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Review

Global distribution of summer chlorophyll blooms in the oligotrophic gyres

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ABSTRACT

Chlorophyll blooms consistently develop in the oligotrophic NE Pacific in late summer, isolated from land masses and sources of higher chlorophyll waters. These blooms are potentially driven by nitrogen fixation, or by vertically migrating phytoplankton, and a better understanding of their ubiquity could improve our estimate of the global nitrogen fixation rate. Here, global SeaWiFS chlorophyll data from 1997 to 2007 are examined to determine if similar blooms occur in other oligotrophic gyres. Our analysis revealed blooms in five other areas. Two of these are regions where blooms have been previously identified: the SW Pacific and off the southern tip of Madagascar. Previously, unnoticed summer blooms were also identified in the NE and SW Atlantic and in a band along 10°S in the Indian Ocean. There is considerable variation in the intensity and frequency of blooms in the different regions, occurring the least frequently in the Atlantic Ocean. The blooms that develop along 10°S in the Indian Ocean are unique in that they are clearly associated with a hydrographic feature, the 10°S thermocline ridge, which explains the bloom within a conventional upwelling scenario. The environment and timing of the blooms, developing in oligotrophic waters in late summer, are conducive to both nitrogen fixers and vertically migrating phytoplankton, which require a relatively stable water column. However, the specific locations of the chlorophyll blooms generally do not coincide with areas of maximum levels of nitrogen fixation or *Trichodesmium*. The NE Pacific chlorophyll blooms develop in a region with a very high SiO_4/NO_3 ratio, where silicate will not be a limiting nutrient for diatoms. The blooms often develop between eddies, wrapping around the periphery of anti-cyclonic features. However, none of the areas where the blooms develop have particularly high eddy kinetic energy, from either a basin-scale or a mesoscale perspective, suggesting that other factors, such as interactions with a front or dynamics associated with the critical latitude, operate in conjunction with the eddy field to produce the observed blooms.

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1. Introduction

The general paradigm in biological oceanography is that the vertical upwelling of deep nutrients drives production in the nutrient-limited regions of the surface ocean (Lewis et al., 1986). This process is well documented, particularly in the equatorial ocean, where surface chlorophyll increases with shoaling of the thermocline bringing more nutrients to the surface (Chavez et al., 1998; Ryan et al., 2002; Siegel et al., 1999; Turk et al., 2001; Wilson and Adamec, 2001). Nitrate is assumed to be the limiting nutrient on short time scales (Lewis et al., 1986), outside of high-nutrient, low-chlorophyll (HNLC) regions, where Fe becomes a factor. However, diazotrophs, organisms that fix atmospheric nitrogen, can thrive in warm, nitrate-deplete waters, and could shift the ocean from nitrogen to phosphorus limitation (Cullen, 1999; Karl et al., 1997; Tyrrell, 1999). The most well-known oceanic diazotroph is *Trichodesmium*, but nitrogen fixation occurs in multiple organisms, including both unicellular cyanobacteria (Church et al., 2005; Hewson et al., 2007; Montoya et al., 2004; Zehr et al., 2001, 2007), and the endosymbiontic *Richelia* that is found within several species of large diatoms, most notably *Rhizosolenia* and *Hemiaulus* (Heinbokel, 1986; Mague et al., 1974; Sundström, 1984; Venrick, 1974; Villareal, 1991). The contribution of these other organisms could be significant, as it has been estimated that *Trichodesmium* accounts for only 25–50% of the nitrogen fixation in the global oceans (Mahaffey et al., 2005).

