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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 SiO₄/NO₃ 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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Contents

1. Introduction	108
2. Data	109
3. Results	109
3.1. NE Pacific	110
3.2. NE Atlantic	111
3.3. SW Atlantic	115
3.4. SW Pacific	116
3.5. South Indian	118
3.6. Madagascar	120
4. Regional intercomparison	120
5. Mechanisms of chlorophyll bloom formation	120
5.1. Enhanced phytoplankton growth	120
5.1.1. Nitrate	120
5.1.2. Iron and dust	123
5.1.3. Phosphate	124
5.1.4. Silicate	124

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5.2.	Reduced mortality	124
5.3.	Chlorophyll/C changes	125
5.4.	Physical factors	125
5.4.1.	Eddies	125
5.4.2.	Fronts	126
5.4.3.	Mixing	128
5.4.4.	Convergence	128
6.	Conclusions	128
	Acknowledgements	129
	References	129

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 endosymbiotic *Richelia* that is found within several species of large diatoms, most notably *Rhizosolenia* and *Hemiaulus* (Heinboekel, 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 CO₂ 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 measured 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/m³ (Hood et al., 2002; Subramaniam 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*, epifluorescence 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; Subramaniam 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; Subramaniam 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

(Dandonneau et al., 2004; Dupouy et al., 1988, 2000). In the oligotrophic Pacific, northeast of Hawaii, large blooms of chlorophyll usually develop in late summer (Wilson, 2003; Wilson et al., 2008). Based on non-synoptic, in situ observations, the nutrient source for these blooms has been attributed to new N either from nitrogen fixation from *Richelia*-diatom associations or from vertically migrating *Rhizosolenia* diatom mats (Wilson, 2003; Wilson et al., 2008). Coles et al. (2004b) used results from a biological-physical model to show that the anomalous summer chlorophyll maximum that occurs throughout the western tropical Atlantic is due to nitrogen fixation. A large summer chlorophyll bloom develops east of the southern tip of Madagascar nearly every year (Uz, 2007), and nitrogen fixation is one of several explanations that have been put forth to explain this feature (Longhurst, 2001; Srokosz et al., 2004; Uz, 2007).

It is possible that these chlorophyll blooms are not directly composed of nitrogen fixing organisms, but rather are “echo” blooms (Boushaba and Pascual, 2005; Lenes et al., 2001; Mulholland et al., 2006), fuelled from new N in the euphotic zone that was generated either from nitrogen fixation or brought in from vertically migrating phytoplankton. There is indication of this effect in the North Pacific, where elevated levels of both *Rhizosolenia* mats and diatoms with nitrogen fixing endosymbionts were sampled several weeks before the development of a chlorophyll bloom visible by satellite data (Wilson et al., 2008).

Here we examine the global distribution of summer blooms in the oligotrophic oceans, as observed by satellite chlorophyll data. The satellite data indicates isolated areas where there are fairly rapid increases in surface chlorophyll, which we refer to here as chlorophyll blooms. It should be noted that a chlorophyll bloom is not necessarily a phytoplankton bloom, since the chlorophyll increase could be the result of factors other than phytoplankton growth in excess of phytoplankton loss (i.e. physical aggregation or physiological changes). What constitutes a bloom has regional, seasonal and community-structure aspects, and is not merely a matter of biomass accumulation (Smayda, 1997).

The development of intermittent large summer chlorophyll blooms is observed in all ocean basins, however, there are significant differences in the interannual frequency between basins. Existing physical and biological data from the bloom regions are reviewed to look for commonalities in their environments, and to see if there is evidence that the blooms are supported by either nitrogen fixation or vertically migrating phytoplankton. Generally, there is a paucity of biological data, given that: (1) most surveys focus on more dynamic regions with higher productivity than the oligotrophic gyres, and (2) the potential organisms of interest, including *Trichodesmium*, unicellular diazotrophs, diatoms such as *Hemiaulus* and *Rhizosolenia* that can contain nitrogen fixing endosymbionts, and vertically migrating phytoplankton are not routinely sampled. There is, however, a considerable dataset for the Atlantic Ocean, as a result of the Atlantic Meridional Transect (AMT) program. Since 1995 this program has conducted cruises twice a year between the UK and the Falkland Islands (50°N to 52°S), to assess mesoscale to basin-scale phytoplankton processes across the North and South Atlantic (Aiken and Bale, 2000; Aiken et al., 2000). The locations of the chlorophyll blooms are discussed in the context of the global distributions of nitrogen fixation and other factors that might explain the development of these features.

2. Data

Eleven years of monthly 9 km, level-3 chlorophyll *a* data from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) ocean color sensor were analyzed for the period between September 1997 and November 2007. Extensive work has gone into the calibration and

validation of the SeaWiFS chlorophyll *a* product and the dataset is periodically reprocessed as improvements are made to the algorithms (Eplee et al., 2007; Hooker and McClain, 2000; McClain et al., 2004a; O'Reilly et al., 1998). The data used here were generated from the July 2007 reprocessing, which used version 5.2 of the algorithm. Within this paper the SeaWiFS chlorophyll *a* data is simply referred to as chlorophyll data. In addition to the monthly data, timeseries from the 8-day composites of SeaWiFS chlorophyll were also used to examine the development of individual blooms, and monthly climatology data were used to show the seasonal chlorophyll cycle within the bloom regions. A number of auxiliary data sets were also analyzed to provide a broader environmental characterization of the blooms locations. Weekly composites of sea-surface temperature (SST) from the NOAA Pathfinder re-analysis of AVHRR data, and sea-surface height (SSH) altimetry from AVISO, were used to examine the physical dynamics around the blooms. Weekly files of geostrophic velocity fields from AVISO were used to calculate the average eddy kinetic energy (EKE) field over the period 2000–2006 following the method of Duce et al. (2000). Nutrient data from NOAA's World Ocean Atlas 2005 (Garcia et al., 2006) were used to map global distributions of both the reactive silicate/nitrate ratio and N⁺. Gruber and Sarmiento (1997) defined the N⁺ parameter as

$$N^* = (\text{NO}_3 - 16\text{PO}_4 + 2.9) \times 0.87$$

with positive N⁺ values indicating net nitrogen fixation and negative N[−] values indicating net denitrification.

3. Results

Bloom regions are identified using the percentage of time that the monthly 9 km chlorophyll data is greater than 0.15 mg/m³ in late summer, July–October in the northern hemisphere, and January–April in the southern hemisphere (Fig. 1). With an 11-year (1997–2007) timeseries, a bloom lasting 1-month has an associated value of ~2%, since N = 44 in the southern hemisphere and N = 42 in the northern hemisphere (no data for July–August 1997). The chlorophyll value of 0.15 mg/m³ for the bloom threshold was chosen based on previous work with the NE Pacific blooms, where the ambient background level of chlorophyll is ~0.08 mg/m³, and hence the bloom threshold represents nearly a doubling of chlorophyll (Wilson, 2003; Wilson et al., 2008). Since the objective was to identify persistent blooms the analysis in Fig. 1 was done using monthly data, however, the results are the same when done using 8-day composites (not shown). This method is an efficient way to pinpoint episodic chlorophyll blooms in oligotrophic areas characterized by low-chlorophyll, excluding blooms in areas with higher background levels of chlorophyll, such as in coastal areas, the equatorial band, and higher latitudes (the red regions in Fig. 1).

Blooms occur in six different areas. Three of these are regions where blooms have been previously identified: the NE Pacific (Wilson, 2003; Wilson et al., 2008), the SW Pacific (Dupouy et al., 1988, 2000) and off of Madagascar (Longhurst, 2001; Srokosz et al., 2004; Uz, 2007). Previously, unreported summer blooms also occur in the NE and SW Atlantic and in a band along 10°S in the Indian Ocean.

The extent of the oligotrophic gyres changes seasonally (McClain et al., 2004b), and the blooms generally occur within the transition zone, which is oligotrophic only in the summertime (Fig. 2). The oligotrophic gyres have a weak seasonal cycle of chlorophyll, with a winter increase due to enhanced chlorophyll production by phytoplankton as a photoadaptive response to lower light levels (Letelier et al., 1993). Analyses of the global spatial variability of chlorophyll have not identified these blooms, although they have reported surprisingly high variability in oligotrophic regions

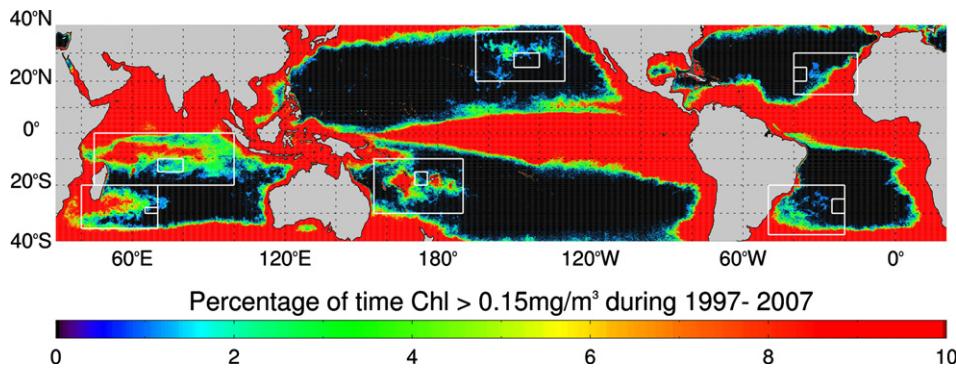


Fig. 1. Global map of percentage of chlorophyll $>0.15 \text{ mg/m}^3$ during the late summer months, July–October in the northern hemisphere, and January–April in the southern hemisphere. A 1-month long bloom in a region is a frequency of 1% (turquoise). The large white boxes indicate the regions of blooms discussed in the paper, the smaller white boxes within these regions indicate the areas used to calculate the climatological seasonal chlorophyll cycle shown in Fig. 3.

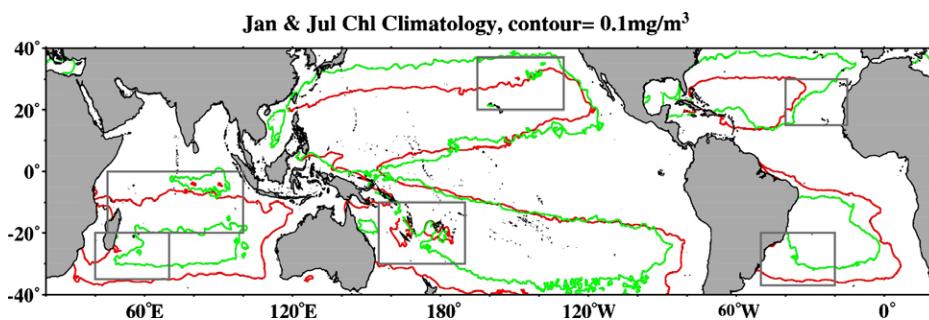


Fig. 2. Global map showing the climatological location of the 0.1 mg/m^3 chlorophyll concentration in January (red) and in July (green).

(Doney et al., 2003; Uz and Yoder, 2004). However, the area where the NE Pacific blooms develop is characterized by large temporal scaling in chlorophyll, which was attributed to the development of the chlorophyll blooms (Zhan, 2008). Doney et al. (2003) and Uz and Yoder (2004) focused on spatial scales of $\sim 2^\circ$ or less and time scales of days to a few weeks, both of which are smaller than the scales associated with the blooms, which are on the order of $\sim 5^\circ$ and weeks to months. Uz and Yoder (2004) attributed most of the variability observed in the oligotrophic gyres to noise bias, which is clearly not the cause of the summer increases in chlorophyll. Relative to the seasonal cycle, the chlorophyll increase during the summer blooms is substantial (Fig. 3). For most of the bloom regions the chlorophyll maximum during the summer blooms is two to three times larger than the local seasonal chlorophyll maximum in the winter. The one exception occurs along 10°N in the Indian Ocean, where the chlorophyll maximum during the bloom is of similar magnitude to the winter maximum (Fig. 3e). In the following sections, each region is discussed in further detail.

3.1. NE Pacific

The late summer chlorophyll blooms near 30°N are consistent events, having occurred in eight of the first 11 years (1997–2007) of SeaWiFS data (Fig. 4). These blooms have been discussed at length by Wilson (2003) and Wilson et al. (2008). While usually the blooms last 4–6 weeks, the large blooms in 1997 and 2000 lasted 4 months. Some years (2000, 2003 and 2006) had multiple blooms that developed in slightly different regions. The only years blooms did not develop near 30°N were 1998, 2001 and 2005.

The blooms occur in a region isolated from landmasses and sources of higher chlorophyll water, developing ~ 700 km north of Hawaii, and ~ 500 km south of the Transitional Zone Chlorophyll Front (TZCF). The TZCF migrates seasonally (Bograd et al., 2004;

Polovina et al., 2001), and it is present in the northern extent of the bloom region in the wintertime, after the blooms have dissipated (Fig. 2). The blooms develop in the approximate position of the subtropical front (STF, Roden, 1974), and the front could play a role in their formation. 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. The blooms occur over the Murray fracture zone that runs along 30°N between 140°W and 160°W , with water depths >5000 m.

Blooms, as observed by satellite chlorophyll data, have also occurred less frequently in two other locations in the NE Pacific: just north of Hawaii in July 2000, September 2005 and July 2006 (Fig. 2), and west of Hawaii, near 165°W , in August 1998 (Fig. 1). However, in situ sampling, done as part of the Hawaii Ocean Timeseries (HOT), has observed summer phytoplankton blooms more frequently, 10 times in 17 years (Dore et al., 2008). These blooms often develop in the lower euphotic zone, where they are not detectable by satellite data. While the Hawaii blooms are characterized by high levels of nitrogen fixers (Dore et al., 2008; White et al., 2007b), nitrogen fixation rates measured at HOT are lower than rates measured along 30°N (Mahaffey et al., 2005). It is possible that the difference in satellite bloom frequency observed between HOT and 30°N is due to a difference in vertical distribution of phytoplankton. For example, the diatom bloom observed at 26°N by Brzezinski et al. (1998) was vertically distributed throughout the surface 50 m, and probably would have been detected by satellite observations, had one been flying then, and Venrick (1974) saw a similar vertical distribution in the summer diatom blooms observed at CLIMAX at 28°N .

