Deep-Sea Research II 134 (2016) 141–156

Contents lists available at ScienceDirect

Deep-Sea Research II

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

Regular article

Seasonal and geographic variations in modeled primary production and phytoplankton losses from the mixed layer between warm and cold years on the eastern Bering Sea shelf

C.L. Liu [a,b], L. Zhai [c], S.I. Zeeman [d], L.B. Eisner [e], J.C. Gann [e], C.W. Mordy [f], S.B. Moran [g], M.W. Lomas [b,*]

[a] *Marine College, Shandong University, Weihai 264209, China*
[b] *Bermuda Institute of Ocean Science, St. George's GE 01, Bermuda, USA*
[c] *Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada B2Y4A2*
[d] *Department of Marine Sciences, University of New England, Biddeford, ME 04005, USA*
[e] *Alaska Fisheries Science Center, Juneau, AK 99801, USA*
[f] *Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, WA 98195, USA*
[g] *Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882-1197, USA*

ARTICLE INFO

Available online 28 July 2016

Keywords:
Primary production
Bering Sea
Grazing
Carbon export
Climate variability

ABSTRACT

The total daily phytoplankton loss from the mixed layer can be estimated as the difference between gross primary production (GPP) and the realized change in phytoplankton carbon biomass. Here a modeling approach is used to estimate the total loss rates for five hydrographic domains on the eastern Bering Sea Shelf during a warm (2000–2006) and a cold (2007–2010) period. Model results indicate that the average daily rate of GPP in the mixed layer for all domains is on average slightly higher than in warm years (950 ± 726 mg C m^{-2} d^{-1}) than in cold years (859 ± 640 mg C m^{-2} d^{-1}), but is not significantly different. Similarly, the daily phytoplankton total loss rate from the mixed layer in all domains is on average slightly higher in warm years (961 ± 747 mg C m^{-2} d^{-1}) than in cold years (888 ± 691 mg C m^{-2} d^{-1}), but the difference is not significant. That total loss rates show the same warm vs. cold year pattern as GPP, suggests similar seasonal and latitudinal variations and magnitudes of change for both processes. The annual total loss is compared with the sum of individual process losses (e.g., mixing, grazing, sinking, etc.), with the discrepancy being generally larger than $\sim$15% of the total loss both in warm and cold years. The model results also show that annual respiration is generally greater than losses due to zooplankton grazing and sinking both in warm and cold years. Compared among domains, significant differences (t-test, $P < 0.05$) between northern and southern domains (defined as North and South of 60°N) are observed for GPP rate, total daily loss rate and each of the individual loss terms in cold years, while values for southern domains are higher than those of northern domains. In warm years there were no significant differences between domains. Furthermore, these results indicate that total loss rates reflect patterns in GPP rate implying a similar metabolic balance within the ecosystem in both warm and cold years.

1. Introduction

The Bering Sea is one of the most productive marine ecosystems in the world's oceans (Walsh et al., 1989). This region accounts for almost half of the annual U.S. pelagic fishery catch (Overland and Stabeno, 2004) and supports a productive benthic community (Grebmeier et al., 1995). The Bering Sea is susceptible to climate change and has exhibited a high degree of variability in the areal extent of sea ice, as well in water temperatures, and the distribution and abundance of key species at multiple trophic levels over the past four decades (Stabeno et al., 2012a).

For example, during 1972–2000, high interannual variability in the areal extent of sea ice during spring (March–April) was associated with alternating annual warm and cold climate conditions. Beginning in 2000, the ecosystem experienced a continuous warm period (2001–2006) of approximately six years with low ice extent

---

[*] Corresponding author. Current address: Bigelow Laboratory for Ocean Sciences, East Boothbay, MN 04544, USA. Fax: +1 207 315 2329.
E-mail address: mlomas@bigelow.org (M.W. Lomas).

http://dx.doi.org/10.1016/j.dsr2.2016.07.008
0967-0645/

during spring, followed by a contiguous cold period (2007–2011) of about the same period when the sea ice was more extensive. For the remainder of each growing season, high or low areal extents of the sea ice during spring were associated, respectively, with relatively cold or warm water column temperatures, as well as with related changes in the areal extent of the bottom water 'cold pool' (defined as <2 °C). In the southeastern Bering Sea, ocean circulation also differs between warm and cold years; during cold years, monthly-mean currents over the shelf were largely westward, while in warm years the direction of the currents were more variable, with northward flows occurring during December–February and relatively weak flows for the remainder of the year (Stabeno et al., 2012a).

