Summer blooms of diatom-diazotroph assemblages and surface chlorophyll in the North Pacific gyre: A disconnect

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[1] The discovery of large summer chlorophyll blooms in oligotrophic regions of the ocean has led to questions about the relationship between these blooms and the frequently cooccurring outburst of nitrogen-fixing phytoplankton. We compared diatom-diazotroph assemblage (DDA) abundance to size-fractionated chlorophyll (chl) and satellite ocean color chlorophyll estimates to evaluate how DDAs affected ocean color estimates in the eastern and central North Pacific gyre at 28–30°N. DDA blooms were dominated by either *Hemiaulus hauckii* (in the central Pacific in 2003 and the eastern Pacific in 2002) or by *Rhizosolenia* (eastern Pacific in 2002), both with nitrogen-fixing *Richelia* symbionts. The 2002 DDA bloom was measured a week prior to the development of a satellite-observed chlorophyll bloom at the same location. In contrast, the 2003 *Hemiaulus* bloom was not within a clearly defined satellite feature. Although DDA abundance increased 10^4–10^5-fold relative to the background and they dominated the net plankton (≥5 μm or >10 μm chl size) fraction, the in situ chl (maximum ≤0.11 mg m^{-3}) never reached the 0.15 mg m^{-3} threshold used to define satellite-observed chlorophyll blooms in oligotrophic waters. The DDA blooms were not evident in the in situ fluorometer data; however, the blooms occurred within high beam attenuation features observed in the transmissometer data. *Trichodesmium* was not a component of either diatom bloom although elevated levels of *Trichodesmium* were observed at two stations where DDAs were not abundant. While DDA blooms and satellite ocean chlorophyll blooms are sometimes coincident, our data do not support that DDAs are the sole source of the satellite-observed chlorophyll in summertime blooms. DDA blooms are likely underreported in the North Pacific, particularly in the waters west of Hawaii, due to their frequent lack of distinctive ocean color, fluorescence, and chlorophyll signatures. The source of the ocean color signature in the blooms remains elusive, but scattered literature observations suggest that cooccurring members of the near-surface flora such as the small pennate diatom *Mastogloia* may play an important role.

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1. Introduction

[2] Satellite oceanography has transformed oceanographic research by providing basin scale, synoptic data that reveal detail and complexity only suspected from shipboard surveys. The ability to quantify phytoplankton biomass and productivity has provided remarkable insights into the spatial and temporal variability of the oceans [*Behrenfeld et al.*, 2005]. In most cases, productivity patterns are related to known physical features such as upwelling or river plumes; however, an interesting exception has been the discovery of summer chlorophyll blooms in open ocean regions. In this literature, "chlorophyll bloom" has been defined as chlorophyll >0.15 mg m^{-3} as measured by satellite ocean color data for oligotrophic waters [*Wilson*, 2003; *Wilson et al.*, 2008], and we will use this convention hereafter. While chlorophyll (chl) of 0.15 mg m^{-3} is quite low, in this region the ambient background chl level is ~0.08 mg m^{-3} or less; hence the bloom threshold represents nearly a doubling of chl [*Wilson*, 2003; *Wilson et al.*, 2008]. These chl blooms have been observed in all oceans, but those in the eastern North Pacific subtropical gyre (NPSG) are unique both in their interannual consistency and in their isolated location far from any landmass effects

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[*Wilson and Qiu*, 2008]. Since the North Pacific summer chl blooms often occur in the same area as blooms of diatom-diazotroph assemblages (DDAs) [*Dore et al.*, 2008; *Wilson and Qiu*, 2008], it has been assumed that DDA blooms are responsible for the satellite chlorophyll signature, and by inference, that DDA blooms will be visible in satellite ocean color data [*Wilson*, 2003; *Wilson et al.*, 2008]. However, this relationship has not been directly tested with concurrent measures of pigment and cell abundance.

[3] DDAs are symbioses of the diatoms *Hemiaulus* or *Rhizosolenia* with the endosymbiont *Richelia intracellularis*. There is also a much less abundant association between the diatoms *Chaetoceros*, *Bacteriastium*, and *Climacodium*, and various intra or extracellular symbionts [*Guillard and Kilham*, 1977; *Carpenter and Janson*, 2000; *Foster and Zehr*, 2006; *Gómez et al.*, 2005]. The *Richelia* symbiont of *Hemiaulus* and *Rhizosolenia* is diazotrophic, and at least in the case of *Rhizosolenia* can fully support the host diatom's N needs [*Villareal*, 1990, 1991]. Nitrogen fixation by these DDAs can be significant in both oceanic [*Kitajima et al.*, 2009] and nearshore systems [*Subramaniam et al.*, 2008]. DDAs and *Trichodesmium* [*Dore et al.*, 2008; *White et al.*, 2007b] are part of a upper euphotic zone flora distinctly different than the deeper community found near the pycnocline [*Venrick*, 1988, 1999]. The existence of DDA blooms in the North Pacific west of Hawaii remains largely unknown save for the report by *Brzezinski et al.* [1998].

[4] While the same species are generally seen at both the Hawaii Ocean Time series (HOT) station near 23°N and along 30°N where the satellite chlorophyll blooms develop, there are differences in floristic composition. For example, blooms of *Trichodesmium* are frequent at HOT but the species is only rarely observed at 30°N [*Dore et al.*, 2008; *Venrick*, 1997]. Nitrogen fixation rates measured at HOT are lower than rates measured along 30°N [*Mahaffey et al.*, 2005]. Satellite-observed chlorophyll blooms are much more frequent at 30°N than at HOT [*Dore et al.*, 2008; *Wilson and Qiu*, 2008].

[5] As a result of the HOT program [*Karl and Lukas*, 1996], there is a great deal of information available about the biological dynamics just north of Hawaii relevant to DDAs. Summer blooms of nitrogen fixers (DDAs, *Trichodesmium*, and coccoid cyanobacteria) commonly occur at HOT [*Dore et al.*, 2008; *White et al.*, 2007b]. These blooms generally develop in the lower euphotic zone above the nutricline [*Dore et al.*, 2008], and often do not have an associated satellite chl signal due to their depth [*Dore et al.*, 2008; *Wilson and Qiu*, 2008]. The blooms at HOT are sometimes associated with eddies [*Fong et al.*, 2008] and they frequently (but not always) occur with a shoaling mixed layer, and iron and phosphorus (or both) are potential limiting elements [*Dore et al.*, 2008; *White et al.*, 2007b]. DDAs may be responsive to P inputs from a variety of sources at different scales such as winter mixing [*Dore et al.*, 2008], eddy dynamics [*Fong et al.*, 2008], hypoxia-driven P fluxes [*White et al.*, 2007a], or riverine processes [*Subramaniam et al.*, 2008]. The increases in phycoerythrin, which are presumably DDA blooms, at HOT are not clearly associated with changes in chlorophyll [*White et al.*, 2007b].

[6] *Scharek et al.* [1999b] reported export by *Hemiaulus* spp. at HOT; and *Hemiaulus*-dominated sediments in the Mediterranean [*Kemp et al.*, 1999] and in the Arctic [*Davies et al.*, 2009] suggest a broader geological importance of this group. Although symbionts cannot be detected in sediments, nitrogen isotope work conducted on sapropels in the Mediterranean suggests that nitrogen fixation was common during late Pleistocene summer diatom bloom events [*Sachs and Repeta*, 1999]. Summer diatom blooms can result in significant export production, the so-called "fall dump" [*Kemp et al.*, 2000]. *Dore et al.* [2008] noted that export flux from the surface, such as occurs at HOT, rather than from the nutricline, deviates considerably from the traditional concept that most oligotrophic ocean export production (high *f* ratio) occurs deep in the water column near the nutricline [*Goldman*, 1988; *Platt et al.*, 1989]. This paradigm was developed from observations in the Atlantic Ocean near Bermuda, where considerably different seasonality exists and eddy characteristics may dominate export [*McGillicuddy et al.*, 2007].

[7] It is difficult to assess how widespread DDA blooms are using standard shipboard techniques. Detection of the endosymbiont requires using either transmitted light microscopy or epifluorescence, neither of which are standard measurements. A global compilation of DDA observations was summarized by *Monteiro et al.* [2010], in conjunction with a model simulation of the global distribution of DDAs. Their model predicted the largest DDA abundances in the Indian Ocean and the subtropical Atlantic Ocean. They also predicted DDAs in a band between 20°–40°N in the Pacific, which our study area falls within, but with smaller biomass values relative to the Indian and Atlantic Oceans [*Monteiro et al.*, 2010]. Curiously, their DDA distribution was not constant across the Pacific, and had a conspicuous absence of DDAs northeast of Hawaii. This is the region where most of the Pacific DDA observations have occurred, including the ones at or near the HOT station [*Fong et al.*, 2008; *Heinbokel*, 1986; *White et al.*, 2007b], the CLIMAX station (28°N, 155°W) [*Venrick*, 1974], and observations further to the east [*Mague et al.*, 1974; *Wilson et al.*, 2008].

[8] In this paper, we present the direct microscopic enumeration of net plankton flora and size-fractionated chlorophyll from two cruises along 28–30°N in the Pacific, one in 2002 and one in 2003. The size fractionation is done to isolate the DDA component, given that both *Hemiaulus* and *Rhizosolenia* are fairly large phytoplankton (the cell dimension of *Hemiaulus* is several tens of μm, and *Rhizosolenia-Richelia* in this region of the Pacific can range from 10 to 15 μm in diameter and exceed 90–100 μm in their pervalvar axis). We operationally define a DDA bloom to refer to individual or combined abundances >100,000 cell m^{-3}, as determined by in situ sampling (bottle samples or net tows). The relationships between DDA abundance, size-fractionated chlorophyll and satellite measured chlorophyll fields are examined.

