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# Spring phytoplankton in the eastern coastal Gulf of Alaska: Photosynthesis and production during high and low bloom years

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ABSTRACT

Primary production associated with the spring bloom in high-latitude seas constitutes a substantial fraction of annual total in those environments, and provides a seasonally timed bounty to benthic and pelagic organisms at higher trophic levels. Light is widely believed to regulate the timing and magnitude of spring production in the coastal Gulf of Alaska, although few data are available on the relationship between light and photosynthesis or primary production in that region. In two cruises to the coastal waters of southeast Alaska (May 2011 and April 2013), we observed strongly contrasting early-season phytoplankton communities, although environmental conditions were largely similar. An early, diatom-dominated spring bloom occurred in April 2013, while the anomalously low chlorophyll conditions of spring 2011 were widely observed in May of that year. Integrated chlorophyll *a* (Chl) was substantially higher in April 2013 than in May 2011 (median 62 versus 29 mg $m^{-2}$), and April 2013 saw a greater contribution by large cells ( > 20 μm size fraction) to total Chl. The < 20 μm size fraction, however, had a higher median carbon biomass in the low-Chl spring of 2011 (74 versus 47 μg C $l^{-1}$). Other interannual differences in the < 20 μm size class included a higher C:Chl ratio (76 versus 41 g:g), a lower specific growth rate (0.18 versus 0.65 $d^{-1}$), and a greater biomass of picophytoplankton (cells ≤ 2 μm) in 2011. Photosynthesis-irradiance experiments in both years revealed low light-acclimated spring communities, with high photosynthetic efficiencies ($\alpha^B$) and low irradiances for the onset of light saturation, contrasting strongly with the high light-acclimated summer Gulf of Alaska community previously described. Photoinhibition was seen in both springs but was more frequent and severe in the small cell-dominated community of 2011. Maximum photosynthetic rates ($P^B_M$) were higher in the high-Chl month of April 2013 than in May 2011, averaging 5.3 versus 3.4 μg C μg $Chl^{-1}$ $h^{-1}$ across all depths and both size classes. In May 2011, $P^B_M$ showed a strong negative correlation with salinity, while several photosynthetic parameters were correlated to light exposure history. In contrast, we found no environmental correlates to photosynthetic parameters in April 2013. Estimated primary production was considerably higher in April 2013 than in May 2011 (medians 2.5 versus 0.9 g C $m^{-2}$ $d^{-1}$). Characteristics of the May 2011 phytoplankton community were broadly consistent with a role for iron limitation on this narrow shelf, where cross-shelf exchange processes with nearby iron-limited open ocean waters may vary with larger-scale environmental conditions. Understanding the factors that regulate spring phytoplankton biomass, composition, and photophysiology will be key to understanding the large interannual variations in spring production in the coastal Gulf of Alaska.

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## 1. Introduction

Waters of the coastal Gulf of Alaska support highly productive fisheries as well as large populations of seabirds and marine mammals, both resident and migrant (Mundy, 2005). Marine phytoplankton largely comprise the base of the food web supporting these species. Remote sensing of chlorophyll *a* (Chl) has revealed that intense seasonality, pronounced interannual variability, and mesoscale patchiness are hallmarks of coastal Gulf of Alaska phytoplankton communities (Brickley and Thomas, 2004; Waite and Mueter, 2013). Understanding the drivers of this temporal and spatial variability is key to understanding variability in marine bird and animal populations in the Gulf.

The major spatial contrast in the Gulf of Alaska is between the coastal waters over the continental shelf and the open ocean waters of the deep basin. The oceanic habitat of the open Gulf is constrained to low levels of phytoplankton biomass by chronic iron limitation and consequent close coupling between production

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and microzooplankton grazing (Boyd et al., 2004; Miller, 1993). The oceanic Gulf ecosystem is characterized by year-round low Chl and high macronutrient concentrations, and a small cell-dominated phytoplankton community in which diatoms are scarce. In contrast, the coastal Gulf of Alaska supports higher Chl levels year-round (Brickley and Thomas, 2004). An intense spring diatom bloom dominates the annual cycle, and macronutrients (nitrate, silicate) in surface waters can be depleted in spring and summer (Childers et al., 2005; Strom et al., 2006; Waite and Mueter, 2013).

Regulation of phytoplankton production in these coastal waters is complex, involving light, macronutrients, iron, and grazing by micro- and mesozooplankton (Aguilar-Islas et al., 2016; Dagg et al., 2009; Fiechter et al., 2009; Strom et al., 2006, 2007, 2010). Regulation of the spring bloom is of particular interest. This feature represents the largest near-surface Chl accumulation of the year in most shelf locations, although a fall bloom can also be substantial (Brickley and Thomas, 2004). In addition, the timing of the bloom almost certainly relates to the phasing of life histories in zooplankton populations that rely, directly or indirectly, on this production pulse at the start of the growing season (Mackas and Tsuda, 1999; Pinchuk et al., 2008). Average peak bloom timing as estimated from satellite ocean color imagery is between May 11th and May 17th, depending on shelf region (Waite and Mueter, 2013). However, satellite images also reveal that both the timing of bloom onset and the timing and magnitude of peak Chl biomass can vary interannually by many weeks (Brickley and Thomas, 2004; Henson, 2007).

