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Spring and fall phytoplankton blooms in a productive subarctic ecosystem, the eastern Bering Sea, during 1995–2011

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ABSTRACT

The timing and magnitude of phytoplankton blooms in subarctic ecosystems often strongly influence the amount of energy that is transferred through subsequent trophic pathways. In the eastern Bering Sea, spring bloom timing has been linked to ice retreat timing and production of zooplankton and fish. A large part of the eastern Bering Sea shelf (~500 km wide) is ice-covered during winter and spring. Four oceanographic moorings have been deployed along the 70-m depth contour of the eastern Bering Sea shelf with the southern location occupied annually since 1995, the two northern locations since 2004 and the remaining location since 2001. Chlorophyll *a* fluorescence data from the four moorings provide 37 realizations of a spring bloom and 33 realizations of a fall bloom. We found that in the eastern Bering Sea: if ice was present after mid-March, spring bloom timing was related to ice retreat timing (p < 0.001, df=1, 24); if ice was absent or retreated before mid-March, a spring bloom usually occurred in May or early June (average day 148, SE=3.5, n=11). A fall bloom also commonly occurred, usually in late September (average day 274, SE=4.2, n=33), and its timing was not significantly related to the timing of storms (p=0.88, df=1, 27) or fall water column overturn (p=0.49, df=1, 27). The magnitudes of the spring and fall blooms were correlated (p=0.011, df=28). The interval between the spring and fall blooms varied between four to six months depending on year and location. We present a hypothesis to explain how the large crustacean zooplankton taxa Calanus spp. likely respond to variation in the interval between blooms (spring to fall and fall to spring).

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1. Introduction

The timing and magnitude of phytoplankton blooms in subarctic ecosystems often strongly influence the amount of energy transferred through subsequent trophic pathways. In the southeastern Bering Sea, spring bloom timing has been linked to production of large crustacean zooplankton and walleye pollock (*Gadus chalcogrammus*) (Hunt et al., 2002, 2011; Coyle et al., 2011);

0967-0645/\$ - see front matter Published by Elsevier Ltd. http://dx.doi.org/10.1016/j.dsr2.2013.12.007 if ice is present after mid-March, an early ice-associated bloom occurs there; otherwise a spring bloom usually occurs in May (Hunt et al., 2002; Stabeno et al., 2001). Although spring bloom timing is well-characterized in the southeastern part of the shelf (Brown and Arrigo, 2011, 2013; Hunt et al., 2002, 2011; Rho and Whitledge, 2007; Stabeno et al., 2001), less is known about the spring bloom elsewhere in the eastern Bering Sea (Brown and Arrigo, 2013), as well as the characteristics of the fall bloom (Rho and Whitledge, 2007).

The eastern Bering Sea is dominated by a broad continental shelf (\sim 500 km wide), a large part of which is ice-covered during winter, with the maximum extent varying > 100 km among years. In ice-covered areas, the seasonal cycle of primary production begins with ice algae (primarily large diatoms), which begin to grow in the spring when light level becomes adequate. Ice algae are adapted to lower light levels than pelagic phytoplankton (Kirst and Wiencke, 1995) and grow within the ice and at the ice–water

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interface depending on the amount of overlying snow cover. Ice algae begin to grow in mid-February in the Bering Sea (R. Gradinger, University of Alaska, Fairbanks, pers. comm.) and may provide an early concentrated food source (chlorophyll a maximum $\sim 300\,\mu g\,l^{-1}$; Mock and Gradinger, 2000; Niemi et al., 2011) for zooplankton (e.g. O'Brien, 1987; Runge and Ingram, 1991). Sea ice algae that are not grazed can seed the spring phytoplankton bloom or may aggregate and sink out of the upper water column (Tremblay et al., 1989, Riebesell et al., 1991; Haecky et al., 1998; Fortier et al., 2002) with seeding more likely if the release from ice is not followed by a strong mixing event that breaks down stratification (lin et al., 2007). Sedimentation of ice algae occurs during and immediately after growth of water column phytoplankton starts over the Bering Sea middle shelf (R. Gradinger, University of Alaska, Fairbanks, pers. comm.). Ice algae net growth within the ice typically is terminated during ice melt in late spring or early summer.

