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Biological and physical forcings of late summer chlorophyll blooms at 30°N in the oligotrophic Pacific

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Abstract

Large chlorophyll blooms have been observed with ocean color satellite data in late summer near 30°N, 135–155°W in the oligotrophic subtropical Pacific. Although blooms do not develop every year, their timing and location are consistent when they do appear. Their biological and physical forcings are unknown. Here we examine biological and physical data from a number of cruises along 30°N in the eastern Pacific between 1980 and 2004, focusing on biological data from a cruise that fortuitously sampled a small chlorophyll bloom in July 2002. The climatological bloom location is characterized by elevated levels of *Rhizosolenia* diatom mats as well as endosymbiotic and unicellular nitrogen fixation. We conclude that nitrogen fixation and the vertical migration of *Rhizosolenia* diatom mats below the nutricline are likely mechanisms for the supply of new nitrogen to fuel the chlorophyll blooms and that both mechanisms could be at work. The blooms occur in the eastern gyre of the North Pacific, a region characterized by converging weak surface currents that create an environment favorable for accumulation of positively buoyant particles such as *Rhizosolenia* mats. These blooms could have important ecosystem consequences by impacting local carbon fluxes and serving as an aggregation point for pelagic animals.

Keywords: Chlorophyll blooms; Diatoms; Nitrogen fixation; Satellite sensing; *Rhizosolenia* mats; Surface currents; Convergence zones

1. Introduction

Large chlorophyll blooms, observable with ocean color satellite data, frequently develop in the late summer in the oligotrophic subtropical Pacific northeast of Hawaii (Wilson, 2003). The blooms are quite large, sometimes reaching the size of California (400,000 km^2). They have been observed in 11 of 16 years of satellite ocean color data (CZCS, OCTS and SeaWiFS) and can last up to 4–5 months. The blooms are as yet uncharacterized, with no information available on either what species form the blooms or on the mechanisms that supply nutrients to support this elevated biomass. The two most consistent aspects of the blooms are the timing of their development, occurring in late summer, and their location, centered along 30°N between 135° and 155°W. They do not appear to be caused by topographic features or by subsurface mixing (Wilson, 2003). Drawing upon

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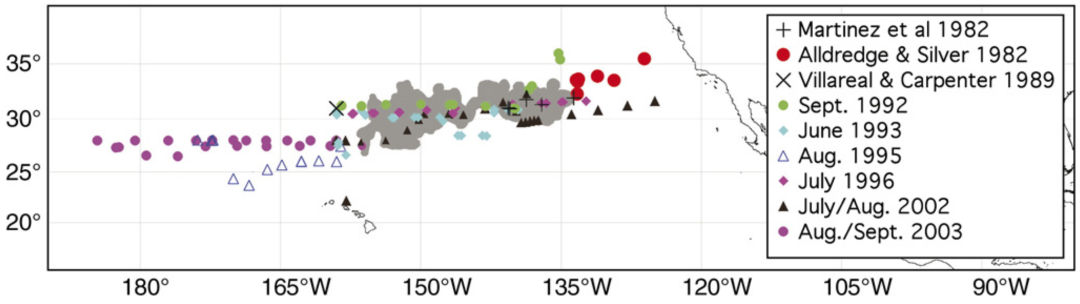

Fig. 1. Map showing the location of cruises whose biological data are presented in this paper. References resulting from these cruises are summarized in Table 1. The gray area indicates the region where chlorophyll blooms are observed from satellite data (see Fig 2).

published results from studies near or within the blooms, Wilson (2003) hypothesized that they are fuelled by either nitrogen fixation or by new N brought in by the vertical migration of *Rhizosolenia* diatom mats between the surface and the nutricline.

Here we expand upon the work of Wilson (2003) by (1) examining the available biological data along 30°N in the Pacific, (2) presenting analysis of the first biological samples taken near a bloom and (3) evaluating the location of the chlorophyll blooms in a basin-scale context. Most in situ biological observations from this part of the Pacific come from the Hawaii Ocean Time-series (HOT, 23.75°N) and CLIMAX (28°N) sites, neither of which is directly within the region where the blooms develop. However, there have been a number of cruises that have sampled *Rhizosolenia* diatom mats along ~30°N (see Fig. 1 and Table 1). These data are examined here, with a particular focus on data from a 2002 cruise (Montoya et al., 2004; Singler and Villareal, 2005; Pilskaln et al., 2005) that serendipitously sampled the boundary of a small chlorophyll bloom in this region. These are the only existing data from a 30°N chlorophyll bloom, and they have not been previously examined in the context of the blooms. The consistent position of the blooms within the eastern Pacific basin suggests a strong link to large-scale physical forcing. We discuss physical characteristics of the eastern Pacific that could contribute to the formation of the chlorophyll blooms in this localized area.

2. Data

Satellite ocean color data from the Coastal Zone Color Scanner (CZCS), the Ocean Color and Temperature Scanner (OCTS) and the SeaWiFS (Sea-viewing Wide Field-of-view Sensor) sensors were used to identify chlorophyll blooms between 1979–1985 and 1996–2004. For CZCS and OCTS, monthly data were examined, for SeaWiFS, both 8-day and monthly composite data were examined (using the 9 km, level-3 dataset). Blooms are defined as regions with chlorophyll >0.15 mg/m^3 in Jul.–Oct., when the ambient background level of chlorophyll is ~0.08 mg/m^3.

A compilation of *Rhizosolenia* mat abundances from cruises between 1980 and 2003 is examined in relation to bloom location. In situ biological data from a 2002 cruise that went through the southern edge of a small chlorophyll bloom is compared with the satellite observations. This cruise measured *Rhizosolenia* mats abundances (by SCUBA divers using methods described in Villareal et al., 1996), the abundance of diatoms with *Richelia* endosymbionts (collected from a series of 64 μm mesh MOCNESS tows), and rates of unicellular nitrogen fixation (using methods described in Montoya et al., 2004). Diatom abundance was collected

