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

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Abstract

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

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1. Introduction

1.1. Physical environment

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

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

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

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

1.2. History of bloom observations

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

Table 1
Summer phytoplankton bloom observations in the NPSG

Date	Location	Dominant organism(s)	Type of observation	Reference
September 1969	27–31°N, 155°W	*Rhizosolenia* w/*Richelia*	Shipboard	Venrick (1974)
September 1969	18–30°N, 155°W	*Hemiaulus*; *Rhizosolenia* w/*Richelia*; *Trichodesmium*	Shipboard	Marumo and Asaoka (1974)
June 1972	Appx. 29°N, 156°W to appx. 31°N, 155°W	*Hemiaulus*; *Rhizosolenia* w/*Richelia*; some *Trichodesmium*	Shipboard	Mague et al. (1974)
June 1972	27–31°N, 155°W	*Rhizosolenia* w/*Richelia*	Shipboard	Venrick (1974)
August 1972	34.5°N, 145.6°W	*Rhizosolenia* w/*Richelia*	Shipboard	Venrick (1974)
October 1972	21.4°N, 158.2°W	*Trichodesmium*	Shipboard	Gundersen et al. (1976)
August–September 1973	Appx. 28°N, 140°W to appx. 23°N, 157°W	*Rhizosolenia* w/*Richelia*; *Trichodesmium*	Shipboard	Mague et al. (1977)
October–December 1981	Satellite Bloom Region[a]	Unknown	Satellite (CZCS)	Wilson et al. (2007)
September 1982	21.3–21.5°N, 158.2–158.8°W	*Hemiaulus* and *Rhizosolenia* w/*Richelia*	Shipboard	Heinbokel (1986)
October–December 1982	Satellite Bloom Region	Unknown	Satellite (CZCS)	Wilson et al. (2007)
September–December 1984	Satellite Bloom Region	Unknown	Satellite (CZCS)	Wilson et al. (2007)
September–December 1985	Satellite Bloom Region	Unknown	Satellite (CZCS)	Wilson et al. (2007)
August 1989	22.8°N, 158.2°W	*Trichodesmium*	Shipboard	Karl et al. (1992)
August 1991	22.75°N, 158°W	*Trichodesmium*	Shipboard	Letelier and Karl (1996)
June 1992	22.75°N, 158°W	*Trichodesmium*	Shipboard	Letelier and Karl (1996)
July 1992	23°N, 158.1°W	*Mastogloia*; *Hemiaulus* and *Rhizosolenia* w/*Richelia*	Deep moored sediment trap	Scharek et al. (1999a)
July–August 1994	23.1°N, 157.9°W	*Mastogloia*; *Hemiaulus* w/*Richelia*	Deep moored sediment trap	Scharek et al. (1999a)
July–August 1994	22.75°N, 158°W	*Mastogloia*; *Hemiaulus* w/*Richelia*; *Trichodesmium*	Shipboard and floating sediment trap	Scharek et al. (1999b)
August 1995	26°N, 159°W	*Mastogloia*; *Hemiaulus* w/*Richelia*	Shipboard	Brzezinski et al. (1998)
August 1995	22.75°N, 158°W	Diatoms	Deep moored sediment trap	This study
July 1996	24.2°N, 157.1°W to 26.4°N, 156.2°W	Diatoms, *Trichodesmium*	Shipboard	Ondrusek and Bidigare (1997); this study
November 1996	Satellite Bloom Region	Unknown	Satellite (OCTS)	Wilson et al. (2007)
June–July 1997	23.5°N, 158.1°W	Unknown	Mooring O_2 sensor at 50 m	Emerson et al. (2002)
July 1997	22.75°N, 158°W	Diatoms	Deep moored sediment trap and benthic respirometer	Smith et al. (2002)
September–October 1997	Satellite Bloom Region	Unknown	Satellite (SeaWiFS)	Wilson (2003), Wilson et al. (2007)
July–August 1998	22.75°N, 158°W	Diatoms	Shipboard, moored sensors and deep moored sediment traps	Letelier et al. (2004); this study
August 1998	22.75°N, 158°W	Diatoms	Deep moored sediment trap and benthic respirometer	Smith et al. (2002)
August 1999	22.75°N, 158°W	Unknown	Satellite (SeaWiFS)	This study
August–September 1999	Satellite Bloom Region	Unknown	Satellite (SeaWiFS)	Wilson (2003), Wilson et al. (2007)
October 1999	22.75°N, 158°W	Unknown	Export based on thorium/uranium disequilibrium	Benitez-Nelson et al. (2001)

Table 1 (*continued*)

Date	Location	Dominant organism(s)	Type of observation	Reference
June–July 2000	22.75°N, 158°W	*Hemiaulus* and *Rhizosolenia* w/*Richelia*; *Mastogloia*; *Trichodesmium*	Shipboard and deep moored sediment trap	Landry (2002), Letelier et al. (2004); this study
June–December 2000	Satellite Bloom Region	Unknown	Satellite (SeaWiFS)	Wilson (2003), Wilson et al. (2007); this study
September–October 2001	22.75°N, 158°W	*Trichodesmium*; diatoms	Shipboard	Landry (2002); this study
June–July 2002	28–31°N, 140–155°W	*Hemiaulus* and *Rhizosolenia* w/*Richelia*	Shipboard	Montoya et al. (2004), Wilson et al. (2007)
July–August 2002	Satellite Bloom Region	Unknown	Satellite (SeaWiFS, MODIS)	Wilson (2003), Wilson et al. (2007)
September 2002	22.75°N, 158°W	Unknown	Satellite (SeaWiFS)	This study
July–September 2003	Satellite Bloom Region	Unknown	Satellite (SeaWiFS, MODIS)	Wilson (2003), Wilson et al. (2007)
August–September 2003	28°N, 172–180°W	*Hemiaulus* w/*Richelia*	Shipboard	Singler and Villareal (2005)
July–September 2004	Satellite Bloom Region	Unknown	Satellite (SeaWiFS, MODIS)	Wilson (2003), Wilson et al. (2007)
July 2005	22.4°N, 157.5°W to 22.8°N, 158.3°W	*Hemiaulus* w/*Richelia*; *Trichodesmium*	Shipboard	Fong (2006); this study
July–August 2005	22.75°N, 158°W	Unknown	Satellite (SeaWiFS)	This study

[a] Satellite Bloom Region denotes irregular area centered along 30°N between about 130–160°W where satellite observations indicate a high frequency of summer bloom occurrences, as described by Wilson et al. (2007) and approximately delineated in Fig. 1.

spring bloom in the lower layer of the euphotic zone (Letelier et al., 2004), but there is no obvious manifestation of this phenomenon in the upper layer.

In the summer, however, surface phytoplankton blooms appear in the NPSG with some regularity (Table 1). Such blooms are typically dominated by microphytoplankton with some degree of buoyancy control; these organisms appear to be limited to a few genera of diatoms and cyanobacteria. From 1969–1988, a handful of shipboard observations of these phenomena were recorded, but research cruises to the NPSG during these years were relatively infrequent and irregularly spaced in time (Table 1). In October 1988, the Hawaii Ocean Time-series (HOT) program was established, with its primary study site at Station ALOHA (22.75°N, 158°W). Since the program's inception, HOT scientists have carried out a suite of physical and biogeochemical measurements throughout the water column at this site at a cruise frequency of more than ten per year (Karl and Lukas, 1996; Karl et al., 2001b). To date, direct HOT observations (shipboard and from moored instruments) have revealed evidence for a summer phytoplankton bloom in 10 of the 17 years from 1989 to 2005. Although the HOT program represents the most intensive effort to study the NPSG ecosystem, a few additional shipboard observations of summer blooms were made by other investigators as well during this timespan (Table 1). In addition to the observations from ships and moorings, satellite ocean color sensors have produced images of these summer blooms with unprecedented detail. These images reveal summer blooms in the NPSG during four of the 6 years from 1979–1985 and during eight of the 10 years from 1996 to 2005 (Table 1; Wilson et al., 2007). All of these bloom observations have been made in the eastern part of the NPSG; curiously, none has been reported from farther west than about 160°W (Fig. 1).

1.3. Nitrogen fixation

The two-layer model of the euphotic zone assumes that the only exogenous source of fixed nitrogen is the deep pool of nitrate, which is brought into the system by mixing, upwelling or entrainment (Dugdale and Goering, 1967; Eppley and Peterson, 1979). Because the surface waters are effectively cut off from this N source, another source of nitrogen must be available to meet the needs of growing phytoplankton within summer blooms. It is therefore not surprising that organisms capable of dinitrogen fixation (*Trichodesmium* and diatoms harboring diazotrophic endosymbionts) are implicated in the majority of bloom observations (Table 1). N_2 fixation is

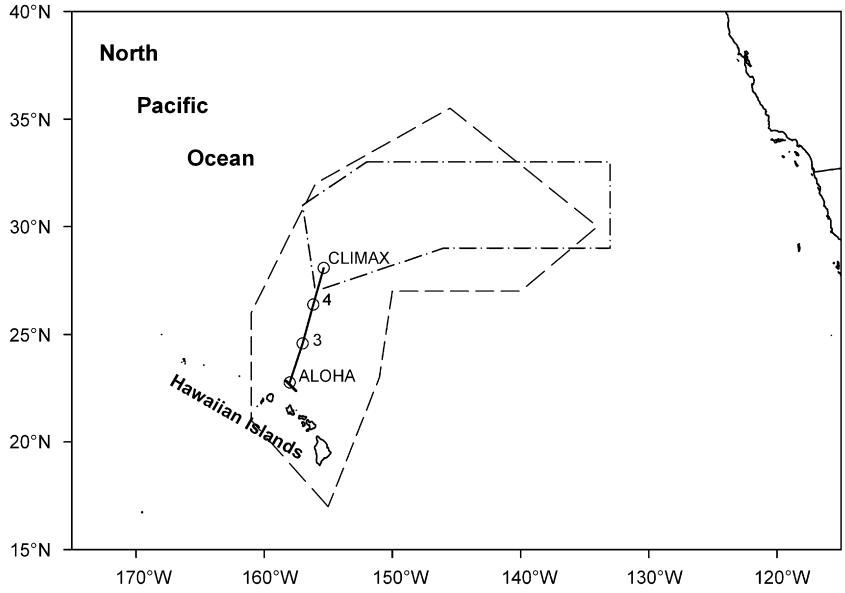


Fig. 1. Map of the eastern subtropical North Pacific Ocean, showing the location of the Hawaiian Islands and the study sites. Open circles denotes stations occupied during the July 1996 AC1 transect (bold line) from Station ALOHA (22.75°N, 158°W) to a station at the center of the CLIMAX region (28°N, 155°W). The July 2005 WHOTS transect is indicated by the short bold line immediately south of Station ALOHA. The narrow dashed line bounds the area which includes all of the summer bloom direct observations listed in Table 1. The narrow dot-dashed line defines the approximate area of most frequent summer sea surface chlorophyll intensifications as detected by satellite ocean color sensors (Wilson et al., 2007).