Phytoplankton in the Bering Sea exhibit net growth in the spring once the water becomes stratified and the mixed layer is shallower than the critical depth (*sensu* Sverdrup, 1953). Prior to this, phytoplankton are considered to be light-limited, but have adequate nutrients due to the advection of nutrient rich slope water onto the shelf during the previous winter, which is mixed throughout the water column (Niebauer et al., 1995); nutrient recycling on the shelf also is important (Granger et al., 2011). The phytoplankton spring bloom typically ends when the surface nutrient supply is exhausted and phytoplankton growth becomes nutrient limited (typically below 1 μ M nitrate). Grazing pressure from mesozooplankton and microzooplankton also increases as the spring progresses, which can reduce the net accumulation of phytoplankton standing stocks.

In the summer, phytoplankton concentration in the surface mixed layer is typically low due to nutrient limitation and continued grazing pressure. Episodic wind events can break down stratification and mix nutrients and viable phytoplankton cells to the surface during this period (Sambrotto et al., 1986; Stabeno et al., 2010; Mordy et al., 2012). During fall, increased frequency and intensity of storms and overall cooling of the water column reduces stratification and deepens the mixed layer so that nutrients are mixed to the surface to fuel fall phytoplankton blooms. The fall bloom ends when phytoplankton become light limited, due to decreased day length and deepening of the mixed layer. Pelagic-benthic coupling (Grebmeier et al., 2006) and luxury nutrient consumption by diatoms near the sediment interface may also be important (Droop, 1973), since the Bering Sea shelf is a shallow shelf system with 1% light levels located 10-20 m below the pycnocline (Mordy et al., 2012). Phytoplankton present in the water column during late fall, when ice begins to form, can be incorporated into the ice with large diatom cells preferentially selected (Gradinger and Ikavalko, 1998; Niemi et al., 2011). Ice algal cells may grow slowly during winter when light levels are very low (Melnikov, 1998) and then begin to grow faster when light increases in spring.

In this paper we focus on the middle domain of the eastern Bering Sea shelf where four oceanographic moorings have been located. The measurements on the moorings include temperature and chlorophyll *a* fluorescence. In summer, the middle domain is strongly stratified into two layers, with a wind-mixed upper layer and a tidally-mixed lower layer. The middle domain typically extends from the 50 m isobath to the 100 m isobath, and is bounded by oceanic fronts or transition zones (Iverson et al., 1979). In winter, the middle domain is usually well mixed and cold, with a large part (>50%) ice-covered. These four oceanographic moorings provide the longest, daily record of in situ oceanographic measurements in the eastern Bering Sea. This paper is the first examination of the chlorophyll *a* fluorescence data,



excepting previous analyses of the spring bloom at the southernmost mooring (Hunt et al., 2002, 2011; Stabeno et al., 2001). In this paper our objectives are to: characterize spring and fall blooms over the eastern Bering Sea middle shelf; relate their timing and strength to physical characteristics including spring ice retreat and fall overturn; and discuss some implications of these results for one of the large crustacean zooplankton taxa characteristic of that domain (*Calanus* spp.).

2. Data and methods

2.1. Moorings

Four oceanographic moorings have been deployed along the 70-m depth contour of the eastern Bering Sea shelf with two southern locations sampled almost continually since 1995 (M2) and 1999 (M4), and two northern locations since 2004 (M8) and 2005 (M5) (Fig. 1). Prior to 2005, moorings were recovered and redeployed twice a year, once in the spring (April/May) and again in the late summer or early fall (September/October). Since 2006, there has been extensive ice on the northern shelf in spring and M8 (and sometimes M5) has only been recovered and redeployed once a year in August or September. Data collected by instruments on the moorings included temperature (miniature temperature recorders, SeaBird⁵ SBE-37 and SBE-39) and chlorophyll *a* fluorescence (WET Labs DLSB ECO Fluorometer). A transition to fluorometer sensors with wipers that sharply reduced fouling occurred during 2001-2004. Data were collected at least hourly. During autumn, winter, and early spring, the shallowest instrument was at 11 m at M2 and M4, at 15 m at M5 and at 20 m at M8. During late spring to early autumn (the ice-free period), the mooring at M2 included a surface toroid measuring temperature at a depth of 1 m, and the upper instrument at M4 was at 11 m, as was the upper instrument at M5 and M8 if a summer mooring was deployed. For consistency, our analyses focus on data recorded at

⁵ Use of trade names does not constitute an endorsement by NOAA.

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