Table 1
Summary of the cruises that collected the data presented in this paper

Cruise	Dates	References
R/V *Cayuse*	Oct. 1980	Alldredge and Silver (1982)
R/V *Cayuse*	Sep. 1981	Martínez (1982), Martínez et al. (1983)
R/V *Thomas Washington*	Mar./Apr. 1989	Villareal and Carpenter (1989)
R/V *Wecoma*	Aug. 1992	Villareal et al. (1996)
R/V *Wecoma*	Sep. 1992	Villareal et al. (1993)
R/V *New Horizon*	May./Jun. 1993	Villareal et al. (1996)
R/V *Moana Wave*	Aug. 1995	Brzezinski et al. (1998), Shipe et al. (1999)
R/V *New Horizon*	Jul./Aug. 1996	Brzezinski et al. (1998), Shipe et al. (1999), Villareal et al. (1999), McKay et al. (2000)
R/V *Melville*	Jul./Aug. 2002	Montoya et al. (2004), Singler and Villareal (2005), Pilskaln et al. (2005)
R/V *New Horizon*	Aug./Sep. 2003	Singler and Villareal (2005), Pilskaln et al. (2005)
R/V *Melville*	Jun./Jul. 2004	CLIVAR P2, leg 1
R/V *Melville*	Jul./Aug. 2004	CLIVAR P2, leg 2

using a 1/4 m^2 MOCNESS (64 µm mesh) system towed from 0–300 m. The surface abundances presented here were calculated from the volume filtered after enumerating an aliquot from the surface (0–15 m) sample. *Hemiaulus* forms chains that are up to cm in size, and will be retained by mesh sizes larger than the cell diameter. However, cell breakage is an inevitable part of net sampling, as is the change in retention efficiency of small particles as the net clogs. For this reason, we consider these numbers to be useful only for relative comparison to other MOCNESS samples collected on this cruise. Symbiont enumeration from the 1993 cruise was conducted as described in Villareal (1994).

To characterize the physical environment of the bloom region, climatological near-surface currents, calculated from a combined analysis of drifter, satellite altimetry and wind data as in Niiler et al. (2003) and Maximenko and Niiler (2005) are presented, as well as output from a model of passive tracer concentrations (Maximenko, manuscript in prep.). Hydrographic data is also analyzed from the P2 transect (http://whpo.ucsd.edu) across 30°N in the summer of 2004. Although the 2004 bloom occurred a month prior to this transect, these data reveal differences between the western and eastern Pacific basins.

3. Bloom demographics

The blooms can be identified as regions in the oligotrophic subtropical Pacific gyre with chlorophyll >0.15 mg/m^3 during Jul.–Oct. (Fig. 2, images of the individual blooms can be seen at http://www.pfeg.noaa.gov/~cwilson/bloom). The location of the blooms is relatively consistent from year-to-year between 135° and 155°W at 30°N. Additionally, there were two, month-long blooms that developed south of this area, one near 165°W, 20°N in Aug. 1998, and one on the north side of Hawaii in Jul. 2000. The focus of this paper is on the 30°N blooms. While the analysis in Fig. 2 used only data from Jul.–Oct., all months were examined, and blooms do not develop outside of this time period. The blooms develop ~10° south of the Transition Zone Chlorophyll Front (TZCF), defined as the location of the 0.2 mg/m^3 surface chlorophyll across the basin (Polovina et al., 2001), although in the winter the TZCF migrates into the bloom region and engulfs any blooms still existing. The blooms are not forced by positive topography, occurring over the Murray fracture zone (>5000 m depth) with no nearby seamounts. The blooms do not appear to be associated with concurrent SSH or SST anomalies, suggesting that processes other than subsurface mixing are likely important (Wilson, 2003). While blooms have been seen near Hawaii associated with mesoscale isopycnal doming (Brzezinski et al., 1998; Vaillancourt et al., 2003), such features typically can be identified by SSH or SST anomalies.

While the blooms have a consistent seasonality and location, there is variability in their interannual development and magnitude (Fig. 3). The local chlorophyll variability in Jul.–Nov. illustrates the timing and duration of the different blooms. They generally develop in Jul. or Aug., and can sometimes last into Dec., although more commonly the blooms last 4–6 weeks. In 2003, two separate blooms developed at slightly different locations, each lasting about a month. The location of the TZCF drives the winter chlorophyll variability, with chlorophyll >0.1 mg/m^3 indicative of proximity to the TZCF. In winter, the TZCF penetrates into the western bloom region, but not into the eastern bloom region.

Blooms have occurred in 11 of the 16 years of satellite ocean color comprising the CZCS, OCTS and

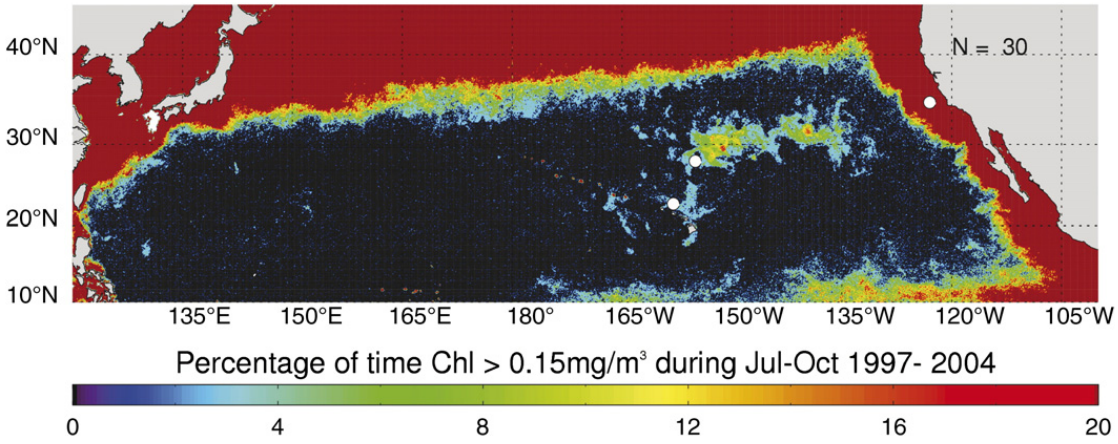

Fig. 2. Percentage of time (using monthly images) that SeaWiFS chlorophyll is above 0.15 mg/m^3 during July–October, of 1997–2004, showing the integrated region of the episodic chlorophyll blooms at 30°N between 140° and 155°W. A bloom lasting a single month has an associated value of ~3%. White dots indicate the locations of the HOT, Climax and "M" stations.