2. Materials and Methods

2.1. Cruise Data

[9] Data were collected during two cruises (R/V *Melville*, 20 June–16 July 2002 and R/V *New Horizon*, 22 August to 14 September 2003) that were part of the *Rhizosolenia* Mats in the Pacific (RoMP) project. The 2002 cruise sampled the eastern North Pacific between Hawaii and San Diego along roughly 30°N, and the 2003 cruise sampled the central North Pacific westbound along 28°N from Hawaii to past

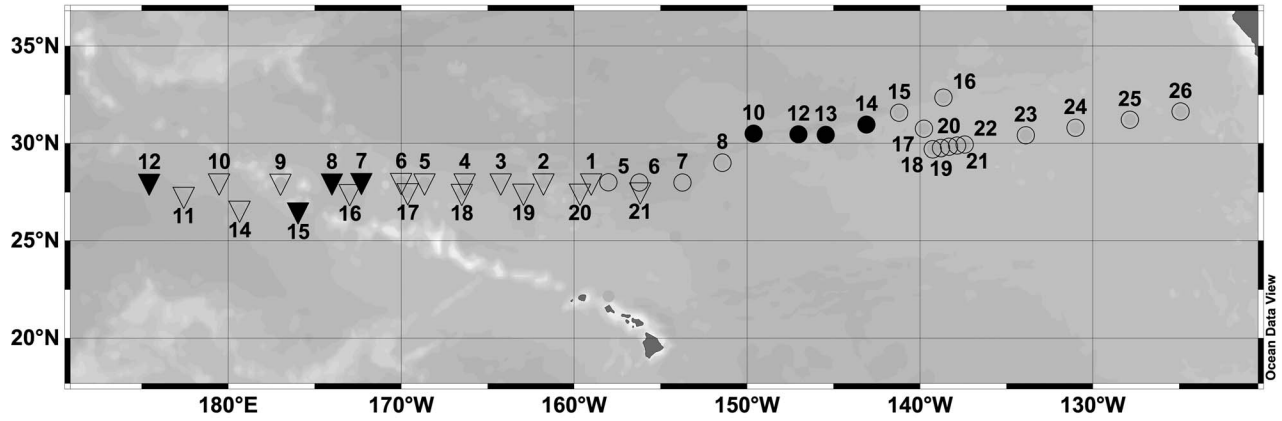

Figure 1. Cruise stations for 2002 (R/V *Melville*, circles) and 2003 (R/V *New Horizon*, inverted triangles). Note the area of overlap between the cruises at approximately 159°W. Bloom stations (>100,000 DDA cells m^{-3}) are shown as solid symbols.

the dateline, and returned to Hawaii on an eastbound transect slightly south of 28°N (Figure 1). Profiles and discrete water samples were collected with a rosette equipped with a Sea-Bird SBE 9 CTD and a Seapoint fluorometer. In 2002, water samples were collected at the surface, 20, 40, 60, 80, 100, 115, 125, 150, and 200 m as well as at the deep fluorescence maximum. In 2003, samples were collected at the surface and at 10, 25, 50, 60, 80, 90, 100, 110, 125 and 150 m. Percent transmittance (Tr) data were collected with a Wet Labs C-Star Seatech transmissometer (25 cm path length, 6 km depth range, calibrated for 100% transmittance in pure water) interfaced with the Sea-Bird CTD. Differences in optical window cleanliness between casts were removed by assuming that the transmittance was equal at 150 m for all stations. The normalized particle abundance (PA_{Ni}) for each depth at every station was determined by (1) determining the range (R_S) between the highest (T_{SH}) and lowest (T_{SL}) transmittance values from the surface to 150 m depth, (2) subtracting the lowest value found in that range from each data point (T_i) for that station, (3) dividing the resultant values by the range found in step 1, and (4) subtracting each of those values from one

$$PA_{Ni} = 1 - \frac{[T_i - T_{SL}]}{[T_{SH} - T_{SL}]}. \quad (1)$$

Each station had PA_{Ni} values that ranged from zero (highest transmittance, fewer particles) to one (lowest transmittance, more particles). The transmittance ranges for all stations on both cruises were collected and the highest range (R_{CH}) was identified. The data were then normalized to the cruise high transmittance range by multiplying the normalized particle abundances for each station by the ratio of the range for that station to the cruise high range. These normalized values (PA_{NCi}) have a maximum of one, indicating the highest particulate concentration for the cruise

$$PA_{NCi} = PA_{Ni}\frac{R_S}{R_{CH}}. \quad (2)$$

While this calculation does not produce quantitative results, it permits a rough method to evaluate the distribution of particles for each cruise.

[10] *Hemiaulus* and *Rhizosolenia* spp. were enumerated using a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) with 64 μm mesh nets. Aliquots were enumerated under a compound microscope (Sedgwick-Rafter cell), corrected for cod end volume and volume filtered, and reported as cell m^{-3}. The *Richelia* symbiont was visible in *Rhizosolenia clevei* in transmitted light and only cells with symbionts present were counted. Epifluorescence was not useful for the enumerating the *H. hauckii* symbiont in formalin-preserved samples; however, careful transmitted light microscopy in the laboratory on the preserved samples revealed the presence of the *Hemiaulus* symbiont at all stations. *Foster and Zehr* [2006] also reported *Richelia*-containing *H. hauckii* collected within the diatom bloom at station 12 (this study) in the eastern Pacific (2002). Subsequent field work in this area has found that *H. hauckii* symbionts are frequently only pale red in blue light epifluorescence (excitation 470, emission >575 nm), and can be extremely difficult to locate (T. A. Villareal, unpublished observations, 2008–2009). However, by careful transmitted light microscopy (including crushing cells and teasing apart the contents), we found they were present in 98–100% of the cells we examined in this region in subsequent cruises. We present the *Hemiaulus* data with a high degree of confidence that they represent symbiont-containing cells. At selected stations in 2002, discrete water samples from the CTD were preserved in 1% buffered formalin for enumeration (50 mL settled volume) with an inverted microscope [*Hasle*, 1978] to allow comparisons between net and discrete water samples. Since net samples of phytoplankton are frequently regarded as nonquantitative, this step was necessary for validation. *Trichodesmium* was enumerated (MOCNESS) only from 2003; qualitative records note it as "rare" from 2002 samples.

[11] Two size-fractionated chl concentrations were determined fluorometrically after extraction overnight in methanol at −20°C [*Welschmeyer*, 1994]. In 2002, we used 0.4 μm (total) and 10 μm (>10 μm) pore size polycarbonate filters and in 2003, we used 0.4 μm (total) and 5 μm (>5 μm) filters. Each size fraction had a separate filtration (0.4 μm and 5 or 10 μm for 200 mL and 250 mL filtered, respectively). We

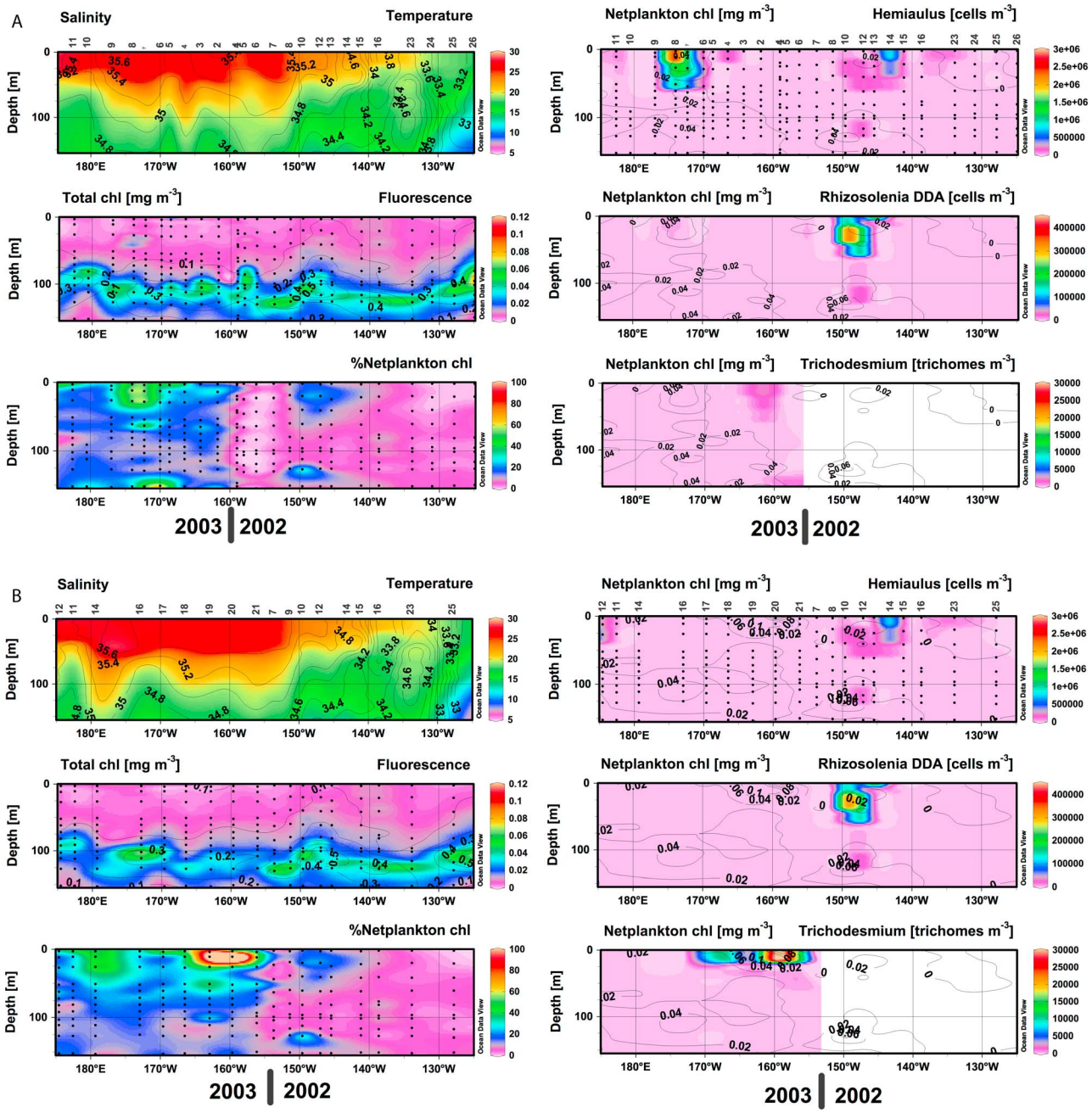

Figure 2. Contour plots of temperature, fluorescence, percentage of net plankton chlorophyll, *Hemiaulus* cell count (cells m^{-3}), *Rhizosolenia-Richelia* cell count (cells m^{-3}), and *Trichodesmium* counts (trichomes m^{-3}) from 2002 and 2003. (a) Eastern Pacific 2002 and northern leg of central Pacific 2003 (stations 1–12). (b) Eastern Pacific 2002 and southern leg of central Pacific 2003 (stations 12–21). Salinity field contours are overlaid on the temperature section, total chl contours are overlain on the fluorescence section, and net plankton chl (>10 μm in 2002, >5 μm in 2003) contours are overlaid on the *Hemiaulus*, *Rhizosolenia*, and *Trichodesmium* sections.

will refer to the larger size fraction (either 5 μm or 10 μm as net plankton and the 0.4 μm fraction as total chl.