now recognized as a quantitatively significant source of new nitrogen in tropical and subtropical waters worldwide (Capone, 2001; Karl et al., 2002b; Capone et al., 2005), and several independent lines of evidence indicate that dinitrogen fixation meets approximately half of the new nitrogen demand of the NPSG phytoplankton annually (Karl et al., 1997; Deutsch et al., 2001; Dore et al., 2002). At Station ALOHA, >80% of the N_2 fixation occurs in the upper 60 m, and the highest depth-integrated rates occur in the summer (Dore et al., 2002; Grabowski, 2005). Large (>10 μm) phycoerythrin-containing particles also increase dramatically above 60 m in summer, suggesting that at least part of the summer increase in diazotrophy may be due to *Trichodesmium* and/or cyanobacterial endosymbionts of large diatoms (Dore et al., 2002; Grabowski, 2005). *Trichodesmium* may excrete 80–90% of its recently fixed nitrogen as ammonium (NH_4^+) or dissolved organic nitrogen (DON) compounds (Mulholland and Bernhardt, 2005), thus it may serve as a source of new N for other non-diazotrophic phytoplankton. Nitrogen transfer is similarly thought to occur between *Rhizosolenia* diatom cells with and without the diazotrophic endosymbiont *Richelia intracellularis* (Villareal, 1988).

Another potentially significant source of new fixed nitrogen to the surface layer of the NPSG is associated with certain mat-forming *Rhizosolenia* species that have the capability to vertically migrate to tap nitrate from the nutricline (Villareal et al., 1996; Singler and Villareal, 2005). Although these mats do not appear to be responsible for the observed blooms themselves, they are common in the eastern NPSG (Villareal et al., 1993; Pilskaln et al., 2005) and may contribute to the nitrogenous nutrition of the surface phytoplankton. *Rhizosolenia* mats also may at times harbor endosymbiotic non-pigmented bacteria (Alldredge and Silver, 1982); a report of N_2 fixation by these presumably heterotrophic microorganisms (Martínez et al., 1983) was not corroborated in a subsequent study (Villareal and Carpenter, 1989). At present, the quantitative importance of the net nitrate flux resulting from vertical migrations by *Rhizosolenia* mats is not well constrained.

Although nitrogen fixation can relieve N-limitation of growth by the phytoplankton community, blooms must also be fueled by sources of phosphorus, iron and (in the case of diatoms) silicon. Dissolved iron measurements at Station ALOHA suggest that the near-surface phytoplankton are unlikely to be chronically limited by this element (Johnson et al., 2003; Boyle et al., 2005; Brown et al., 2005). Iron concentrations at this site decrease with depth to a minimum in the lower euphotic zone, and remain less than surface concentrations even at the

depth of greatest observed winter mixing (~130 m), so delivery of new iron is likely not from deep-water but from the atmosphere (Boyle et al., 2005). However, the input of iron from atmospheric dust is spatially and temporally patchy. Hence, surface iron levels at Station ALOHA may not be suitably representative of the entire NPSG in this regard. Also, it is not clear how much of the measured iron is truly bioavailable (Wu et al., 2001).

Dissolved silicate concentrations in surface waters at Station ALOHA are (on a molar basis) 1–3 orders of magnitude larger than either nitrate or phosphate concentrations. Although it is conceivable that silicate could become sufficiently depleted in a dense diatom bloom and limit the maximum biomass achieved, the onset and development of such a bloom is unlikely to be prevented at these silicate concentrations, especially given the relatively low silica quotas of the bloom-forming diatoms (Brzezinski et al., 1998). These observations suggest that any bioelemental limitation to the extent of summer bloom development is likely to be due to insufficient phosphorus and/or iron.

It is also important to consider that the N_2-fixing organisms themselves are often limited in their capability for diazotrophy by the availability of other elements, especially iron and phosphorus (Doremus, 1982; Vitousek and Howarth, 1991; Mills et al., 2004; Grabowski, 2005). Therefore, without a sufficient supply of these two elements, nitrogen limitation of phytoplankton growth may never be alleviated. N_2 fixation is also an energetically costly process (Karl et al., 2002), hence the extent to which cyanobacterial diazotrophs may support the N requirements of the phytoplankton bloom may depend critically on the amount of light energy available to them. Co-limitation by light, Fe and/or P is also possible at different stages of the blooms.

In addition to specific bioelements, trace organic compounds such as B vitamins may in some cases limit the growth of eukaryotic microorganisms including phytoplankton (Provasoli and Carlucci, 1974; Karl, 2002; Croft et al., 2006). For example, many diatoms have an absolute requirement for vitamin B_{12} but lack the ability to synthesize this compound; these phytoplankton may rely on symbiotic relationships with prokaryotes for their vitamin B_{12} supply (Croft et al., 2005), but the quantitative significance of such relationships has been called into question (Droop, 2007). Evidence for stimulation of the growth of large phytoplankton by B vitamins in nutrient-rich temperate and Antarctic coastal waters has been presented (Sañudo-Wilhelmy et al., 2006; Panzeca et al., 2006), but it is not known to what extent B vitamins influence plankton community structure in the usually prokaryote-dominated oligotrophic gyres.

1.4. Metabolic imbalance

Recently, it has been suggested that the euphotic zones of the oceanic gyres are net heterotrophic systems, consuming more organic carbon in respiration than they produce through photosynthesis (del Giorgio et al., 1997; Duarte and Agustí, 1998). Even high-precision time-series measurements of photosynthesis and respiration rates over a complete annual cycle have failed to reach a metabolic balance (Williams et al., 2004). Nevertheless, oxygen and carbon tracer methods (chemical and isotopic) have been used in the NPSG that reveal net autotrophy (Emerson et al., 1997; Quay and Stutsman, 2003; Keeling et al., 2004; Juranek and Quay, 2005). Such tracer methods integrate production and respiration signals over larger space and time scales than do incubation methods, suggesting that the apparent metabolic imbalance between photosynthesis and respiration might be explained in terms of heterogeneity in primary production that is inadequately resolved through bottle sampling (Karl et al., 2003). Short-lived bursts of oxygen production have been observed from moored oxygen sensors at Station ALOHA (Emerson et al., 2002). Some of these are associated with positive sea surface height anomalies and increases in dissolved nitrogen gas, and thus may be influenced by mixing or eddy pumping of nutrients. Others are clearly not so associated; these bursts of productivity could potentially be manifestations of N_2 fixation-supported summer blooms. Moreover, the mismatch between tracer and incubation results is greatest during the summer (Juranek and Quay, 2005), suggesting that patchy distributions of primary production in space and time during summer may prevent us from accurately quantifying the different components of the metabolic budget using discrete sampling approaches.

1.5. What is a summer bloom?

A bloom may be defined as "the rapid growth of one or more species which leads to an increase in biomass of the species" (Richardson, 1997). Unfortunately, it is much more common in practice to observe the result of

a bloom (an area of elevated phytoplankton biomass) than the mechanisms that led to its development. The accumulation of phytoplankton biomass is a result of an imbalance in the tightly coupled rates of production (photosynthesis) and loss (grazing, sinking, and lysis) of phytoplankton cells; such accumulation often represents only a small fraction of the total phytoplankton production that occurs over the course of a bloom (Longhurst, 1998). In many respects, what defines a bloom will depend on what methods were used to observe the bloom. With regard to summer blooms in the NPSG, Wilson (2003) used a definition that was convenient and reasonably unambiguous when applied to a satellite ocean color data set: "sustained chlorophyll values $>0.15\ mg\ m^{-3}$." This definition is problematic when the elevated chlorophyll is found below the first optical depth that is observed by the satellite (about 5–25 m at Station ALOHA, depending mainly on phytoplankton abundance). It also fails to clarify what constitutes "sustained" in the context of the temporal sequence of bloom development, cessation and decay. In this paper we define a bloom as a rapid (days–weeks) increase in observed phytoplankton biomass in the surface ocean ($\leqslant$60 m) relative to the background condition, regardless of the mode of observation. We recognize that an observation of increasing biomass does not necessarily indicate new biomass production, and that the background condition itself is spatially and temporally variable. Also, we will accept that observations based on the export of surface-derived material (e.g., sediment trap collections) are as valuable as surface observations, despite the fact that they sample the removal of the accumulated biomass rather than its growth. We define "summer bloom" as a bloom that is observed in the NPSG during the months of June through September, while recognizing that conspicuous surface accumulations of phytoplankton biomass may sometimes last into December (Table 1).

2. Methods

2.1. Station locations

Most of the data presented in this study were collected at Station ALOHA (22.75°N, 158°W), the benchmark site of the ongoing Hawaii Ocean Time-series (HOT) research program (Fig. 1). This oligotrophic deep-water location lies within the eastern portion of the NPSG. Beginning with the HOT-1 cruise in October 1988, program scientists have visited Station ALOHA approximately ten times annually, completing HOT-176 in December 2005. During each HOT cruise, a suite of physical and biogeochemical measurements are conducted in order to characterize the state of this oceanic ecosystem; repeated observations allow for assessment of ecosystem variability over seasonal to decadal timescales (Karl and Lukas, 1996; Karl et al., 2001b).

Approximately 660 km NNE of Station ALOHA lies the CLIMAX region, a loosely defined area within a few degrees surrounding 28°N, 155°W. From the mid-1960s through the mid-1980s, a number of research expeditions were conducted in this area, providing the first comprehensive description of the NPSG ecosystem (Hayward et al., 1983; Hayward, 1987). In July 1996, HOT program scientists conducted a transect, termed AC1, from Station ALOHA to the nominal center of the CLIMAX region, in order to directly compare the physical and biogeochemical conditions at these two sites in nearly real time. Underway surface ocean data were collected during the cruise, and two intermediate stations in addition to ALOHA and CLIMAX were occupied for full water column sampling.