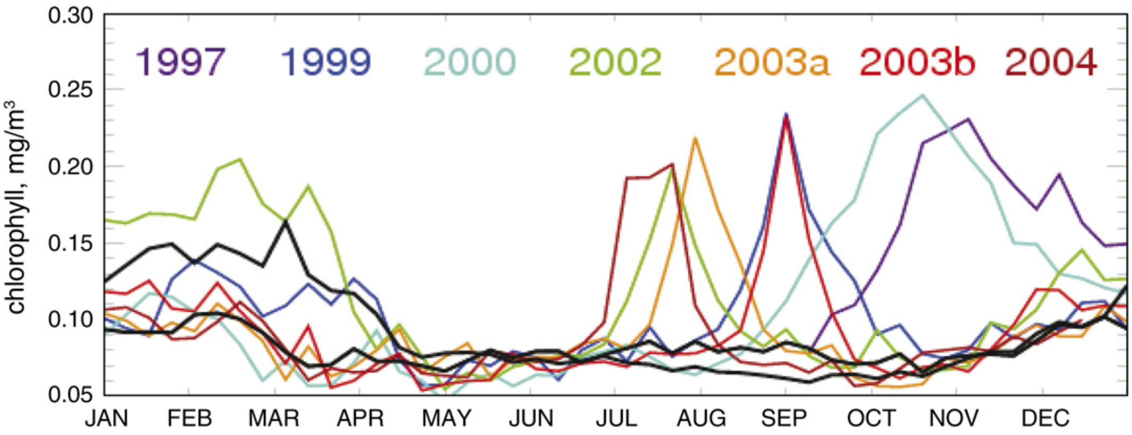

Fig. 3. The annual chlorophyll cycle from the region of each year's bloom as observed by SeaWiFS data (1997–2004). The black lines are the average chlorophyll concentration from two boxes west (160–162°W, 29–33°N) and east (160–162°W, 29–33°N) of the bloom region to demonstrate how the meridional change in the location of the TZCF affects the winter chlorophyll variability in the bloom region.

SeaWiFS datasets. This is a minimum count, however, since some of the CZCS years did not have enough coverage in this area to determine whether there was a bloom. There has been sufficient spatial coverage between 1996 and 2004 to know that there were only 2 years (1998 and 2001) without any significant bloom development. The bloom's interannual occurrence does not appear to be tied to ENSO variability (Fig. 4). The frequency of the blooms is much higher than that of strong El Niño or La Niña events, which occur every 5–7 years. The two largest blooms observed with SeaWiFS occurred in 1997 and 2000, which were El Niño and La Niña years, respectively.

4. Biological forcing

Possible sources of new nitrogen fueling the blooms are a biologically mediated flux of nitrate by vertically migrating diatom mats and nitrogen fixation (Wilson, 2003). These processes are not mutually exclusive, and both could play a role in the formation and maintenance of the observed chlorophyll blooms.

4.1. Nitrate transport by vertically migrating diatoms

Vertically migrating *Rhizosolenia* diatom mats have been observed extensively in the bloom region (Villareal and Carpenter, 1989; Villareal et al., 1996, 1999). *Rhizosolenia* mats change buoyancy to descend below the nutricline to acquire nitrate and return to the surface for photosynthesis. This dynamic is evidenced by a variety of indirect measures: (1) the δ15N isotopic composition of the mats is similar to the deep nitrate pool and distinctly heavier than the surface particulate δ15N (Villareal et al., 1993) (2) the presence of high internal nitrate pools found in diatoms only after exposure to elevated external nitrate far higher than the ~5 nM nitrate concentrations in surface waters in the gyres (Villareal et al., 1996) (3) nitrate reductase (an inducible enzyme) activity sufficient to provide for cellular N needs (Joseph et al., 1997) (4) the presence of mats below the nutricline (Villareal et al., 1999) (5) *Rhizosolenia* is capable of dark nitrate uptake (Richardson et al., 1996) and (6) C/N and protein/carbohydrate ratios co-vary with buoyancy status in a

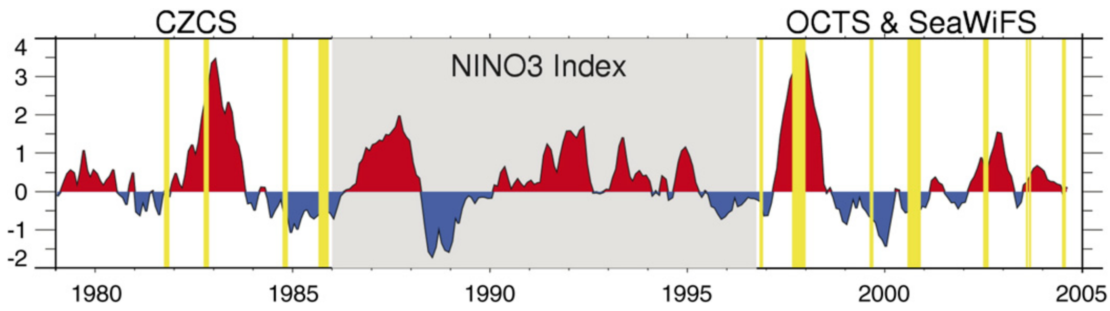

Fig. 4. Interannual occurrence of the chlorophyll blooms (shown in yellow) superimposed on the NINO3 index. Large positive (negative) anomalies indicate El Niño (La Niña) events. The gray box indicates a period with no available satellite data.

manner consistent with increasing N depletion along a gradient of positively to negatively buoyant mats (Villareal et al., 1999). A variety of large diameter *Rhizosolenia* species are capable of positive buoyancy at rates of 3–5 m h^{-1} (Moore and Villareal, 1996; Villareal et al., 1996). Carbohydrate ballasting has been suggested as the likely mechanism of buoyancy regulation based on known patterns in limnetic cyanobacteria, the above-mentioned co-variation of carbohydrate/protein ratios with buoyancy status, and the relationship between carbohydrate and buoyancy in *Rhizosolenia* (Moore and Villareal, 1996). *Rhizosolenia* mats have been observed at nutricline depths (Villareal et al., 1993; Pilskaln et al., 2005); however, attempts to collect them from these depths (~100–250 m) have generally been unsuccessful. The mats leak nitrate at rates sufficient to replace the ambient nitrate pool (~5 nM) in as little as 3 days, although rates vary considerably with environmental conditions and abundance (Singler and Villareal, 2005). Locally, new production resulting from vertical mat migration can be nearly 50% of the export production measured at HOT (Villareal et al., 1999) depending on mat abundance. Other buoyant species have many of the same characteristics of *Rhizosolenia* mats, suggesting that vertical migration as a life-history strategy is not limited to *Rhizosolenia* spp. (Villareal and Lipschultz, 1995; Villareal et al., 1999).