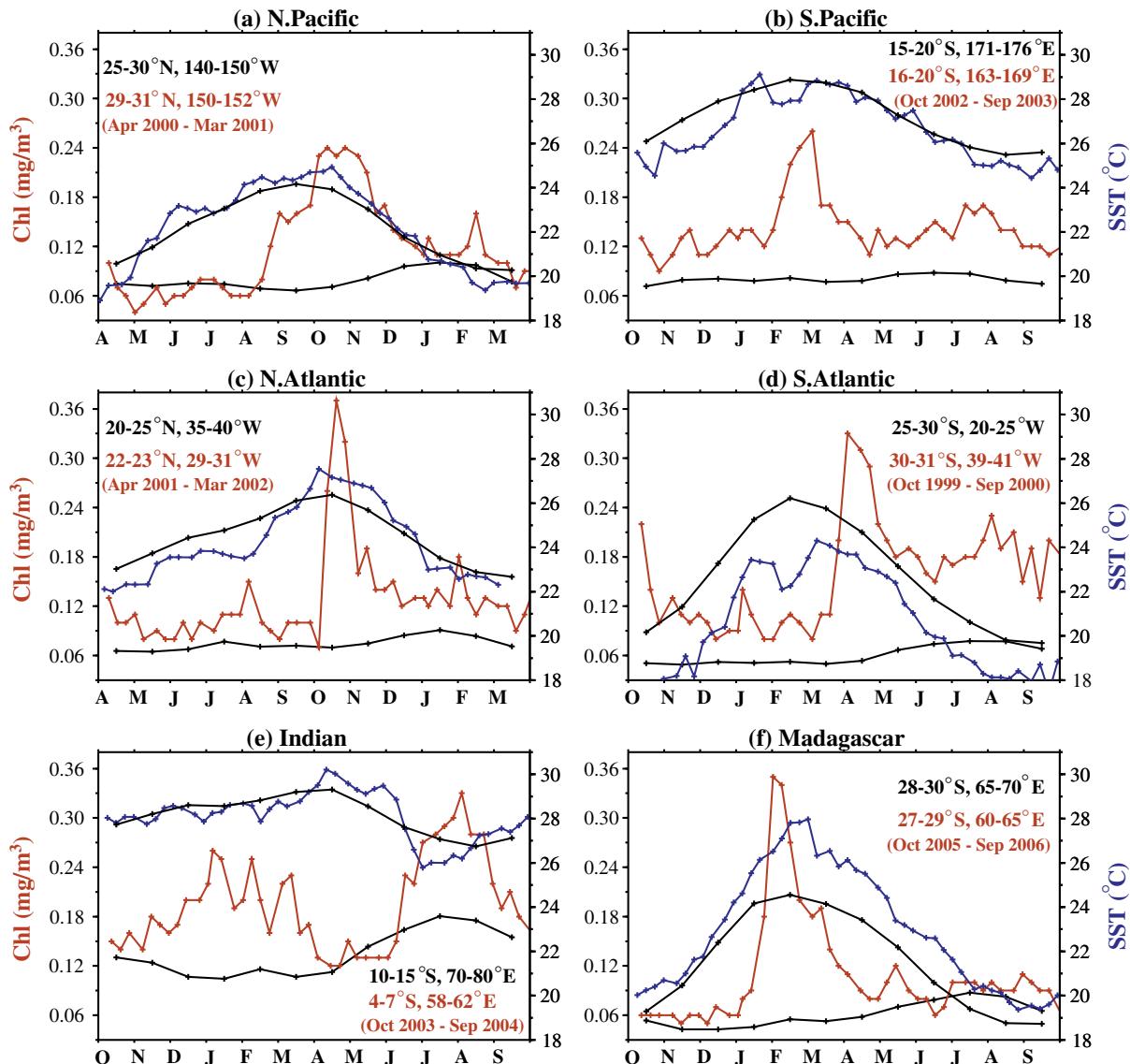


Fig. 3. Weekly timeseries of 1 year of chlorophyll (red) and SST (blue) from a point within a bloom in each of the six regions: (a) NE Pacific, (b) SW Pacific, (c) NE Atlantic, (d) SW Atlantic, (e) Southern Indian and (f) off Madagascar. Also shown are the monthly climatologies (black) of the seasonal cycle of chlorophyll and SST for a nearby region, which is outside of the bloom influence (see Fig. 1). To best show the buildup and decline of the blooms, the data is plotted from April onward in the Northern hemisphere, and from October in the Southern hemisphere.

Both nitrogen fixation and the vertical migration of *Rhizosolenia* diatom mats across the nutricline are possible mechanisms for a supply of new nitrogen to fuel the chlorophyll blooms, and both processes could be at work (Wilson, 2003; Wilson et al., 2008). There is also indication that these blooms could be “echo” blooms, fuelled from new N in the euphotic zone that was generated either from nitrogen fixation or brought in from the vertical migration of *Rhizosolenia* mats (Wilson et al., 2008). However, it remains uncertain what physical conditions consistently stimulate blooms in this specific location of the NE Pacific. Wilson et al. (2008) argued that the weak and convergent surface flow of the region creates a favorable environment for the accumulation of positively buoyant particles such as *Rhizosolenia* mats, and they also noted the nutricline is shallower in the eastern North Pacific than in the western North Pacific, making nutrients more readily available in the bloom region for migrating mats. Dore et al. (2008) hypothesized that the blooms off of Hawaii are limited by phosphorus, and that they are controlled in part by the local depth of winter mixing and the phosphocline depth.

3.2. NE Atlantic

The global distribution of elevated summer chlorophyll shows a bloom in the NE Atlantic just north of 20°N near 30°W (Fig. 1). The bloom developed at the end of September 2001, and lasted through November 2001 (Fig. 5), hence the months shown for the NE Atlantic are one later than those for the NE Pacific (Fig. 4) to better show this one bloom. Unlike the NE Pacific, where blooms occur almost every year, there has been only one bloom in the NE Atlantic in the last 11 years of satellite observations. This bloom has not been previously noted in the literature.

The NE Atlantic bloom develops slightly west of the Mauritanian upwelling zone off of Cape Blanc (Briauaud et al., 1987; Gabric et al., 1993; McClain et al., 1990; Van Camp et al., 1991). Conditions are favorable year-round for upwelling off the NW African coast between 20°N and 25°N (Gabric et al., 1993; Mittelstaedt, 1991), and “giant filaments” of chlorophyll often develop here due to the convergence of the southward flowing Canary Current and the poleward flowing countercurrent (Van Camp et al.,

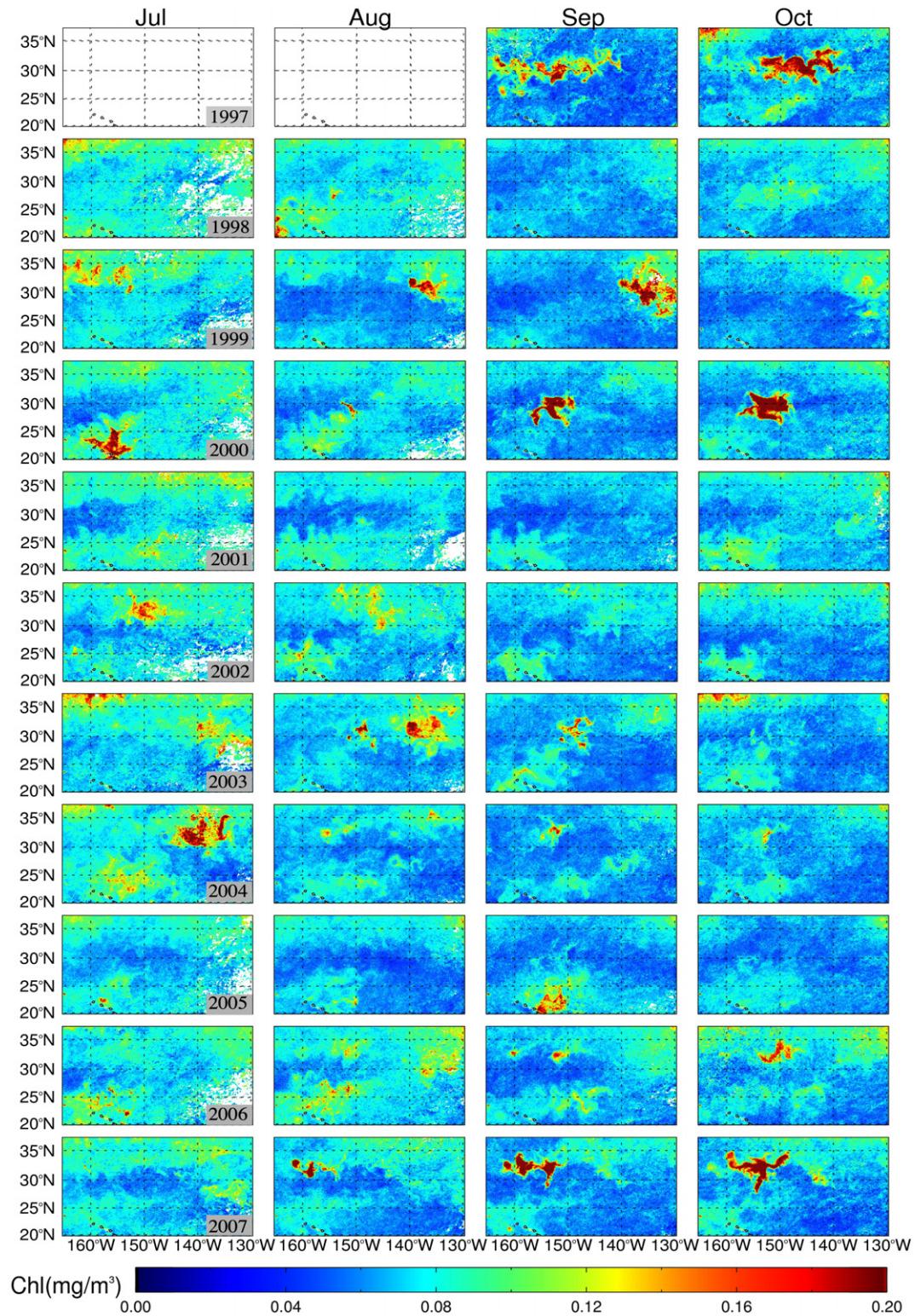


Fig. 4. Monthly maps of chlorophyll for July–October in the NE Pacific between 1997 and 2007.

1991). There is considerable offshore advection of this upwelled water via the westward flowing North Equatorial Current (Álvarez-Salgado et al., 2007; McClain et al., 1990; Mittelstaedt, 1991). The coastal advection is usually confined to 200–300 km offshore (Álvarez-Salgado et al., 2007; Mittelstaedt, 1991), but sometimes extends as far as 450 km past the shelf break (Van Camp et al., 1991).

While on a basin-scale, the NE Atlantic bloom appears to be an offshoot of the high chlorophyll coastal water associated with the Mauritanian upwelling (Fig. 1), a closer look at the bloom does not support this idea. The bloom initiated at 33°W, 22–24°N (Fig. 6a); at this time the maximum chlorophyll value, >0.3 mg/m³, was more than 1000 km offshore of water with the same value in the coastal zone. As the bloom developed it expanded eastward

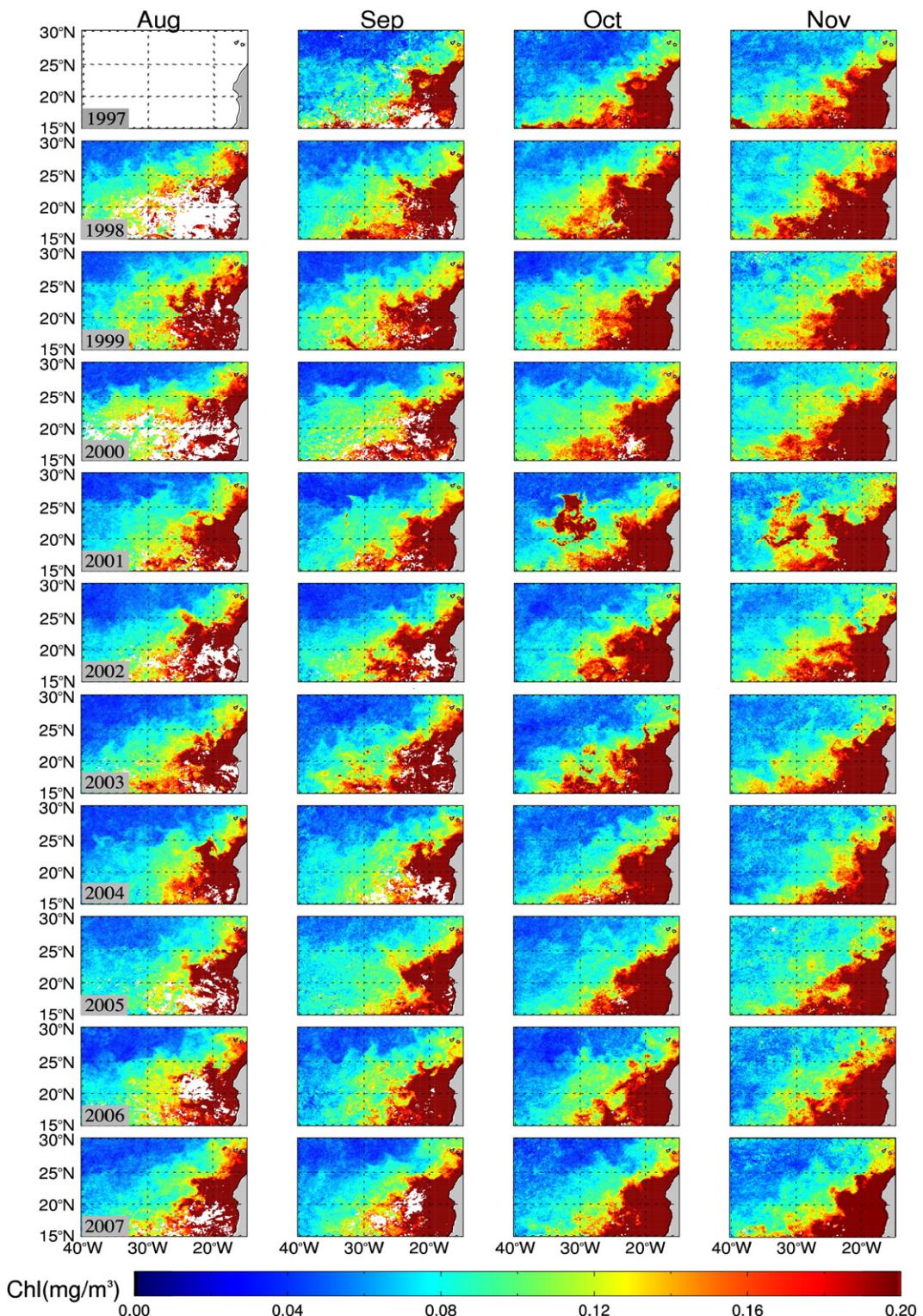


Fig. 5. Monthly maps of for August–November in the NE Atlantic between 1997 and 2007. To better show the one bloom in this region, which started in October and extended into November, the images shown here are 1-month later than those shown for the NE Pacific.

(Fig. 6b and c). At its largest, in October 2001, it occupied the area between 20–27°N and 28–34°W ($\sim 300,000 \text{ km}^2$), but always remained distinct from the high chlorophyll at the coast (Figs. 5 and 6). While subsurface advection of upwelled coastal water to this region cannot be ruled out, the large distances involved, and the lack of a surface connection between the bloom and the high chlorophyll coastal water suggests that advection is not factor in the development of this bloom.

