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Summer phytoplankton blooms in the oligotrophic North Pacific Subtropical Gyre: Historical perspective and recent observations

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Abstract

The export of organic matter from the oceanic euphotic zone is a critical process in the global biogeochemical cycling of bioelements (C, N, P, Si). Much of this export occurs in the form of sinking particles, which rain down into the unlit waters of the deep sea. Classical models of oceanic production and export balance this gravitational loss of particulate bioelements with an upward flux of dissolved nutrients, and they describe reasonably well those areas of the ocean where deep winter mixing occurs. The surface waters of the North Pacific Subtropical Gyre (NPSG), however, are strongly stratified and chronically nutrient-depleted, especially in summer. Nevertheless, there is ample evidence that blooms of phytoplankton and subsequent pulses of particle export occur during the height of summer stratification in these waters, especially to the northeast of the Hawaiian Islands. These blooms impact regional bioelemental cycling and act as a food source to the deep-sea benthos. We review here numerous published observations of these events in the NPSG, and present new data collected at Station ALOHA (22.75°N, 158°W) during the first 176 cruises of the Hawaii Ocean Time-series program (1988–2005), along with results from transect cruises conducted in the region in 1996 and 2005. We suggest that the summer phytoplankton bloom can be considered a frequent, perhaps annual feature in the northeastern NPSG, and that its perceived stochastic nature is a manifestation of chronic undersampling in time and space. The bloom is typically dominated by only a few genera of large diatoms and the cyanobacterium *Trichodesmium*. It appears to be consistently supported by dinitrogen fixation, but the fate of the organic matter produced during the summer depends critically on the species composition of the responsible diazotrophs. We estimate that the summer bloom is responsible for up to 38% of N_2 fixation and up to 18% of N-based new production annually at Station ALOHA. We hypothesize that the spatial distribution, timing and magnitude of the bloom may be determined largely by the physical and biological processes controlling new phosphorus delivery into the euphotic zone during the summer and the preceding winter.

Keywords: North Pacific Subtropical Gyre; Phytoplankton blooms; Nitrogen fixation; Particle flux; Diatoms; Nutrient cycles

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1. Introduction

1.1. Physical environment

The central gyres of the oceans occupy 40% of the world's surface, yet their waters house some of the most poorly sampled ecosystems on Earth (Karl, 1999, 2002). These vast and deep regions, far from the influence of land, have historically been considered the oceanic equivalent of terrestrial deserts, with low standing stocks of biomass and low production rates. In part, this view has resulted from a dearth of comprehensive investigations of central gyre habitats due to their remoteness and expansiveness. However, the view of these biomes as supporting homogenous and static ecosystems has been challenged over the past two decades, as more frequent field observations of the gyre habitats have revealed substantial complexity and variability on a variety of time and space scales (Karl, 1999, 2002).

The largest of these open ocean habitats is the North Pacific Subtropical Gyre (NPSG), a great anticyclonic circulation feature extending roughly from 15°N to 35°N latitude and from 135°E to 135°W longitude. With its surface area of approximately 2×10^7 km^2, it is considered to be the Earth's largest contiguous biome (Karl, 1999; Karl et al., 2002a). The surface waters of the NPSG are characterized by vanishingly low nutrient concentrations and low standing stocks of living organisms. The low biomass results in very clear water, allowing net photosynthesis to occur to a substantial depth (Letelier et al., 1996). Despite the low biomass, fairly high rates of primary production are maintained through rapid recycling of nutrients. This recycling is highly efficient; typically less than 10% of the annual primary production is lost from the euphotic zone as sinking particles (Pace et al., 1987; Knauer et al., 1990; Karl et al., 1996).

The euphotic zone of the NPSG has been typically modeled as a two-layer system (Dugdale, 1967; Eppley et al., 1973; Small et al., 1987). The upper, nutrient-limited layer accounts for most of the primary production, supported primarily by nutrients recycled from organic matter *in situ*. The lower layer lies at the top of the nutricline, where nutrients are more readily available but photosynthesis is light-limited. A persistent chlorophyll maximum is found in this lower layer, where high cellular pigment quotas increase the efficiency of light harvesting by phytoplankton under nutrient-replete conditions. Because of persistent thermal stratification of the upper ocean in the NPSG, surface mixed layers seldom penetrate to the depth of the nutricline, hence delivery of exogenous nutrients to the upper, more productive layer is severely constrained (Winn et al., 1995; Karl, 1999; Dore et al., 2002).

In this classic two-layer model, the origin of the sinking export flux of particulate organic matter from the euphotic zone is thought to be the lower, nutrient-replete layer (Coale and Bruland, 1987). The upper layer is considered to be the equivalent of a "spinning wheel," which drives little export because it is supported largely by regenerated nutrients (Goldman, 1984). Without a mechanism for introducing new nutrients to the upper layer, large, rapid increases of phytoplankton biomass within this layer would be impossible. Such blooms of phytoplankton would be particularly inhibited during the summer and fall, when thermal stratification of the water column is strong and mixed layers are particularly shallow. Nevertheless, numerous observations of enigmatic summer blooms have been made in the NPSG (Table 1); moreover, there is mounting evidence that a significant fraction of the particulate organic matter export from the euphotic zone originates in the upper layer during summer stratification (Scharek et al., 1999a,b; Dore et al., 2002). These phenomena are inconsistent with the classical two-layer model, and yet are critical to any mechanistic understanding of ecosystem dynamics in the NPSG.

1.2. History of bloom observations

The spring bloom of phytoplankton is a seasonal phenomenon in polar and temperate latitudes, where abundant nutrients, brought to the surface by deep winter convection, fuel rapid growth as the water column stabilizes and light levels increase (Sverdrup, 1953; Siegel et al., 2002). In the NPSG, no such seasonally recurring surface bloom occurs in spring, because winter mixing fails to penetrate deeply into the nutricline. Nevertheless, rapid increases in surface phytoplankton biomass are occasionally observed in the spring in association with cyclonic mesoscale eddies (Letelier et al., 2000) or intense atmospheric disturbances (DiTullio and Laws, 1991). In addition, the deepening of isolumes into the nutricline during spring creates a sort of