2.2. Satellite Data

[12] Ocean color data from both Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on NASA's Aqua satellite were used to examine the regional scale chlorophyll variability during the two RoMP cruises. The data were obtained from the west coast regional node (WCRN) of NOAA's CoastWatch program, and had been mapped to an equal angle grid of 0.05° latitude by 0.05° longitude using simple arithmetic means to produce 8 day composite images. Due to persistent cloudiness in this

Table 1. Average Cell Counts of *Hemiaulus*, *Rhizosolenia*, and *Trichodesmium* in the Top 60 m From the 2002 and 2003 Cruises[a]

Station	Date	Longitude (°W)	*Hemiaulus* (cell m^{-3})	*Rhizosolenia* (cell m^{-3})	*Hemiaulus/ Rhizosolenia*	*Trichodesmium* (trichomes m^{-3})
			2002			
4	24 Jun	158.98	1768	232	7.6	rare
5	26 Jun	158.00	2147	247	8.7	rare
6	28 Jun	156.23	2225	189	11.8	rare
7	30 Jun	153.73	5096	466	10.9	rare
8	2 Jul	151.42	1741	215	8.1	rare
10	*3 Jul*	*149.63*	*76,752*	*189,194*	*0.4*	*rare*
12	*4 Jul*	*147.02*	*122,369*	*138,091*	*0.9*	*rare*
13	*5 Jul*	*145.47*	*74,061*	*34,331*	*2.2*	*rare*
14	*6 Jul*	*143.08*	*433,026*	*4782*	*90.6*	*rare*
15	7 Jul	141.20	62,344	1449	43.0	rare
16	8 Jul	138.64	32,592	227	143	rare
23	11 Jul	133.88	82,758	1264	65.5	rare
24	12 Jul	131.01	501	1128	0.4	rare
25	13 Jul	127.86	317	158	2.0	rare
			2003			
1	22 Aug	159.00	17	7	2.4	644
2	25 Aug	161.76	0	11	0	2210
3	26 Aug	164.23	337	55	6.1	719
4	27 Aug	164.23	53,157	7	7594	0
5	28 Aug	168.65	23	8	2.9	0
7	*30 Aug*	*172.29*	*988,030*	*1100*	*898*	*0*
8	*31 Aug*	*174.00*	*1,628,354*	*4333*	*376*	*0*
9	1 Sep	176.98	3282	20	164	0
10	3 Sep	179.48°E	202	26	7.8	0
11	4 Sep	177.44°E	25,949	25	1038	0
12	*5 Sep*	*175.43°E*	*203,335*	*199*	*1021*	*0*
14	7 Sep	179.34	8889	0	∞	0
15	*8 Sep*	*175.96*	*690,882*	*0*	∞	*0*
16	9 Sep	172.97	8116	0	∞	0
18	11 Sep	166.49	9383	0	∞	9852
19	12 Sep	162.92	4285	8	535	4655
20	13 Sep	159.66	1838	420	4.4	31,322
21	14 Sep	156.18	2061	275	7.5	13,019

[a]Values for stations 16–25 in 2002 represent only the 0–15 m strata abundance. *Trichodesmium* abundance includes only the upper 20 m and is only qualitative in 2002. Stations in italic are bloom stations, defined as stations with total DDA abundance >100,000 cell m^{-3}.

region, daily images are rarely sufficient for effectively viewing features. The first data available from the MODIS/Aqua satellite is in early July 2002 coincident with the RoMP 2002 cruise. Therefore, to look at the development of the 2002 chlorophyll bloom SeaWiFS data were used, both daily and 8 day composites.

[13] Altimetry data from the Archiving, Validation and Interpretation of Satellite Oceanographic data (AVISO) program were also obtained from the CoastWatch WCRN. The AVISO Sea Surface Height (SSH) anomaly product combines data from multiple satellites. The 2002 data used here included data from TOPEX/POSEIDON and ERS-2, and the 2003 data included data from Jason-1 and ENVISAT. The data were on an equal angle grid of 0.25° latitude by 0.25° longitude and 7 day composite images.

3. Results

3.1. DDA Abundances

[14] Three *Hemiaulus* blooms were observed. One in the eastern North Pacific (2002) between 143° and 150°W and two in the central North Pacific (2003), one between 172° and 175°W and one at 175°E (Figure 2). The one bloom station on the return leg of the 2003 cruise, station 15, was ~250 km southwest of the closest bloom station (station 8) on the westbound leg (Figure 1) and these blooms are probably the same feature. It is curious; however, that station 16, which is only 60 km south of the westbound bloom stations (stations 7 and 8), did not have significant DDA abundances (Table 1). However, DDA abundances can change dramatically in short distances; along the westbound leg abundances of *Hemiaulus* changed by 3–4 orders of magnitude at the boundaries of the bloom (Table 1). This pattern of sharp bloom boundaries is also evident in the chlorophyll blooms that have been observed by satellite [*Wilson and Qiu*, 2008]. *Hemiaulus* in the central Pacific bloom exceeded the *Hemiaulus* abundance in the eastern bloom by nearly fourfold (Table 1). *Hemiaulus* abundance decreased sharply in the California Current transition region at 131°W (stations 24 and 25, Table 1).

[15] Only one bloom of *Rhizosolenia-Richelia* was observed. It occurred in the eastern (2002) North Pacific between 143° and 150°W (stations 10 and 12, Figure 2). This bloom overlapped the *Hemiaulus* bloom, but their maximum abundances occurred at different stations. The *Rhizosolenia-Richelia* maximum occurred at the western most bloom station (station 10, 149.6°W), while the maximum in *Hemiaulus* in abundance occurred over 600 km further east (station 14, 143°W). All the DDA blooms were localized in the top 50 m of the water column well above the pycnocline (Figure 2).

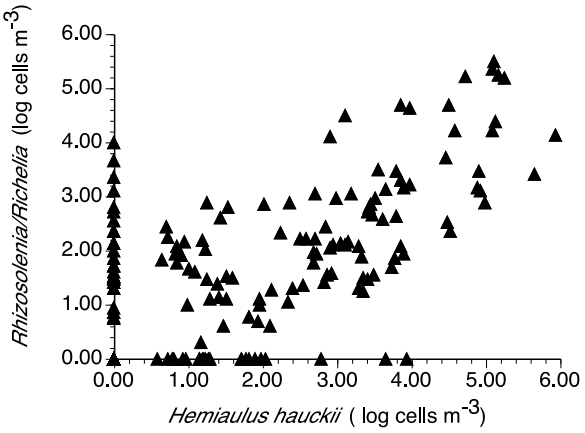

Figure 3. *Rhizosolenia-Richelia* abundance versus *Hemialus hauckii* abundance from all stations. Values were log transformed by log (value +1).

[16] *Hemiaulus* and *Rhizosolenia-Richelia* abundance did not covary in a predictable way (Figure 3). The two taxa bloomed together, but about 25% of the time they bloomed separately and with many orders of magnitude difference between the DDA abundance. For example, *Rhizosolenia-Richelia* abundance of 10^2 cells m^{-3} cooccurred with *Hemiaulus* abundance ranging from zero to 10^4 cells m^{-3}. The very highest abundance for either taxon had the other DDA present at some level. While both taxa were usually present, *Hemiaulus* was usually the dominant taxon. *Hemiaulus* was only absent at one station (station 2, 162°W), whereas *Rhizosolenia-Richelia* was absent at four stations (stations 14–18, 166.5°–179.3°W) and very low (<100 cells m^3) throughout most of the central North Pacific (Table 1). Even within the *Rhizosolenia-Richelia* bloom, *Hemiaulus* abundance was significant (Table 1).

[17] *Trichodesmium* was rarely observed in the eastern North Pacific. In the central Pacific, it was abundant from 159 to 166.5° W (stations 1–3 and 18–21), and was absent at stations farther west (Table 1 and Figure 2). The DDA abundances were very low at the stations with any significant amount of *Trichodesmium* (Table 1).

[18] Net collections are usually considered to undersample phtyoplankton since even very fine meshes (10 μm) will pass many cells, and this is particularly the case with the 64 μm mesh used by the MOCNESS. The individual cell dimensions of *Hemiaulus* (several tens of μm) would permit passage through the net mesh and result in undersampling. However, net-collected and bottle-collected cell counts generally agreed within a factor of 2 (Figure 4) with the MOCNESS recording higher abundance than the bottle counts at low DDA abundance. The agreement between the two was probably facilitated by the tendency of *Hemiaulus* to form long chains that frequently produced macroscopic aggregates (Figure 5) that were larger than the mesh size. These relatively rare aggregates would likely be missed by the 50 mL volume settled for counts.

3.2. In Situ Chlorophyll

[19] Across the study area, the surface chlorophyll concentrations (0–40 m) ranged from 0.04 to 0.11 mg m^{-3} (Figure 2). These surface values are below the 0.15 mg m^{-3}

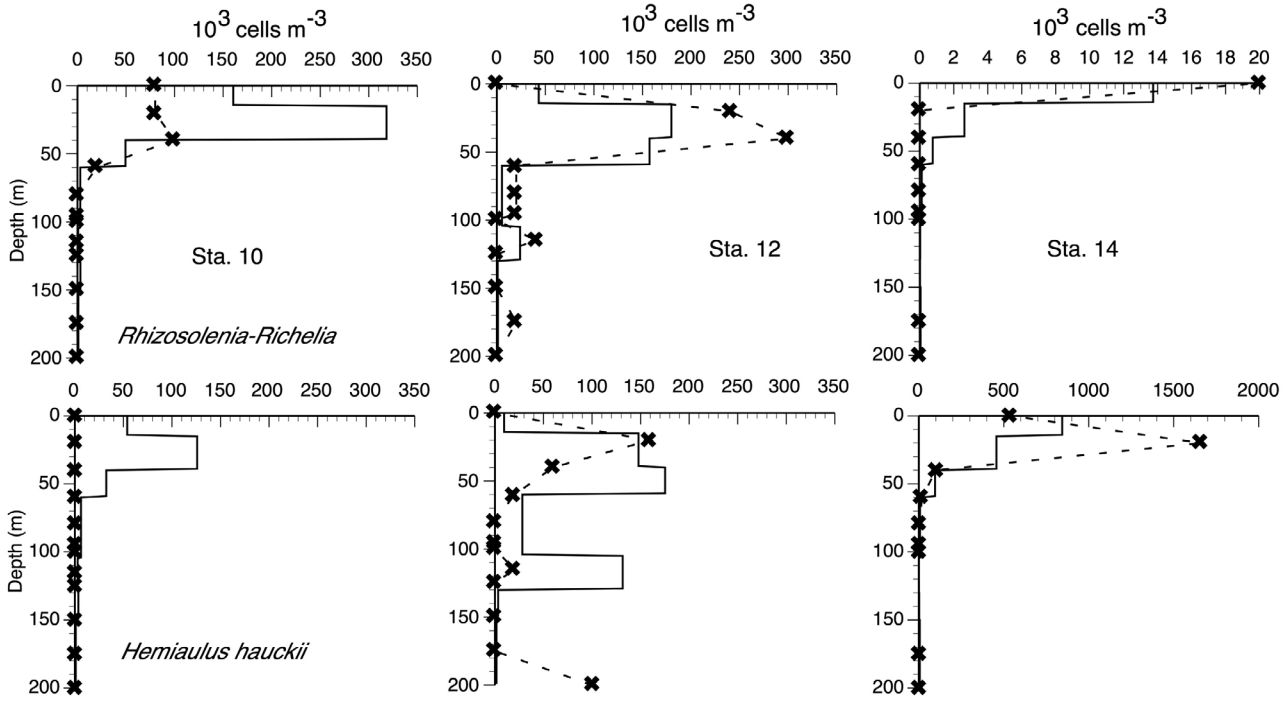

Figure 4. Comparison of 64 μm mesh MOCNESS samples and discrete water samples for *Rhizosolenia-Richelia* and *Hemialus hauckii* from the 2002 cruise. Individual strata sampled by the MOCNESS are outlined by solid lines. Dashed lines indicate the discrete water samples. All values are reported as 10^3 cells m^{-3}.

