Pseudocalanus* spp., suggest that shifting oceanographic patterns and climate warming will have unequal impact on this group of organisms. Currently, the arctic *P. acuspes* dominates the genus contribution (50-90 %) within the Chukchi Sea; however, the contribution and northward penetration of the two temperate species, *P. newmani* and *P. mimus*, is expected to increase with warming temperatures and increasing inflow from the Pacific during the summer months. My results highlight how species that are very similar morphologically may nevertheless play different roles in an ecosystem.

In my final chapter (*Chapter 4*), I examine the long-term changes that may have occurred in the zooplankton communities within the Chukchi Sea, associated with the dramatic changes in climate that have been observed in the region over the past century. Despite the patchiness and variable quality of the available data, my results indicate a significant increase in zooplankton biomass within the southern Chukchi region, mostly driven by the advected copepod *Calanus glacialis.* This increase likely reflects increasing inflow of biomass-rich Pacific water during the extended summer season. A trend is also observed suggesting a northward shift of Pacific species into the Chukchi Sea, likely driven by a longer ice-free period and extended warmer summer temperatures, as well as a shifting phenology favoring earlier development of species. While these results are far from a conclusive time series, they present the first evidence of change within planktonic communities within the western Chukchi Sea over the last 70 years. Although summer zooplankton communities of the Chukchi Sea have contained Pacific species for as long as observations exist, continued warming and sea ice loss could further increase the influence of Pacific fauna within the Chukchi region. I showed that the success of several of the key advected species is largely correlated with water temperature. My findings are consistent with numerous other studies reporting climate related changes propagating from the environment to the biological communities, such as the significant increase in planktivorous birds that was observed in this region compared to reports from the 1970's (Gall et al., 2016). However, despite the observed trend of increasing zooplankton biomass in the region, it is likely that the trend may level out or reverse with continued warming as was the case in 2004.

Unequivocally, the Chukchi Sea is currently in a state of rapid transition. The changes in the physical environment are influencing the biological systems within the region, as manifested within the zooplankton communities, both on short- and long-term scales. These changes are often best observed at the species level, as responses to environmental stressors by different organisms within the same communities may be vastly different. To become robust, future sampling efforts need to be directed towards creating a continuous time series, with consistent methods and sampling periods to better understand and predict the distribution of communities in a changing Chukchi Sea.

5.1 References

Eisner, L. B., Hillgruber, N., Martinson, E., and Maselko, J. (2012). Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi seas. *Polar Biol.*, 36(1):87–113.

Gall, A. E., Morgan, T. C., Day, R. H., and Kuletz, K. J. (2016). Ecological shift from piscivorous to planktivorous seabirds in the Chukchi Sea, 1975–2012. *Polar Biol.*

Matsuno, K., Yamaguchi, A., Hirawake, T., and Imai, I. (2011). Year-to-year changes of the mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and 2007, 2008. *Polar Biol.*, 34(9):1349–1360.

Questel, J. M., Clarke, C., and Hopcroft, R. R. (2013). Seasonal and interannual variation in the planktonic communities of the northeastern Chukchi Sea during the summer and early fall. *Cont. Shelf Res.*, 67:23–41.