While the spatial distribution of *Rhizosolenia* mat data is limited, there is a clear peak in abundance at 30°N and 140–160°W (Fig. 5), the same region where the chlorophyll blooms develop. Most of these data were collected in the June–Sept. period, again consistent with bloom development. A 2002 cruise that sampled *Rhizosolenia* mats along a transect near 30°N (Montoya et al., 2004; Singler and Villareal, 2005; Pilskaln et al., 2005) fortuitously went through the southern edge of a small chlorophyll bloom centered on 32°N, 150°W. The highest *Rhizosolenia* mat abundance was observed near 155°W, although prior to the bloom occurring in this region in 2002 (Fig. 6a and b). Elevated chlorophyll developed at the station with high *Rhizosolenia* mat abundance at the end of July, several weeks after the mat measurements. However, this does not rule out the mats as a nutrient source for the chlorophyll bloom. For example, the maximum chlorophyll increase associated with Fe enrichment experiments typically occurs 2–3 weeks after the addition (Gall, 2001; Boyd et al., 2004). We also cannot rule out other requirements for bloom development such as threshold *Rhizosolenia* mat concentrations or coupling/uncoupling from grazers.

4.2. Nitrogen fixation

Nitrogen fixation is common in the bloom area and is associated with several distinct prokaryote taxa including *Trichodesimium* (Karl et al., 1992), endosymbiotic cyanobacteria (*Richelia*) contained within *Hemialus* and *Rhizosolenia* diatoms (Mague et al., 1974; Venrick, 1974; Scharek et al., 1999a,b) and unicellular cyanobacteria (Zehr et al., 2001; Falcón et al., 2004; Montoya et al., 2004). While large *Trichodesimium* blooms have been observed near Hawaii (Karl et al., 1992), *Trichodesimium* appears less common further north in the bloom vicinity (Venrick, 1997, Villareal, unpublished observation). Summer diatom blooms have been observed and sampled at the HOT and CLIMAX sites (Mague et al., 1974; Venrick, 1974; Heinbokel, 1986; Brzezinski et al., 1998; Scharek et al., 1999a,b), but never at times with available satellite chlorophyll data. Some of these events are quite significant with *Hemiaulus* and *Rhizosolenia* spp. densities reaching 10^3 cells/l, or 1–2 orders of magnitude above winter

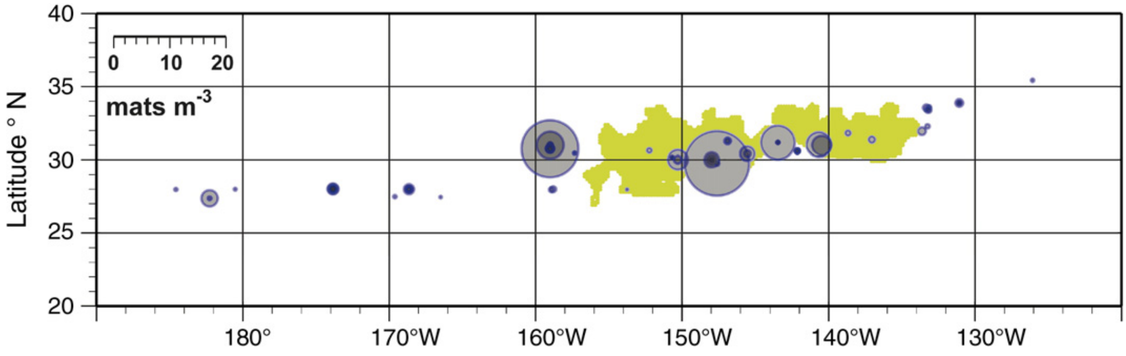

Fig. 5. Spatial distribution of the abundance of *Rhizosolenia* mats in the North Pacific, compiled from cruises listed in Table 1. The concentration of samples near 30°N is due to weather conditions; the trade winds increase north and south of 30°N, impeding sampling. The shaded green area indicates the bloom region.

