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Comparison of spring-time phytoplankton community composition in two cold years from the western Gulf of Alaska into the southeastern Bering Sea



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ABSTRACT

The Bering Sea is a highly productive ecosystem providing the main oceanographic connection between the North Pacific and Arctic oceans. The atmospheric connection with the Arctic Ocean leads to seasonal sea ice formation in the Bering Sea, the areal extent and timing of retreat of which have important implications for primary productivity and phytoplankton community composition in this region. Hydrographic data from cruises and satellite sea ice and sea surface temperature data in spring 2011 and 2012 suggest classification of these years as relatively warmer and colder years, respectively. Locations in the western Gulf of Alaska (Pavlof Bay), at the north end of an eastern pass through the Aleutian Islands (Unimak Pass), and on the continental shelf of the Bering Sea (M2) were visited in both years. Stratification was apparent on the shelf in 2012, while the water column was comparatively well-mixed at other locations in both years. Phytoplankton biomass was highest in 2011 overall and specifically on the shelf in both years, while minimal biomass was measured within the well-mixed Unimak Pass in 2012. Surface phytoplankton size distributions included substantial contributions of picoplankton ($< 3 \mu\text{m}$) in 2011 (21–35%), while micro- (20–200 μm) and nanoplankton (3–20 μm) comprised 79% and 95% of biomass in Pavlof Bay and at M2, respectively, in 2012. Analyses of similarity revealed spatial variability in the phytoplankton assemblages within each year (2011: $R=0.588$, $p < 0.004$; 2012: $R=0.646$, $p < 0.004$). Additionally, between-year variability had a strong and significant effect on differences between assemblages across all locations ($R=0.579$, $p < 0.0003$), likely masking differences between sites when years were grouped ($R=0.134$, $p < 0.079$). These differences were likely driven by the dominance (up to 75% in Unimak Pass) of the colonial prymnesiophyte *Phaeocystis* sp. at all sites in 2011, resulting in reduced community diversity, compared to more widespread abundance of large diatoms of the genera *Thalassiosira*, *Thalassiothrix*, and *Chaetoceros* in 2012. The current study shows that within-regime differences in phytoplankton community composition between years can be almost as great as that between locations with vastly different oceanographic settings. High between- and multi-year variability may combine with a potential overall decline in sea ice in the Bering Sea to produce significant changes in the productive base of the food web with potential cascading effects on higher, economically and ecologically important trophic levels.

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1. Introduction

The Bering Sea provides the major connection between the North Pacific and Arctic oceans. The area of the Bering Sea is almost evenly divided between shallow waters of the continental shelf ($< 200 \text{ m}$) and deeper waters ($> 200 \text{ m}$) southwest of the

continental slope (Hunt et al., 2010), and its physics have been well discussed in other sources (e.g. Stabeno et al., 2001, 2012a, 2002, 1999). Through geostrophic transport, water enters the eastern Bering Sea from the North Pacific through a series of passes along the Aleutian Island chain. Unimak Pass is one of the shallow ($< 80 \text{ m}$) eastern passes through which warm, low-salinity, southward-flowing waters of the Alaska Coastal Current (ACC) first enter the Bering Sea, constituting the only major connection between the shelves of the North Pacific Ocean and Bering Sea (Stabeno et al., 2002; Ladd and Stabeno, 2012). Unimak Pass also allows for advection of zooplankton populations (Longhurst, 1998)

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and some nutrients (Stabeno et al., 2002) onto the shelf. Circulation within the Bering Sea is dominated by a cyclonic gyre, and waters exit the sea via geostrophic flow northward through the Bering Strait into the Arctic Ocean or southward through the Kamchatka Strait into the western North Pacific Ocean (Stabeno et al., 1999; Hunt et al., 2010).

The oceanography of the Bering Sea is strongly influenced by the in- and outflow of waters of differing origins and by atmospheric coupling with the Arctic Ocean (Hunt et al., 2010; Brown and Arrigo, 2012). Wind direction is largely a function of the location and magnitude of the Aleutian Low and shows variability on interannual, multi-year, and multi-decadal time scales (Jin et al., 2009; Overland et al., 2012). Wind direction has significant implications for the Bering Sea, with warm periods (e.g. 2001–2005) dominated by spring wind anomalies out of the south, and cool periods (e.g. 2007–2010) dominated by spring wind anomalies originating in the northwest (Hunt et al., 2010; Brown and Arrigo, 2012; Stabeno et al., 2012b). Warm years are characterized by higher than average sea temperatures, low sea ice area, decreased sea ice extent, and early retreat of ice, relative to cool years (Stabeno et al., 2012b). The date of ice retreat, in combination with water column stabilization by solar heating and cessation of winter storm activity, directly affects the timing of the spring phytoplankton bloom especially in the southeastern Bering Sea sea-shelf which supports a large portion of the food web (Hunt et al., 2002; Sigler et al., 2014).