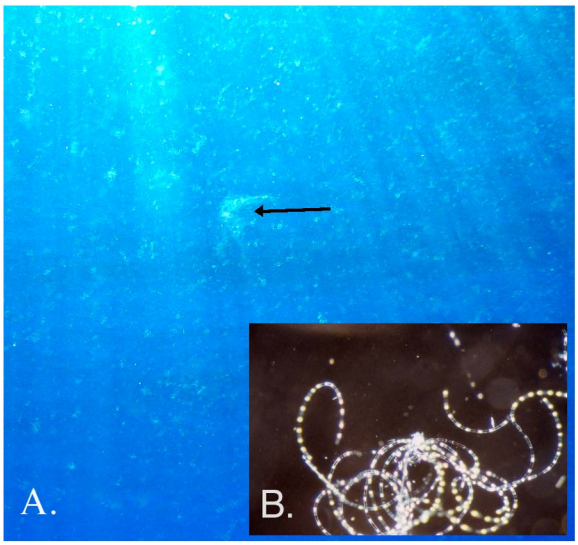

Figure 5. (a) An underwater photograph of *Hemiaulus hauckii* aggregates taken at ~5 m showing dense accumulations at 172.3°W, 28°N on 31 August 2003 (station 7). The arrow indicates a *Rhizosolenia* mat approximately 8 cm in size. (b) Stereomicrograph of a single *Hemiaulus hauckii* aggregate (~1 cm in size). The individual light dots in the circular/spiral chains are single cells of *H. hauckii*.

threshold value defined for satellite chlorophyll blooms in the NPSG [*Wilson et al.*, 2008]. The highest surface value, 0.11 mg m^{-3}, occurred within the eastern DDA bloom at 147°W (station 12), slightly east of the *Rhizosolenia* maximum at 149.6°W (station 10). The deep chlorophyll maximum shoaled by ~50 m, and more than doubled to >0.8 mg m^{-3} between 145° and 150°W, coincident with the DDA bloom. In contrast to the eastern DDA bloom, there was no discernable change in the subsurface chlorophyll structure associated with either of the two DDA blooms in the central North Pacific. There was an increase in surface chlorophyll associated with the *Hemiaulus* bloom at 172°–174°W (stations 7 and 8). Chlorophyll values on either side of the bloom were ~0.05 mg m^{-3} and increased to 0.10 mg m^{-3} within the bloom.

[20] There was considerable difference across the study area in the percentage of net plankton chlorophyll, defined as the percentage of total extracted chlorophyll that is retained on a 5 μm (2003) or 10 μm (2002) filter. In the central North Pacific (2003), the percentage of net plankton in the subsurface was between 10 and 25%, whereas in the eastern North Pacific (2002) it was ≤7% (Figure 2). Additionally, in the eastern Pacific (2002) the surface and subsurface had similar percentages, while in the central Pacific (2003), the surface layer had a considerably larger percentage of net plankton (>40%) relative to the subsurface

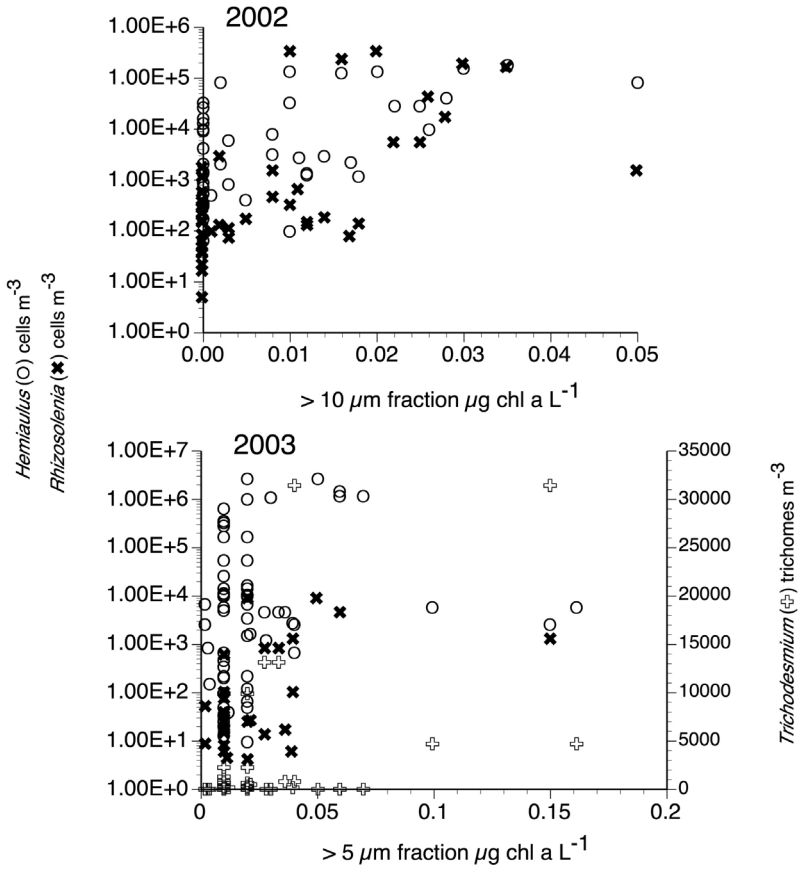

Figure 6. DDA abundance (*H. hauckii* and *Rhizosolenia-Richelia*) relationship to size-fractionated chlorophyll for (top) 2002, >10 μm chl size fraction versus abundance and (bottom) 2003, >5 μm chl size fraction versus abundance. Note the difference in scale for both the x and y axes.

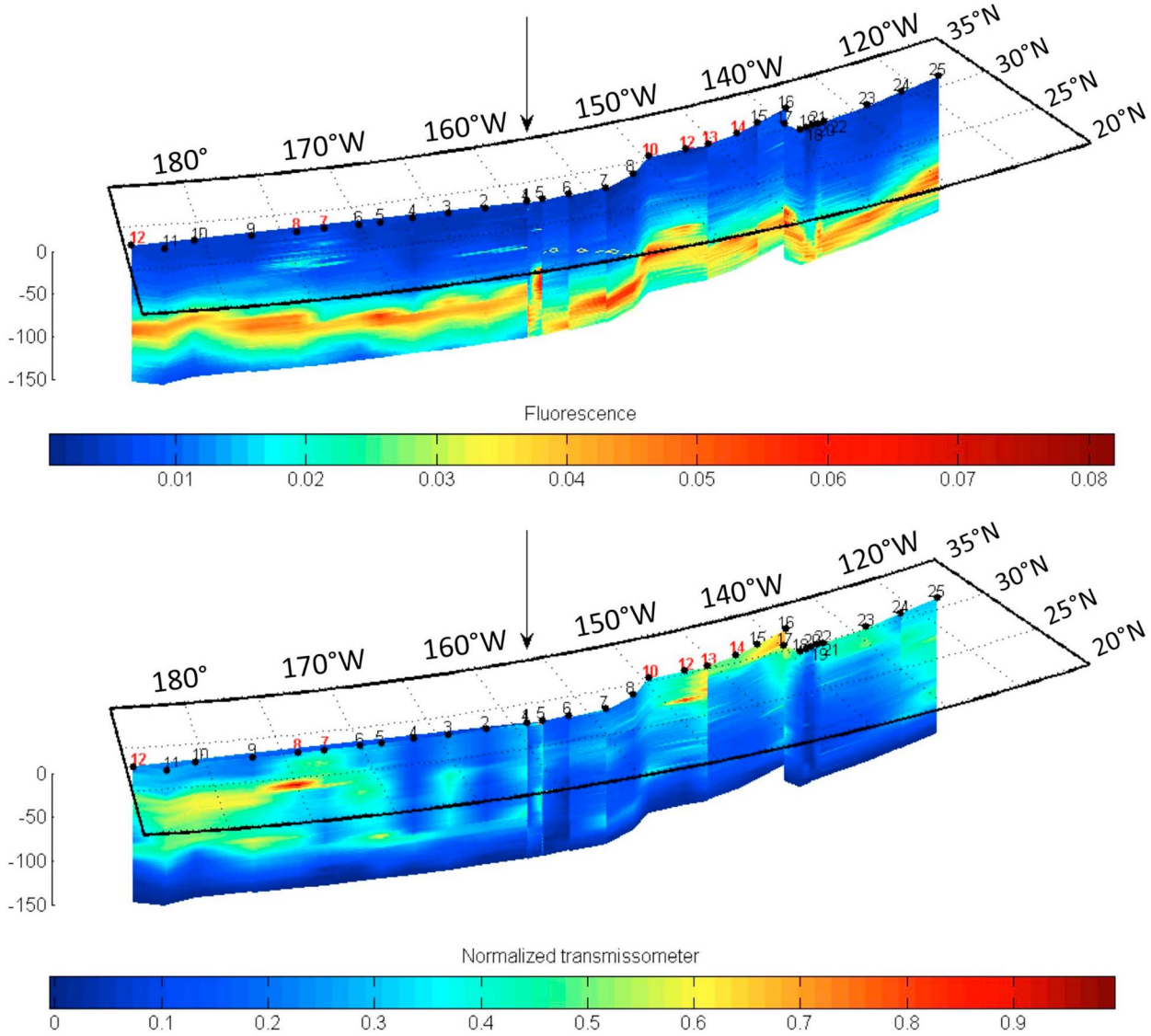

Figure 7. Curtain plots of (top) CTD fluorescence and (bottom) normalized transmissometer for both cruises. The 2002 data extends east of Hawaii, and the 2003 data extends west of Hawaii. The 2003 data shown is just the westbound portion. The arrow marks the division between the two cruises.