Numerous studies have shown that nitrogen fixation, and *Trichodesmium* in particular, makes a major contribution to the nitrogen budget of the North Atlantic (Carpenter and Romans, 1991; Carpenter et al., 2004; Montoya et al., 2002, 2007). Most studies have suggested that both nitrogen fixation rates and *Trichodesmium* biomass abundances are higher in the western tropical Atlantic than in the eastern basin (Capone et al., 2005; Coles et al., 2004a; Davis and McGillicuddy, 2006; Gruber and Sarmiento, 1997; Hood et al.,

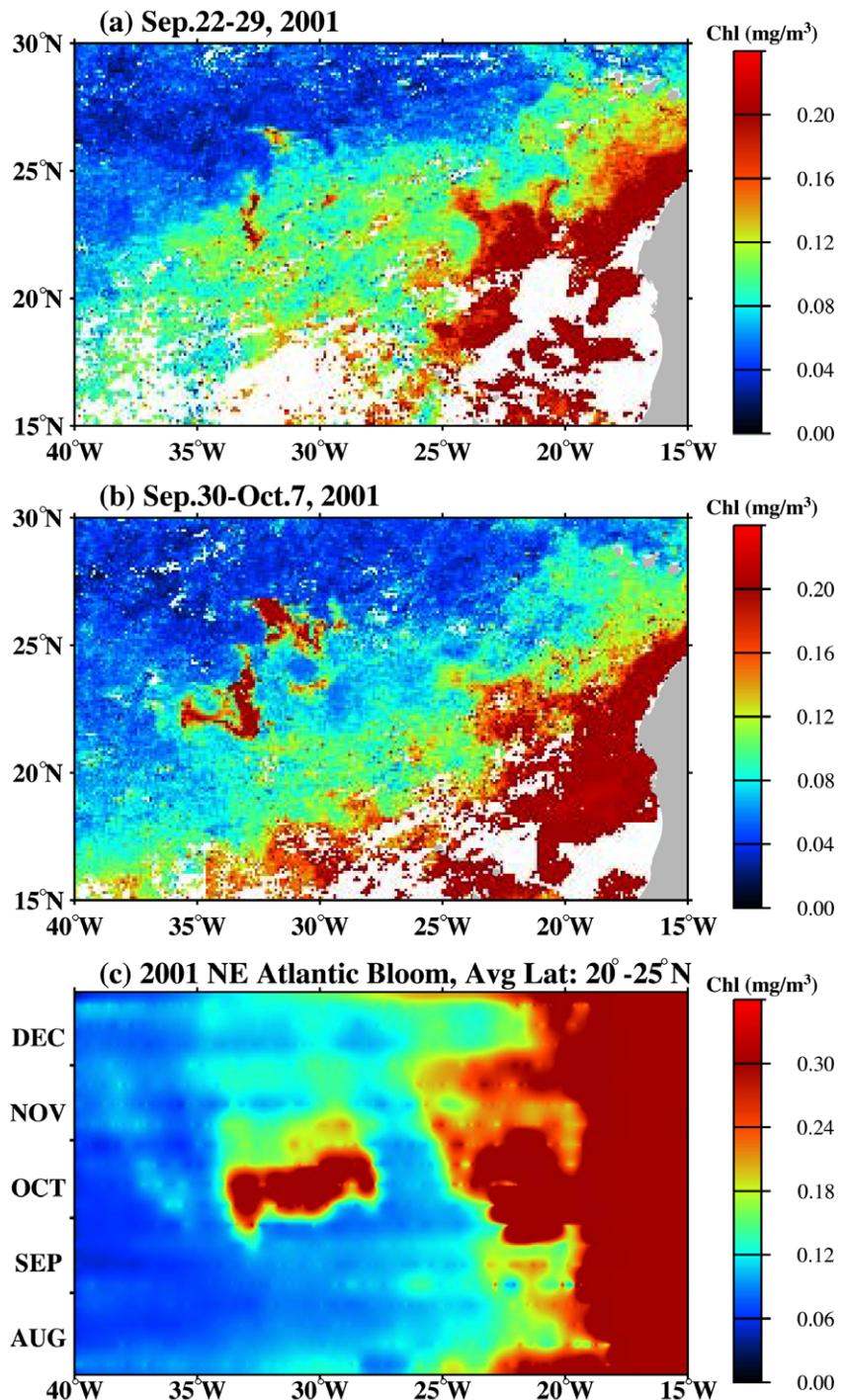


Fig. 6. Hovmöller diagram of 8-day chlorophyll data from August to December, 2001 along 15–40°W in the NE Atlantic, averaged between 20°N and 25°N.

2004; Lee et al., 2002). In the NW Atlantic the seasonal cycle of chlorophyll is distinct from the rest of the subtropical Atlantic in that chlorophyll peaks in the summertime. For this reason our analysis does not indicate any blooms in this area, as the entire region has chlorophyll greater than the bloom threshold of 0.15 mg/m³ (Fig. 1). This anomalous summer peak in chlorophyll has been attributed to nitrogen fixation based on a joint analysis of satellite data and model results (Coles et al., 2004b).

However, nitrogen fixation is not absent in the eastern Atlantic, as evidenced by observations of *Trichodesmium* (Carpenter, 1983a; McCarthy and Carpenter, 1979; Ramos et al., 2005; Tyrrell et al., 2003), nitrogen fixation measurements (Staal et al., 2007) and geo-

chemical studies (Mahaffey et al., 2003; Reynolds et al., 2007). Some studies have in fact indicated greater levels of nitrogen fixation in the eastern half of the Atlantic, where both higher densities of *Trichodesmium* (McCarthy and Carpenter, 1979) and higher rates of nitrogen fixation (Voss et al., 2004) were observed in cross-Atlantic transects. However, since *Trichodesmium* is not the only oceanic diazotroph, it can be misleading to use *Trichodesmium* abundances as a proxy for nitrogen fixation. For example, Montoya et al. (2007) observed no significant difference in the overall rate of nitrogen fixation across the Atlantic, but *Trichodesmium* was the dominant contributor to nitrogen fixation in the west, whereas unicellular diazotrophs dominated in the east. *Rhizosolenia* mats

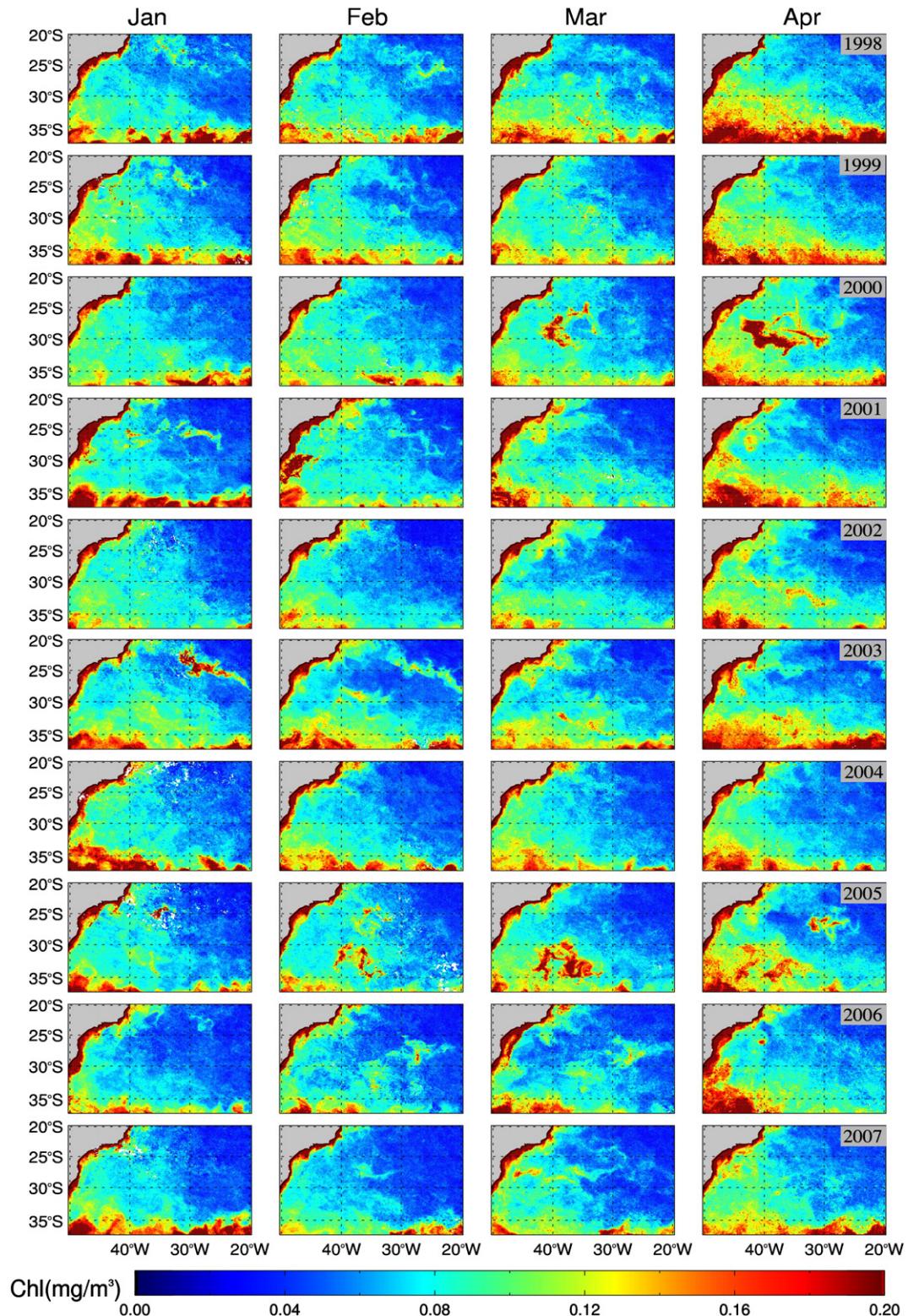


Fig. 7. Monthly maps of chlorophyll for January–April in the SW Atlantic between 1998 and 2007.

have also been observed in the region of the NE Atlantic bloom (Carpenter et al., 1977).

3.3. SW Atlantic

Summer chlorophyll blooms occur in the SW corner of the South Atlantic subtropical gyre, near 30°S and 30–40°W (Figs. 1

and 7). Significant blooms developed in 4 years: 2000 (March–April), 2003 (January), 2005 (February–March) and 2007 (March), and there were also smaller, weaker blooms in other years, such as in 2001 (January), 2002 (April) and 2006 (February–March). The blooms develop near the Rio Grande Plateau between 30–40°W and 30°S, but they are clearly not tied to this geographic feature, as they do not develop in exactly the same place from year to

year, but are generally confined to the region between 25–35°S and 20–40°W. In some years there are multiple blooms, for example, between January and April 2005 there were three blooms in different locations.

While on a basin-scale (Fig. 1) the blooms develop relatively close to the high chlorophyll waters associated with both the SW coast of Brazil and the Brazil-Malvinas Confluence (BMC) at ~35°S, it is clear from examination of the individual blooms (Fig. 7) that the blooms are geographically distinct from both areas. The blooms occur hundreds of kilometers away from the sharp chlorophyll gradients associated with the shelf break and with the BMC. One exception is the small, eddy-shaped bloom near 40°W, 26°S in April 2006. The 8-day images preceding the development of this offshore bloom show tendrils of elevated chlorophyll leaving the coast (not shown), suggesting that this bloom was an offshore injection of coastal waters.

The Brazil Current (BC) forms the western boundary of the South Atlantic gyre, flowing south and bringing oligotrophic subtropical waters poleward. In the summer, the BC spreads further onto the shelf break, resulting in lower productivity (Brandini, 1990). The BMC forms the southern boundary of the western South Atlantic gyre. It occurs several degrees south of where the blooms develop, migrating seasonally from ~30°S in the austral winter to ~40°S in the austral summer (de Souza and Robinson, 2004). Upwelling of South Atlantic Central Water injects nutrients onto continental shelf waters off Brazil (Lopes et al., 2006; Metzler et al., 1997). While the upwelling occurs more frequently during the austral summer (Lima et al., 1996; Valentin, 1984), it is unlikely that the chlorophyll blooms are induced by upwelling, as they develop hundreds of kilometers offshore, and the upwelling is confined to a narrow band ~20 km wide (Valentin et al., 1987). There are also no cold temperature anomalies associated with the blooms, which would be indicative of upwelling.

Compared to the North Atlantic, *Trichodesmium* seems conspicuously absent in the South Atlantic. In the first 8 AMT cruises there was only one observation of elevated *Trichodesmium* in the South Atlantic, which occurred off Brazil at ~49°W and 34°S in October 1998 (Tyrrell et al., 2003). But there have been other observations of *Trichodesmium* in the vicinity of the chlorophyll blooms, both offshore (Carpenter, 1983a), and in the coastal and shelf regions (Méndez and Medina, 2004; Metzler et al., 1997; Siqueira et al., 2006), and as far south as the BMC (Hart, 1934, as reported by Carpenter (1983)). Additionally, there are organisms other than *Trichodesmium* that could be associated with the chlorophyll blooms. Sundström (1986) reported on observations of *Rhizosolenia debaryana* in the coastal area of Brazil near 24°S. *R. debaryana* is one of the species that makes up the composition of the vertically migrating *Rhizosolenia* mats (Villareal and Carpenter, 1989), which have been hypothesized to account for the chlorophyll blooms consistently observed in the NE Pacific (Wilson et al., 2008).

3.4. SW Pacific

Summer chlorophyll blooms occur in the SW Pacific subtropical gyre between New Caledonia and Vanuatu (Figs. 1 and 8). Blooms are observed in this region in every year of satellite observations, although there is significant interannual variability in the strength and extent of the blooms, for example the blooms were much less extensive in 2000–2002. The most extensive bloom occurred between February–April 1998 and was centered in the North Fiji basin (west of Fiji) between 15°S and 25°S, and extended eastward off the southern tip of New Caledonia along 25°S.

Unlike the blooms in the North Pacific and in the Atlantic, the SW Pacific blooms develop interspersed around islands and shallow topographic features. Geographically, the higher chlorophyll areas in the SW Pacific fall into two different categories. One type

is the large, amorphous features that are not directly tied to bathymetry, such as the blooms in the North Fiji basin, and southeast of Fiji. The other type is found encircling the islands, and over shallow bathymetry (<500 m depth), such as the Chesterfield Islands (19–22°S, 159°E), the hook at the northern tip of the Fiji Ridge (16–19°S, 177°E to 178°W) and the northern part of Tonga Ridge (174°W, 20°S), where chlorophyll is always higher than in the nearby ocean. These features are most easily visible in 2000–2002, when the open ocean blooms, offshore of the islands, were not well-developed (Fig. 8).

It is well-known that different physical dynamics associated with islands and shallow topography can elevate surface nutrient levels, resulting in a near-shore chlorophyll increase, the “island mass effect” (Coutis and Middleton, 2002; Doty and Oguri, 1956; Heywood et al., 1990; Sokolov and Rintoul, 2007). There are a number of mechanisms that can cause this increase, including benthic interactions (Doty and Oguri, 1956), land drainage (Dandonneau and Charpy, 1985; Signorini et al., 1999), and flow disturbance which can lead to eddy shedding and isopycnal doming downstream of islands (Coutis and Middleton, 2002; Heywood et al., 1990). While the spatial scales vary depending on both the mechanism involved and environmental conditions, the effects can be quite large, extending over 1000 km (Signorini et al., 1999; Sokolov and Rintoul, 2007). It is interesting to note that the high chlorophyll is usually bounded between New Caledonia in the south and Vanuatu in the north, and seldom develops offshore of the southwest coast of New Caledonia. Blooms also develop consistently southeast of Fiji, and there appears to be a geographic break between these two blooms areas (Fig. 1). As the blooms occur within the eastward flow of the South Tropical Countercurrent (Qiu and Chen, 2004), and the largest ones develop downstream of New Caledonia and Fiji, island mass effects could play a role in the formation of the blooms. While the chlorophyll blooms do not structurally resemble typical island wakes (Coutis and Middleton, 2002; Heywood et al., 1990; Palacios, 2002), retention is strongly controlled by coastal bathymetry (Coutis and Middleton, 2002), which is complex in this region.