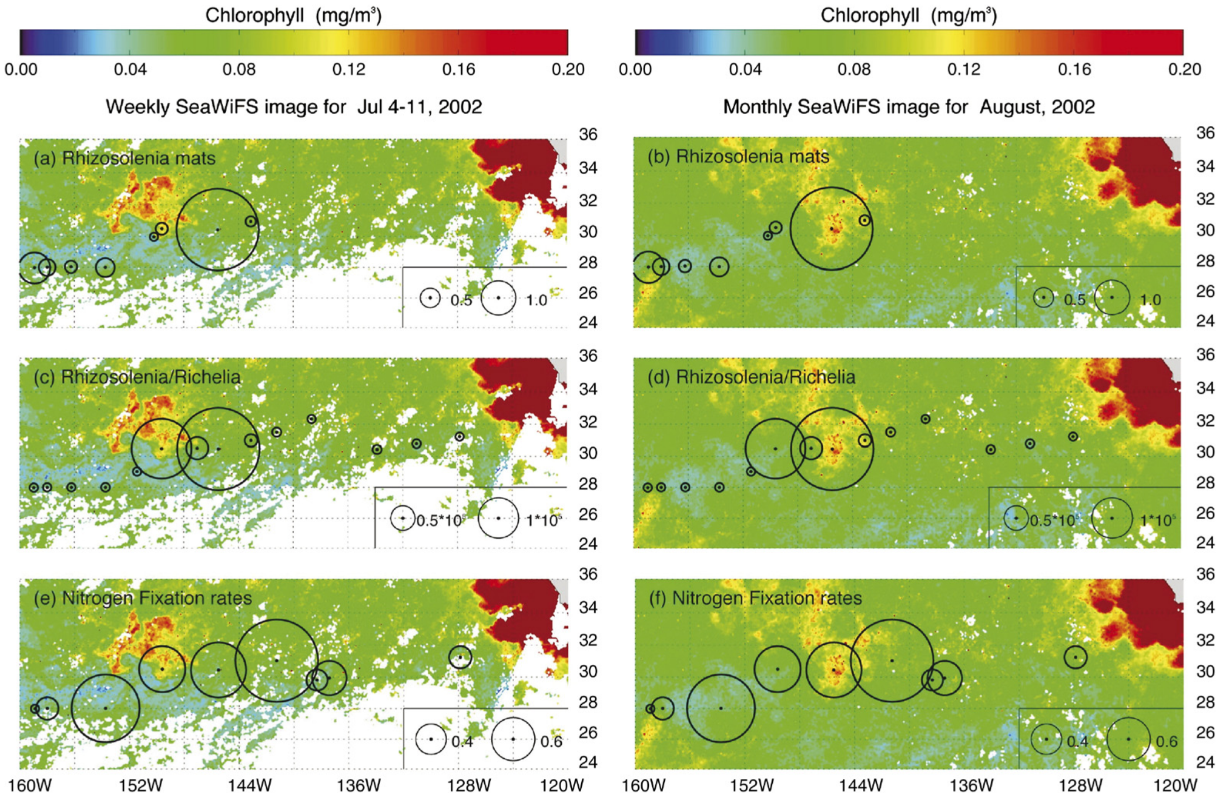

Fig. 6. SeaWiFS image of the 2002 chlorophyll bloom overlaid with the relative abundances of (top) *Rhizosolenia* mats, mats/m^3 (middle) *Rhizosolenia* diatoms containing the symbiotic *Richelia*, cell/m^3 and (bottom) unicellular rates of nitrogen fixation, nmol l^{-1} h^{-1}. On the left is the weekly image from July 4–11, 2002 (most concurrent with the in situ samples), on the right is the monthly composite from August, demonstrating changes in the bloom's shape and location. The in situ data were collected between June 24 and July 10.

background. Both of these genera can contain the nitrogen-fixing endosymbiont *Richelia intracellularis* at times (Mague et al., 1974; Villareal, 1991). Recent work has suggested that unicellular cyanobacteria could fix as much nitrogen in the Pacific as *Trichodesimium* and *Richelia* (Zehr et al., 2001; Falcón et al., 2004; Montoya et al., 2004).

Since almost all of these observations come from either the HOT or CLIMAX study area, they provide little information about the spatial distribution of their abundance, especially as neither site is within the main area where the blooms occur (see Fig. 2). During the 2002 cruise to this area, the highest abundances of the *Rhizosolenia–Richelia* symbiosis were found within the chlorophyll bloom (Fig. 6c and d). Of the two stations with elevated levels of *Rhizosolenia–Richelia*, one was within the chlorophyll bloom, and one sampled an area several weeks before the development of the chlorophyll bloom at that location. There are two other stations within the bloom region that do not have elevated levels of the *Rhizosolenia–Richelia* association. Similar small-scale (tens of kilometers) heterogeneity was also observed within diatom blooms at the CLIMAX site (Venrick, 1974). The highest rates of nitrogen-fixation values (<100 µm size fraction, Montoya et al., 2004) are also associated with the region of the bloom (Fig. 6e and f). However, the spatial distribution of elevated nitrogen-fixation rates are spread further away from the bloom than the high values of *Rhizosolenia* mats and *Rhizosolenia–Richelia*. The areal rate of nitrogen fixation measured at 30°N, 520 µmol N m^{-2} day^{-1}, is much higher than rates observed at HOT, which are less than 100 µmol N m^{-2} day^{-1} (Montoya et al., 2004).

Another diatom that can contain the *Richelia* symbiont in the Pacific is *Hemiaulus*. The symbiont is not always present, and the level of symbiosis may be a proxy for allochthonous nutrient injection. For example, in an eddy off of Hawaii subsurface nutrient injection reduced the percentage of symbiosis to near zero (Vaillancourt et al., 2003). Data from the 1993 cruise showed a large increase in the percentage of *Hemiaulus* with symbionts between 135° and 145°W, from less than 10% to 45–65% (Fig. 7). While it is not clear what would cause this regional change in percent symbiosis, the size and location of this feature is consistent with nitrogen-fixation playing an important role in the chlorophyll bloom region. One interpretation is that *Hemiaulus* populations outside the bloom area may be supported by N sources other than nitrogen fixation. Unfortunately, there are no satellite data from this time period to determine whether the variation in symbiosis percentage was associated with a chlorophyll bloom.

4.3. Nutrient limitation

While both biological processes, mat migration and N_2 fixation, alleviate nitrogen limitation, potential limitation by Fe, Si and P must be considered. The biological pathways involved in both processes utilize more Fe than those in regular phytoplankton (Raven, 1988, 1990; Singler and Villareal, 2005). Fe concentrations are low in this part of the Pacific, but there is an aeolian flux from Asian dust storms in the springtime (Duce and Tindale, 1991). Fluorescence values of phytoplankton in this area indicate that they are not Fe-stressed (Johnson et al., 2003), and the same result has been seen for *Rhizosolenia* mats in the bloom region (Singler and Villareal, 2005). However, mats west of 160°W (outside of the bloom region) have lower fluorescence values (F_v:F_m), a response consistent with Fe-stress (Singler and Villareal, 2005). It is possible that Fe limitation, and the interannual variability in aeolian deposition, could play a role in the development of the observed chlorophyll blooms.

Silicate concentrations show a pronounced westerly decrease across the eastern basin of the central N. Pacific. Brzezinski et al. (1998) noted high rates of particulate production in the bloom region in 1995 with production rates declining in the water west of 160°W in 1996. Although additional silicate always stimulated higher particulate Si production rates, elevated concentrations of *Hemiaulus* did not appear to require high ambient concentrations. For example, a bloom of >15,000 cell l^{-1} was noted at 26°N, 159°W and was not coincident with elevated Si concentrations. However there did appear to be a regional difference in the Si dynamics within *Rhizosolenia* mats. The western transect Si concentrations

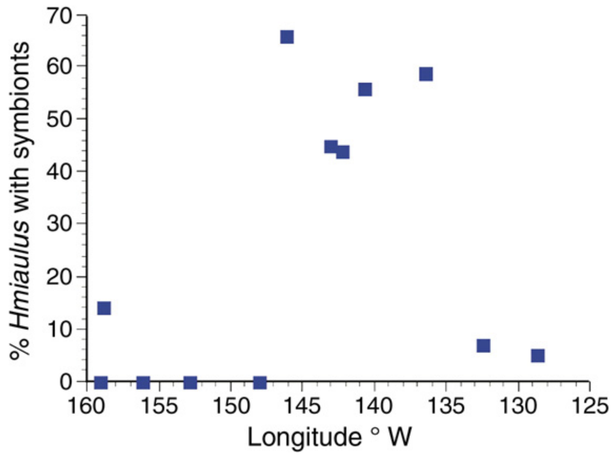

Fig. 7. *Hemiaulus* cells in surface samples containing symbiotic *Richelia* as a percentage of all *Hemiaulus* against longitude. The transect extended from 27.5° to 31.1°N in May–June, 1993.

were sufficiently low that *Rhizosolenia* mats could only acquire sufficient Si for doubling at depth; whereas, in the eastern transect, Si concentrations were high enough at the surface to permit continuous uptake (Shipe et al., 1999).