(10–25%). However, different filter sizes were used on the two cruises: 5 μm in 2003 (central Pacific) and 10 μm in 2002 (eastern Pacific). While interannual variability cannot be ruled out, this difference suggests that the 5–10 μm fraction of phytoplankton comprises ~15% of the subsurface phytoplankton community, and an even larger percent in the surface water. Regardless of the filter size used, the percentage of net plankton appears to track the DDA blooms better than the total chlorophyll. In the eastern Pacific the net plankton percentage increased from <10% to 15–25% within the DDA bloom. In the central Pacific, the net plankton increased from background levels of 30% to ~50% in the DDA bloom. The greatest net plankton fraction (100% of the total chl) was within the region of elevated *Trichodesmium* (Figure 2b).

[21] Despite the increase in net plankton fraction within the DDA blooms, the relative increase in chl was fairly small (Figure 6). Logarithmic changes in DDA abundance produce only minor increases in the net plankton chl, and cooccur with a chlorophyll dynamic range that only varies fivefold. In 2002, for example, a *Hemiaulus* abundance of 1×10^5 cells m^{-3}, produced anywhere from 0.002 to 0.05 mg chl m^{-3}. In 2003, an abundance of 1×10^6 cells m^{-3} resulted in less than 0.05 mg m^{-3} while abundances 10^4 less had nearly as much chl in the net plankton fraction.

3.3. Fluorometer and Transmissometer Data

[22] The CTD fluorescence did not substantially increase at either of the DDA blooms (Figure 7). There was a shoaling of the fluorescence maximum in the eastern DDA bloom between 140° and 155°W (stations 10 and 12–14), as was seen in the total chlorophyll data (Figure 2). There was a slight subsurface peak at 30–40 m between 172° and 174°W in the 2003 central Pacific *Hemiaulus* bloom at stations 7 and 8 (Figure 7).

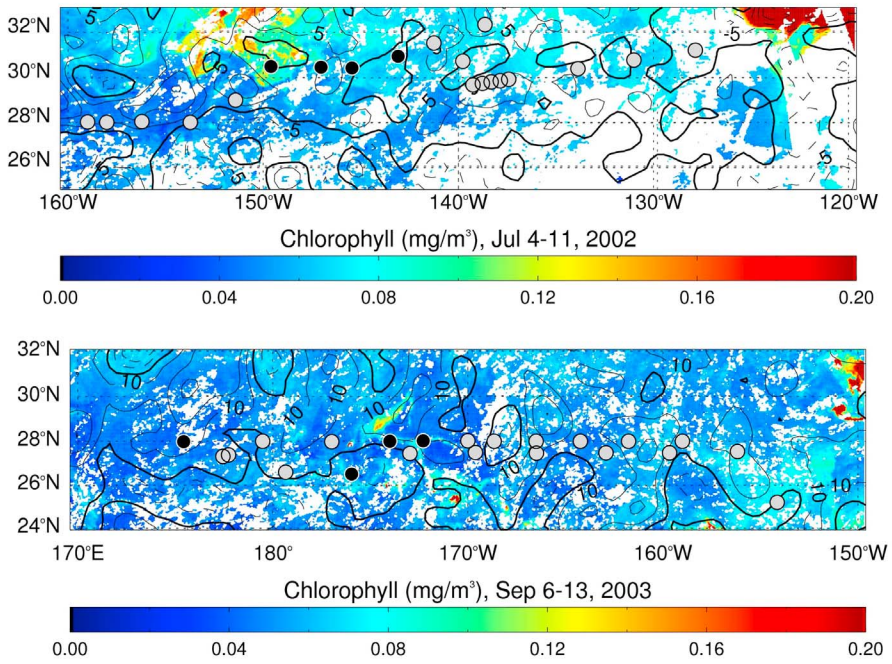

Figure 8. Ocean color chlorophyll data from the 2002 and 2003 cruise. (top) An 8 day composite of MODIS chlorophyll data from 4 to 11 July 2002, overlain with the RoMP 2002 stations (24 June and 13 July 2002). (bottom) An 8 day composite of MODIS chlorophyll data from 6 to 13 September 2003, overlain with the RoMP 2003 stations (22 August to 14 September). Bloom stations are shown as black circles. Contours of the SSH anomalies (5 cm contour interval) are also shown.

[23] In contrast to the fluorescence data, both the eastern (2002) and central (2003) DDA blooms were visible in the normalized transmissometer data (Figure 7). In the eastern Pacific, there was a substantial decrease in water clarity in the upper 40 m at the location of the DDA bloom, and lower transmittance (higher particulate matter) values which extended well past the DDA bloom (Figure 7). Divers noted visible, although not abundant, *Hemiaulus* aggregates in the upper 15 m at the eastern (2003) Pacific DDA bloom (stations 10 and 12–14). There was also a significant surface increase in normalized transmissometer values at the central (2003) Pacific DDA bloom near 170°W (stations 7 and 8), as well as a subsurface maximum. This subsurface maximum extended between 40 and 80 m depth from the DDA bloom westward to the end of the cruise track (Figure 7). However, there were few *Hemiaulus* recorded from this subsurface region (stations 9–12, Figure 2). Stations 7 and 8 sampled a region of extensive *Hemiaulus* aggregate formation (Figure 5). These 1–2 cm aggregates were composed of long chains of intertwining *H. hauckii* chains with the larger aggregates containing ~10^3 cells per aggregate.

3.4. Satellite Chlorophyll Data

[24] The DDA bloom in the eastern North Pacific in 2002 occurred adjacent to chlorophyll bloom observed with satellite data (Figure 8). In comparison to chlorophyll blooms from other years in this area [*Wilson et al.*, 2008], the 2002 bloom was fairly weak in magnitude, with not much chlorophyll above the bloom threshold of 0.15 mg m^{-3}. However, the satellite data clearly identifies the area of 30–34°N, 150–155°W as anomalously higher in chlorophyll relative to the rest of the waters in the study region.

[25] The most western 2002 DDA bloom station (station 10) was located on the boundary of the chlorophyll bloom, approximately 300 km southeast of the chlorophyll maximum of 0.2 mg m^{-3} at 32.7°N, 152°W. The satellite image is fairly synoptic with the bloom station sampling; the bloom stations were sampled 3–6 July 2002 (Table 1) and the satellite image in Figure 8 is an 8 day composite from 4 to 11 July 2002. The time series of daily satellite chlorophyll data from station 10 shows that it was sampled less than a week after initiation of the bloom, and about a week before the maximum chlorophyll value at this location (Figure 9). While the other three bloom stations seem spatially disjoint from the synoptic chlorophyll bloom (Figure 8), later satellite images [*Wilson et al.*, 2008] show that the bloom center migrated ~650 km southeast in the subsequent month. This is evident in the time series of satellite chlorophyll for station 13 (Figure 9), which has values above the bloom threshold in late July and early August. *Wilson et al.* [2008] suggested an "echo bloom" phenomena was at work, whereby the new N brought in by the diazotroph observed during the RoMP cruise led to the chlorophyll bloom that developed a month later.

[26] The cloudiness in this region in the summertime makes it difficult to analyze either daily images or daily time series due to the sparse frequency of observations. For example there is a gap of 19 days in the satellite chlorophyll time series at station 13 during the period when the bloom was developing there (Figure 9). A bigger picture view of

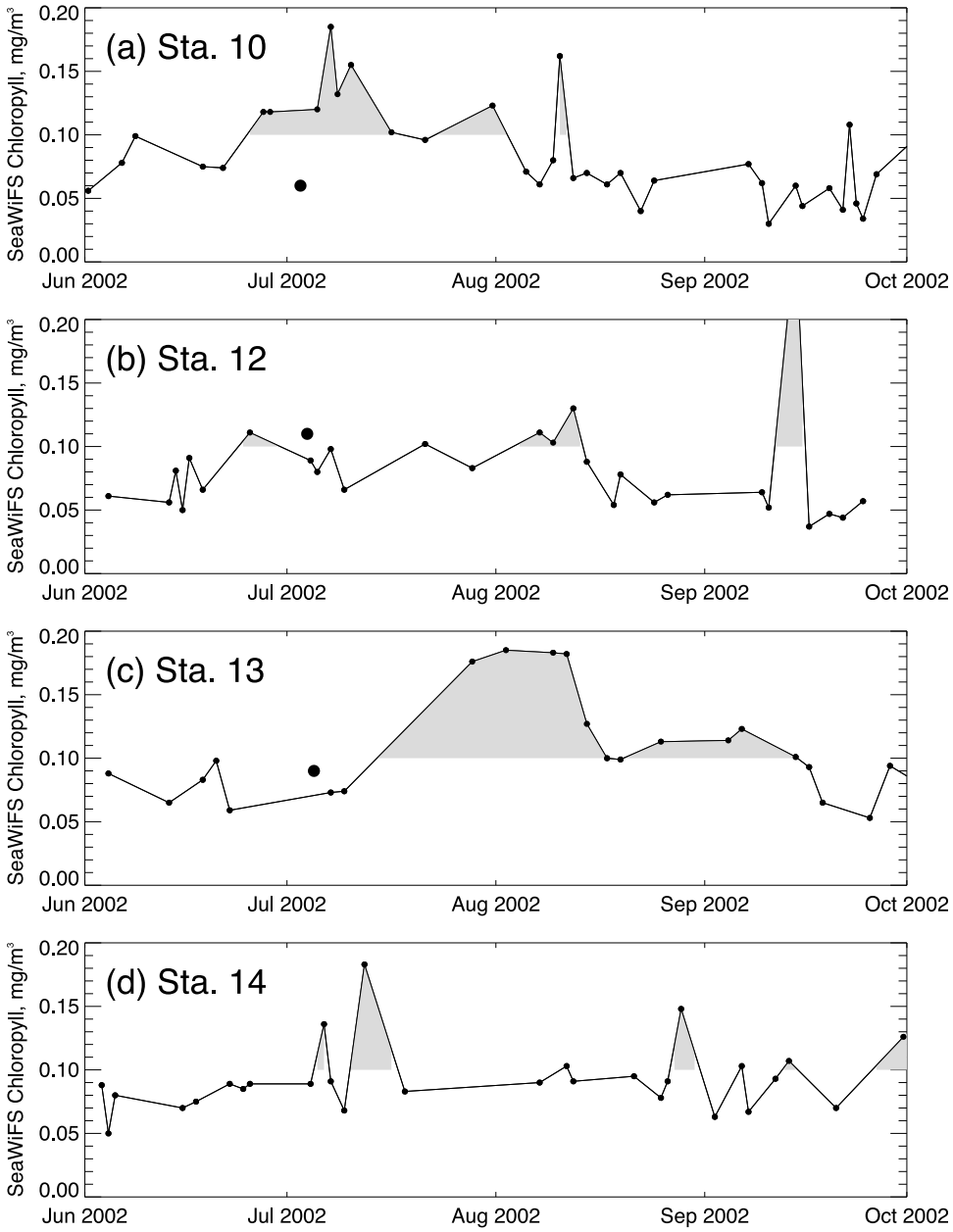

Figure 9. Daily time series from June to October of SeaWiFS satellite chlorophyll from each of the four DDA stations during the 2002 cruise. Values greater than 0.1 mg m^{-3} are shaded gray. The in situ chlorophyll value for that station is shown as a black circle. The chlorophyll sample for station 14 was lost.

the temporal relationship between the station sampling and the development and peak of the chlorophyll bloom is shown in the Hövmoller plot in Figure 10. While stations 7 and 8 were temporally as close to the chlorophyll bloom as the bloom stations, their positions were further south (28°N and 29°N), hence they were spatially further from the chlorophyll bloom than the bloom stations (Figure 8).