The SW Pacific blooms have been previously noted in satellite data and attributed to *Trichodesmium* (Dandonneau et al., 2004; Dandonneau and Gohin, 1984; Dupouy et al., 1988, 2000), which can occur in high densities in the summertime near New Caledonia (Campbell et al., 2005; Dandonneau and Gohin, 1984; Garcia et al., 2007; Le Borgne et al., 1997; Masotti et al., 2007; Moutin et al., 2005) and off of Tonga (Bowman and Lancaster, 1965), which at 21°S, 175°W is the eastern extent of the chlorophyll blooms. High densities of *Trichodesmium* were observed in the New Caledonia area coincident with the chlorophyll blooms in February–April 1998 (Campbell et al., 2005) and in February 2003 (Garcia et al., 2007). In addition to *Trichodesmium*, significant amounts of nitrogen fixation occur in this region from unicellular diazotrophs (Campbell et al., 2005; Garcia et al., 2007). The SW Pacific blooms also occur within the band of high precipitation associated with the South Pacific Convergence Zone (Vincent, 1994), and it has been suggested that enhanced water column stratification in this region, caused by the high precipitation, would favor the enhanced rates of nitrogen fixation observed here (Hansell and Feely, 2000).

Because of the high Fe requirement of the nitrogenase enzyme, diazotrophic growth is often limited by the availability of iron (Berman-Frank et al., 2001; Hood et al., 2000; Rueter, 1983; Rueter et al., 1992). The North Fiji basin is hydrothermally active (Halbach et al., 1999; Koschinsky et al., 2002), and local iron enrichment from regional venting could promote the apparent extensive amount of nitrogen fixation in this region. A large hydrothermal plume, centered at 1700 m depth, extends over the entire region where the chlorophyll blooms develop (Lupton et al., 2004) and appears to emanate from the Lau Basin, due east of Fiji (German et al.,

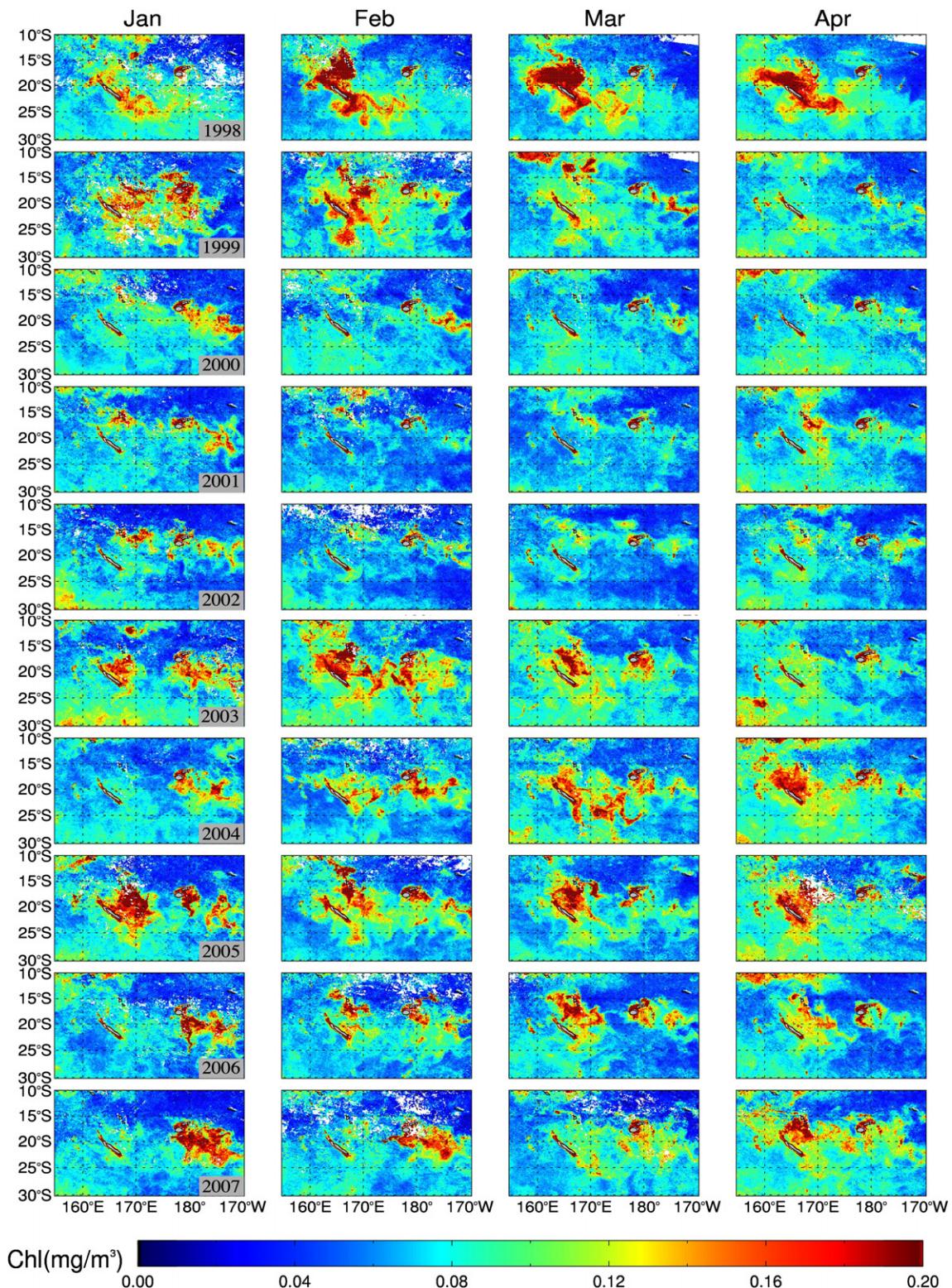


Fig. 8. Monthly maps of chlorophyll for January–April in the SW Pacific between 1998 and 2007.

2006). While this plume is too deep to directly enhance surface waters, shallower venting occurs east of Samoa within the summit crater of the Vaolulu'u seamount (Hart et al., 2000; Staudigel et al., 2006), with a hydrothermal plume encircling the summit between 650 and 700 m depth (Hart et al., 2000). Dissolved iron concentrations throughout the region are higher than typical for oligotrophic regions (Campbell et al., 2005; Van Den Broeck et al., 2004). Open

ocean concentrations of dissolved iron in the Pacific and Atlantic Oceans are <0.2 nmol/kg, with an average value of 0.07 nmol/kg (Johnson et al., 1997). In contrast, Campbell et al. (2005) reported a range of median surface concentration of 0.09 nmol/kg in the non-coastal waters between New Caledonia and Fiji, but also measured values as high as 0.7 nmol/kg. The median value increases to 0.35 nmol/kg in coastal regions (Campbell et al., 2005), and at

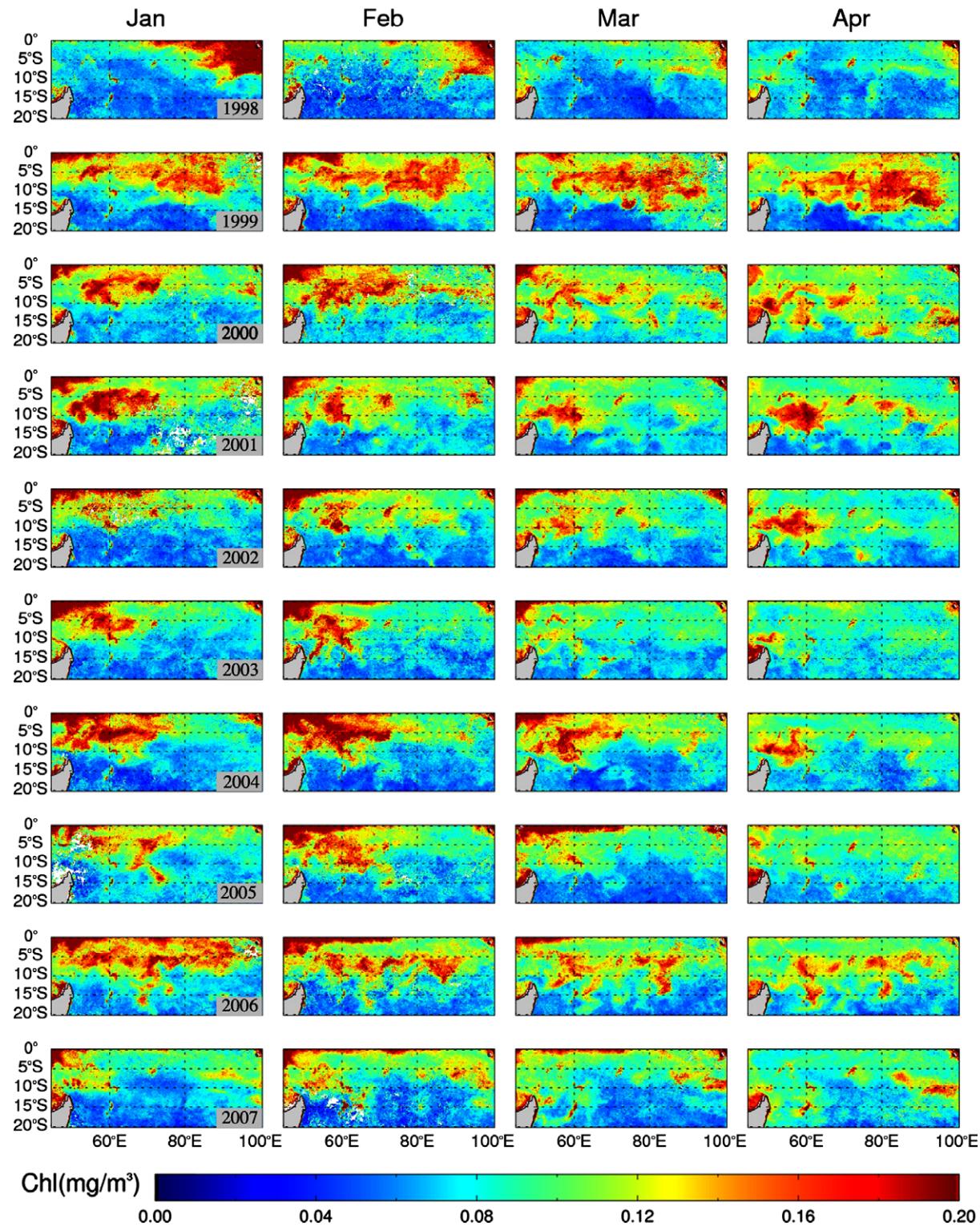


Fig. 9. Monthly maps of chlorophyll for January–April in the SW Indian, 0–20°S, between 1998 and 2007.

plume depths (between 1500 and 2000 m depth) can increase to values on the order of 10–100 nmol/kg (German et al., 2006; Koschinsky et al., 2002; Staudigel et al., 2006).

In regions where higher iron concentrations alleviate iron limitation, such as the North Atlantic (Mills et al., 2004; Sañudo-Wilhelmy et al., 2001; Wu et al., 2000), nitrogen fixation can become limited by phosphorus, and there is evidence that this is also the case in the SW Pacific (Moutin et al., 2005; Van Den Broeck et al., 2004). Moutin et al. (2005) found phosphate to be the systemic

limiting nutrient for nitrogen fixation in this region, and they argued that the seasonal variations in dissolved phosphate controlled the growth and decay of *Trichodesmium* blooms here.

3.5. South Indian

Summer chlorophyll blooms occur between 5°S and 10°S in the southern subtropical Indian Ocean over a wide band extending across most of the basin (Figs. 1 and 9). Some of the areas of high

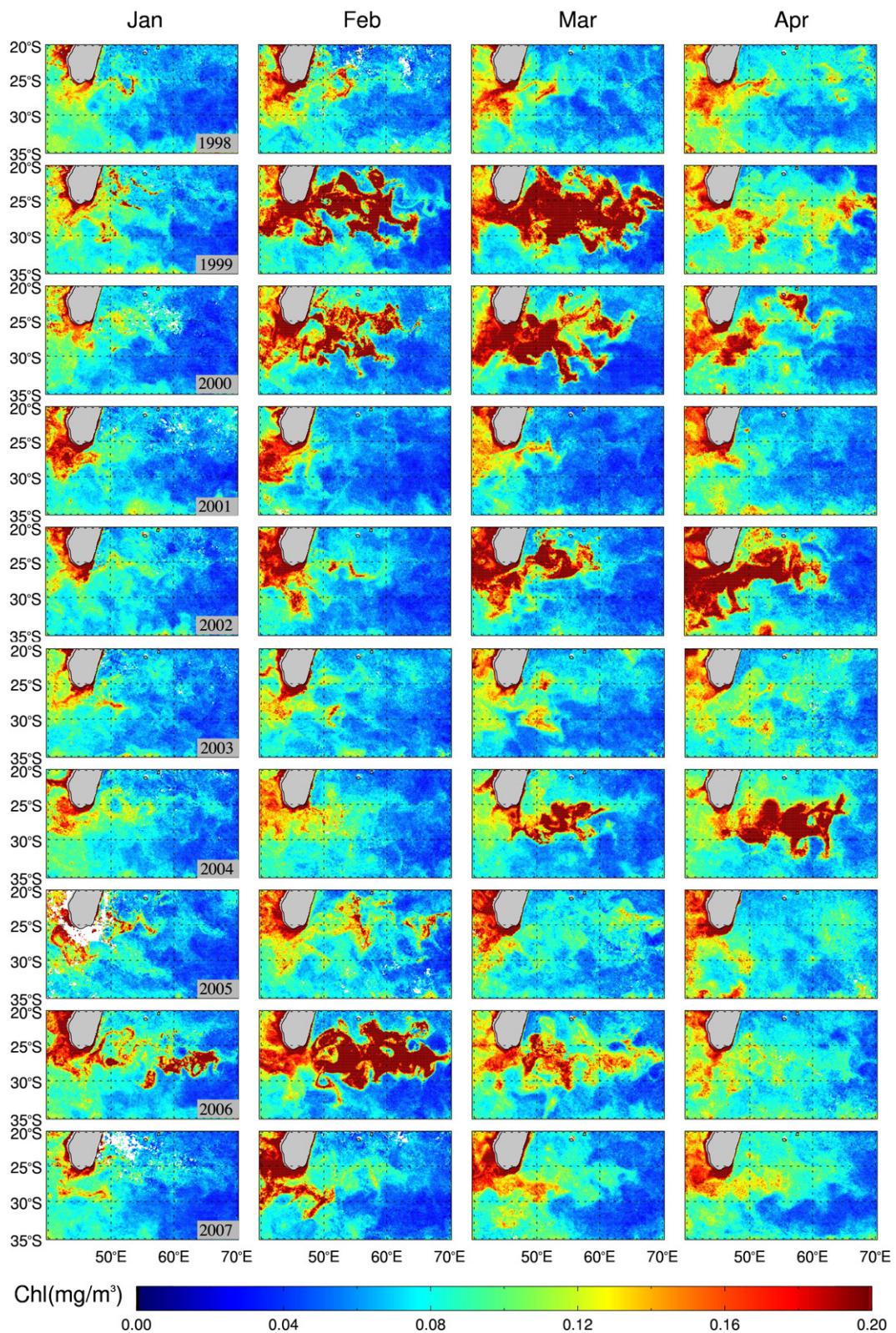


Fig. 10. Monthly maps of chlorophyll for January–April off Madagascar, 20–35°S, between 1998 and 2007.

chlorophyll occur consistently in the same locations and are clearly tied to topographical features. For example, the Mascarene Plateau ($4\text{--}20^{\circ}\text{S}$, $\sim 56^{\circ}\text{E}$) and the Chagos Archipelago (5°S , 72°E) always have higher chlorophyll than the surrounding ocean. This association is most evident in 1998 when these topographic features are

the only areas with elevated chlorophyll. The lower chlorophyll in 1998 was associated with a reversal in the Indian Ocean dipole mode that resulted in widespread warming of the Indian Ocean and a deepening of the thermocline (Feng et al., 2001; Murtugudde et al., 2000; Webster et al., 1999; Yu and Rienecker, 2000).