In July 2005, HOT scientists conducted a short transect near Station ALOHA, from 22.37°N, 157.5°W to 22.83°N, 158.3°W, in order to sample a bloom feature that had been observed in satellite images. This cruise of opportunity is referred to here as the WHOTS transect, because the expedition's primary mission was to recover and redeploy the Woods Hole Oceanographic Institution – Hawaii Ocean Time-series Station mooring.

2.2. Water column continuous profiles

A lowered CTD-rosette package was used to collect continuous profiles of key parameters. The procedures used for calibration of the pressure, conductivity and temperature sensors are described elsewhere (Lukas and Santiago-Mandujano, 1996). Density was determined from conductivity and temperature, and the depth of the surface mixed layer was estimated by determining the depth at which the density differed from the surface density by $0.125\ kg\ m^{-3}$ (Levitus, 1982). From October 1988 to September 2001, induced fluorescence profiles were obtained with a SeaTech flash fluorometer interfaced with the CTD (Winn et al., 1995). This instrument

was replaced in October 2001 with a Seapoint chlorophyll fluorometer. The calibration of the flash fluorometers to yield chlorophyll *a* concentrations is described below. For purposes of presentation, the raw data from all sensors have been averaged into 2 dbar pressure bins from 0 to 200 dbar, and depths have been calculated from pressures assuming a mean density of 1.024 kg m^{-3} throughout this pressure range. A separately lowered Biospherical Profiling Reflectance Radiometer (PRR) was used for measurement of photosynthetically active radiation (PAR; 400–700 nm wavelength) as described in Letelier et al. (2004).

2.3. Water column biogeochemical measurements

The CTD-rosette package included 24 PVC sampling bottles of 12-l capacity for collection of discrete water samples. Subsamples were collected from these for a variety of analyses; HOT sampling strategy and core measurements are described in detail elsewhere (Karl and Lukas, 1996; Karl and Dore, 2001).

Nitrate (plus nitrite) was determined using the chemiluminescence method (Garside, 1982; Dore and Karl, 1996), in order to accurately quantify its concentration at low levels. Phosphate was colorimetrically measured at low levels as soluble reactive phosphorus, using the MAGIC preconcentration method (Karl and Tien, 1992). Particulate biogenic silica (PBSi) was collected on 0.8 μm Nuclepore polycarbonate membrane filters and analyzed colorimetrically after time-course carbonate digestion (DeMaster, 1981; Scharek et al., 1999a).

Primary photosynthetic production was measured by the incorporation of ^{14}C-labeled bicarbonate into particulate matter during dawn-to-dusk *in situ* or simulated *in situ* incubations (Karl et al., 1996; Letelier et al., 1996). Six to eight depths from 5 to 175 m were sampled in triplicate, spiked with a solution of $NaH^{14}CO_3$, incubated and filtered onto Whatman GF/F filters. Trace metal-clean techniques were employed for sampling and incubations. We report primary production as the net carbon incorporation into particulate matter during the daylight period with no dark corrections or other adjustments.

Phytoplankton accessory pigments, including the diatom marker fucoxanthin, were determined by HPLC following acetone extraction of GF/F-filtered samples (Wright et al., 1991; Letelier et al., 1993). Chlorophyll *a* was determined by conventional fluorometry after acetone extraction of GF/F-filtered samples (Strickland and Parsons, 1972; Letelier et al., 1996). This technique also yields a separate estimate of chlorophyll degradation products (''pheopigments'') following acidification of the extracted sample; however, at Station ALOHA the ''pheopigment'' signal is largely due to interference from chlorophyll *b* (Karl et al., 2001c).

The sum of fluorometrically measured extracted ''pheopigments'' and chlorophyll *a*, henceforth termed ''chloropigment,'' describes well the chlorophyll fluorescence signal perceived by the lowered flash fluorometer. We were therefore able to standardize the voltage output of the flash fluorometer to units of chloropigment (mg m^{-3}) through a simple linear calibration. To subsequently convert chloropigment to chlorophyll *a*, we then multiplied the chloropigment derived from the flash fluorometer by the measured ratio of chlorophyll *a* to chloropigment. Unfortunately, at Station ALOHA this ratio varies strongly with depth, somewhat with season, and possibly with changes in fluorometers or fluorometer filters. During each cruise, however, we have been able to utilize a cubic spline interpolation of our discrete measurements of the chlorophyll *a*:chloropigment ratio to produce a vertical profile of this ratio with 2-dbar resolution. We then multiplied these interpolated ratios by the 2 dbar binned chloropigment data from the flash fluorometer, on a cruise-by-cruise basis, to yield high-resolution chlorophyll *a* profiles.

Because chlorophyll *a* profiles during bloom events display spikes that probably correspond to phytoplankton aggregation in distinct layers (Fig. 2), we used the high-resolution data to calculate a chlorophyll *a* profile ''roughness'' index, which serves as a measure of the frequency of such laminae within the surface layer. We call this factor the ''Holm-Hansen Index'' (HHI), after O. Holm-Hansen, who introduced us to its utility. It is calculated by taking the mean of the absolute differences in chlorophyll *a* concentration between adjacent 2 dbar bins from 0 to 46 dbar. Normalizing this mean absolute concentration difference (in mg m^{-3}) to the thickness of the bin (approximately 2 m) yields the HHI (in mg m^{-4}).

2.4. Sediment trap collections

The flux of sinking particles was sampled at 4000 m using moored PARFLUX MK 7-21 time-sequencing sediment traps (0.5 m^2 aperture). The exact locations of the sediment trap mooring deployments varied, but

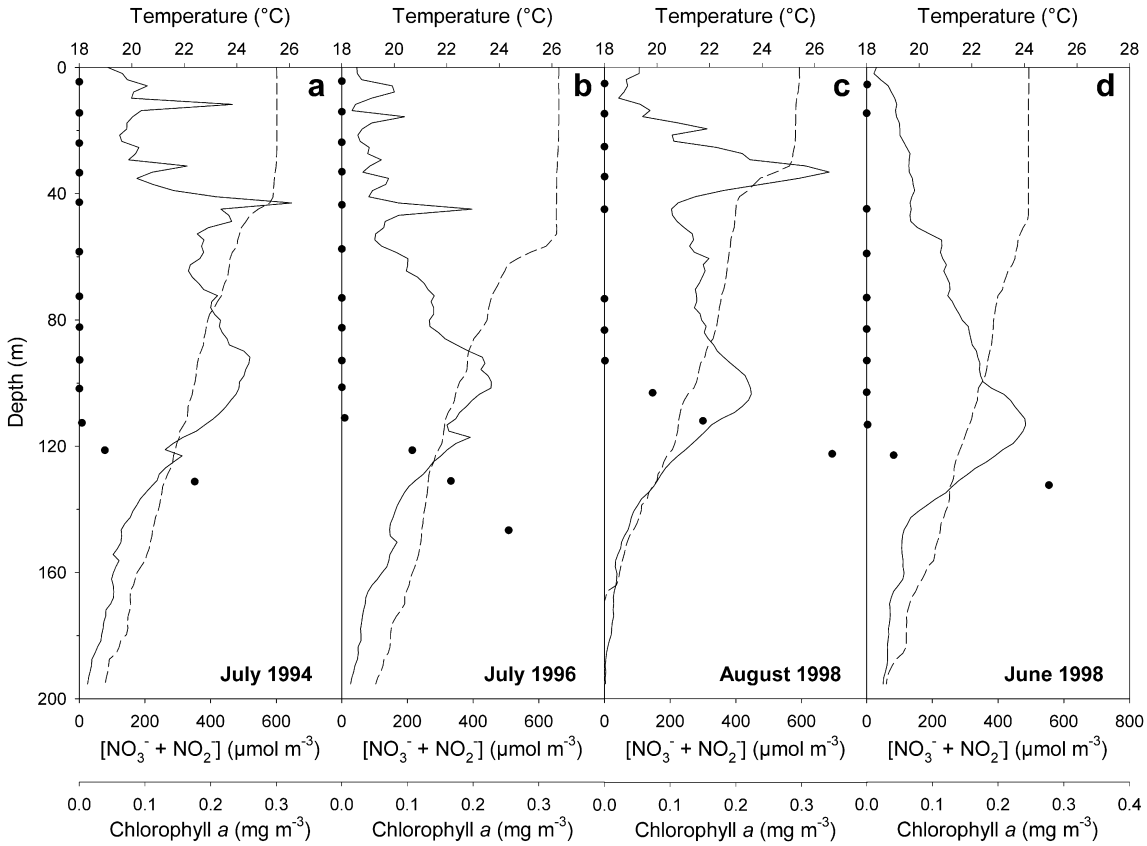


Fig. 2. Depth profiles of selected water column parameters in summer at Station ALOHA. Three profiles (a–c) are shown which display near-surface blooms as evidenced by laminae of elevated chlorophyll *a* concentrations (solid lines). A pre-bloom example (d) is shown for comparison. Temperature and nitrate concentration are indicated by dashed lines and solid symbols, respectively.

were always within 10–40 km of Station ALOHA and >100 km north of the Hawaiian Islands. Data presented here are from nine deployments spanning the period from September 1993 through June 2003. The 21 formalin-preserved collections from each trap deployment were split and subsampled as described in Karl et al. (1996) and Scharek et al. (1999a). Individual samples represent collection periods of 15–18 days in duration, except in summer 1995 when each collection period was only 7 days. PBSi was analyzed as described above for water column samples. Particulate carbon (PC) was determined on GF/F-filtered samples by combustion and gas chromatography using a conventional CHN analyzer. Particulate inorganic carbon (PIC) was determined on replicate filters by direct acidification and infrared detection of the liberated CO_2 with a LI-COR detector. Particulate organic carbon (POC) was calculated by difference (POC = PC − PIC). No correction was made for possible solubilization of the analytes into the buffered formalin solution, thus the fluxes presented here should be considered minimum estimates.

2.5. Towed and moored sensors

During the AC1 transect, a towed package (Endeco fin) was deployed at 45 m. This package included an optical plankton counter and a WETStar minifluorometer, as described in detail by Huntley et al. (2006). Data from the fluorometer were calibrated with bottle chlorophyll *a* samples collected at three stations along the transect, using the calibration method described above for the lowered flash fluorometers.