While the two potential sources of N (mat migration and N_2 fixation by *Richelia*) are similar in their needs for Fe and Si, they are distinctly different in their P needs. *Rhizosolenia* mats show no buoyancy related differences in their N/P ratios, and probably acquire P at depth as well (Villareal, unpublished analysis). *Hemiaulus* and *Rhizosolenia* diatoms with endosymbiotic *Richelia* would require a P supplement to maintain Redfield stoichiometry. Since the relatively small *Hemiaulus* and *Rhizosolenia* species are unlikely to vertically migrate due to size requirements (Villareal, 1988), and there is not data to suggest unusual advective or diffusive sources of P, the source of additional P remains problematic. The sources and roles of these potentially limiting nutrients on both processes needs to be studied further.

5. Physical forcing

Previous analyses have not revealed any obvious linkages between the blooms and local physical forcing. The blooms are not associated with SST or SSH anomalies that would be indicative of mixing or breaking internal waves (Wilson, 2003). However, we cannot reject the possibility that physical processes may be responsible directly, or indirectly, for the blooms. In fact, their consistent location at 30°N, 135–155°W, and their absence in the western part of the Pacific Ocean (Fig. 2), suggest that large-scale physical forcing may provide necessary conditions for bloom development.

If the biological processes discussed above are responsible for the chlorophyll blooms, then the physical requirements of these processes could dictate when and where they develop. For example, since cell buoyancy is crucial to mat migration, this process would be most effective under calm conditions that permit sea surface accumulations of *Rhizosolenia* mats (Villareal and Carpenter, 1989; Villareal et al., 1996). The relationship of physical forcing with N_2-fixation is less clear. *Hemiaulus* is preferentially associated with the shallow mixed layer typical of late summer, calm conditions (Venrick, 1988). Calm conditions may minimize the vertical flux of NO_3, and thus increase the selective advantage of N_2-fixation as a strategy. Both habitat patterns are consistent with the timing of the chlorophyll blooms, which develop in late summer when wind speeds are lowest.

5.1. Latitudinal position

In the summer, there is a zone of minimum wind speed and shallow mixed layer depths along 30°N (not

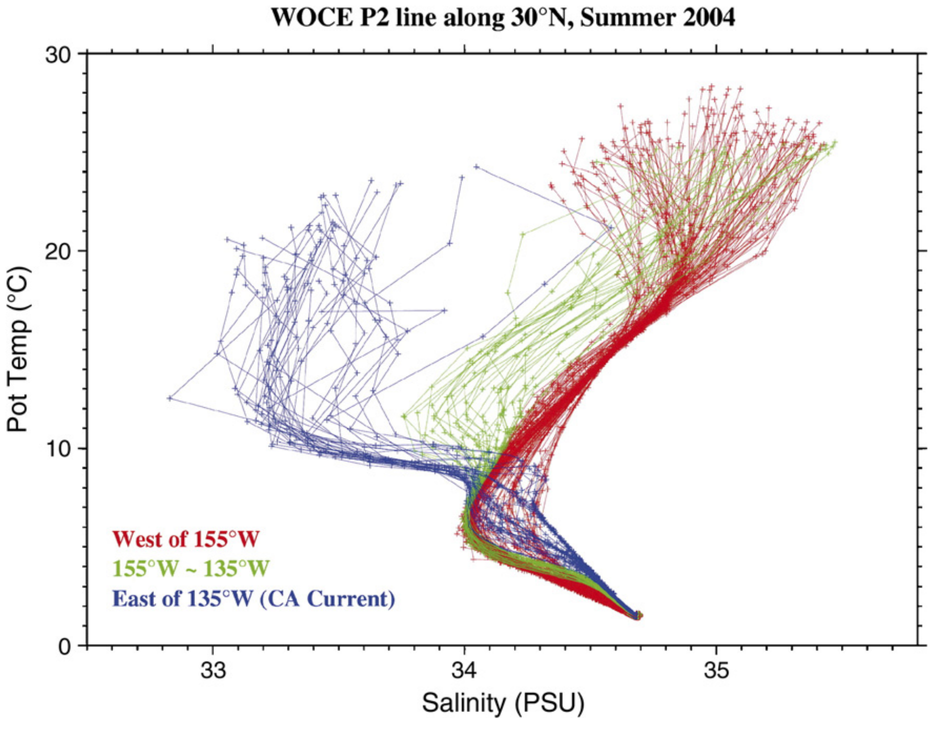

Fig. 8. Temperature–salinity diagram from the P2 line in summer 2004 along 30°N. Data from the western Pacific (west of 155°W) are in red, the eastern Pacific (135–155°W) are in green, and the fresher water from the California Current (east of 135°W) are in blue.

shown). In fact the minimal wind speed at 30°N dictated the latitude of the biological cruises as their sampling procedures (getting SCUBA divers into and out of small inflatable boats launched off of research vessels) required the winds <10–15 knots. 30°N is also the approximate position of the subtropical front (STF, Roden, 1974). It has been suggested that there is summer upwelling associated with the front that does not have a surface expression (Niiler and Reynolds, 1984), in which case it is possible that a subsurface nutrient injection drives the blooms. The surface signature of the STF is seasonal, being most intense in winter, when it has a clear SST signature, and weaker in summer due to strong frontolysis (Kazmin and Rienecker, 1996). In summer, the front is manifest mainly by a salinity, rather than a temperature, gradient (Roden, 1974, 1975), and hence is not distinguishable by satellite data. Thus, it is not possible to evaluate the relationship between the blooms' appearance and location, and the strength and position of the front. However, the STF is a relatively uniform feature across the Pacific basin, and the presence of blooms only in the eastern half of the Pacific suggests other physical dynamics are responsible.