[27] In contrast to the 2002 DDA bloom, the two DDA blooms observed in 2003 were not associated with any significant increase in satellite chlorophyll, neither synoptically nor with a time delay (Figures 8 and 10). This result is not surprising as historically the satellite chl blooms do not develop west of Hawaii [*Wilson and Qiu*, 2008]. However, there was a small filament of elevated chlorophyll slightly northwest of the DDA bloom at station 8 (the yellow feature in Figure 8). The highest chlorophyll within the filament was just above the bloom threshold value of 0.15 mg m^{-3} [*Wilson*, 2003]; however, due to its small size and short duration (less than a month) this feature was not apparent in the analysis of *Wilson and Qiu* [2008] who used monthly composites. Station 8 was located in a curvature of this filament, but the part of the filament with the largest chlorophyll values was ~100 km away (data not shown). The chlorophyll filament curved around the zero SSH anomaly contour, consistent with dynamics associated with

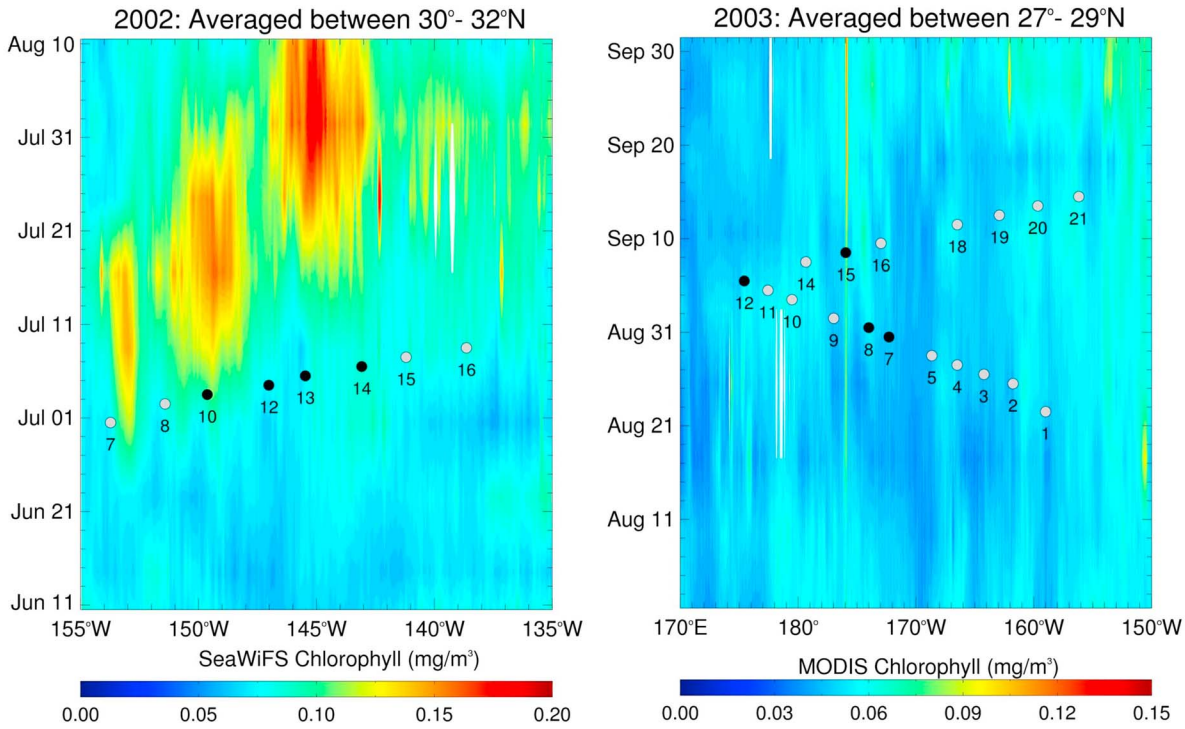

Figure 10. (left) Hovmöller diagram of SeaWiFS chlorophyll along 155°–135°W, averaged over 30°–32°N, between 10 June and 10 August 2002, overlain with the RoMP 2002 stations. (right) Hovmöller diagram of MODIS chlorophyll along 170°E–150°W, averaged over 27°–29°N, between 1 August and 1 October 2003, overlain with the RoMP 2003 stations. The black circles indicate the bloom stations.

unstable manifolds that *Calil and Richards* [2010] investigated in this area.

3.5. Hydrography

[28] Differences between the physical environment of the central and eastern North Pacific are evident from both the hydrographic data and the SSH topography. Both cruises were in the vicinity of the subtropical front located near 30°N, but there is significant interannual, longitudinal, and seasonal variation in the front's location [*Laurs and Lynn*, 1977; *Saur*, 1980; *Seki et al.*, 2002]. It has been suggested that the subtropical front and frontal mechanisms could play a role in the formation of the 30°N chlorophyll blooms [*Wilson et al.*, 2008]. The front's temperature signature weakens considerably in the summer, and it is best detected by salinity data [*Roden*, 1974, 1975]. As seen by the underway salinity data (Figure 11), the 2002 cruise in the eastern Pacific crossed the subtropical front, defined by a surface salinity of 34.8 [*Roden*, 1970], once near 145°W and twice near 140°W. The front is evident in the salinity contours as the intrusion of fresher water (at stations 15–17) and a surface manifestation was visible from the ship as a large slick extending perpendicular to the ship's course and extending to the horizon near station 20. The satellite chlorophyll bloom in 2002 was located on the warm, salty side of the subtropical front.

[29] The 2003 cruise in the central Pacific did not cross the subtropical front. The small chlorophyll filament in 2003 was wrapped around a mesoscale eddy feature, but it was not associated with the subtropical front and there was little variability in the surface salinity structure in the central North Pacific.

4. Discussion

[30] The DDA blooms observed in 2002 and 2003 represent features separated by nearly a year in time and over 2000 km in distance. While these data represent a set of snapshots and cannot resolve time-dependent processes, there are some general features from the two cruises that provide insights into DDA blooms.

[31] DDA bloom taxa frequently cooccurred, but the ratio of *Hemiaulus* to *Rhizosolenia* DDAs varied considerably (Table 1). This quantitative data supports other observations that the DDA community is not homogeneous, but has considerable dominance variation [*Mague et al.*, 1974]. In some cases, *Rhizosolenia-Richelia* was absent (station 15, 2003) and in other cases, it dominated (station 10, 2002). *Trichodesmium* had a distinctly different distribution than the DDA taxa and rarely overlapped at abundance. Observations by *Venrick* [1997] and *Dore et al.* [2008] have led to the inference that diatom blooms likely dominate at 30°N while *Trichodesmium* is of greater importance at HOT (22.75°N 158°W). In the western Pacific, *Kitajima et al.* [2009] reported maximum abundance of DDAs at 8° and 30°N, and maximum *Trichodesmium* abundance at 26.5°N. Our results support these patterns, showing little *Trichodesmium* along an east-west line at 28–30°N. The one region where elevated *Trichodesmium* (10^4–10^5 trichomes m^{-3}) was observed, between 156 and 164°W at 28°N,

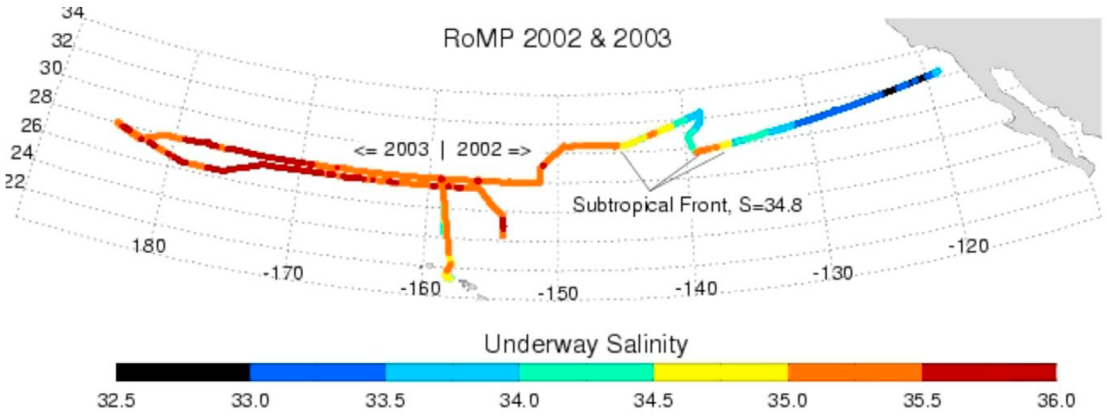

Figure 11. Surface salinity from the underway system for the 2002 and 2003 cruises. The subtropical front was crossed near 145°W and twice near 140°W. Both cruises are plotted for comparison of the regional differences. The separation between the two cruises at ~159°W is indicated. The 2002 data extends east of Hawaii, and the 2003 data extends west of Hawaii. The transect slightly south of 28°N was collected in 2003 on the return leg and terminated northeast of Hawaii.

occurred in the same longitude band as the HOT station. This bloom was dominated by the >10 μm chl size fraction and had a paucity of DDAs. Further work is needed clarify the regional role of *Trichodesmium*.

[32] We found no evidence that DDA blooms contribute sufficient chl to account for satellite chl blooms. Phycoerythrin increases at HOT (cyanobacteria blooms) linked to diatom increases (presumably DDA) also showed no consistent surface chlorophyll increases [*White et al.*, 2007b]. *Dore et al.* [2008] note discordances between satellite chlorophyll blooms and phytoplankton blooms at HOT. Our observations support these analyses and extend it to direct microscopic confirmation of DDA blooms on a wider regional scale. *Hemiaulus* and *Rhizosolenia-Richelia* blooms did not have a distinctive ocean color signature nor was there an obvious in situ chlorophyll signature. The nearly fourfold increase in cell abundance between the 2002 and 2003 *Hemiaulus* DDA blooms yielded virtually identical extracted chlorophyll values (~0.08–0.11 mg m^{-3}), values that were only slightly above the background. Although the most intense ocean color chlorophyll blooms were not sampled in either year (Figure 10), the data suggest that either these satellite chlorophyll blooms are truly massive diatom events, or that the ocean color data is capturing a signal linked to, but not due to, DDA blooms.