Temperature and optical data from the summer 1998 deployment of an instrumented full-ocean depth mooring (HALE–ALOHA; Letelier et al., 2000) are also presented here. Temperature was measured by thermistors placed at eleven depths between 2 m and 149 m. A Satlantic downwelling irradiance spectroradiometer,

attached to the mooring at 25 m depth, was used to estimate the mean 0–25 m chlorophyll *a* concentrations as described in Letelier et al. (2000). Bottle chlorophyll *a* samples from six HOT cruise occupations of Station ALOHA during the deployment period were used to validate the chlorophyll *a* calibration.

2.6. Remote sensing and climatology

Surface chlorophyll *a* images from the SeaWiFS satellite ocean color sensor were obtained from the NASA Level 3 browser (http://oceancolor.gsfc.nasa.gov/cgi/level3.pl). Surface chlorophyll data for the region surrounding Station ALOHA were derived using the SeaWiFS OC4 chlorophyll algorithm (O'Reilly et al., 1998).

Climatological nitrate and phosphate data were obtained from NOAA/NODC (http://www.nodc.noaa.gov/) using the World Ocean Atlas 2001 database (Conkright et al., 2002). Climatological mixed layer depths (based on density) were also obtained from NOAA/NODC using the Monterey and Levitus (1997) compilation. The climatological data were analyzed and plotted using the Ocean Data View software (Schlitzer, 2002; http://odv.awi-bremerhaven.de/home.html).

3. Results

3.1. Vertical and spatial distributions

The vertical distribution of chlorophyll *a* at Station ALOHA is typical of oligotrophic open ocean waters, with relatively low surface concentrations and a persistent chlorophyll maximum layer in the lower euphotic zone. During nearly every summer since the HOT program began making observations, discrete layers of elevated chlorophyll *a* have appeared in the upper water column. These bands are often numerous and typically range from <2 to a few meters thick, but sometimes they may form a single layer up to 50 m thick, with peak concentrations exceeding those of the deep chlorophyll maximum. Example "bloom" profiles from 1994, 1996 and 1998 (Fig. 2a–c) may be compared with a "pre-bloom" profile from 1998 (Fig. 2d). Although the highest chlorophyll concentrations in such blooms are usually associated with the base of the mixed layer, those at the surface may also be elevated above pre-bloom levels. These summer chlorophyll accumulations are positioned above 80 m, in the zone of depleted nitrate.

Surface chlorophyll was also measured at 45 m depth using an underway system on a transect from Station ALOHA to Station CLIMAX at 28°N in July 1996. During this transect, a large bloom was encountered, at least 250 km across (Fig. 3). Phytoplankton pigment analyses conducted at two stations within the bloom revealed high levels of the marker pigment fucoxanthin, suggesting diatom dominance (Ondrusek and Bidigare, 1997); however, visual inspection of net tow collections also revealed a conspicuous presence of *Trichodesmium*. The underway 45 m chlorophyll varied by up to an order of magnitude within the bloom, and revealed considerable spatial heterogeneity. Water column chlorophyll *a* profiles through the bloom showed that the vertical distribution of chlorophyll *a* could be quite different between stations with similar surface values. Chlorophyll *a* levels at 45 m were about 200% of surface values at Station 3, yet only about 20% of surface values at Station 4 (Fig. 3).

3.2. Temporal evolution and demise

The SeaWiFS satellite ocean color sensor, launched in August 1997, has revealed approximately fivefold variability in surface chlorophyll *a* at Station ALOHA (Fig. 4). Note that these data represent 8-day averages over a 729 km^2 area, thus the observed variability is not due to small patches or thin filaments of enhanced surface phytoplankton biomass. Winter increases in chlorophyll *a* are likely due to a combination of photoadaptation of phytoplankton (Winn et al., 1995) and growth following stochastic mixing events that bring nutrients up from depth (Karl et al., 2001a). However, in summer, cellular chlorophyll *a* quotas are at their minimum and the water column is highly stratified below a shallow mixed layer, hence the peaks in surface chlorophyll *a* detected around Station ALOHA each summer from 1998 to 2005 are enigmatic. Several of these summer maxima rival the largest winter chlorophyll *a* peaks, particularly those in 1999, 2000, 2002 and 2005. Shipboard sampling during HOT cruises was generally successful at capturing the chlorophyll *a*

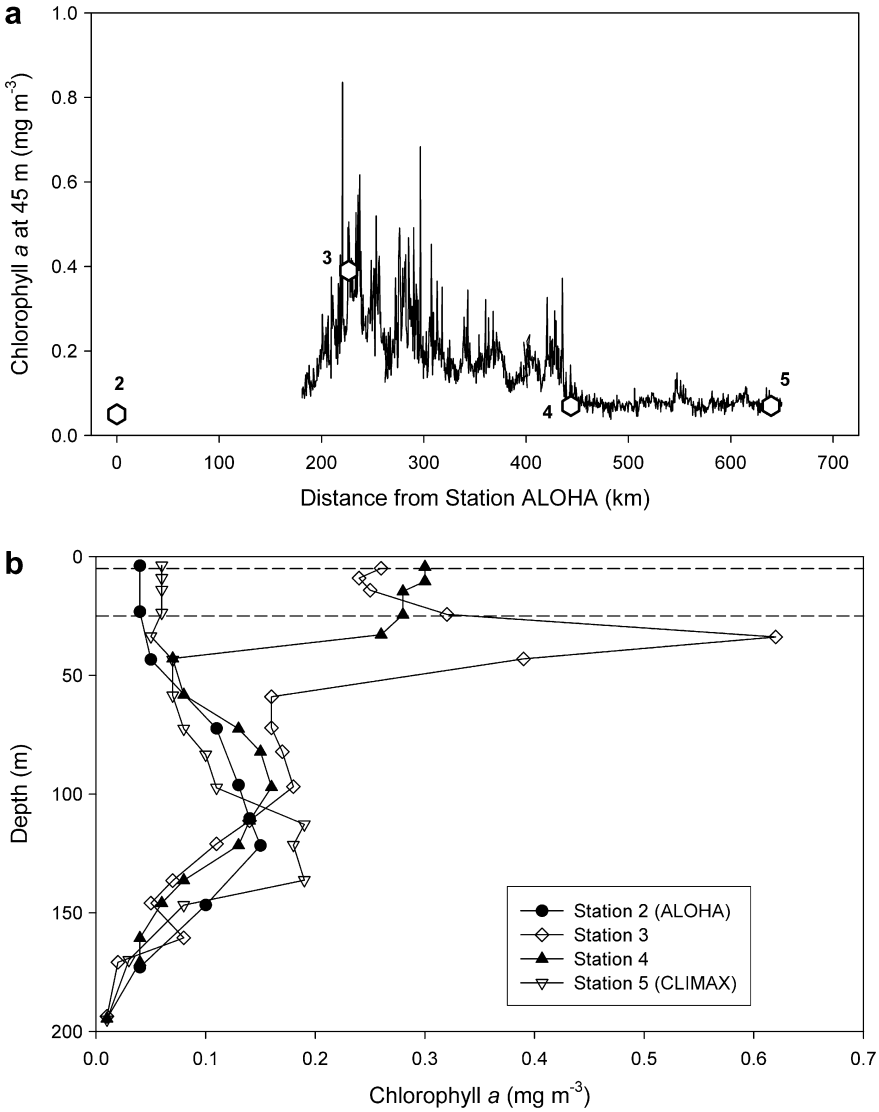


Fig. 3. Chlorophyll *a* concentrations along the July 1996 AC1 transect. (a) Underway towed sensor measurements of chlorophyll *a* at a depth of 45 m from 24.2°N to 28.1°N; bloom conditions were present over at least 250 km of the transect. Symbols indicate bottle chlorophyll *a* data collected during station occupations and used for sensor calibration (see Section 2). (b) Water column profiles of chlorophyll *a* concentration at four stations occupied along the transect. Station numbers correspond to those shown in panel (a) and in Fig. 1. The dashed lines at 5 and 25 m indicate approximately the range of the first optical depth in Station ALOHA waters during high and low surface chlorophyll *a* conditions, respectively; this depth defines the base of the layer observable by satellite ocean color sensors.

variability, however, short-lived peaks were sometimes missed when cruise spacing was too broad, such as in September 2002 (Fig. 4). Conversely, shipboard collections sometimes indicated large chlorophyll *a* peaks that were not detected by the satellite, as seen in September 1998. Such a situation could be the result of a small spatial scale of the feature sampled from the ship, and/or it could be due to the majority of the phytoplankton biomass residing below the first optical depth perceived by the satellite.

Summer blooms display complex spatial patterns as they evolve over time. The evolution of the 2000 NPSG bloom (at least the surface manifestation thereof) was well documented by the SeaWiFS satellite ocean color sensor and may serve as an example of a bloom cycle (Fig. 5). Not visible in May, the 2000 bloom began to develop near Station ALOHA in June, and through July it spread across a large area to the north, east and south of the main Hawaiian Islands. In August, the bloom diminished in this area but began to intensify

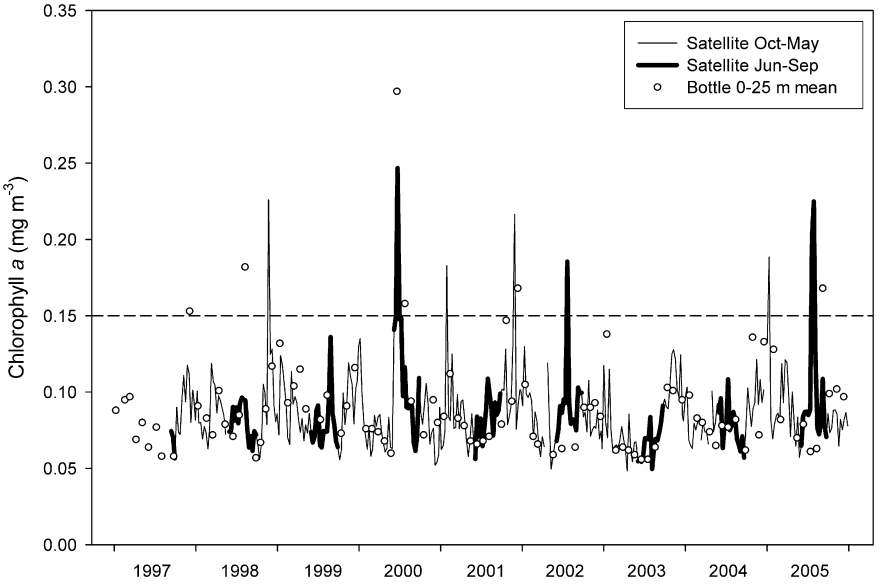


Fig. 4. Comparison of remotely sensed surface chlorophyll *a* with bottle measurements at Station ALOHA, 1997–2005. Solid lines indicate 8-day moving averages of data from the SeaWiFS satellite ocean color sensor for a 27 km × 27 km square centered on the station. Bold and narrow lines represent the June–September and October–May seasonal periods, respectively. Open circles indicate HOT cruise mean values in the upper 25 m during each station occupation. The horizontal dashed line indicates the 0.15 mg m^{-3} chlorophyll *a* threshold for defining bloom conditions from satellite data proposed by Wilson (2003).

farther to the northeast, centered at approximately 30°N, 152°W. The bloom reached its peak surface expression in September–October, and had a total area (defined by surface chlorophyll >0.15 mg m^{-3}) of some 148,000 km^2 (Fig. 5; Wilson, 2003). Through November and December, the bloom gradually dissipated. Shipboard observations at Station ALOHA in June and July revealed that the 2000 bloom was dominated by diatoms (*Hemiaulus* and *Rhizosolenia)*, which harbored the diazotrophic cyanobacterial endosymbiont *Richelia* (Table 1).