The chlorophyll blooms develop along a thermocline “ridge”, which occurs between 5°S and 10°S due to Ekman pumping (Murtugudde et al., 1996; Rao and Sivakumar, 2000; Schott et al., 2002). Murtugudde et al. (1996) and Wiggert et al. (2006) have discussed the higher chlorophyll resulting from this open ocean upwelling, but noted that the bloom occurred during the Southwest Monsoon (SWM), in July–September (austral winter). While seasonally the maximum chlorophyll does occur in this region during austral winter (Fig. 3e), it is clear from Fig. 9 that there are also isolated regions of elevated chlorophyll that develop in the austral summer, during the Northeast Monsoon (NEM). The development of these summer chlorophyll blooms is consistent with the Ekman divergence and thermocline doming at 5–10°S being strongest during the NEM (Rao and Sivakumar, 2000; Schott et al., 2002). Subsurface (50 m) temperatures are coldest in January, and the dome of cold water disappears July–August because of changes in the wind pattern (Rao and Sivakumar, 2000). However, upwelling along the 10°S thermocline ridge, and the cold water dome at 100 m depth, are both present year-round (Rao and Sivakumar, 2000). The disconnect between stronger upwelling in the summer, yet with a weaker chlorophyll bloom than occurs in the winter, is probably a consequence of the difference in mixed layer depth (MLD). The MLD is shallower in summer, 30–50 m deep, versus 50–60 m deep in winter (Rao et al., 1989), so the upwelled water will have a greater impact on the surface water in the winter, leading to a stronger bloom.

3.6. Madagascar

Chlorophyll blooms develop east of Madagascar in February–April (Figs. 1 and 10). These blooms originate at the southern tip of Madagascar and extend eastward to 70°E, covering a distance of ~2500 km. The only years that blooms did not develop were 1998 and 2001, though the blooms in 2003 and 2005 were not as well-developed as the other bloom years. The Madagascar blooms differ from blooms in the other regions in that they are characterized by consistent eastward propagation, which is the opposite direction to both the mean flow and Rossby wave propagation (Longhurst, 2001; Srokosz et al., 2004). With the exception of the 1997 bloom in the NE Pacific, which also appeared to propagate eastward (Wilson, 2003; Wilson et al., 2008), none of the blooms in the other regions display consistent propagation in any direction. The southern boundary of the Madagascar blooms coincides with the South Indian Counter Current (SICC), a narrow eastward flowing current between 22°S and 26°S (Palastanga et al., 2007; Siedler et al., 2006).

Different mechanisms have been put forth to explain the Madagascar blooms (Longhurst, 2001, 2007; Srokosz et al., 2004; Uz, 2007). Longhurst (2001) first described this phenomenon, and classified it as an “entrainment” bloom resulting from upwelling at the center of cyclonic eddies, and at the periphery of anti-cyclonic eddies. Given their association with localized upwelling that would bring nitrate to the surface, Longhurst (2001) does not think the blooms are *Trichodesmium*, suggesting instead that they are comprised of eukaryotic algal cells. However, Uz (2007) argues that these blooms are fuelled by nitrogen fixation, and used subsurface data from ARGO floats to show that the blooms occur in regions with a shallow MLD over a strong pycnocline, a condition that would retain nitrogen fixers at the surface. Uz (2007) also suggests that runoff from Madagascar alleviates the iron limitation of diazotrophy. Srokosz et al. (2004) postulates that the bloom is a plankton wave, originating in the high chlorophyll water off Madagascar and spreading against the mean flow by a combination of phytoplankton growth and eddy diffusion. They assume sufficient nutrients were available for phytoplankton growth and do not address the question of whether nitrogen fixers are involved.

There are numerous reports of *Trichodesmium* blooms in the Indian Ocean. While the northern Indian Ocean has been studied more extensively, there are reports of *Trichodesmium* in the southern Indian Ocean, and large blooms of them have been observed in the coastal waters off Tanzania (Bryceson and Fay, 1981; Carpenter, 1983a; Karsten, 1907; Taylor, 1966). Concentrations appear highest during the austral summer (Carpenter, 1983a).

4. Regional intercomparison

Commonalities among the different regions where episodic summer chlorophyll blooms develop could help identify their underlying forcing mechanisms. The blooms along 5–10°S in the Indian Ocean occur in a region of open ocean upwelling that is intensified in the summer. These blooms are unique in that they are clearly associated with a hydrographic feature, the 10°S thermocline ridge, which explains the bloom development within a conventional upwelling scenario. The rest of the discussion focuses on the blooms in the other regions, and the possible physical mechanisms associated with them. Since the NE Pacific bloom region is the most well-studied (Dore et al., 2008; Pilskaln et al., 2005; White et al., 2007b; Wilson, 2003; Wilson et al., 2008) the discussion will largely revolve around comparisons to that region. The blooms in the North and South Atlantic appear most similar to those in the NE Pacific, being isolated from both land masses and any hydrographic features that could explain them, however, the Atlantic blooms occur much less frequently than the NE Pacific blooms. Blooms in the two other regions, the SW Pacific, and southeast of Madagascar, are probably influenced by “island mass effects”. The SW Pacific blooms are usually bounded between the islands of New Caledonia and Vanuatu, and the blooms along 25°S in the Indian Ocean develop within the dynamic eddy field and current system emanating off the southern tip of Madagascar.

5. Mechanisms of chlorophyll bloom formation

The chlorophyll blooms discussed here are regions with higher surface chlorophyll concentrations than occurs in the nearby vicinity. An obvious interpretation of these features is that they represent blooms of phytoplankton, or net excess phytoplankton growth. However, from only satellite data it is not possible to definitively classify an increase in surface chlorophyll as a phytoplankton bloom, as other factors, such as reduced mortality, surface chlorophyll accumulation, and changes in cellular chlorophyll/C ratios, could also lead to the observed chlorophyll blooms. In the following sections, each of these factors is discussed in further detail.

5.1. Enhanced phytoplankton growth

Assuming that the chlorophyll blooms do represent blooms of phytoplankton, understanding their development requires knowledge of the predominant controlling nutrient limitation, i.e., nitrate, iron, phosphate or silicate, in their region, and the processes that will alleviate that limitation. While low light can also be limiting to phytoplankton growth, this dynamic will not be a factor in the subtropics during the summer, when the chlorophyll blooms develop.

5.1.1. Nitrate

Throughout most of the oceans, nitrate is the limiting nutrient to phytoplankton growth on short time scales, and its primary source into the euphotic zone is the vertical flux across the nutricline (Lewis et al., 1986). However, this vertical flux is not sufficient to support the observed level of new production in the

ocean, and it is presumed that nitrogen fixation accounts for the bulk of the discrepancy (Eppley and Peterson, 1979). The most well-known oceanic diazotroph is *Trichodesmium*, but nitrogen fixation occurs in multiple organisms (Church et al., 2005; Hewson et al., 2007; Mague et al., 1974; Montoya et al., 2004; Villareal, 1991; Zehr et al., 2001, 2007). Another biologically mediated process that can deliver new N to the euphotic zone is vertically migrating phytoplankton (Richardson et al., 1998; Villareal and Lipschultz, 1995; Villareal et al., 1999).

5.1.1.1. Nitrogen fixation. 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 CO₂ and export of carbon (Hood et al., 2000). Estimates of the global ocean nitrogen fixation rate keep steadily increasing, from an initial estimate of ~10 Tg N yr⁻¹ in 1970 to current estimates of ~135 Tg N yr⁻¹ (Codispoti, 2007; Delwiche, 1970; Gruber, 2004; Karl et al., 2002), and recent studies have suggested that current estimates still need to be revised upwards (Codispoti, 2007; Davis and McGillicuddy, 2006). The increasing trend is primarily a reflection of advances made both in measuring nitrogen fixation rates, and in identifying diazotrophy in organisms, i.e. it is a matter of "the more we look, the more we find" (Codispoti, 2007), rather than representing a temporal change. There is however, evidence from the HOT station that nitrogen fixation rates in the North Pacific gyre have been increasing over the past 20 years (Karl, 2007).

The total oceanic nitrogen fixation rate can be estimated by extrapolating direct in situ measurements of nitrogen fixation, or from indirect geochemical methods. Both methods require assumptions for factors that are not well understood, resulting in large uncertainties in the estimates (Hansell et al., 2004; Karl et al., 2002; Mahaffey et al., 2005). Geochemical estimates are generally three to four times larger than estimates extrapolated from direct measurements (Mahaffey et al., 2005). This discrepancy could be due to the geochemical estimates measuring processes that are integrated over larger spatial and temporal scales than the spot measurements, which are highly variable. The geochemical estimates should also integrate the effects of all diazotrophy, and most of the estimates based on direct measurements are based solely on measurements of nitrogen fixation from *Trichodesmium* (Mahaffey et al., 2005).

An advantage to the geochemical measurements is that they provide a means to globally map nitrogen fixation rates. Gruber and Sarmiento (1997) introduced the quasi-conservative tracer N*, a linear combination of nitrate and phosphate, to examine the global distribution of nitrogen fixation and denitrification. The N* parameter does not quantify rates of nitrogen fixation, but areas with positive (negative) values of N* indicate prevailing nitrogen fixation (denitrification) (Gruber and Sarmiento, 1997). All of the bloom regions occur within areas with positive N*, with the exception of the Indian Ocean between 5°S and 10°S, but nitrogen fixation is not thought to contribute to these blooms. Deutsch et al. (2007) expanded on this methodology and used P' (defined as (PO₄³⁻-NO₃⁻)/16) and an ocean circulation model to estimate nitrogen fixation rates. While the N* distribution suggests that there is more nitrogen fixation in the N. Atlantic relative to the North Pacific, the Deutsch et al. (2007) results suggest that there is more nitrogen fixation in the Pacific than in the Atlantic (Fig. 11b). They argue that nitrogen fixation rates are coupled more to denitrification zones than to the availability of iron. With the exception of the SW Atlantic and 5–10°S Indian Ocean, the chlorophyll blooms

all occur in (or adjacent to) regions with moderate nitrogen fixation rates, according to Deutsch et al. (2007).

5.1.1.2. *Trichodesmium*. *Trichodesmium* is the most well-known oceanic diazotroph; an overview of the existing knowledge on its physiology and ecology was recently summarized by LaRoche and Breitbarth (2005). It is found throughout the subtropical ocean and has been reported in all the regions where chlorophyll blooms develop. However, it is difficult to construct a global view of *Trichodesmium* abundance from spot sampling, especially since there is significant temporal and spatial variability in the measurements of both *Trichodesmium* biomass and its associated rates of nitrogen fixation (Capone et al., 2005; Mahaffey et al., 2005; Montoya et al., 2007; Stihl et al., 2001). Additionally, it is possible that traditional sampling methods have underestimated the abundance of *Trichodesmium*. Recent observations using a video plankton recorder (VPR) show that *Trichodesmium* does not just congregate at the surface, as generally thought, but rather is distributed throughout the surface layer down to 100 m (Davis and McGillicuddy, 2006; Kolber, 2006). Nitrogen fixation rates using VPR data are up to five times higher than rates derived from standard net sampling, suggesting that previous estimates of the global *Trichodesmium* nitrogen fixation rate, based on traditional sampling methods, need to be revised upwards (Davis and McGillicuddy, 2006).

To estimate the global distribution of *Trichodesmium* Westberry and Siegel (2006) used a bio-optical algorithm applied to SeaWiFS radiometric data (Westberry et al., 2005). They calculated *Trichodesmium* persistence, defined as the percent time *Trichodesmium* blooms were present, as estimated from the satellite data, scaled to the frequency of clear-sky occurrences. They found the greatest occurrence of *Trichodesmium* in the southeast tropical Pacific, the western Arabian Sea and at low latitudes in the south central Atlantic Ocean. The locations of the chlorophyll blooms are overlaid on top of the Westberry and Siegel (2006) *Trichodesmium* distribution in Fig. 11c. Summer chlorophyll blooms have not been observed in the regions where they estimate the highest persistence of *Trichodesmium*. However, the analysis used here would not detect chlorophyll blooms within either the southeast tropical Pacific or the western Arabian Sea, as these areas are outside the boundaries of the oligotrophic gyres (see Fig. 1). The chlorophyll blooms in the NE Atlantic and the SW Pacific do occur within regions of *Trichodesmium* occurrence, and the ones in the SW Atlantic and off of Madagascar occur at the edges of regions of *Trichodesmium* occurrence. The NE Pacific blooms develop in an area that is devoid of *Trichodesmium* according to the Westberry and Siegel (2006) analysis. However, their algorithm is specific for *Trichodesmium*, and observations suggest that *Trichodesmium* is not the primary diazotroph in the region of the NE Pacific blooms (Wilson et al., 2008).