The implications of warm years on primary production and the spring bloom are multidimensional. The spring bloom of phytoplankton requires stratification of the water column; in cool years the bloom occurs in cold water (-1.5 – 2 °C) as sea ice melts, while in warm years the bloom is delayed until solar heating stratifies the water column and, as a result, occurs in warm (5 – 8 °C) waters (Stabeno et al., 2012b). There tends to be a generally positive response of net primary production with sea surface temperature (Hare et al., 2007; Mueter et al., 2009; Hunt et al., 2010); the effects of temperature on composition of the phytoplankton community, however, are less clear. Cells > 5 μm in size have generally comprised the bulk of the standing stocks (Lomas et al., 2012), and early work in the Bering Sea documented distinct spring-time ice edge and shelf break communities dominated by large diatoms (Schandelmeier and Alexander, 1981). Furthermore, recent evidence suggests a shift within the phytoplankton community towards smaller cells (Noiri et al., 2005; Hare et al., 2007; Fujiwara et al., 2011) and reduced microzooplankton grazing of the spring bloom (Strom and Fredrickson, 2008) in warm years. This combination of smaller cells and lower microzooplankton grazing has been suggested to lead to observed reductions in the abundance of large zooplankton, including the copepod *Calanus marshallae* in warmer years (Hunt et al., 2008, 2011; Lomas et al., 2012; Stabeno et al., 2012b). More generally, shifts in diversity and community structure have been shown to significantly affect stability and functioning in complex aquatic food webs via a combination of direct and indirect effects (Downing and Leibold, 2002; Narwani and Mazumder, 2012). Unfortunately, community composition remains a parameter that is difficult to measure remotely (e.g. via satellite) or with in situ instrumentation (e.g. on moorings) with the result that trends in phytoplankton community structure in environments such as the Bering Sea are still rather poorly understood.

The effects of multi-year variability between warm and cold conditions on the Bering Sea ecosystem have been investigated for several decades, largely motivated by the economic role of the region as a major producer of seafood for the United States and its direct connection to the rapidly changing Arctic ecosystem (Stroeve et al., 2007; Brown and Arrigo, 2012; Overland et al., 2012). The Bering Sea generates approximately 40% of the United

States finfish and shellfish landings in the U.S., employs a large population of fishers, processors, and distributors, and supports subsistence for over 50,000 local residents, many of whom are Alaskan natives (Stabeno et al., 2012b). Hunt et al. (2002) proposed an Oscillating Control Hypothesis, suggesting bottom-up or top-down control of fisheries in cold or warm regimes, respectively, largely as a result of changes in the timing of the spring phytoplankton bloom, differential temperature-regulated zooplankton production, and impacts of secondary production on survival and recruitment of piscivorous fish. This hypothesis has been revised since its original inception to incorporate evidence for a lack of large zooplankton in warm years (Hunt et al., 2008; Lomas et al., 2012; Stabeno et al., 2012b), despite increased primary production (Hunt et al., 2011). However, the effects of changes in the community composition of primary producers on these dynamics remain largely unknown.

Climate-driven trends in sea ice decline have been documented in the Arctic Ocean (e.g. Stroeve et al., 2007); however, the impacts of climate change on sea ice and temperature in the Bering Sea remain somewhat obscured. Satellite-based observations of sea ice do not indicate a long-term decline in the last six decades (Brown and Arrigo, 2012), while model-based predictions suggest a potential air temperature increase and severely reduced sea ice extent in the Bering Sea by 2050 (Wang et al., 2012). Continued high variability and the potential for long-term change in temperatures and sea ice extent may have significant implications for the dynamics of the spring bloom, affecting the composition of phytoplankton communities with potentially significant effects on the food web of the Bering Sea. However, such information is still rare.

The current study compares spring-time phytoplankton communities from the western Gulf of Alaska, through Unimak Pass, and into the southeastern Bering Sea shelf during a relatively warm (2011) and cold (2012) year. These years follow the documented cold years of 2007–2010 and fall within the range of conditions described by Stabeno et al. (2012b), namely increased ice extent and cooler temperatures, suggesting that 2011 and 2012 likely also fall within this cold regime. Given the importance that the timing, magnitude, and composition of spring blooms in the Bering Sea have on the greater ecosystem, the current study's focus on within-regime variability provides important insights into the significantly different communities that even small changes in environmental conditions can affect. With variability in environmental conditions, especially sea ice coverage in the southern Bering Sea, expected to increase with continued climate change (Stabeno et al., 2012a), an understanding of the potential effects on community structure of primary producers is of great importance.

2. Methods

2.1. Remote sensing

Sea surface temperature (SST) data for the region was accessed for the day of 15 May in each year through the Group for High Resolution Sea Surface Temperature (GHRSSST; <http://podaac.jpl.nasa.gov/GHRSSST>). The GHRSSST global level 4 analysis is produced daily on a 0.25° grid at the NOAA National Climatic Data Center and employs optimal interpolation (OI) using data from the 4 km Advanced Very High Resolution Radiometer (AVHRR) Pathfinder Version 5 time series and in situ ship and buoy observations. Sea ice extent data were obtained from the National Snow & Ice Data Center (http://nsidc.org/data/seaice_index/archives/) and regional estimates of areal extent (m^2), excluding data north of the Bering Strait, were calculated in ArcMap (v. 10, Esri). Rates of sea-ice

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