3.3. Biomass and production

Depth profiles of chlorophyll *a* from three HOT cruises spanning a summer bloom occurrence (May, June and July 2000) reveal large temporal changes during bloom development and decay (Fig. 6a). The buildup of phytoplankton biomass in the upper 60 m from 23 May to 20 June resulted in a significant reduction in light penetration to the lower euphotic zone (Fig. 6b). The position of the deep chlorophyll maximum layer (DCML) correspondingly shoaled and chlorophyll *a* at depths below the DCML declined. By the decaying phase of the bloom (26 July), the DCML had shoaled by some 60 m, while light penetration was increasing as the bloom itself had begun to diminish in the surface layer. Largely due to these temporal changes in chlorophyll *a* distributions both in the upper and lower euphotic zones, the total euphotic zone (0–180 m) integrated chlorophyll *a* was not linearly related to surface or maximum chlorophyll *a* levels. Compared to the pre-bloom condition (23 May), the euphotic zone integrated chlorophyll *a* was elevated by only 52% on 20 June (mid-bloom) and by only 5% on 26 July (late-bloom).

In order to evaluate the full magnitude of NPSG bloom events on phytoplankton biomass levels, we compared the available full euphotic zone (0–180 m) water column bottle chlorophyll *a* data with bottle data more representative of what might be sensed by satellites (mean 0–25 m) or a towed sensor (45 m). We extended the Station ALOHA data set by including information from both the 1996 AC1 transect and the 2005 WHOTS transect (the latter deliberately sampled within and outside of a summer bloom near Station ALOHA). The combined data set revealed a nonlinear relationship between surface chlorophyll *a* (either mean 0–25 m or 45 m) and total euphotic zone chlorophyll *a* (Fig. 7a and b). A similar relationship was found between surface

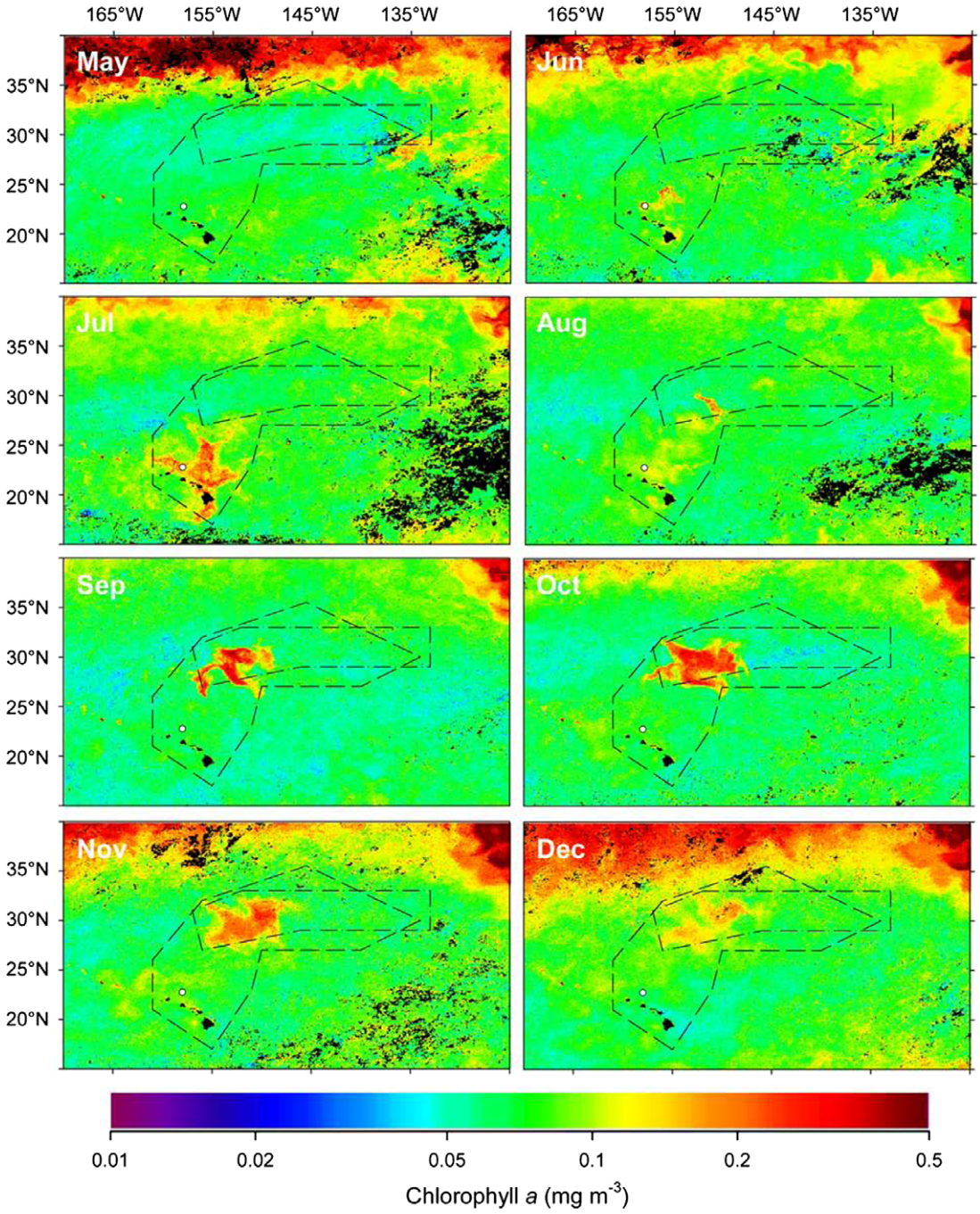


Fig. 5. Surface chlorophyll *a* images from the SeaWiFS satellite ocean color sensor documenting the development and demise of the 2000 summer bloom. Each panel presents the mean condition for the calendar month shown within the area bounded by 15–40°N and 125–170°W. Direct shipboard observations were made of the bloom, dominated by diatoms of the genera *Hemiaulus* and *Rhizosolenia*, in June and July at Station ALOHA (indicated by the white circle). The seasonally varying boundary between high and low chlorophyll *a* seen north of 35°N is the transition zone chlorophyll front between the subtropical and subpolar North Pacific Gyres (Polovina et al., 2001). The dashed and dot-dashed lines indicate the historical bloom observation area and the satellite high-frequency bloom detection area, respectively, as presented in Fig. 1.

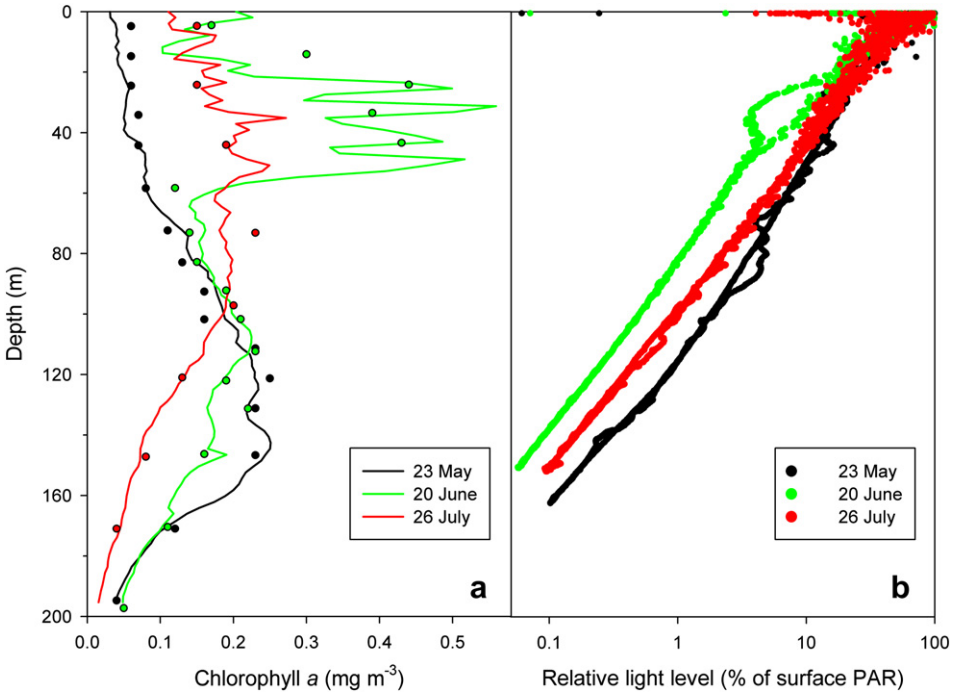


Fig. 6. Progression of the 2000 summer bloom and its effect on light penetration. (a) Water column profiles of chlorophyll *a* from three HOT cruises representing pre-bloom, mid-bloom and late-bloom conditions. Lines indicate continuous chlorophyll *a* profiles determined from flash fluorescence with approximately 2 m vertical resolution. Symbols of corresponding color denote bottle chlorophyll *a* samples collected during each cruise and used to calibrate the sensor (see Section 2). (b) Vertical profiles of relative light penetration measured as the percent of surface photosynthetically active radiation (PAR) reaching a given depth. Symbol colors match corresponding chlorophyll *a* profiles in panel (a). Both downcast and upcast data are shown. Shadows from the ship's superstructure reaching the deck sensor created much of the variability between upcast and downcast profiles seen in the 23 May data, while the deviation between profiles seen at about 20–40 m on 20 June is likely the result of phytoplankton patchiness.

chlorophyll *a* and total euphotic zone primary production (Fig. 7c and d), though fewer productivity data than chlorophyll *a* data were available for defining the full range of values.