5.1.1.3. Other diazotrophs. While *Trichodesmium* is the best studied oceanic diazotroph, it is certainly not the only one. 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 endosymbiotic *Rhizelia* 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) and a variety of other microbes (Karl et al., 2002; Mehta and Baross, 2006). The contribution of these other organisms could be significant, as it has been estimated that *Trichodesmium* accounts for only 25–50% of the global nitrogen fixation rate, with the assumption that activity from diazotrophic nanoplankton and *Rhizelia* explain the difference (Mahaffey et al., 2005), although it is also possible that the *Trichodesmium* rate needs to be revised upwards (Davis and McGillicuddy, 2006). Areal rates of nitrogen fixation from *Rhizelia*

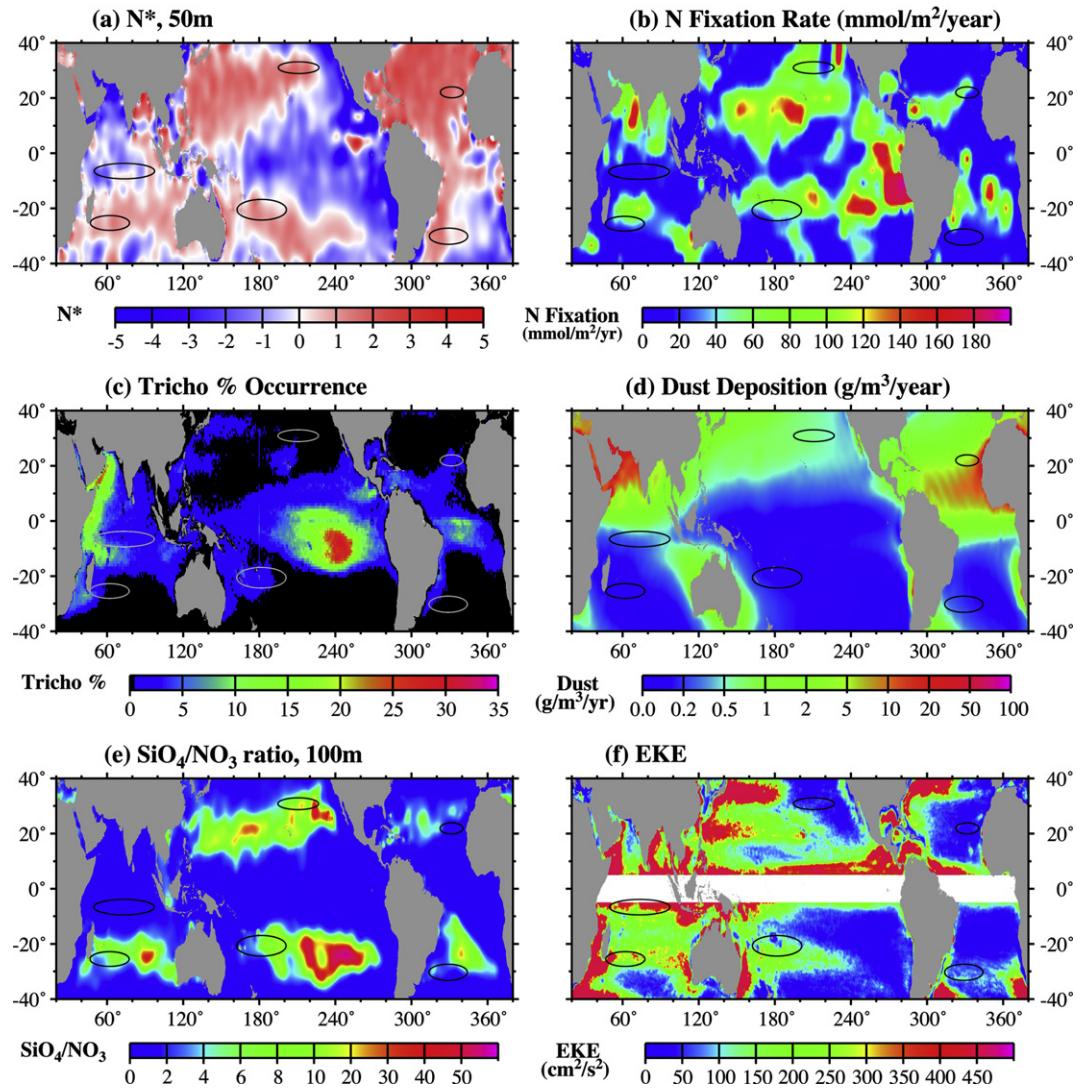


Fig. 11. Global distribution of (a) N^* at 100 m, calculated using nutrient data from the NOAA/NODC World Ocean Atlas 2005, (b) nitrogen fixation rates from Deutsch et al. (2007), (c) *Trichodesmium* persistence (the percentage of time blooms are present, scaled to the frequency of clear-sky occurrences) from Westberry and Siegel (2006), (d) dust deposition from Mahowald et al. (2005), (e) SiO_4/NO_3 ratio calculated using nutrient data from the NOAA/NODC World Ocean Atlas 2005 and (f) eddy kinetic energy (EKE) calculated using geostrophic velocity fields from AVISO. The ovals on the maps represent, schematically, the areas where chlorophyll blooms develop.

and diazotrophic nanoplankton are of the same magnitude (and as variable) as those from *Trichodesmium* (Mahaffey et al., 2005). Diatoms with diazotrophic symbioses are capable of rapid growth and forming localized blooms (Villareal, 1992), and they commonly develop near the NE Pacific chlorophyll blooms (Wilson et al., 2008). These other types of diazotrophs they have not been studied as much as *Trichodesmium*, but their distribution appears fairly ubiquitous. Diatoms containing *Richelia* have been observed in the NE Pacific (Heimbokel, 1986; Mague et al., 1974; Venrick, 1974; Villareal, 1992), the western Pacific off of Japan (Gómez et al., 2005), the Gulf of California (White et al., 2007a), the Indian Ocean (Bergman, 2001) and the western tropical Atlantic (Carpenter et al., 1999; Foster et al., 2007; Villareal, 1994). Unicellular diazotrophs have been observed in the Atlantic Ocean (Falcón et al., 2002; Langlois et al., 2005), the NE Pacific Ocean (Church et al., 2005; Montoya et al., 2004; Zehr et al., 2001, 2007) and the SW Pacific (Campbell et al., 2005; Garcia et al., 2007).

It is very likely that the N fixed from these different types of nitrogen fixation will have different fates. For example, *Trichodesmium* is not readily grazed (O'Neil and Roman, 1992), while unicellular diazotrophs probably are (Mahaffey et al., 2005). Questions

still remain about the fate of N fixed by *Trichodesmium*, the most well understood marine diazotroph, and even less is known about the fate of N fixed by other diazotrophs (Mahaffey et al., 2005).

5.1.1.4. Vertical migrators. Vertically migrating phytoplankton could provide a new source of N into the euphotic zone to fuel chlorophyll blooms. Mats of *Rhizosolenia* diatoms change buoyancy to descend below the nutricline to acquire nitrate, and return to the surface for photosynthesis (Richardson et al., 1996; Villareal et al., 1993, 1996, 1999). In the North Pacific the estimated N flux into the euphotic zone from mats is on the order of 40–50 $\mu\text{mol N m}^{-2} \text{ day}^{-1}$ (Pilskaln et al., 2005; Richardson et al., 1998; Villareal et al., 1996, 1999), which is comparable to the low end of estimated rates of nitrogen fixation, 2–520 $\mu\text{mol N m}^{-2} \text{ day}^{-1}$ for the same area (Dore et al., 2002; Montoya et al., 2004). Most studies of *Rhizosolenia* mats (Alldredge and Silver, 1982; Martínez et al., 1983; Villareal et al., 1993, 1996; Villareal and Carpenter, 1989) have been in the NE Pacific, and the largest densities of mats observed occur in the same region where the chlorophyll blooms develop (Wilson et al., 2008). As little is known about their global distribution it is not possible to

Table 1

Range of values reported for different types of N flux

	N flux ($\mu\text{mol N m}^{-2} \text{ day}^{-1}$)	Reference
Nitrogen fixation		
<i>Trichodesmium</i>	0.61–898 ^a	As summarized in Mahaffey et al. (2005)
<i>Richelia</i> or nanoplankton	2.2–3955 ^a	As summarized in Mahaffey et al. (2005)
<i>Rhizosolenia</i> mats	40–50	Pilskaln et al. (2005), Richardson et al. (1998) and Villareal et al. (1996, 1999)
Vertical NO ₃ flux	2.7–1760	As summarized in Mahaffey et al. (2005)
Estimated flux needed to support the 2000 NE Pacific bloom	360 ^b	This work

^a Range of average areal estimates.^b Estimate based on ΔChl of 0.16 mg/m³ over 6 weeks, a C/Chl ratio of 150, Redfield stoichiometry, a MLD of 25 m and a nitrogen fixation assimilation rate of 50%.

speculate on their association with chlorophyll blooms outside of the NE Pacific. However, *Rhizosolenia* mats have also been observed in the north Atlantic (Carpenter et al., 1977) and in the south Atlantic and Indian Oceans (Wallich, 1858).

In addition to *Rhizosolenia* mats, many different types of large phytoplankton are capable of vertical migration (Moore and Villareal, 1996; Villareal, 1988; Villareal and Lipschultz, 1995; Villareal et al., 2007; Woods and Villareal, 2008). Genera with this capability include the prasinophyte *Halosphaera*, the dinoflagellate *Pyrocystis* and the diatoms *Ethmodiscus* and *Rhizosolenia* (Villareal and Lipschultz, 1995; Woods and Villareal, 2008). While large phytoplankton are rare in the ocean, they are ubiquitous, and probably undersampled due to the inherent difficulties in sampling them (Goldman, 1993). Villareal and Lipschultz (1995) concluded that all of the large phytoplankton ($>100 \mu\text{m}$) in the Sargasso Sea are capable of vertical migration, and that they use this mechanism to acquire nitrate. Diatom blooms can develop rapidly, and also sink rapidly, resulting in large episodic fluxes out of the euphotic zone (Goldman, 1993; Sancetta et al., 1991). Subsequent to fall stratification these fluxes can be significant, the so-called “fall dump”, which represents the diatom production integrated over the period of summer stratification (Kemp et al., 2000). Goldman (1993) speculated on the potential for sizable blooms of diatoms to occur in the open ocean without being noticed. It is possible that with the advent of satellite chlorophyll data we are now observing such blooms.

5.1.1.5. Estimated fluxes. A rough estimate can be made of the N flux necessary to produce the observed increases in chlorophyll associated with the summer blooms. The chlorophyll timeseries of the 2000 bloom in the NE Pacific (Fig. 3a) indicates a ΔChl of 0.16 mg/m³ over 6 weeks. Using a C/Chl ratio of 150 (Taylor et al., 1997; Villareal and Carpenter, 1989), Redfield stoichiometry, and a MLD of 25 m yields a corresponding nitrate biomass change of $180 \mu\text{mol N m}^{-2} \text{ day}^{-1}$. This rate is comparable to the average areal rate of nitrogen fixation of $100–300 \mu\text{mol N m}^{-2} \text{ day}^{-1}$, although rates $>8000 \mu\text{mol N m}^{-2} \text{ day}^{-1}$ have also been reported (Mahaffey et al., 2005). However, all N fixed will not be converted into biomass. In a similar calculation for a bloom in the Atlantic, Coles et al. (2004b) used results from a model of *Trichodesmium* ecosystem dynamics to estimate that only 5% of N fixed is converted into phytoplankton biomass. From a review of data in the literature, Mulholland (2007) estimated the amount of N released from nitrogen fixation from *Trichodesmium*, and found rates that varied from 12% to 97%. Ohlendieck et al. (2000) demonstrated that the amount of N released can change through the evolution of a diazotrophic bloom, with more being released in the early stages. Using a median efficiency rate of 50% would necessitate a nitrogen fixation rate of $360 \mu\text{mol N m}^{-2} \text{ day}^{-1}$ to sustain the observed chlorophyll bloom in the NE Pacific in 2000. Estimates of the physical flux of N range from 3 to 1760 $\mu\text{mol N m}^{-2} \text{ day}^{-1}$ (Mahaffey et al., 2005). These different flux estimates are summarized in Table 1.

5.1.2. Iron and dust

Iron is often cited as the limiting factor in the growth of diazotrophs because of the high Fe requirement of the nitrogenase enzyme (Berman-Frank et al., 2001; Hood et al., 2000; Raven, 1988; Rueter, 1983; Rueter et al., 1992). However, the degree to which Fe limits nitrogen fixation is still an open question (Hood et al., 2000). Some recent work has suggested that the diazotrophic Fe requirement is not as high as previously thought (Kustka et al., 2003), and in regions with higher Fe inputs, such as the Atlantic and the SW Pacific, there is evidence that phosphorus limits nitrogen fixation (Moutin et al., 2005; Sañudo-Wilhelmy et al., 2001; Webb et al., 2007; Wu et al., 2000). The major input of Fe to the surface ocean comes from aeolian dust deposition, and is highest in the North Atlantic (Jickells et al., 2005; Mahowald et al., 2005). Alleviation of iron limitation from dust deposition has been suggested to stimulate nitrogen fixation by *Trichodesmium* off of West Florida (Lenes et al., 2001; Walsh and Steidinger, 2001), although the dust and bloom correlation is not always consistent (Stumpf et al., 2008).

If the chlorophyll blooms are the result of enhanced nitrogen fixation stimulated by an episodic iron input, one would expect a relationship between their occurrence and dust events. Dust deposition has significant seasonality, and the highest deposition rates in the NE Pacific occur in spring (Prospero and Savoie, 1989). In this region dissolved dust has a residence time in the surface water of ~ 6 months, and surface concentrations stay relatively moderate through the summer, decreasing in the early winter when the mixed layer deepens (Boyle et al., 2005). While the observed inter-annual variability in the development and strength of the chlorophyll blooms could be driven by the amount of dust deposition during the preceding spring no correlation has been detected between bloom occurrence and dust deposition in the NE Pacific (Wilson, 2003). Years with the most intense Asian dust storms, 1998 and 2001 (Husar et al., 2000; Yu et al., 2003), were also years without the development of any surface chlorophyll blooms (see Fig. 4), although a subsurface bloom was observed at the HOT site in August 1998 (Letelier et al., 2004). Additionally, dust storms track along 40–45°N (Zhao et al., 2006), quite a bit further north of where the blooms develop.

The bloom locations are overlaid on top of dust deposition rates from Mahowald et al. (2005) in Fig. 11d. On a global scale there is also no clear relationship between bloom occurrence and dust deposition rates. The greatest deposition occurs in the North Atlantic, where only one bloom has been observed in 11 years, whereas the consistent blooms that develop in the SW Pacific and off of Madagascar occur in areas with extremely low dust deposition.

Dust deposition however is not the only source of Fe to the oceans. The fluxes of Fe from hydrothermal venting and from river inputs are both comparable in magnitude to the estimated global atmospheric deposition (Street and Paytan, 2005). However, the distribution patterns of these different sources vary greatly, with atmospheric deposition being the primary source input for open ocean areas, as riverine and hydrothermal sources are mostly

removed from solution and deposited near their sources. Two of the regions where chlorophyll blooms develop occur near active hydrothermal venting: the SW Pacific and the NE Pacific. However, while venting from the Lo'ihi Seamount in the NE Pacific is a possible Fe source for the blooms that develop just north of Hawaii, it seems a less likely source for the blooms further north near 30°N. That latitude is north of the Lo'ihi hydrothermal plume, as mapped by helium (Lupton et al., 2004), which is a much more conservative in seawater than iron. Additionally, as the hydrothermal plume is centered at 1000 m depth, it seems unlikely to contribute significantly to surface Fe concentrations.

Other factors that can impact the availability of Fe in the surface water are regional differences in both dust solubility and residence times of Fe. Boyle et al. (2005) used both these factors to account for surprising differences between Fe distributions in the Atlantic and the Pacific. For instance Fe concentrations in the Atlantic are only a factor of two to three higher than those at the HOT station off Hawaii, despite the dust flux being on the order of 40-fold higher (Boyle et al., 2005).

5.1.3. Phosphate

The process of nitrogen fixation will naturally lead to P limitation, as there is not a supply of phosphate coupled to the N derived from nitrogen fixation, and dissolved inorganic phosphate is generally negligible in the surface oligotrophic ocean. Two additional sources of P that could be available for diazotrophs are dissolved organic phosphate (DOP) and inorganic phosphate from depth, accessed either through biological depth mining or from seasonal mixing. Since the DOP pool is considerably larger than the inorganic pool, access to this pool could significantly alleviate P limitation (Abell et al., 2000; Ammerman et al., 2003; Björkman et al., 2000; Yoshimura et al., 2007). Geochemical field studies have demonstrated that the DOP pool is more biologically labile than the dissolved organic nitrate (DON) pool (Abell et al., 2000). It has been suggested that this differential recycling rate provides the excess P needed to support nitrogen fixation rates observed in the Atlantic and in the subtropical North Pacific (Abell et al., 2000; Wu et al., 2000). *Trichodesmium* and some unicellular diazotrophs (*Crocospheara watsonii*) have specific physiological strategies that increase the scavenging of phosphorus from DOP (Dyrhman et al., 2006; Dyrhman and Haley, 2006; Mulholland et al., 2002; Sohm and Capone, 2006; Stihl et al., 2001).