[33] The literature also does not support DDA blooms having a strong chl signature. Previous DDAs blooms have been observed in this region of the Pacific (Table 2). The observed cell abundances were an order of magnitude higher than the highest values measured in 2002 or 2003, but yet the surface chl values were not anomalously high. Only one of these blooms had a surface chlorophyll concentration (0.14–0.19 mg m^{-3}) above the threshold for satellite chl blooms. In our direct size fractionated data, the net plankton chlorophyll content was well below the 0.15 mg m^{-3} threshold for bloom detection, and this size fraction never contained sufficient chlorophyll to account for the observed ocean color signature. We calculate that at the *Hemiaulus* abundance from station 8 in 2003 (Table 1) and the mean >5 μm chl (upper 50 m: 0.038 mg m^{-3}), that a bloom threshold of 0.15 mg m^{-3} would require 6.4×10^6 cells m^{-3}. A similar calculation for station 12 in 2002 (>5 μm chl in the upper 50 m of 0.025 mg m^{-3}) yields 0.7×10^6 cells m^{-3}. From Table 2, even when these cell densities have been reported and sampled, the measured chlorophyll fell well short of the 0.15 mg m^{-3} threshold. The low chlorophyll values in conjunction with the high *Hemiaulus* abundance imply they have a very low chlorophyll/cell content; however, there is no available published data from in situ populations for validation. Clearly, it cannot be assumed that the *Hemiaulus* blooms have (1) sufficient chlorophyll to be solely responsible for summer satellite chlorophyll blooms or (2) a predictable ocean color signature. The signature present in the transmissometer data suggests that this may be a useful method for detecting blooms in archived data, but further work is required to validate this approach.

Table 2. Cell Counts for Other *Hemiaulus* Blooms Reported in This Region and Their Associated Surface Chlorophyll Values

Hemiaulus Abundance (cells m^{-3})	Measured Chlorophyll Value (mg m^{-3})	Location	Year	Reference
25×10^6	0.06–0.08	28°N, 155°W	1969	*Venrick* [1974]
3×10^6	0.14–0.19	26°N, 159°W	1995	*Brzezinski et al.* [1998]
$16–20 \times 10^6$	0.10	31.4°N, 149.9°W	1992	T. A. Villareal (unpublished observations, 1992)
0.1×10^6	0.13 (total)	30°N, 147°W	2002	this work (station 12)
1.6×10^6	0.08 (total)	26°N, 174°W	2003	this work (station 8)

[34] The eastern DDA bloom, which was associated with a satellite chlorophyll bloom, was also different from the 2003 DDA blooms in that it was more mixed, with high abundance of both *Hemiaulus* and *Rhizosolenia*. The in situ total chlorophyll levels associated with the mixed DDA bloom were slightly elevated over nonbloom values (Figure 2), consistent with the satellite signal. The eastern bloom differed from the western bloom in that the increase between 145° and 150°W in net plankton chl was also mirrored by an increase in total chl (Figure 2), suggesting that *Rhizosolenia* has significant higher levels of chlorophyll per cell than *Hemiaulus*. There are also other taxa present in these blooms that have a consistent affiliation with DDAs. The numerically codominant diatom in the 1995 *Hemiaulus* bloom (Table 2) was a small pennate diatom (*Mastogloia woodiana*) [*Brzezinski et al.*, 1998] that would have been undersampled in the 2002/2003 MOCNESS samples. *Mastogloia* spp. (representing small pennate diatoms in general) were commonly seen with *Hemiaulus* in 1995, 2002, and 2003 (T. A. Villareal, unpublished observations, 2008–2009), have been reported in the historical *Richelia* blooms [*Venrick*, 1974], were specifically noted as cooccurring with *Hemiaulus* [*Semina and Levashova*, 1993] and *Rhizosolenia-Richelia* [*Brown et al.*, 2008], and were an important component of sediment traps at HOT [*Scharek et al.*, 1999a] and VERTEX [*Blueford et al.*, 1990]. *Guillard and Kilham* [1977] noted that *Mastogloia* is one of the characteristic and predictable species of oligotrophic regions. Naviculoid diatoms are associated with the *Chaetoceros* DDA as well in the western Pacific [*Gómez et al.*, 2005]. Like the DDA taxa, *Mastogloia* spp. are a member of the shallow community [*Venrick*, 1988]. The small size of many pennate spp. would permit passage through a 10 μm pore size filter but retention on a 5 μm pore size filter, an observation consistent with the greater contribution of the net plankton fraction to the total chlorophyll in 2003 than 2002 (Figure 2). The ecology of this group is largely unknown although it is a notable numerical dominant [*Venrick*, 1990]. This emphasizes that these DDA blooms are not monospecies events and, at the very least, have an additional diatom component, the small pennate community, to consider.

[35] Aggregation appears to be a fundamental part of *Hemiaulus* biology, and the biological association with pennate diatoms is probably not unrelated since many pennates are substrate oriented and are seen to live directly on aggregates [*Fryxell*, 2000; *Lee and Fryxell*, 1996] and *Rhizosolenia* mats [*Villareal et al.*, 1996]. The 2003 *Hemiaulus* bloom near the satellite-observed chlorophyll filament was highly aggregated to a degree unexpected for the open ocean as evidenced direct visual observation (Figure 5). *Pilskaln et al.* [2005] reported >13,000 aggregates m^{-3} (of unknown composition) from the 30°N bloom area as well, and *Scharek et al.* [1999a] noted aggregates in sediment traps at HOT. *Hemiaulus* aggregates have been noted by divers throughout the eastern North Pacific [*Villareal et al.*, 1996]. If *Hemiaulus* aggregates are numerically important, discrete water samples probably undersample both *Hemiaulus* and the associated pennate population, much like marine snow aggregates are undersampled by bottles [*Alldredge and Silver*, 1988].

[36] The longitudinal range where DDA blooms occurred extends well outside the HOT-CLIMAX area considered by *Dore et al.* [2008]. *Dore et al.* [2008] suggested that DDA blooms in the HOT-CLIMAX region of the North Pacific were utilizing residual P from winter mixing, and based on nutrient N:P and mixing climatologies, suggested that blooms were not favored in the regions west of Hawaii. In our study, we found substantial blooms of DDAs occurring to at least 175°E suggesting that some of the assumptions used in their calculations cannot be supported. In addition, *Semina and Levashova* [1993] noted *Hemiaulus* extended across the Pacific Ocean to the Japanese coast. The occurrence of a DDA bloom in the faint ocean color feature seen in Figure 8 invites speculations that these features, in general, may represent localized blooms of DDAs. If so, DDA blooms are much more extensive than previously thought in this region west of Hawaii. There are few ways to confirm this hypothesis other than direct shipboard sampling, particularly if these features are at latitudes that the time series station HOT may not represent well.

5. Conclusions

[37] Summer chlorophyll blooms at 28–30°N noted in ocean color satellites in 2002/2003 were associated with increases in the DDA community, but the satellite chlorophyll signature was not due solely to increases in the diatom-diazotroph community. Chlorophyll increases in the DDA size net plankton fraction were not adequate to generate the observed ocean color signature; historical measurements support these observations. Thus, diatom symbioses blooms are coincident with the satellite observed blooms but are not the source of the ocean color signature interpreted as chlorophyll. Large DDA blooms in the central Pacific had only a faint ocean color bloom signature, suggesting that similar faint, transient features in the central Pacific may also be DDA blooms. Bloom species dominance at 28–30°N can alternate and different taxa can dominate at adjacent stations. *Hemiaulus hauckii* aggregates into macroscopic flocs that are both widespread and appear to be linked to a cooccurring community of pennate diatoms. Fluorescence profiles did not identify DDA blooms well, but they were more evident in transmissometer profiles. DDA blooms extend into the central Pacific Ocean west of the 180°W and are more extensive than previously thought.

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References

Alldredge, A. L., and M. W. Silver (1988), Characteristics, dynamics and significance of marine snow, *Prog. Oceanogr.*, *20*, 41–82, doi:10.1016/0079-6611(88)90053-5.

Behrenfeld, M. J., E. Boss, D. A. Siegel, and D. M. Shea (2005), Carbon-based ocean productivity and phytoplankton physiology from space, *Global Biogeochem. Cycles*, *19*, GB1006, doi:10.1029/2004GB002299.

Blueford, J. R., J. J. Gonzales, and K. Van Scoy (1990), Comparing radiolarian and diatom diversity and abundance from the northeast

Pacific, *Mar. Micropaleontol.*, *15*, 219–232, doi:10.1016/0377-8398(90)90012-B.

Brown, S. L., M. R. Landry, K. E. Selph, E. J. Yang, Y. M. Rii, and R. R. Bidigare (2008), Diatoms in the desert: Plankton community response to a mesoscale eddy in the subtropical North Pacific, *Deep Sea Res. Part II*, *55*, 1321–1333, doi:10.1016/j.dsr2.2008.02.012.

Brzezinski, M. A., T. A. Villareal, and F. Lipschultz (1998), Silica production and the contributions of diatoms to new and primary production in the central North Pacific, *Mar. Ecol. Prog. Ser.*, *167*, 89–104, doi:10.3354/meps167089.

Calil, P. H. R., and K. J. Richards (2010), Transient upwelling hot spots in the oligotrophic North Pacific, *J. Geophys. Res.*, *115*, C02003, doi:10.1029/2009JC005360.

Carpenter, E. J., and S. Janson (2000), Intracellular cyanobacterial symbionts in the marine diatom *Climacodium frauenfeldianum* (Bacillariophyceae), *J. Phycol.*, *36*, 540–544, doi:10.1046/j.1529-8817.2000.99163.x.

Davies, A., A. E. S. Kemp, and J. Pike (2009), Late Cretaceous seasonal ocean variability from the Arctic, *Nature*, *460*, 254–258, doi:10.1038/nature08141.

Dore, J. E., R. M. Letelier, M. J. Church, and D. M. Karl (2008), Summer phytoplankton blooms in the oligotrophic North Pacific subtropical gyre: Historical perspective and recent observations, *Prog. Oceanogr.*, *76*, 2–38, doi:10.1016/j.pocean.2007.10.002.

Fong, A. A., D. M. Karl, R. Lukas, R. M. Letelier, J. P. Zehr, and M. J. Church (2008), Nitrogen fixation in an anticyclonic eddy in the oligotrophic North Pacific Ocean, *ISME J.*, *2*, 663–676, doi:10.1038/ismej.2008.22.

Foster, R. A., and J. P. Zehr (2006), Characterization of diatom-cyanobacteria symbioses on the basis of nifH, hetR and 16S rRNA sequences, *Environ. Microbiol.*, *8*, 1913–1925, doi:10.1111/j.1462-2920.2006.01068.x.