Spring in the coastal Gulf is a time of rapid change in solar irradiance on multiple time scales, as the sun angle increases, cloud cover varies day-to-day from heavy to absent, and vertical mixing responds to warming and the passage of storms. Conceptual models of the region posit a strong dependence of spring production on light availability (Gargett, 1997; Henson, 2007). Similarly, in numerical models of the coastal Gulf, predictions of primary production are highly sensitive to the form of the photosynthesis – irradiance function, and particularly to the assumed photosynthetic efficiency ($\alpha^B$) (Coyle et al., 2012; Fiechter and Moore, 2009). To progress in our understanding of climate – production links in this highly productive ecosystem, we need data on light regulation of photosynthesis and primary production. This study provides the first data on the photophysiology of coastal Gulf of Alaska phytoplankton during the crucial spring bloom period.

We visited southeast coastal waters extending from the southern end of Baranoff Island north to the Yakutat Bay region (Fig. 1) in spring of two years: 2011 and 2013. The southeastern region is particularly understudied in comparison with the northern and western Gulf of Alaska. The geography here contrasts strongly with that of coastal waters west of Prince William Sound: the shelf is generally narrower, with deep, cross-cutting canyons and troughs that disrupt the Alaska Coastal Current (ACC) and promote cross-shelf exchange. The mountainous shoreline and deep entrances such as Cross Sound and Chatham Strait affect the timing and delivery of runoff, generate intense variability in regional winds (Ladd and Cheng, 2016), and promote the exchange of nutrients and organisms between the shelf and inland waters (Stabeno et al., 2016). The Yakutat and Sitka coasts are both sites of eddy formation (Henson and Thomas, 2008; Ladd, 2007); due to the narrow shelf, eddy circulation readily effects cross-shelf exchange over the entire shelf width. However, tidal mixing energy and freshwater inputs are both lower in the southeast than on the northern shelf (Stabeno et al., 2016). Satellite imagery indicates that patterns of Chl intensity and timing also contrast between southeastern and western coastal waters: on average, the southeast has lower Chl concentrations and an earlier spring bloom peak, and there is a tendency for Chl anomalies in the two regions to vary out-of-phase (Brickley and Thomas, 2004; Waite and Mueter, 2013).

As part of the Gulf of Alaska Integrated Ecosystem Research Program (GOA-IERP), our goal was to characterize the photophysiology of the spring phytoplankton, to relate the photosynthesis-light responses to the physical and chemical environment of the southeast shelf, and to estimate primary productivity in spring of two years: 2011 and 2013. We were provided with a natural experiment in that spring of 2011 had a greatly reduced bloom, while the bloom in 2013 was early and intense. Characterizing spring photosynthesis-light responses will contribute to our understanding of how environmental variability regulates primary production in the coastal Gulf of Alaska.

## 2. Materials and methods

### 2.1. Environmental conditions.

Observations were made on cruises to the southeast coastal Gulf of Alaska from 3–18 May 2011 (R.V. Thomas G. Thompson)

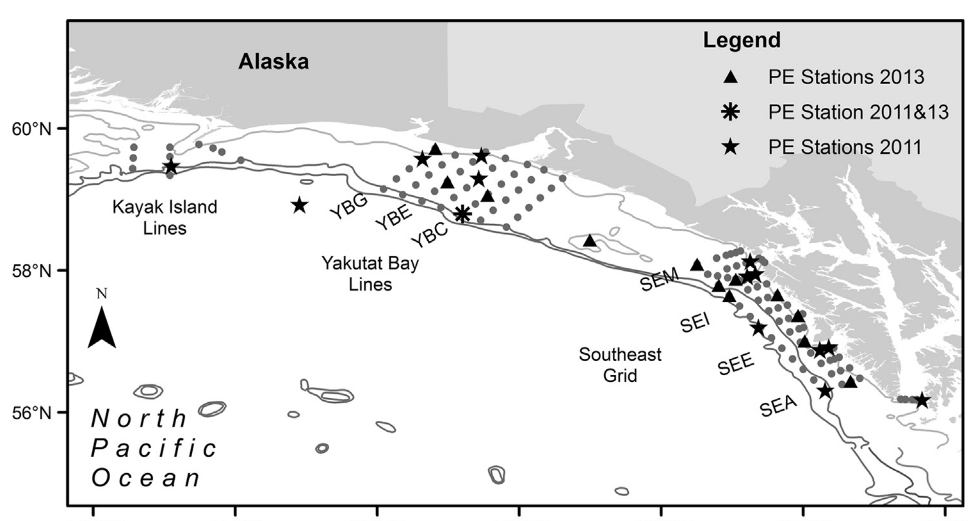


**Fig. 1.** Map of southeast coastal Alaska study region showing program sampling grid (smaller gray dots) and P – E experiment sites. For stations on the Southeast (SE) or Yakutat Bay (YB) grids, numbers in the station names (Table 1) refer to approximate distance offshore in nautical miles.

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