Karl et al. (1992) proposed that *Trichodesmium* overcomes P limitation by migrating vertically below the nutricline to acquire phosphate. There is some evidence of this, lower internal N:P ratios have been measured in positively buoyant *Trichodesmium*, relative to negatively buoyant ones, in both the North Pacific and the Gulf of Mexico (Letelier and Karl, 1998; Villareal and Carpenter, 2003). However, large abundances of non-migratory *Trichodesmium* have also been observed (Letelier and Karl, 1998), as have ascending and descending *Trichodesmium* colonies without differing N:P ratios, suggesting that vertical mining of P is not the universal solution for *Trichodesmium* (Villareal and Carpenter, 2003). Additionally, in many oligotrophic regions the phosphocline is deeper than physiological depth limit for *Trichodesmium*, which should prohibit P mining from being a viable mechanism (Villareal and Carpenter, 2003). Vertical migration has shown to be the mechanism for the N supply for *Rhizosolenia* mats (Richardson et al., 1996; Villareal et al., 1993, 1996, 1999), and it is possible that the mats similarly acquire other nutrients, such as P and Fe, at depth (Villareal and Lipschultz, 1995; Villareal et al., 1996, 1999). However, this question has only been examined for Fe, where results from a field study showed no indication of Fe uptake at depth for *Rhizosolenia* mats (McKay et al., 2000).

There are also physical mechanisms that could deliver phosphate to the surface layer from depth. Moutin et al. (2005) argued that the development of the summer blooms of *Trichodesmium* in

the SW Pacific is tied to the seasonal availability of phosphate from winter mixing. Similarly, Dore et al. (2008) hypothesized that the spatial distribution, timing and magnitude of summer blooms in the NE Pacific are determined largely by the physical and biological processes controlling new phosphorus delivery into the euphotic zone during the summer and the preceding winter. At the ALOHA station upwelled water has a low N:P ratio, so this source is more important for its supply of P rather than N (Dore et al., 2008).

There is growing evidence showing the importance of phosphate availability in regulating nitrogen fixation in the ocean. Phosphate limitation of nitrogen fixation seems widespread in the Atlantic (Sañudo-Wilhelmy et al., 2001; Webb et al., 2007; Wu et al., 2000), although there is also evidence that it is co-limited by both Fe and P, with dust deposition apparently acting as a source of not just Fe, but also of P (Mills et al., 2004). And, as discussed above, the supply of phosphate has been attributed to control diazotrophic processes in both the SW Pacific (Moutin et al., 2005) and the NE Pacific (Dore et al., 2008). However, there are important regional differences that still have not been well mapped out. For instance, the limiting control on nitrogen fixation appears to change across the southern Pacific, with the dominant factor being phosphate in the west, and temperature and/or iron in the central and eastern South Pacific (Moutin et al., 2008).

5.1.4. Silicate

In situ observations in the NE Pacific suggest that the summer chlorophyll blooms are composed of diatoms, either diatoms containing diazotrophic endosymbionts or vertically migrating diatom mats (Wilson et al., 2008), which raises the question as to whether silicate is the limiting nutrient in this region. The ratio of dissolved SiO_4/NO_3 has been used as diagnostic for whether silicate or nitrate is limiting to diatoms (Conley and Malone, 1992; Dugdale et al., 1995; Smetacek, 1999). Values of dissolved $\text{SiO}_4/\text{NO}_3 > 1$, the Redfield ratio for these two nutrients (Brzezinski, 1985; Redfield et al., 1963), result in diatom dominance within the phytoplankton population (Sommer, 1994, 1998). The area where the NE Pacific chlorophyll blooms develop is characterized by $\text{SiO}_4/\text{NO}_3 > 10$ (Fig. 11e), which is considerably higher than the Redfield ratio. The SiO_4/NO_3 ratio of diatoms can vary under different nutrient limitations and different physiological states (Brzezinski, 1985; Harrison et al., 1977). However, even the highest SiO_4/NO_3 ratios reported by Brzezinski (1985), which were >3 , are considerably smaller than the ratios observed in parts of the Pacific (Fig. 11e), indicating that silicate is not a limiting nutrient in the NE Pacific, and that this region should favor the dominance of diatoms within the phytoplankton population, providing other nutrients are not limiting. This is consistent with field studies showing that in the eastern Pacific the silicate supply in the euphotic zone is sufficient for migrating *Rhizosolenia* mats, and they do not have to rely on silicate uptake at depth (Shipe et al., 1999). The Madagascar and SW Pacific bloom areas also occur in regions with elevated SiO_4/NO_3 ratios. However, there are also vast areas of the ocean with elevated SiO_4/NO_3 ratios, but no chlorophyll blooms.

5.2. Reduced mortality

The alleviation of a nutrient limitation, as discussed in the previous sections, assumes a bottom-up control mechanism for bloom formation, but a top-down mechanism is also possible. The main source of phytoplankton mortality in the oceans is grazing by microzooplankton (Calbet and Landry, 2004) and failure of the microzooplankton population to contain phytoplankton production can generate a bloom (Irigoin et al., 2005). Under this scenario the question becomes what would cause a sudden decrease in grazing pressure? High light and poor nutrient content in the food source have been shown to constrain grazing growth (Ander-

sen et al., 2007; Urabe and Sterner, 1996), and both factors are likely under summer conditions in the oligotrophic gyres. Theoretical studies of the maintenance of phytoplankton blooms fuelled from point sources of nutrient fertilization have shown mixing is critical, as it keeps the phytoplankton and zooplankton populations temporally decoupled, allowing expansion of the bloom (Abraham et al., 2000; Martin, 2000; Neufeld et al., 2002). Without in situ biological data it is not possible to elucidate the specific dynamics that result in the observed summer chlorophyll blooms.

5.3. Chlorophyll/C changes

It is possible that the chlorophyll blooms do not represent an increase in phytoplankton, but rather an increase in the cellular content of chlorophyll. However, this scenario seems unlikely, as the primary variation in chlorophyll/carbon ratios in oligotrophic waters occurs in wintertime, with higher chlorophyll arising from an adaptation to lower light levels (Taylor et al., 1997). Different taxon of phytoplankton can have different chlorophyll cellular content, so potentially the chlorophyll blooms could correspond to a change in the dominant phytoplankton, rather than an increase in phytoplankton biomass, relative to the non-bloom water. For instance, diatoms, which potentially compose the bloom, have a much higher chlorophyll/C ratio than dinoflagellates (Geider, 1987). However, environmental effects, such as light and nutrient levels, appear to impact the chlorophyll/C ratio more than inter-genera differences (Goldman, 1990; Veldhuis et al., 2005).

5.4. Physical factors

There are a number of physical factors that can lead to surface chlorophyll blooms by different mechanisms. In much of the nutrient-limited ocean, both upwelling and entrainment of water below the nutricline into the mixed layer will stimulate a phytoplankton bloom, and an increase in surface chlorophyll, providing sufficient light levels are present (McCreary et al., 1996). A growth-induced bloom can also result from changes in water column stratification or turbulence that provide a more suitable habitat for the bloom species. For example, weak winds and low turbulent mixing can favor *Trichodesmium* growth (Carpenter and Price, 1976). Surface blooms can be produced by the physical accumulation of chlorophyll, through either convergence (Dandonneau et al., 2003, 2008; Stumpf et al., 2008) or upwelling of the subsurface chlorophyll maximum (Charria et al., 2003), in which case phytoplankton growth is not involved. An important distinction is that the different mechanisms are generally associated with different biological processes: for example upwelling of nutrient-rich water will not favor diazotrophs, as they will be outcompeted by non-diazotrophic organisms, whereas physical changes resulting in convergent, stratified conditions will favor diazotrophs. As with any generality, however, there will be exceptions. For instance, it has been proposed that upwelling of low N:P water in the Pacific fuels P-deficient diazotrophs (Dore et al., 2008). Biomass accumulation in well-lit, stratified conditions could be due either to diazotrophic growth, or to the passive accumulation of phytoplankton. The potential role of eddies, fronts, mixing and convergence in the formation of the chlorophyll blooms is discussed within the context of these different scenarios in the following sections.

5.4.1. Eddies

Upwelling at the center of cyclonic (cold-core) eddies typically results in higher chlorophyll levels within the eddy core (Falkowski et al., 1991; McGillicuddy and Robinson, 1997; Seki et al., 2001). In contrast, anti-cyclonic (warm-core) eddies are characterized by downwelling in the eddy core, but upwelling around the eddy periphery, which can result in a ring of higher chlorophyll encircling

the eddy (Olson, 1986; Tranter et al., 1983; Yamamoto and Nishizawa, 1986). Some anti-cyclonic eddies, mode-water eddies, have a shoaling of the seasonal thermocline, but a depression of the main thermocline, resulting in upwelling into the euphotic zone (Brundage and Dugan, 1986; McGillicuddy et al., 1999), which can lead to long-lasting blooms in their cores (McGillicuddy et al., 2007). So far mode-water eddies have only been identified in the North Atlantic; it is not known how prevalent they are elsewhere.

The chlorophyll blooms often develop within eddy fields (Fig. 12), although they are not the typical blooms observed in the core of cyclonic eddies (Falkowski et al., 1991; McGillicuddy and Robinson, 1997; Seki et al., 2001), which are coherent circular structures, and map closely with cold SST and negative sea-surface height (SSH) anomalies. By contrast, the blooms are filamentary or amorphous in structure, do not have associated SSH or SST anomalies, and, except for those off Madagascar and the 2000 bloom in the NE Pacific, they remain stationary and do not propagate. In none of the areas is the eddy field, as depicted by the SSH data, reflected in the SST data (Fig. 12). Almost all of the blooms develop between eddies, wrapping around the periphery of anti-cyclonic features, which are characterized by elevated SSH. The meanders of elevated chlorophyll follow the contours of the SSH field, centered on the zero SSH anomaly isoline, rather than at the maximum anomalies in the eddy centers (Fig. 12). This dynamic is better developed in some regions than others, and is the least well-developed in the North Atlantic. The one bloom that occurred there developed in a region with very little gradient in the SSH field, and while there is some indication that the chlorophyll follows the SSH isoline, it is not as pronounced as in the other regions. The one area where the chlorophyll blooms are clearly not associated with eddy dynamics is the 5–10°S region of the Indian Ocean, where blooms are located within the center of a large expanse of negative SSH and colder SST (Fig. 12e and f), consistent with the blooms being associated with upwelling at the thermocline ridge, as was previously discussed.

Different mechanisms have been put forth to explain elevated biomass around anti-cyclonic (warm-core) eddies: upwelling at the eddy periphery (Yentsch and Phinney, 1985), convergence at the eddy periphery (Olson and Backus, 1985) and entrainment (Evans et al., 1985; Yamamoto and Nishizawa, 1986). Since most of the studies of warm-core rings have involved eddies spun off a current (the Gulf Stream or the Kuroshio) with a strong chlorophyll gradient (Joyce, 1985; Olson, 1991; Wiebe and McDougall, 1986), separating vertical from horizontal (entrainment) effects has been difficult. However, none of the chlorophyll blooms described here develop in areas with nearby high chlorophyll that would be entrained around the eddies, leaving only upwelling or convergence as possible mechanisms.

If upwelling of nutrient rich water fuelled the enhanced chlorophyll, a coincident signature of colder SST would be expected, however, this is not observed (Fig. 12), nor is it seen in SST data prior to bloom development (see Fig. 3). The lack of SST signals suggests that convergence within the eddy field is playing a role in the formation of the chlorophyll blooms. Phytoplankton capable of regulating their buoyancy will be concentrated along the convergent ring of an anti-cyclonic eddy, whereas passive tracers will not be (Olson and Backus (1985). Convergence as a mechanism for bloom formation is discussed in more detail in Section 5.4.4.

The eddy-bloom association is the most well-developed in the Madagascar region, and was also noted by Longhurst (2001). He described the evolution of the chlorophyll blooms, which initially appear along the periphery of anti-cyclonic features and mature into anomalies that completely overlie the feature they initially encircled. Given their association with localized upwelling that would bring nitrate to the surface, Longhurst (2001) did not think the blooms are diazotrophic, but he did not mention the absence of SST anomalies. Uz (2007) argued that this absence of SST anom-

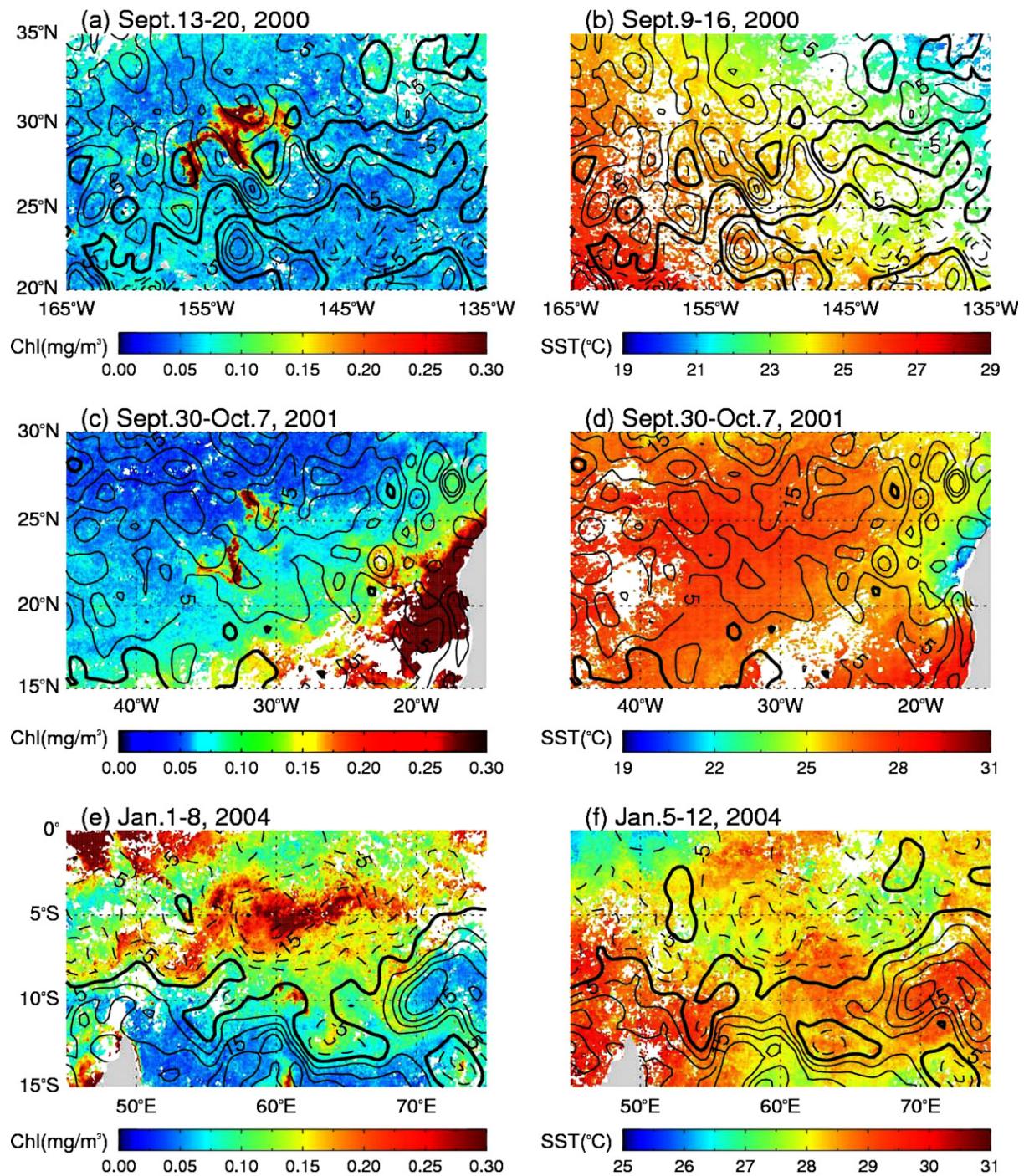


Fig. 12. Contours of weekly SSHA overlaid over weekly composite images of chlorophyll (left) and SST (right) from bloom periods in the (a and b) NE Pacific, (c and d) SW Pacific, (e and f) NE Atlantic, (g and h) SW Atlantic, (i and j) Southern Indian and (k and l) off Madagascar. Positive (negative) contours of SSHA are solid (dashed), and the zero contour line is thicker.

lies, together with the lack of agreement between interannual wind forcing and bloom development, suggested that the blooms develop in areas where strong stratification confines diazotrophs to a warm, shallow, well-lit layer.