3.4. Export

The various time-series records at Station ALOHA allow us to compare surface expressions of summer blooms with their impact on the export of bioelements to the deep sea. The presence of distinct phytoplankton strata associated with summer blooms (Fig. 2) can to an extent be quantitatively assessed, by looking to the variability of chlorophyll *a* between depths in flash fluorometer profiles collected during HOT cruises. The time-series of the 0–45 m chlorophyll *a* profile roughness index (Holm-Hansen Index, or HHI; see Section 2) reveals distinct summer peaks during most of the years of observation (Fig. 8a). Because of a change in fluorometer to a more sensitive instrument, the "background" HHI signal is noisier from October 2001 onward (Fig. 8a); however, the 2 dbar binning of the data ensures that the presence of thicker laminae associated with blooms stands out above such noise. The most conspicuous of the summer HHI peaks occurred in 1989, 1992, 1994, 1996, 1998, 2000, 2001 and 2005. The presence of elevated fucoxanthin (Fig. 8b) and particulate biogenic silica (PBSi; Fig. 8c) coincident with the 1998, 2000, 2001 and 2005 HHI peaks suggests that at least in these summers, diatoms were a significant component of the 0–45 m phytoplankton.

Bottom-moored sediment traps were used to collect sinking particles at 2800 and 4000 m at Station ALOHA. From 1994 to 2002, the fluxes of PBSi measured at 4000 m revealed summer maxima in each year except 1999 (Fig. 8d). Fluxes of particulate organic carbon (POC) displayed a nearly identical pattern

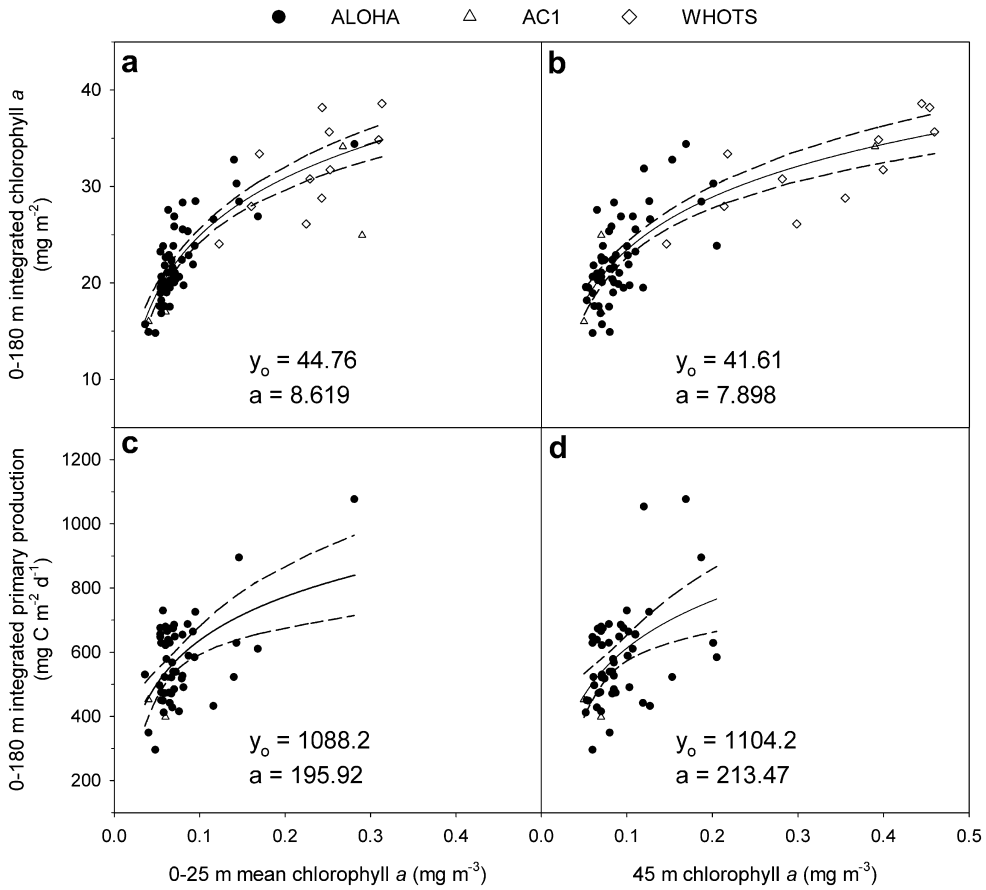


Fig. 7. Relationships between surface chlorophyll *a* and depth-integrated (0–180 m) euphotic zone chlorophyll *a* and primary productivity during summer (June–September). Data included are from HOT program summer occupations of Station ALOHA during 1989–2005 (filled circles), the July 1996 AC1 transect (open triangles) and the July 2005 WHOTS transect (open diamonds). (a and b) Euphotic zone depth-integrated chlorophyll *a* as a function of mean surface (0–25 m) and 45 m chlorophyll *a*, respectively. (c and d) Euphotic zone depth-integrated primary productivity as a function of mean surface (0–25 m) and 45 m chlorophyll *a*, respectively. Panels (a) and (c) relate total euphotic zone properties to the chlorophyll *a* that would be determined from satellite observations (see Figs. 4 and 5), while panels (b) and (d) relate these properties to the chlorophyll *a* that would be detected by the towed sensor used along the AC1 transect (see Fig. 3). The curve fits to the data are of the form $y = y_0 + a * \ln(x)$ and are all highly significant ($P < 0.001$). Dashed lines indicate the 5% and 95% confidence limits for the regressions. Note that no primary productivity measurements were made on the WHOTS transect nor at Stations 3 and 4 of the AC1 transect.

(Fig. 8e), suggesting that diatoms contribute to the organic carbon reaching the deep sea during summer. An especially large export pulse in 2000 was nearly coincident in time with the surface bloom expressions. This export pulse of fresh phytodetritus was collected at 2800 m (data not shown) and 4000 m simultaneously (15.75 days resolution), demonstrating rapid settling at >76 m d^{-1}.

3.5. Energetics

The energy required for rapid phytoplankton growth is solar, hence phytoplankton blooms are usually associated with shallow mixed layers. Using only summer (June–September) data from Station ALOHA, we plotted the total chlorophyll *a* in the upper layer (0–80 m) against the depth of the surface mixed layer (Fig. 9a). Although the actively mixing layer may be shallower at any given time than the well-mixed layer, we used the latter in our analysis, because the timescale of bloom development (days–weeks) should be long enough to average out the potential effects of daily variations in mixing depth on phytoplankton production (Brainerd and Gregg, 1995). Furthermore, because the mean daily incident light at the sea surface is fairly

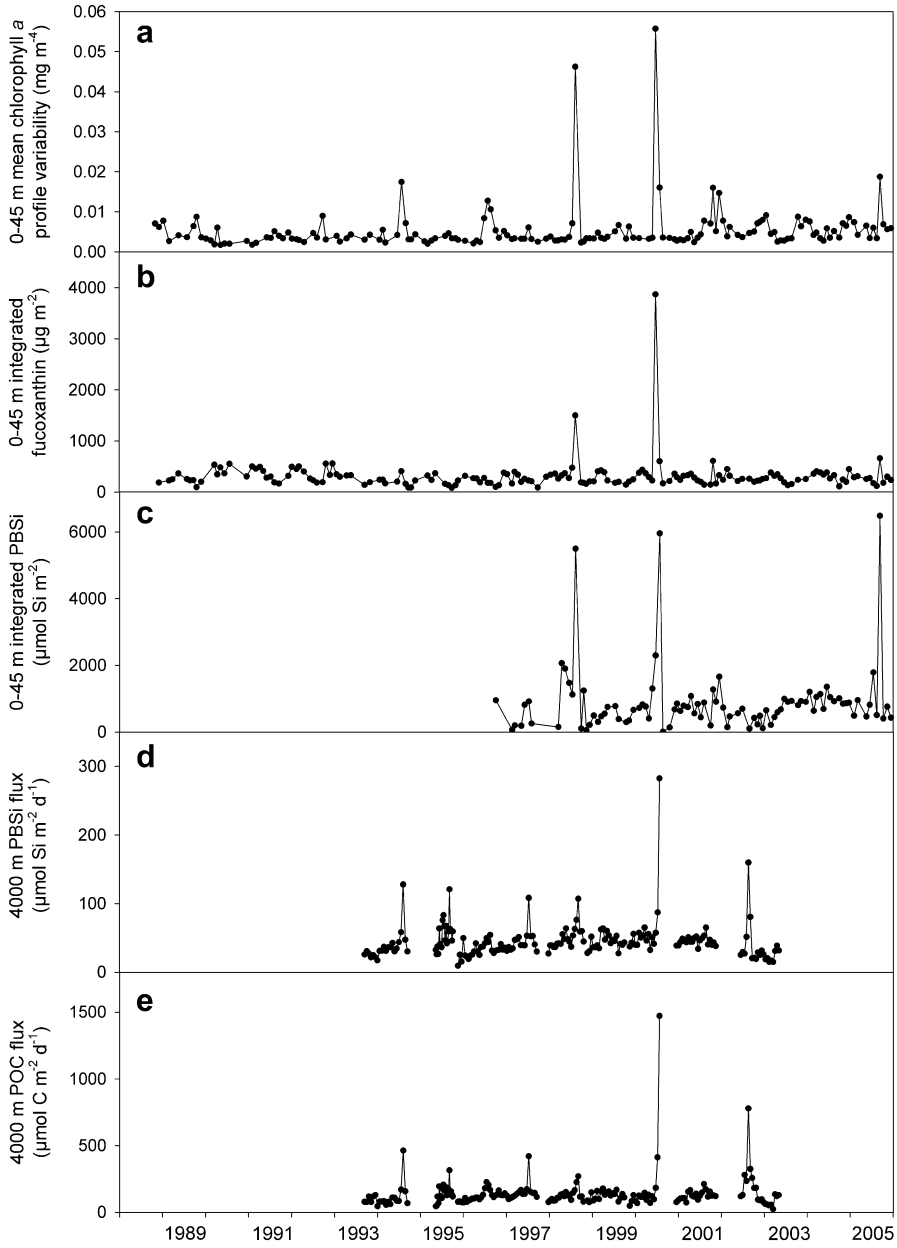


Fig. 8. Time-series of selected parameters at Station ALOHA, October 1988 to December 2005. (a) Mean depth variability in chlorophyll *a* concentration within the upper 45 m of the water column (Holm-Hansen Index; see Section 2). High values indicate the presence of distinct layers of elevated phytoplankton biomass within this upper zone. (b) Concentration of fucoxanthin, a diatom accessory pigment, integrated over the upper 45 m. (c) Concentration of particulate biogenic silica, integrated over the upper 45 m. (d and e) Fluxes of particulate biogenic silica and particulate organic carbon, respectively, captured at 4000 m with bottom-moored time-sequencing sediment traps. Each point is derived from a 15- to 18-day collection period, beginning on the date indicated, except in summer 1995 when each collection period was only 7 days in duration.

constant over the summer months (Letelier et al., 2004), mixed layer depth can be used as a relative measure of light availability to the mixed layer phytoplankton. The data appear to cluster into two groups. During cruises where high chlorophyll *a* was present, the chlorophyll *a* was inversely proportional to mixed layer depth (Fig. 9a). Among summer observations with low chlorophyll *a*, no relationship between chlorophyll *a* and mixed layer depth was apparent.