Historically, research has focused on primary production measurements on the eastern Bering Sea shelf because of its importance to fisheries. Winter primary production over the shelf and summer primary production near the Aleutian are have been reported (McRoy et al., 1972; Mordy et al., 2005) using ^{14}C and ^{13}C measurements. While summer primary production has been reported for areas around the Pribilof Islands (Rho et al., 2005; Sambrotto et al., 2008) and in other areas of the Bering Sea (Kopylov et al., 2002; Stockwell et al., 2011; Whitledge et al., 1998), studies have also estimated net primary production indirectly from nitrate depletion in the euphotic zone (Mordy et al., 2012), and from nitrate tracer uptake experiments (Sambrotto et al., 1986; Whitledge et al., 1986; Hansell et al., 1993). Despite the relatively large volume of data on primary production in this region, there are few that report year-round primary production measurements (Rho and Whitledge, 2007) covering a broad spatial scale (i.e., for the entire southeastern shelf). Instead, most studies have focused either on specific 'events', such as ice-edge blooms (Niebauer et al., 1995), the spring bloom (Sambrotto et al., 1986; Whitledge et al., 1986), different seasons in geographically restricted regions (McRoy et al., 1972), or on a geographically important shelf region such as the Pribilof Islands (Sambrotto et al., 2008). Recently, Lomas et al. (2012) reported primary production on the eastern Bering Sea shelf during cold years (2008–2009). However, the temporal resolution was limited to short time periods (weeks) in spring and summer, although they covered a broader spatial scale than many previous studies. Consequently, since direct primary production measurements reported for the Bering Sea are temporally and spatially disparate, it has been difficult to estimate with confidence both shelf-wide primary production and changes in primary production associated with climate variability (Mathis et al., 2010; Lomas et al., 2012).

Primary productivity models, based upon remotely sensed data, have recently been used to address questions related to the spatial and temporal dynamics of primary production over the Bering Sea shelf. For example, Mizobata and Saitoh (2004) used a model to estimate primary production during warm years (1998–2000). However, their study did not provide a comparison of model output with measured data, and there was no independent validation of whether high values observed in warm years represented a true elevation in primary production in the outer domain. Using a similar model based on remotely sensed data, Brown et al. (2011) and Brown and Arrigo (2013) compared warm, low-ice years with cold, high-ice years, and speculated that annual Bering Sea primary production was likely to increase by as much as 40–50% under future conditions of ocean warming and sea ice loss. While their model output overlapped with measured primary production values, the relative error made it difficult to resolve the 40–50% change, although an increase of that magnitude would clearly have important ecological impacts. Similarly, Lomas et al. (2012) concluded that, based upon the high degree of variability in several primary production metrics, an approximate doubling of primary production in warm years would need to occur in order to come to the conclusion that it was significantly greater than primary production in cold years. While there is a growing consensus that primary production may increase in a warmer Bering Sea, the fate of that increased primary production remains largely unknown.

Phytoplankton production in the pelagic zone is subject to a variety of possible loss processes, including both physical (advection and mixing) and biological (respiration, grazing, sinking and natural mortality). Independent estimates of these loss terms are very important; however, loss rates are difficult to fully quantify in the field. Although some loss processes, such as carbon export and micro- and meso-zooplankton grazing were studied extensively recently in the Bering Sea (Moran et al., 2012; Sherr et al., 2013; Stoecker et al., 2014; Campbell et al., 2016), under-sampling, both spatially and temporally, still poses a significant challenge for estimation of total phytoplankton losses in models (Walsh, 1983). Furthermore, there has been relatively little effort directed towards determining total phytoplankton loss over a wide range of physical and biological conditions and regimes. A remote sensing approach has been used to estimate phytoplankton loss terms in the North Atlantic (Siegel et al., 2002); however, this method was applicable only at the time of spring bloom initiation. More recently, Zhai et al. (2010) used a primary production model based on remotely sensed data and a Monte Carlo procedure to estimate the total phytoplankton loss from the mixed layer in the NW Atlantic. The estimated loss was taken as the difference between expected chlorophyll (Chl-a) concentrations at the $N+1$ time step, based upon the calculated phytoplankton gross primary production (i.e., the growth rate), and satellite observations of Chl-a at the time step N.

In order to assess the influence of climate change on the seasonal and spatial distributions of primary production and total phytoplankton losses, this study used the basic approach of Zhai et al. (2010) to quantify gross primary production (GPP) and total phytoplankton losses from the mixed layer in the Bering Sea. The entire Bering Sea shelf was divided into Northern (Outer and Middle domains) and Southern regions (Outer, Middle and Inner domains) at a latitude of approximately 60°N, based on changes in water column structure and tides (Stabeno et al., 2010, 2012a). The specific goals of this study were (1) to compare the temporal and spatial variations in GPP and total losses between warm and cold years in the different domains of the eastern Bering Sea shelf; and (2) to describe the temporal and spatial variations of individual loss term estimations. By examining how modeled GPP and total losses responded during warm and cold years, the study should provide insights into a potential future Bering Sea carbon cycle and into how climate change may alter the flow of carbon through the ecosystem. This would be crucial to the sustenance of upper trophic levels.

2. Methods and data

2.1. Primary productivity algorithm

An analytical model for daily, mixed-layer GPP was used in conjunction with 8-day composite satellite images of phytoplankton biomass fields (indexed as the concentration of Chl-a) to estimate total phytoplankton loss from the mixed layer. The models were applied to five $4^\circ \times 4^\circ$ regions located on the eastern Bering Sea shelf that primarily align with the broader Outer, Middle, and Inner domains, both North and South, previously used by Mathis et al. (2010) and Lomas et al. (2012) (Fig. 1). While portions of these defined regions cross into geographically-fixed neighboring domains, there were important on/off and within shelf lateral meanders in the fronts that defined these domains