An interesting aspect of the relationship between the chlorophyll blooms and the local eddy field is that the blooms generally do not develop in areas with particularly high eddy kinetic energy (EKE), although the Madagascar blooms do develop in an area with a local EKE maximum (Fig. 11f). In contrast, the region where blooms consistently appear in the NE Pacific has extremely low EKE (Fig. 11f). On a local scale the blooms also do not develop along

the strongest SSH gradients (Fig. 12). This apparent paradox suggests that other factors operate in conjunction with the eddy field to produce the observed blooms.

5.4.2. Fronts

A number of the bloom areas are also coincident with front locations suggesting that eddy–front interactions play a role in the development of the blooms. Oceanic fronts often are associated with enhanced biological activity, at many trophic levels (Franks, 1992a; Liu and Woods, 2004; Olson, 2002; Stumpf et al., 2008; Yoder et al., 1994). The interaction between eddies and fronts can cre-

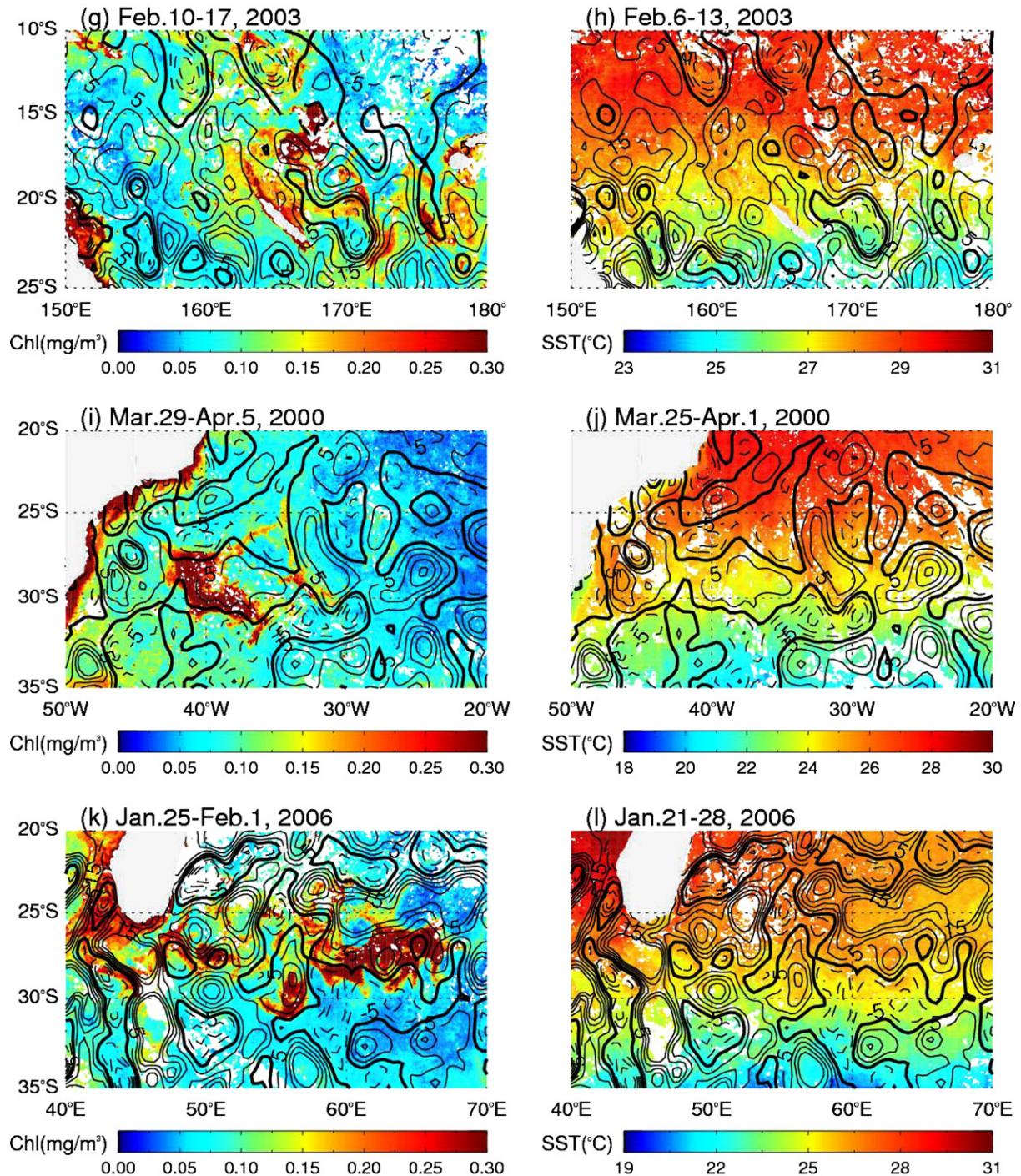


Fig. 12 (continued)

ate convergent flow and the accumulation of phytoplankton along eddy edges (Lima et al., 2002; Yoder et al., 1994). Phytoplankton buoyancy plays a role in this accumulation. Surface diatom patches form along the edges of tropical instability waves, as diatoms float upwards, out of the subducting watermass (Yoder et al., 1994). Giant buoyancy-regulating diatoms such as *Rhizosolenia*, *Thalassiothrix* and *Ethmodiscus* (Villareal and Lipschultz, 1995; Woods and Villareal, 2008) concentrate along oceanic frontal zones (Kemp et al., 2006). It is interesting to note that the surface structure of blooms produced from modeling eddy-front interactions (Lapeyre and Klein, 2006; Lima et al., 2002) is remarkably similar to that of the satellite chlorophyll blooms, particularly those in the NE Pacific.

In the NE Pacific, the blooms develop at the latitude of the summer position of the subtropical front (Roden, 1975, 1980), and in the SW Pacific they develop just south of the South Equatorial Current which is associated with a frontal zone between 13°S and 16°S (Roden, 1998). The blooms off Madagascar develop along the 28°S front (Donohue and Toole, 2003), and just south of the SICC, which could explain the consistent eastward migration of the Madagascar blooms. The blooms in the Atlantic, however, do not appear to be associated with eddy-front interactions. The Atlantic blooms also occur much less frequently than those in the Pacific and Madagascar regions. The subtropical front is not very well-developed in the NE Atlantic, and it occurs ~35°N (Ullman et al.,

2007), considerably further north than the one bloom that developed near 25°N. Similarly in the South Atlantic, the subtropical front occurs between 35°S and 40°S (Burls and Reason, 2006), whereas the blooms develop between 25°S and 30°S. It is also possible that there are subsurface fronts, or fronts driven by salinity rather than temperature gradients, in which case satellite data, the primary tool to identify fronts globally, will not detect them. For example in the NE Pacific, the surface signature of the STF in summer loses its temperature gradient and is manifest only by salinity (Roden, 1974, 1975).

5.4.3. Mixing

During calm conditions *Trichodesmium* is well-known to form large surface aggregations, visible to the naked eye (Carpenter, 1983b; Walsby, 1992). Colonies of *Trichodesmium* are able to regulate their buoyancy, which allows them to return to the surface more quickly after mixing events (Walsby, 1978, 1992). While it has been suggested that surface slicks of *Trichodesmium* are just accumulations, and not actually the result of active growth (Walsby, 1978), there is more evidence that a stable water column, low in nutrients with high light levels, provides conditions conducive for *Trichodesmium* populations to increase (Capone et al., 1997; Hood et al., 2004; Tyrrell et al., 2003). However, there is also evidence that low winds are not always a necessary condition for *Trichodesmium*. For example, Davis and McGillicuddy (2006) observed no discernable change in the abundance of *Trichodesmium* colonies across the wake of a hurricane.

An alternate possibility is that some mixing can be beneficial to bloom formation. For example, recent theoretical studies have demonstrated the importance of horizontal stirring to the development and maintenance of phytoplankton blooms fuelled from point sources of nutrient fertilization (Abraham et al., 2000; Martin, 2000; Neufeld et al., 2002). Mixing is critical to long-term bloom maintenance as it keeps the phytoplankton and zooplankton populations temporally decoupled, allowing expansion of the bloom (Neufeld et al., 2002). A consistent characteristic of the NE Pacific blooms is their development near 30°N, which is close to the critical latitude of 29°, where the local inertial frequency coincides with the diurnal frequency. Enhanced mixing occurs at the critical latitude, due to energy loss and enhanced dissipation rates resulting from the inhibition of internal tides of diurnal frequencies to propagate poleward of the critical latitude (MacKinnon and Winters, 2004, 2005). The NE Pacific bloom region is one of the few regions in the ocean where diurnal, rather than semi-diurnal, tides dominate (Le Provost, 2001). It is possible that at this location enhanced subsurface mixing caused by the confluence of the critical latitude and a maximum in the diurnal amplitude stimulates a chlorophyll bloom by removing “top-down” control, as suggested by Neufeld et al. (2002).

Despite all the work done on *Trichodesmium*, it is still not clear exactly what environmental conditions limit or enhance its growth, and even less is known about other diazotrophs. Without in situ data providing information on the organisms composing the chlorophyll blooms, and the subsurface physical conditions, it

is impossible to do more than speculate on the origins of these blooms. However, sometimes even with in situ data the physical mechanisms are not clear. For example, no discernable differences were observed in the physical conditions during summer blooms of *Richelia*-containing diatoms in the NE Pacific (Venrick, 1974).

5.4.4. Convergence

The chlorophyll blooms appear to develop in the convergent zone at the periphery of anti-cyclonic features. Convergent flow, whether associated with a front or with an eddy, will concentrate small organisms capable of controlling their vertical movement, but not passive tracers (Olson and Backus, 1985). Hence, *Trichodesmium*, and phytoplankton that can control their buoyancy, would be concentrated in convergence zones, but not unicellular diazotrophs. This concentration could result in the observed chlorophyll blooms by either the physical accumulation increasing the surface chlorophyll value, or as an “echo” bloom fuelled by the new N resulting from the concentration of nitrogen fixers. The accumulation and retention zones associated with fronts can have slightly different effects on biomass, for example there are two different types of accumulation: compression zones, which move with the background flow, and convergence zones, which remain stationary (Franks, 1992b). This dynamic could explain some of the variability seen in the propagation of the chlorophyll blooms. Most of them remain stationary, consistent with a convergent accumulation zone, whereas off Madagascar they propagate eastward, consistent with a compression accumulation zone.

It is also possible that convergence acts on a larger scale. Wilson et al. (2008) hypothesized that on a basin-scale the location of the NE Pacific blooms is driven by the combination of both weak and convergent surface flow, creating a favorable environment for the accumulation of positively buoyant particles. The NE Pacific blooms occur in the same part of the Pacific gyre where large amounts of plastic and debris are known to accumulate (Kubota, 1994; Moore et al., 2001; Pichel et al., 2007; Shaw and Mapes, 1979; Venrick et al., 1973; Wong et al., 1977), the so-called “garbage patch” (Moore, 2003). Dandonneau et al. (2003) suggested that the high chlorophyll observed by satellite along convergence zones created by Rossby waves are not actually chlorophyll, but rather floating particles that modify the transfer of light and are erroneously detected by the satellite as higher chlorophyll. It is unlikely however that this mechanism is the explanation for the NE Pacific chlorophyll blooms, since it does not account for the seasonality of the bloom development, nor its absence in some years.

6. Conclusions

Summer chlorophyll blooms appear in all of the oligotrophic basins, although with varying intensity and frequencies, and there does not appear to be one consistent explanation for their development (Table 2). The blooms occur almost every year in the NE and SW Pacific Ocean and off the southern tip of Madagascar, and less frequently in the Atlantic Ocean. The blooms that develop along 5–

Table 2
Summary of bloom regions and possible forcing mechanisms

Region	Possible explanation
NE Pacific	Dynamics associated with the eddy field, high Si/N ratios should favor the dominance of diatoms with nitrogen fixing endosymbionts, providing other nutrients are not limiting ??
NW Atlantic	Dynamics associated with the eddy field
SW Atlantic	Alleviation of Fe limitation via hydrothermal inputs stimulate enhanced nitrogen fixation, in conjunction with the island mass effect
SW Pacific	Seasonal upwelling along thermocline ridge (not associated with diazotrophy)
SW Indian	Dynamics associated with the eddy field, in conjunction with the island mass effect
SW Indian (Madagascar)	

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 development within a conventional upwelling scenario. The blooms in the NE Pacific, and in the NE and SW Atlantic, all occur away from land masses and sources of higher chlorophyll water. The blooms in the two other regions, the SW Pacific, and southeast of Madagascar, both appear to be generated in part by "island mass effects".

The environment and timing of the blooms, developing in oligotrophic waters in late summer, are conducive to nitrogen fixers and organisms requiring a relatively stable water column. *Trichodesmium*, the most common oceanic nitrogen fixer, has been reported in all of the areas where blooms are observed, and other types of diazotrophic organisms have also been observed in many of the bloom locations. Vertically migrating phytoplankton, which are able to acquire nutrients below the nutricline, could also compose the blooms. Only two areas, the NE and SW Pacific, have been sampled synoptically with an ongoing satellite chlorophyll bloom. *Trichodesmium* and unicellular diazotrophs were observed in the SW Pacific (Campbell et al., 2005; Garcia et al., 2007), and diatoms with nitrogen fixing endosymbionts and vertically migrating diatom mats were observed in the NE Pacific (Wilson et al., 2008). All but one of the bloom areas occur in regions with net nitrogen fixation as indicated by N* values. The one exception is the 5–10°S region in the Indian which is not thought to be associated with diazotrophy. However, there is little to explain why blooms do not develop in other areas where net nitrogen fixation is indicated. There is little correspondence between the specific locations of the chlorophyll blooms and global estimates of nitrogen fixation or other factors that might impact nitrogen fixation.

Except for along 5–10°S in the Indian Ocean, almost all of the blooms develop between eddies, wrapping around the periphery of anti-cyclonic features. However, the blooms regions generally are not characterized by particularly high EKE, suggesting that other factors operate in conjunction with the eddy field to produce the observed blooms. It is possible that the convergence brought on by eddy-front interactions, or local mixing generated at the critical latitude (Mackinnon and Winters, 2004, 2005) also play a role in stimulating the blooms.

It is becoming increasingly rare to discover a new natural phenomenon on our planet. The existence of these chlorophyll blooms challenges the assumption that the open sea is characterized well enough to permit extrapolation from heavily studied, presumably typical regions, to less accessible areas of the oligotrophic gyres. A better understanding of the biological and physical mechanisms behind these enigmatic blooms will require both in situ sampling, and modeling studies that can successfully reproduce the observations.

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