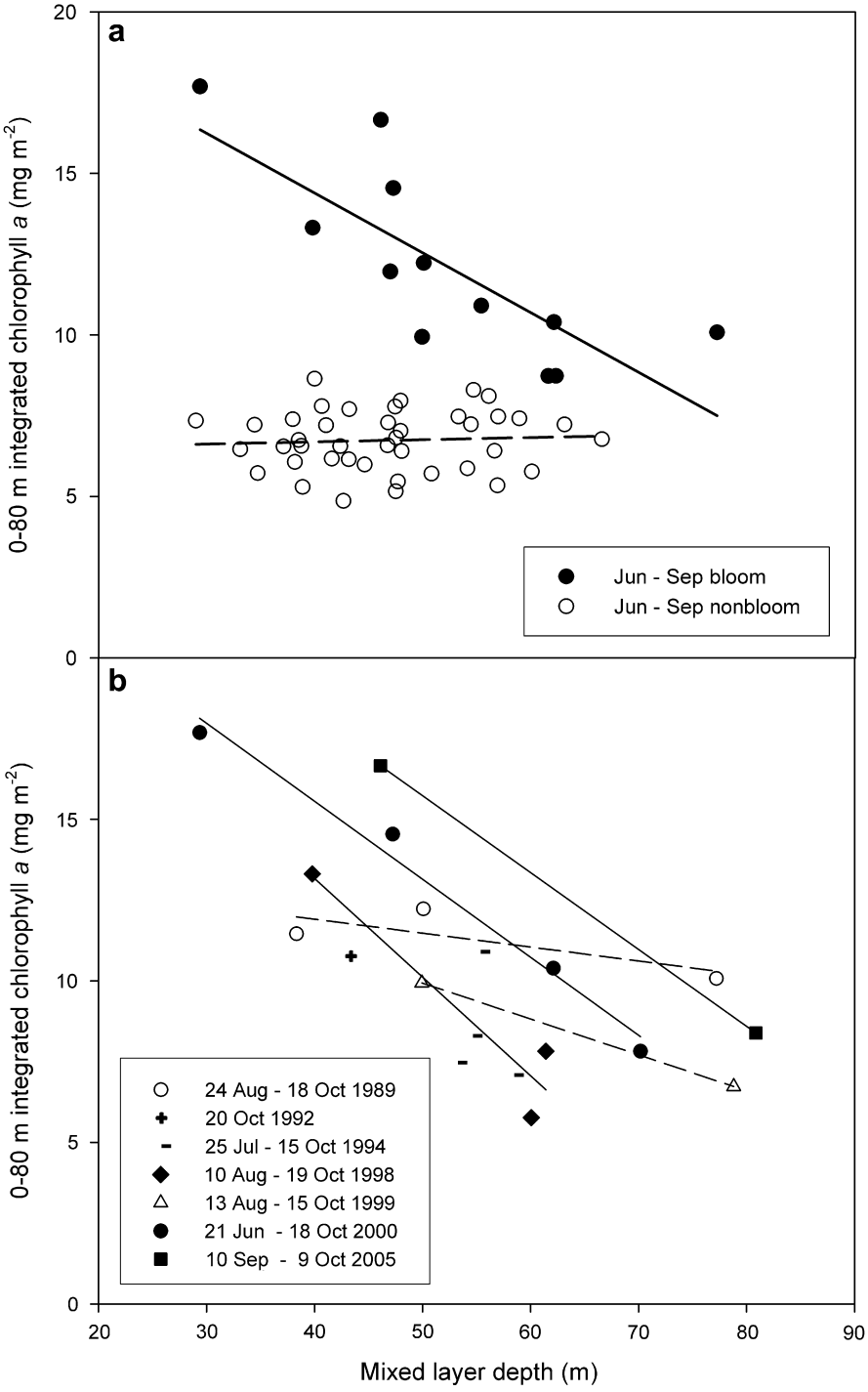


Fig. 9. Upper euphotic zone (0–80 m) chlorophyll *a* as a function of summer mixed layer depth at Station ALOHA, 1989–2005. (a) Data from June–September only, revealing two distinct relationships between chlorophyll *a* and mixed layer depth. Solid circles are considered to represent "bloom" conditions based upon an arbitrary minimum 0–80 m chlorophyll *a* value of 8.7 mg m^{-2}. Open circles similarly represent "non-bloom" summer conditions. (b) Data from the measured bloom maximum through the end of October for the seven "bloom" years in (a). In five cases, 0–80 m chlorophyll *a* declines with increasing mixed layer depth. Open and closed symbols represent blooms believed to be dominated by *Trichodesmium* and diatoms, respectively. Data from 1992 and 1994 are indicated by + and − symbols, respectively.

The data points within the high chlorophyll *a* cluster represent cruises conducted during only seven summers: 1989, 1992, 1994, 1998, 1999, 2000 and 2005. We plotted the 0–80 m integrated chlorophyll *a* during these years against mixed layer depth, from the time of maximum observed chlorophyll *a* through the end of October, in order to investigate the role of deepening mixed layers on the progression of the blooms (Fig. 9b). Decreases in chlorophyll *a* were observed with deepening mixed layer in five of the cruises examined (Fig. 9b). The slopes of the lines fit to these data were nearly identical in 1998, 2000 and 2005, but were less steep in 1989 and 1999. No linear regression was possible for 1992 because the maximum chlorophyll *a* was

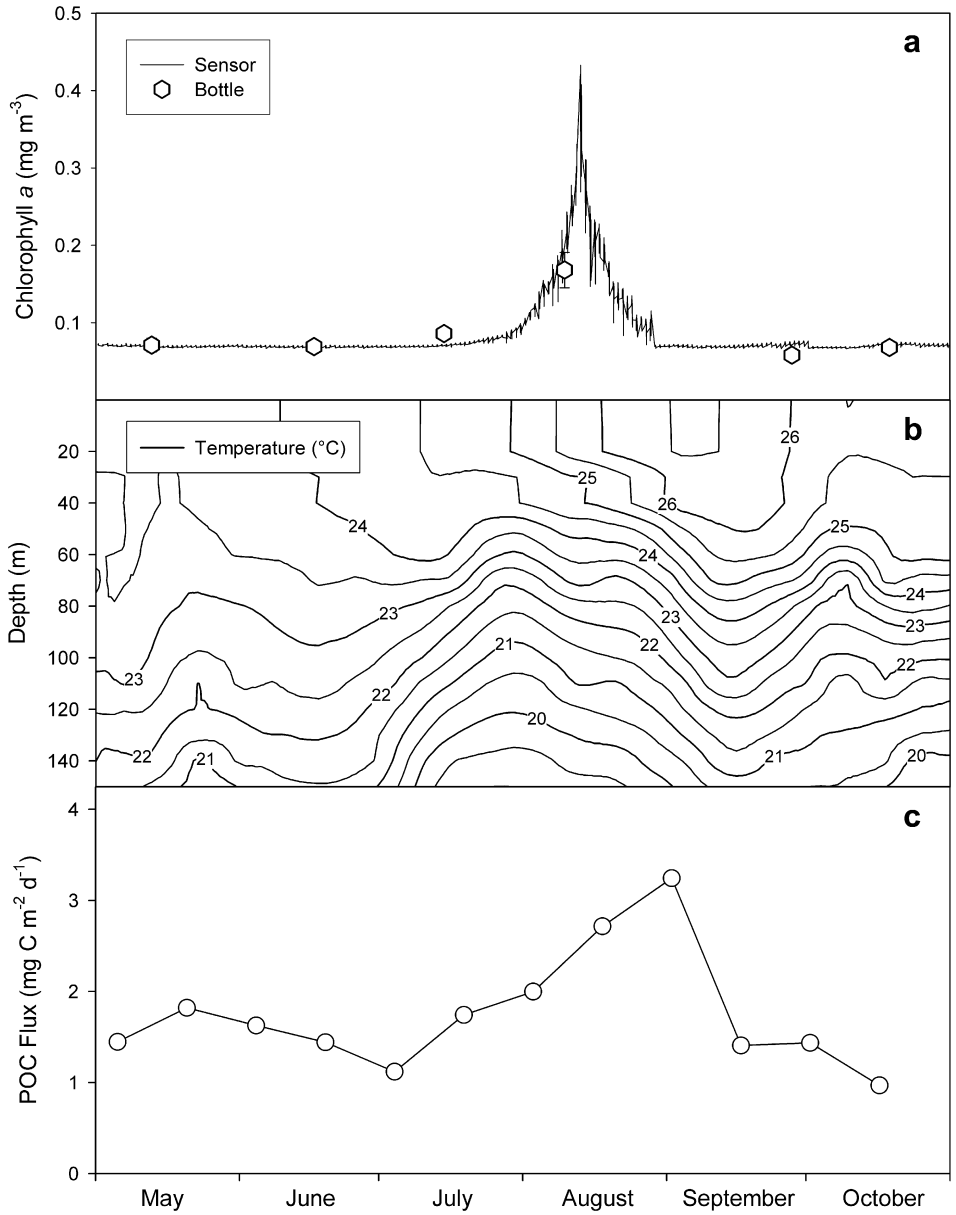


Fig. 10. Temporal evolution and impact of a cyclonic eddy at Station ALOHA during summer 1998. (a) Mean surface chlorophyll *a*. Line represents mean 0–25 m chlorophyll *a* concentration estimated from light measurements using a moored spectroradiometer. Symbols are mean (±sd) of 0–25 m bottle chlorophyll *a* measurements made during HOT cruises and were used to calibrate the sensor (see Section 2). (b) Temperature distribution in the upper 150 m, revealing the doming of isotherms during June–September. (c) Flux of particulate organic carbon collected at 4000 m with a bottom moored time-sequencing sediment trap. Each data point is derived from a 15-day collection period beginning on the date indicated.

not observed until October, and the 1994 data were omitted from the analysis because the mixed layer depths over the period of interest varied only by 5 m or less.