Fryxell, G. A. (2000), *Nitzschia bicapitata* (Bacillariophyceae) and related taxa from oceanic aggregations, *Diatom Res.*, *15*, 43–73.

Goldman, J. C. (1988), Spatial and temporal discontinuities of biological processes in pelagic surface waters, in *Toward a Theory on Biological-Physical Interactions in the World Ocean*, edited by B. J. Rothschild, pp. 273–296, Kluwer Acad., Dordrecht, Netherlands.

Gómez, F., K. Furuya, and S. Takeda (2005), Distribution of the cyanobacterium *Richelia intracellularis* as an epiphyte of the diatom *Chaetoceros compressus* in the western Pacific Ocean, *J. Plankton Res.*, *27*, 323–330, doi:10.1093/plankt/fbi007.

Guillard, R. R. L., and P. Kilham (1977), The ecology of marine planktonic diatoms, in *The Biology of Diatoms*, edited by D. Werner, pp. 372–469, Univ. of Calif. Press, Berkeley, Calif.

Hasle, G. R. (1978), The inverted-microscope technique, in *Phytoplankton Manual*, *Monogr. Oceanogr. Methodol. Ser.*, vol. 6, edited by A. Sournia, pp. 88–96, U. N.. Sci. and Cult. Organ., Page Brothers, Ltd., Norwich.

Heinbokel, J. F. (1986), Occurrence of *Richelia intracellularis* (Cyanophyta) within the diatoms *Hemiaulus Haukii* and *H. membranaceus* off Hawaii, *J. Phycol.*, *22*, 399–403, doi:10.1111/j.1529-8817.1986.tb00043.x.

Karl, D. M., and R. Lukas (1996), The Hawaii Ocean Time-series (HOT) program: Background, rationale and field implementation, *Deep Sea Res. Part II*, *43*, 129–156, doi:10.1016/0967-0645(96)00005-7.

Kemp, A. E. S., R. B. Pearce, I. Koizumi, J. Pike, and S. J. Rance (1999), The role of mat-forming diatoms in the formation of Mediterranean sapropels, *Nature*, *398*, 57–61, doi:10.1038/18001.

Kemp, A. E. S., J. Pike, R. B. Pearce, and C. B. Lange (2000), The "fall dump"—A new perspective on the role of a "shade flora" in the annual cycle of diatom production and export flux, *Deep Sea Res. Part II*, *47*, 2129–2154, doi:10.1016/S0967-0645(00)00019-9.

Kitajima, S., K. Furuya, F. Hashihama, S. Takeda, and J. Kanda (2009), Latitudinal distribution of diazotrophs and their nitrogen fixation in the tropical and subtropical western North Pacific, *Limnol. Oceanogr.*, *54*, 537–547, doi:10.4319/lo.2009.54.2.0537.

Laurs, R. M., and R. J. Lynn (1977), Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters—Distribution, relative abundance, and association with transition zone waters, *Fish. Bull.*, *75*(4), 795–822.

Lee, H. Y., and G. A. Fryxell (1996), Bicapitate *Nitzschia* species: Abundant nanoplankton in aggregates during November–December (1992) in the equatorial Pacific, *J. Plankton Res.*, *18*, 1271–1294, doi:10.1093/plankt/18.8.1271.

Mague, T. H., N. M. Weare, and O. Holm-Hansen (1974), Nitrogen fixation in the North Pacific Ocean, *Mar. Biol. Berlin*, *24*, 109–119, doi:10.1007/BF00389344.

Mahaffey, C., A. F. Michaels, and D. G. Capone (2005), The conundrum of marine nitrogen fixation, *Am. J. Sci.*, *305*, 546–595, doi:10.2475/ajs.305.6-8.546.

McGillicuddy, D. J., Jr., et al. (2007), Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms, *Science*, *316*, 1021–1026, doi:10.1126/science.1136256.

Monteiro, F. M., M. J. Follows, and S. Dutkiewicz (2010), Distribution of diverse nitrogen fixers in the global ocean, *Global Biogeochem. Cycles*, *24*, GB3017, doi:10.1029/2009GB003731.

Pilskaln, C. H., T. A. Villareal, M. Dennett, C. Darkangelo-Wood, and G. Meadows (2005), High concentrations of marine snow and diatom algal mats in the North Pacific subtropical gyre: Implications for carbon and nitrogen cycles in the oligotrophic ocean, *Deep Sea Res. Part I*, *52*, 2315–2332, doi:10.1016/j.dsr.2005.08.004.

Platt, T., W. G. Harrison, M. R. Lewis, W. K. W. Li, S. Sathyendranath, R. E. Smith, and A. F. Vezina (1989), Biological production of the oceans: The case for a consensus, *Mar. Ecol. Prog. Ser.*, *52*, 77–88, doi:10.3354/meps052077.

Roden, G. I. (1970), Aspects of the Mid-Pacific Transition Zone, *J. Geophys. Res.*, *75*, 1097–1109, doi:10.1029/JC075i006p01097.

Roden, G. I. (1974), Thermohaline structure, fronts, and sea-air energy exchange of the trade wind region east of Hawaii, *J. Phys. Oceanogr.*, *4*, 168–182, doi:10.1175/1520-0485(1974)004<0168:TSFASA>2.0.CO;2.

Roden, G. I. (1975), On North Pacific temperature, salinity, sound velocity and density fronts and their relation to the wind and energy flux fields, *J. Phys. Oceanogr.*, *5*, 557–571, doi:10.1175/1520-0485(1975)005<0557:ONPTSS>2.0.CO;2.

Sachs, J. P., and D. J. Repeta (1999), Oligotrophy and nitrogen fixation during eastern Mediterranean sapropel events, *Science*, *286*, 2485–2488, doi:10.1126/science.286.5449.2485.

Saur, J. F. T. (1980), Surface salinity and temperature on the San Francisco-Honolulu route June 1966–December 1970 and January 1972–December 1975, *J. Phys. Oceanogr.*, *10*, 1669–1680, doi:10.1175/1520-0485(1980)010<1669:SSATOT>2.0.CO;2.

Scharek, R., M. Latasa, D. M. Karl, and R. R. Bidigare (1999a), Temporal variations in diatom abundance and downward vertical flux in the oligotrophic North Pacific gyre, *Deep Sea Res. Part I*, *46*, 1051–1075, doi:10.1016/S0967-0637(98)00102-2.

Scharek, R., L. M. Tupas, and D. M. Karl (1999b), Diatom fluxes to the deep sea in the oligotrophic North Pacific gyre at Station ALOHA, *Mar. Ecol. Prog. Ser.*, *182*, 55–67, doi:10.3354/meps182055.

Seki, M. P., et al. (2002), An oceanographic characterization of swordfish longline fishing grounds in the Subtropical North Pacific, *Fish. Oceanogr.*, *11*, 251–266, doi:10.1046/j.1365-2419.2002.00207.x.

Semina, H. J., and S. S. Levashova (1993), The biogeography of tropical phytoplankton species in the Pacific Ocean, *Int. Rev. Gesamten Hydrobiol.*, *78*, 243–262, doi:10.1002/iroh.19930780210.

Subramaniam, A., et al. (2008), Amazon River enhances diazotrophy and carbon sequestration in the tropical North Atlantic Ocean, *Proc. Natl. Acad. Sci. U. S. A.*, *105*, 10,460–10,465, doi:10.1073/pnas.0710279105.

Venrick, E. L. (1974), The distribution and significance of *Richelia intracellularis* Schmidt in the North Pacific central gyre, *Limnol. Oceanogr.*, *19*, 437–445, doi:10.4319/lo.1974.19.3.0437.

Venrick, E. L. (1988), The vertical distributions of chlorophyll and phytoplankton species in the North Pacific central environment, *J. Plankton Res.*, *10*, 987–998, doi:10.1093/plankt/10.5.987.

Venrick, E. L. (1990), Phytoplankton in an oligotrophic ocean: Species structure and interannual variability, *Ecol. Monogr.*, *71*, 1547–1563.

Venrick, E. L. (1997), Comparison of the phytoplankton species composition and structure in the Climax area (1973–1985) with that of ALOHA (1994), *Limnol. Oceanogr.*, *42*, 1643–1648, doi:10.4319/lo.1997.42.7.1643.

Venrick, E. L. (1999), Phytoplankton species structure in the central North Pacific, 1973–1996: Variability and persistence, *J. Plankton Res.*, *21*, 1029–1042, doi:10.1093/plankt/21.6.1029.

Villareal, T. A. (1990), Laboratory culture and preliminary characterization of the nitrogen-fixing *Rhizosolenia-Richelia* symbiosis, *Mar. Ecol. Berlin*, *11*, 117–132, doi:10.1111/j.1439-0485.1990.tb00233.x.

Villareal, T. A. (1991), Nitrogen-fixing by the cyanobacterial symbiont of the diatom genus *Hemiaulus*, *Mar. Ecol. Prog. Ser.*, *76*, 201–204, doi:10.3354/meps076201.

Villareal, T. A., S. Woods, J. K. Moore, and K. Culver-Rymsza (1996), Vertical migration of *Rhizosolenia* mats and their significance to NO_3^- fluxes in the central North Pacific gyre, *J. Plankton Res.*, *18*, 1103–1121, doi:10.1093/plankt/18.7.1103.

Welschmeyer, N. A. (1994), Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments, *Limnol. Oceanogr.*, *39*, 1985–1992, doi:10.4319/lo.1994.39.8.1985.

White, A. E., F. G. Prahl, R. M. Letelier, and B. N. Popp (2007a), Summer surface waters in the Gulf of California: Prime habitat for biological N_2

fixation, *Global Biogeochem. Cycles*, *21*, GB2017, doi:10.1029/2006GB002779.

White, A. E., Y. H. Spitz, and R. M. Letelier (2007b), Whats are driving summer phytoplankton blooms in the North Pacific subtropical gyre?, *J. Geophys. Res.*, *112*, C12006, doi:10.1029/2007JC004129.

Wilson, C. (2003), Late summer chlorophyll blooms in the oligotrophic North Pacific subtropical gyre, *Geophys. Res. Lett.*, *30*(18), 1942, doi:10.1029/2003GL017770.

Wilson, C., and X. Qiu (2008), Global distribution of summer chlorophyll blooms in the oligotrophic gyres, *Prog. Oceanogr.*, *78*, 107–134, doi:10.1016/j.pocean.2008.05.002.

Wilson, C., T. A. Villareal, N. Maximenko, S. J. Bograd, J. P. Montoya, and C. A. Schoenbaechler (2008), Biological and physical forcings of late summer chlorophyll blooms at 30°N in the oligotrophic Pacific, *J. Mar. Syst.*, *69*, 164–176, doi:10.1016/j.jmarsys.2005.09.018.

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