The new N provided by nitrogen fixation is a significant proportion of the total oceanic new production (Capone et al., 1997, 2005; Gruber and Sarmiento, 1997; Karl et al., 1997; Michaels et al., 1996; Zehr et al., 2001). This new production could have an important impact on the overall global carbon cycle since, unlike nitrate brought to the surface from upwelling, nitrogen fixation is not coupled to fluxes of dissolved carbon from the deep ocean, and can potentially drive a net uptake of atmospheric CO_2 and export of carbon (Hood et al., 2000). Another biologically mediated process that delivers new nitrogen to the surface is the vertical migration of phytoplankton. For example, *Rhizosolenia* diatom mats use carbohydrate ballasting to migrate vertically between the nutricline, where they uptake nitrate, and the surface, where they photosynthesize (Richardson et al., 1998; Villareal and Carpenter, 1989; Villareal et al., 1999). Like nitrogen fixation this process results in new production without a flux of deep carbon to the surface, and so can result in removal of carbon from surface waters (Richardson et al., 1998). In the North Pacific the N flux bought into the euphotic zone by these mats is comparable to the low end of the estimated range of nitrogen fixation rates (Pilskaln et al., 2005; Richardson et al., 1998). *Rhizosolenia* mats could also fuel the local ecosystem as some fish are known to directly consume mats (Robison, 1984). In addition to *Rhizosolenia* mats, a number of genera of large phytoplankton vertically migrate to acquire nitrate (Moore and Villareal, 1996; Villareal, 1988; Villareal and Lipschultz, 1995; Villareal et al., 2007; Woods and Villareal, 2008).

It remains difficult to quantify these processes however, because ship-based observations can provide only limited information on the global distribution and temporal variability of the organisms involved. The high spatial and temporal coverage of satellite chlorophyll data provides a mechanism to potentially map the distribution of these processes globally. Satellite data, however, will underestimate these processes, since subsurface activity, which can be important in some places (Davis and McGillicuddy, 2006; Dore et al., 2008), will not be detected. Two different methodologies have been used to identify nitrogen fixation from satellite ocean color data. Genera-specific optical properties can be used to develop algorithms to identify *Trichodesmium* from satellite measured water-leaving radiances (Borstad et al., 1992). Initial algorithms only worked on blooms with chlorophyll values >1 mg/m^3 (Hood et al., 2002; Subramanium et al., 1999, 2002), and therefore could not be applied globally, as throughout most the oligotrophic ocean, where nitrate-deplete waters will favor nitrogen fixation, chlorophyll levels never approach this threshold. Westberry and Siegel (2006) estimated the global distribution of *Trichodesmium* based on a new algorithm better tuned to low-chlorophyll environments (Westberry et al., 2005). However, *Trichodesmium*-specific algorithms will not necessarily identify production stimulated by other forms of nitrogen fixation or by vertically migrating phytoplankton. While there are some algorithms designed to detect diatom blooms from satellite data (Alvain et al., 2005; Sathyendranath et al., 2004), they cannot identify whether the diatoms contain diazotrophic endosymbionts, which can be difficult to detect even with shipboard methods. For example while standard light microscopy can detect *Richelia* in *Rhizosolenia*, epifluoroscence must be used to detect it in *Hemiaulus* (Villareal, 1992). Currently, there are no algorithms to detect unicellular diazotrophs or migrating mats with satellite data.

An alternative approach to identifying nitrogen fixation from satellite data takes into account that the oceanic conditions conducive to nitrogen fixation (and vertical migration) are very different from conditions leading to upwelling-derived production. Populations of *Trichodesmium* and *Rhizosolenia* mats are generally found in stable, stratified waters, with low winds (Capone et al., 1997; Subramanium et al., 2002; Villareal and Carpenter, 1989). *Trichodesmium* is usually not present in waters colder than 20 °C, and rarely blooms below 25 °C (Capone et al., 1997; Carpenter and Capone, 1992; Subramanium et al., 2002). Culture studies indicate that the ideal temperature range for *Trichodesmium* is 24–30 °C (Breitbarth et al., 2007). The conditions conducive to both nitrogen fixation and mat development, i.e. a warm, stably stratified water column, occur in summer and early fall.

There have been a number of studies that have identified anomalous blooms with satellite chlorophyll data and attributed them to nitrogen fixation. Chlorophyll blooms in the southwest Pacific, observed by both the Coastal Zone Color Scanner (CZCS) and SeaWiFS satellites, have been identified as *Trichodesmium*, based on previous reports of *Trichodesmium* in the area and the blooms' summer occurrence, when the surface water is warm and stratified