5.2. Longitudinal position

The chlorophyll blooms occur in the eastern gyre of the North Pacific. This separate gyre was first identified by Sverdrup et al. (1942) from analysis of hydrographic data. Both Munk (1950) and Kenyon (1975) presented theoretical calculations demonstrating how wind patterns could create a closed anticyclonic gyre in the eastern Pacific. The gyre can be seen in the temperature and salinity data from the P2 line at 30°N as the clear distinction between profiles in the eastern (135–155°W) and western (west of 155°W) Pacific (Fig. 8). Water between 10 and 0 °C is significantly fresher in the eastern gyre than in the western Pacific. This temperature range corresponds to water depths between 50 and 400 m. The depth of the nitricline also changes between the eastern and western Pacific, as seen in the vertical section of nitrate from the P2 line in Fig. 9. While there is no longitudinal gradient at 100 m depth, at 200 m the average nitrate (and phosphate, not shown) value east of 180° is double that in the western Pacific (Fig. 9). It is possible that the higher nutrients levels closer to the surface in the east support more abundant *Rhizosolenia* mat populations (Fig. 5), resulting in blooms only in the eastern gyre. The depths with higher nutrient levels are within the range exploited by *Rhizosolenia* mats. Video plankton recorder imagery mounted on an ROV during the 2002 cruise observed mats down to 300 m depth (Pilskaln et al., 2005).

There are other physical differences between the eastern gyre and the rest of the Pacific. There is an abrupt decrease in eddy activity east of 170°W (Bernstein and White, 1977), and the surface currents are weak and more convergent than the same latitude in the western Pacific (Fig. 10). This convergence is clearly evidenced by

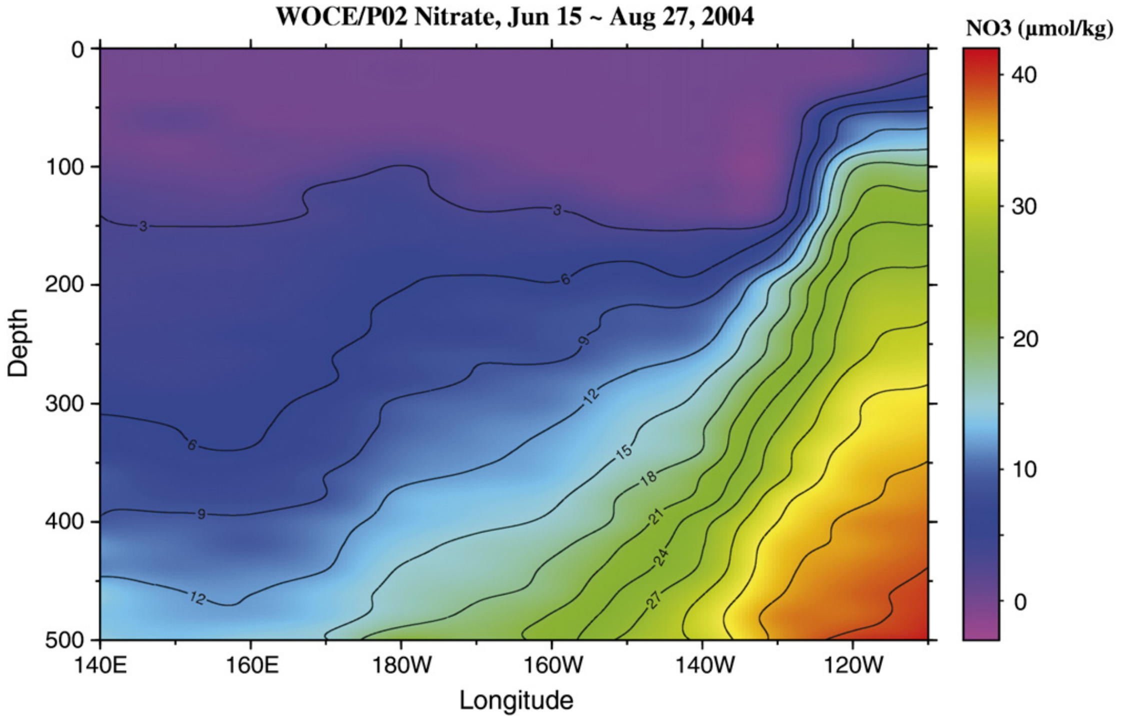

Fig. 9. Nitrate section along 30°N from the P2 line in summer 2004 showing the longitudinal nutrient gradient below 150 m.

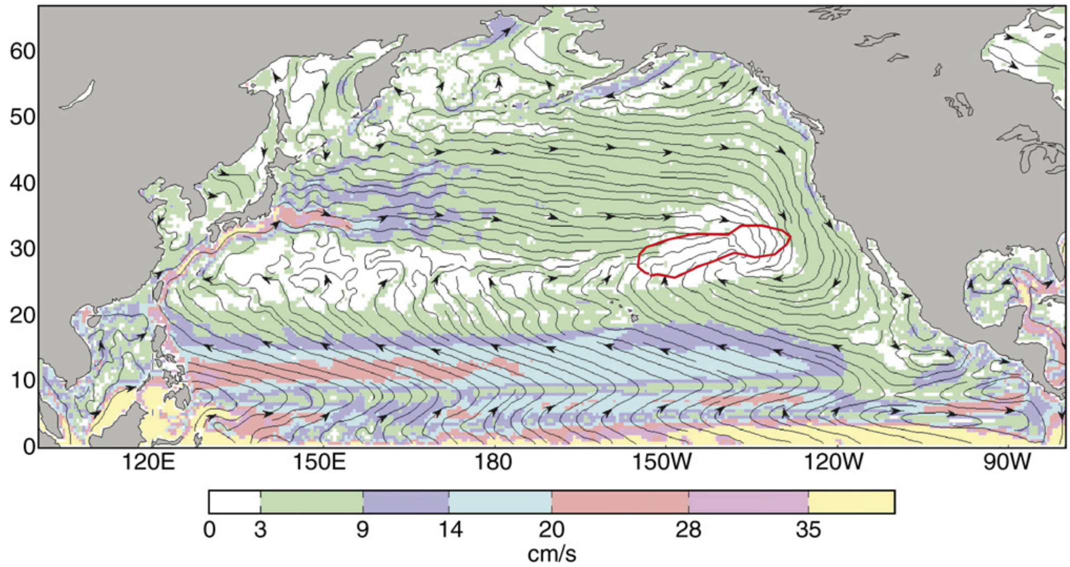

Fig. 10. 1992–2002 mean currents at 15 m depth from Maximenko and Niiler (2004). Colors show velocity magnitude. The bloom region is outlined in red.

