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Climate-mediated changes in zooplankton community structure for the eastern Bering Sea

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ABSTRACT

Zooplankton are critical to energy transfer between higher and lower trophic levels in the eastern Bering Sea ecosystem. Previous studies from the southeastern Bering Sea shelf documented substantial differences in zooplankton taxa in the Middle and Inner Shelf Domains between warm and cold years. Our investigation expands this analysis into the northern Bering Sea and the south Outer Domain, looking at zooplankton community structure during a period of climate-mediated, large-scale change. Elevated air temperatures in the early 2000s resulted in regional warming and low sea-ice extent in the southern shelf whereas the late 2000s were characterized by cold winters, extensive spring sea ice, and a well-developed pool of cold water over the entire Middle Domain. The abundance of large zooplankton taxa such as *Calanus* spp. (*C. marshallae* and *C. glacialis*), and *Parasagitta elegans*, increased from warm to cold periods, while the abundance of gelatinous zooplankton (Cnidaria) and small taxa decreased. Biomass followed the same trends as abundance, except that the biomass of small taxa in the southeastern Bering Sea remained constant due to changes in abundance of small copepod taxa (increases in *Acartia* spp. and *Pseudocalanus* spp. and decreases in *Oithona* spp.). Statistically significant changes in zooplankton community structure and individual species were greatest in the Middle Domain, but were evident in all shelf domains, and in both the northern and southern portions of the eastern shelf. Changes in community structure did not occur abruptly during the transition from warm to cold, but seemed to begin gradually and build as the influence of the sea ice and cold water temperatures persisted. The change occurred one year earlier in the northern than the southern Middle Shelf. These and previous observations demonstrate that lower trophic levels within the eastern Bering Sea respond to climate-mediated changes on a variety of time scales, including those shorter than the commonly accepted quasi-decadal time periods. This lack of resilience or inertia at the lowest trophic levels affects production at higher trophic levels and must be considered in management strategy evaluations of living marine resources.

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1. Introduction

In recent years, climate change in the western Arctic has led to rapid changes in the eastern Bering Sea shelf resulting in variations in seasonal sea ice coverage and water column temperatures, and these variations have affected the entire ecosystem (e.g. Napp and Hunt, 2001; Stabeno et al., 2012b). Zooplankters are essential prey for many fish, seabirds, and marine mammals, therefore there is considerable interest in changes in zooplankton abundance and how these changes may propagate through the food web and impact higher trophic levels (Coyle et al., 2011; Hunt et al., 2011). Many planktivorous fishes, seabirds, and marine mammals inhabit both the northeastern and southeastern Bering Sea during summer (e.g. Piatt and Springer, 2003; Friday et al., 2012; Hollowed et al., 2012; Stevenson and Lauth, 2012). Historical research documented variations in single species abundance and cross shelf patterns of zooplankton in the southeastern Bering Sea (Cooney and Coyle, 1982; Coyle and Pinchuk, 2002; Napp et al., 2002; Stabeno et al., 2010; Coyle et al., 2011; Stabeno et al., 2012a and b). However, there are few modern descriptions of the broad-scale distribution of eastern Bering Sea zooplankton, particularly for the northern Bering Sea (Motoda and Minoda, 1974; Coyle et al., 1996 and references therein). To better understand how climate variability and

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change are affecting the recruitment and broad-scale distributions of planktivores, we need a more thorough understanding of how climate and other forcing affects the production and distribution of zooplankton across the entire region.

The eastern Bering Sea is a large marine ecosystem characterized by a broad continental shelf >500 km wide and >1000 km long oriented in a north westerly direction from the Alaskan Peninsula in the south, to below St. Lawrence Island, approximately 63°N latitude, in the north. Near the northern boundary, the system shifts from a pelagic to benthic dominated system (e.g. Grebmeier et al., 2006; Stevenson and Lauth, 2012; Sigler et al., this issue). The shelf can be divided into regions or domains, each with their characteristic hydrography, circulation, and fauna (Iverson et al., 1979; Cooney and Coyle, 1982; Coachman, 1986; Kachel et al., 2002). Cross shelf domains are most distinct during summer and fall in the southeastern Bering Sea where there are three domains approximated by water depth: Outer (100–180 m), Middle (50–100 m) and Inner (<50 m). The Inner Domain is well mixed, the Middle Domain is stratified into two layers, and the Outer Domain is stratified, but with three layers. In addition to cross shelf variations, there are latitudinal variations in wind fields, water column properties, and most importantly, sea ice coverage (Stabeno et al., 2010, 2012a). The northeastern Bering Sea is ice covered every year; whereas coverage in the south historically varies by more than 100 km (Stabeno et al., 2012a). The cold pool (a layer of <2 °C water that resides on the shelf bottom), is formed as a result of winter cooling and mixing that most often precedes sea ice formation), and typically persists through the following summer. Its extent and magnitude varies with climatic conditions affecting the distribution of many upper trophic level organisms in the region (e.g. Wyllie-Echevarria and Wooster, 1998; Hollowed et al., 2012, Kotwicki and Lauth, 2013).