surface drifters that tend to collect within the eastern gyre. Since direct analysis of these Lagrangian data is biased toward the sparse locations of massive deployments of drifters, a model has been developed using the statistics of drifter trajectories to describe the horizontal advection of a passive tracer (Maximenko, manuscript in preparation). As seen in Fig. 11 a passive tracer advected in the same way as drifters will become heavily concentrated in the eastern gyre relative to the rest of the North Pacific. The calm and convergent conditions in the eastern gyre would allow buoyant organisms such as *Rhizosolenia* to accumulate in large numbers at the surface, and would favor N_2-fixation. The development of surface patches of *Rhizosolenia* diatoms in tropical Pacific instability waves

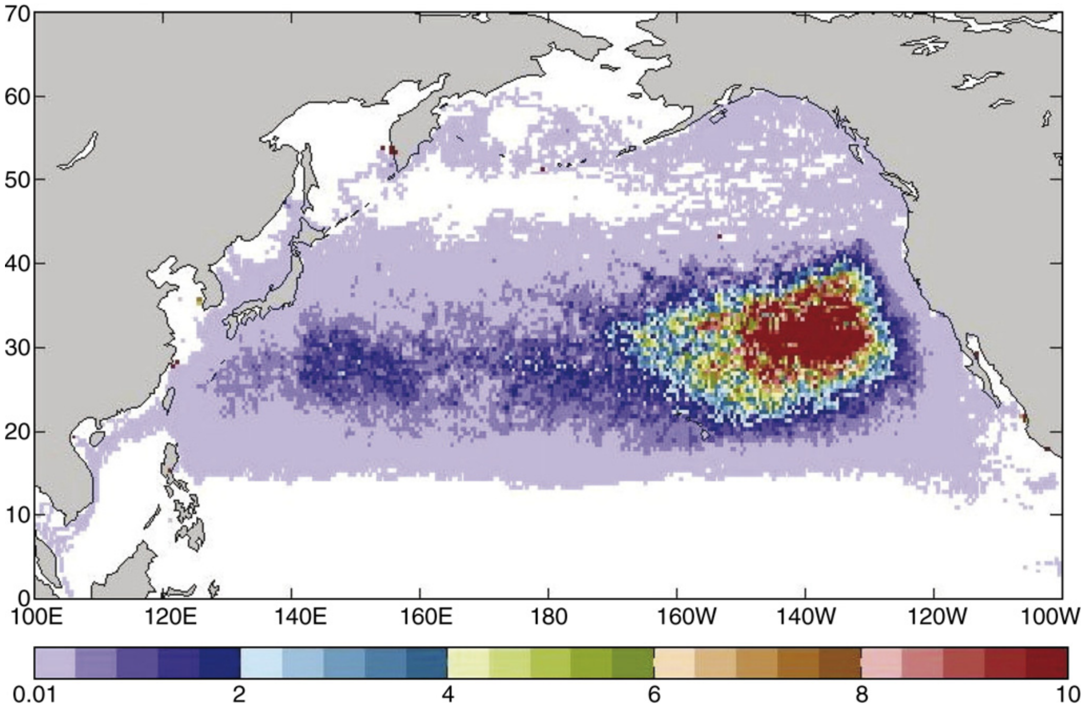

Fig. 11. The relative increase of a passive tracer after 10 years of evolution from an initially uniform state. Output derived from a model using the statistics of drifter trajectories (to remove biases associated with irregularly spaced drifter deployments) to describe the horizontal advection of a passive tracer (Maximenko, manuscript in preparation).

has been associated with areas of convergence (Yoder et al., 1994), and this has been noted for other particles (Dandonneau et al., 2003) including plastic debris and *Velella* (Smith and Hyrenbach, 2003).

6. Potential impacts

The biological forcings hypothesized for the blooms are important since both nitrogen fixation and mat migration introduce new nitrogen into the euphotic zone independently of vertical mixing processes. A phytoplankton bloom responding to upwelled nitrate can produce elevated export rates, but there can be no net carbon flux to depth unless the upwelling of nitrate and CO_2 are uncoupled, whereas a bloom driven by nitrogen fixation is necessarily uncoupled from upward CO_2 flux. Transport of nitrate by phytoplankton vertical migration also uncouples nitrate from subsurface carbon pools, and permits net export of carbon from the euphotic zone. Diatom blooms in particular are important mechanisms for sequestering carbon into the deep ocean (Goldman, 1988), as they can settle rapidly and are capable of highly episodic export from the surface (Scharek et al., 1999a,b). Locally, new production resulting from vertical mat migration could be nearly 50% of that from the diffusive flux of nitrate (Villareal et al., 1999).

The blooms could also have an impact on higher tropic levels in the ecosystem. For example, seabirds use the subtropical convergence as a migratory highway and can smell phytoplankton blooms (Nevitt, 2000; Hay and Kubanek, 2002). The bloom region is also within important habitat for highly migratory species such as albacore, bigeye tuna and billfishes (Laurs et al., 1984; Musyl et al., 2003; Sibert et al., 2003; Anda-Montañez et al., 2004), and within the target area of important longline fisheries (Bigelow et al., 1999; Seki et al., 2002). The blooms may represent a highly localized food source for prey species, and could be important congregation points at various parts of these predators' life histories. However, currently there are insufficient fisheries data coincident within the chlorophyll blooms to ascertain their impact (Wilson, unpublished analysis).

7. Summary

Our analysis of existing data does not rule out either of the hypothesized biological mechanisms for the blooms. Climatologically, the bloom region has higher abundances of vertically migrating *Rhizosolenia* mats, and high mat numbers were observed near the 2002 chlorophyll bloom. More nitrogen fixation was also observed in general proximity to the 2002 bloom, both directly measured, and inferred from higher levels of endosymbiotic diatoms. The blooms occur in the eastern gyre of the North Pacific, a region characterized by weak, yet converging, surface currents, a physical environment conducive for aggregating buoyant organisms in large numbers. More direct in situ sampling of the chlorophyll blooms is needed to better understand their composition and the mechanisms behind their formation. Better understanding of the physical conditions under which blooms develop will be important for efforts to model the global effects of diazotrophy on the carbon cycle (LaRoche and Breitbarth, 2005).

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