The goal of this manuscript is to describe the broad-scale spatial variations in large and small zooplankton community composition in the north and southeastern Bering Sea during warm and cold climate states. Additionally, we address several important questions regarding zooplankton ecology affected by changing climate conditions (see Table 1). The data for these analyses come from broad-scale surveys of zooplankton conducted by the Bering-Aleutian Salmon International Survey (BASIS) program at NOAA, and provide the opportunity to describe the spatial cross-shelf and latitudinal distribution of zooplankton for the entire eastern Bering Sea shelf. These surveys began in 1999 before the Bering Sea Project (Bering Sea Ecosystem Study [BEST] and Bering Sea Integrated Ecosystem Research Program [BSIERP]) was launched in 2007 (Wiese et al., 2012) and have continued into the present after the field components of BEST and BSIERP ended.

Table 1
Questions addressed in manuscript.

Q1	What are the spatial and temporal patterns of large and small zooplankton taxa in the eastern Bering Sea for 2003–2009?
Q2	How do the total abundances and biomasses of large and small zooplankton vary between warm and cold years for the southeastern and northeastern Bering Sea?
Q3a	Are the community compositions of large and small taxa different between warm and cold regimes within each domain?
b	When these communities differed between warm and cold regimes which taxa contributed most to the differences?
c	Did the observed differences in zooplankton community composition between regimes occur exactly during the break between low and high ice years?
d	Which taxa showed the largest variations among years?
Q4	For each domain, which environmental factors explained the greatest amount of variability in zooplankton community composition overall and between warm and cold regimes?

During the 2000s the region experienced different multi-year climate regimes (Stabeno et al., 2012b) above average sea water temperatures and very low sea ice coverage (2000–2005), a single year of average sea water temperatures and sea ice extent (2006), and cold years with extensive sea ice (2007–2009). Thus, in contrast to most regional scientific programs in the last 50 years whose timing or duration allowed limited sampling in a single ecosystem state, our dataset allows us to evaluate changes in the eastern Bering Sea shelf pelagic ecosystem during multiple thermal phases.

2. Methods

2.1. Survey station locations and oceanographic sample collection

From mid August to early October, 2003–2009, samples were collected in the eastern Bering Sea, at stations located from 54.5 to 63.0°N and 159.0 to 174.0°W, and spaced approximately 60 km apart (Cieciel et al., 2009; Farley and Moss, 2009; Fig. 1). Stations were divided into shelf regions for analyses using Eastern Bering Sea Marine Region designations based on oceanographic/hydrographic, fisheries, and oceanographic characteristics (Ortiz et al., 2012; Harvey and Sigler, 2013). We further grouped these regions into five major domains using approximately 60°N to split the shelf into south and north (Stabeno et al., 2010) and approximating cross-shelf domains defined by Coachman (1986) yielding: S Inner (<50 m bathymetry, marine regions 2 and 7), S Middle (50–100 m, regions 3 and 6), S Outer (100–200 m, region 4), N Inner (<~40 m, region11), and N Middle (~40–100 m, regions 9 and 10).

Vertical profiles of temperature, salinity, and chlorophyll a (Chla) fluorescence were collected at each station with a Sea-Bird[1] Model 25 or Model 9plus CTD. A rosette sampler was used to obtain discrete water samples for surface and bottom nutrients, total Chla (Whatman GF/F) and large size-fractionated Chla (>10 μm, Millipore Isopore polycarbonate membrane filters); all samples were stored frozen (−80 °C) for 6 months maximum and analyzed using standard procedures at shore-based facilities (Parsons et al., 1984; Gordon et al., 1993). Vertical profiles of Chla concentrations were derived from regressions between in vivo fluorescence and discrete Chla samples (mean $r^2=0.65$). Water column stability (energy required to mix the water column to 70 m, J m^{-3}) was calculated at each station from CTD temperature and salinity data (Simpson et al., 1977). Ice coverage (number of days of ice at each station during the prior winter) and timing of retreat (the last day of ice in spring) for a 60 km^2 square box centered on each station was obtained from the Advanced Microwave Scanning Radiometer (AMSR) on MODIS Aqua from the National Snow and Ice Data Center (NSIDC) (S. Salo, NOAA PMEL, personal comm.). We assumed no ice when concentrations dropped below 15%. Wind mixing data (wind velocity^3, u^{*3}) for August were obtained from National Centers for Environmental Prediction (NCEP) reanalysis data set (N. Bond, NOAA PMEL, personal comm.). Wind mixing data were averaged over a 2° latitude by 5° longitude box centered on a NOAA PMEL mooring at site M4 (57. 9°N, 168. 9°W; Stabeno et al., 2010). We assumed M4 winds approximated wind fields over our entire survey area, since winds at all four 70 m moorings in the northeast and southeast Bering Sea (M2, M4, M5 and M8) have shown strong coherence during recent years (Stabeno et al., 2010). Winter wind fields for the prior period (October–April) based on shelf-wide model results were used to estimate potential onshore and offshore flow, assuming that southeasterly winds

[1] Use of trade names does not signify an endorsement by the U.S. National Oceanic and Atmospheric Administration.