3.6. Influence of eddies

In 1998, instruments aboard the HALE–ALOHA mooring documented the passage of a cyclonic mesoscale eddy through Station ALOHA (Fig. 10). Beginning in late July, mean 0–25 m chlorophyll *a* increased within a few weeks to >0.3 mg m^{-3}, and then as quickly declined to background levels by the end of August (Fig. 10a). The onset of the rapid chlorophyll *a* increase began at the same time that maximum doming of the thermocline was observed, yet the 45–75 m layer remained stratified throughout the passage of the eddy (Fig. 10b). The development of the 1998 summer bloom therefore appears to have been influenced by the eddy, but it is not clear whether significant physical entrainment of nutrients into the mixed layer occurred during the passage of the eddy. The resulting export flux of POC was captured at 4000 m, mostly in August and early September (Fig. 10c).

3.7. P supply mechanisms

Both deep winter mixing and mesoscale features may bring nutrients into the upper euphotic zone in the NPSG. However, the source waters that are tapped via these mechanisms are highly depleted in nitrate,

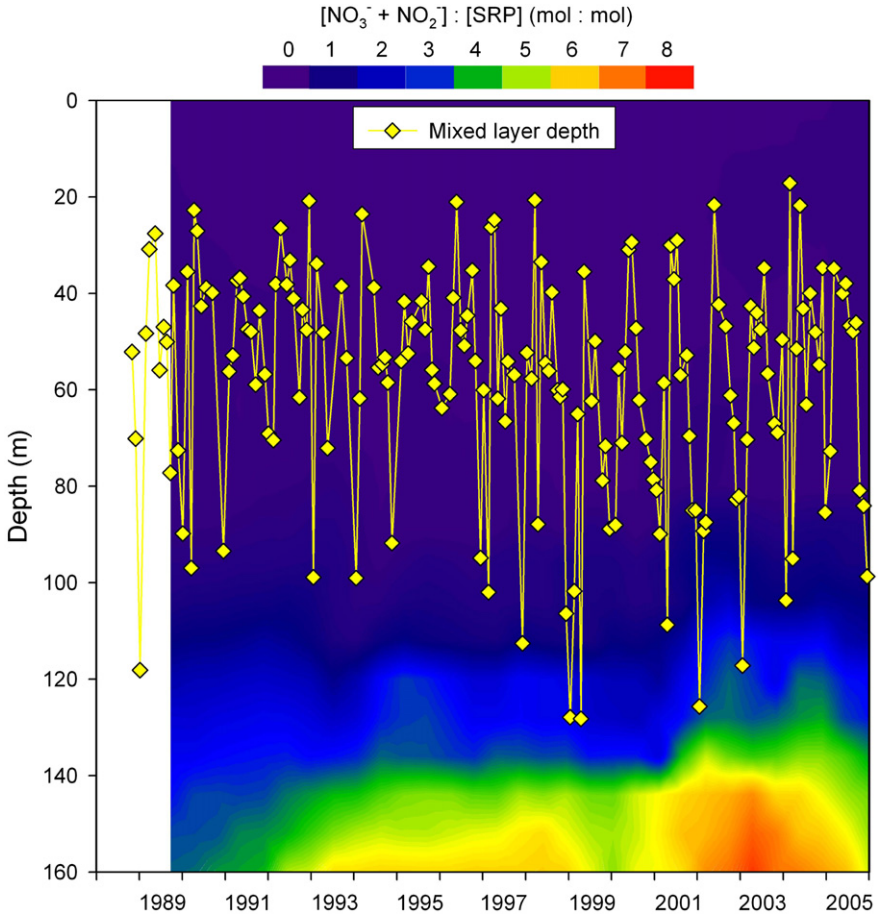


Fig. 11. Distribution of the molar nitrate:phosphate ratio in the upper 160 m at Station ALOHA from 1989 to 2005. Low-level nitrate measurements did not commence until September 1989. Superimposed in yellow symbols are the mean mixed layer depths encountered on each HOT cruise from October 1988 through December 2005.

especially when considered relative to balanced growth at the Redfield molar N:P ratio of 16. From 1989 to 2005 at Station ALOHA, measured nitrate:phosphate ratios in the upper 80 m rarely exceeded 1, and were usually <0.2 mol mol^{-1} (Fig. 11). At the depth of deepest winter mixing, the nitrate:phosphate ratio was seldom >3 mol mol^{-1}, and was most often considerably less. Bringing isopycnals up 50 m or more, such as in the 1998 eddy (Fig. 10), would similarly bring nitrate and phosphate to the upper layer in a very low molar proportion. During the entire period of observation, therefore, nutrient delivery from depth represented a more important source of new P than of new N, relative to cellular needs.

To look more closely at the delivery of phosphate to the upper layer of the euphotic zone at Station ALOHA, the climatologies of mixed layer mean temperature and depth and phosphate concentration in the 60–80 m layer were determined from the HOT data set (Fig. 12). The annual cycle of the 60–80 m mean

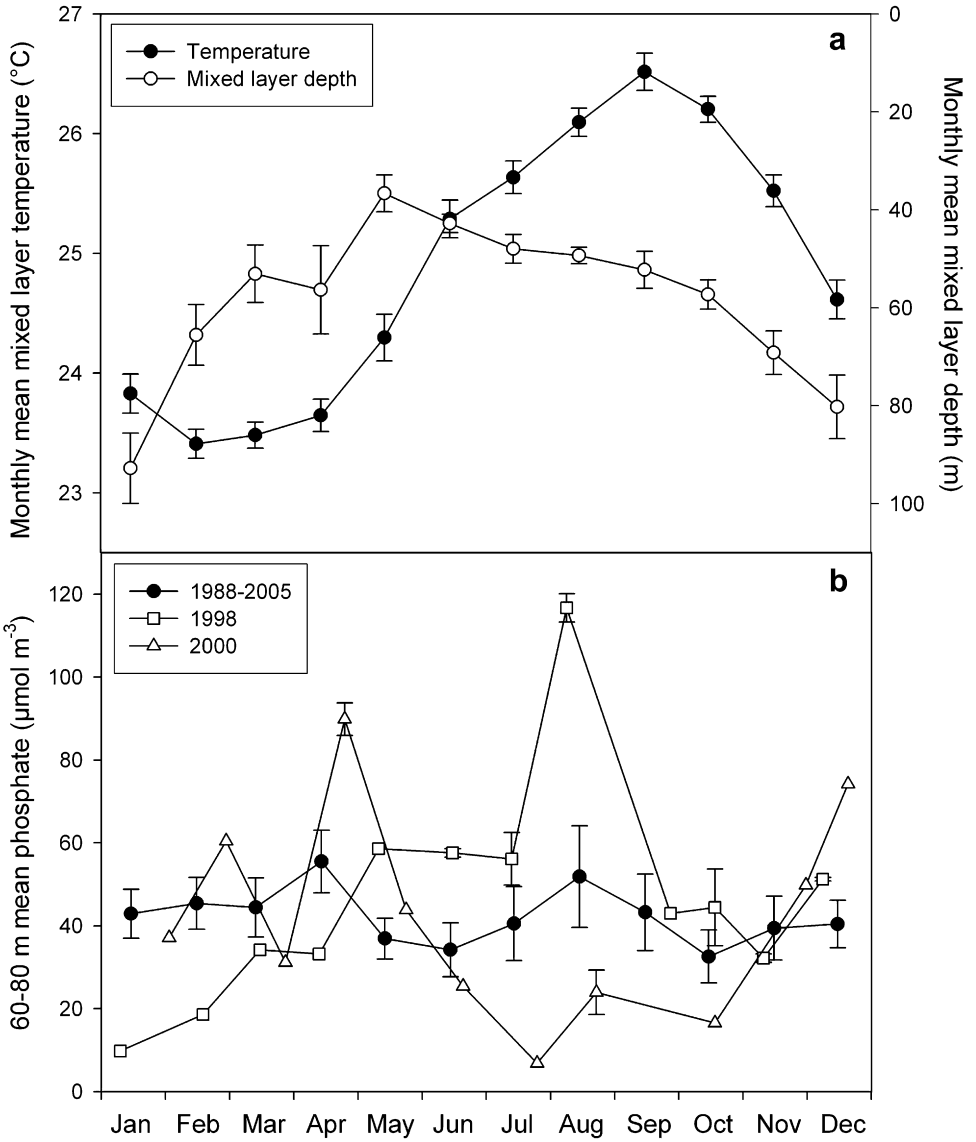


Fig. 12. Monthly climatology of selected parameters at Station ALOHA, 1988–2005. (a) Mean (±se) temperature within the mixed layer (closed symbols) and depth of the mixed layer (open symbols) measured during each month. (b) Mean (±se) phosphate concentration in the 60–80 m depth zone (closed symbols). For comparison, phosphate data from 1998 (open squares) and 2000 (open triangles) bloom years are also presented.

phosphate shows peaks in April and August (Fig. 12b). The April peak comes after a gradual rise in phosphate that begins in November. The August peak, however, rises from June and declines into October, thus occurs during the height of summer, when mixed layers are shallow and warm. Possible mechanistic explanations for the peaks can be seen in the phosphate data from 1998 and 2000 (Fig. 12b). In 2000, there is evidence of phosphate input during the winter and spring, associated with destabilization of the water column. The maximum 60–80 m phosphate came at the end of April, immediately prior to the onset of summer stratification. In 1998, however, there is little evidence of winter phosphate input. Phosphate rises in the spring, and then from July to August rises abruptly. This late season phosphate input may be related to the passage of the cyclonic eddy described above (Fig. 10). It is interesting to note that the 2000 summer bloom developed at Station ALOHA in June (Fig. 5), while the 1998 bloom did not become apparent until late July (Fig. 10).

4. Discussion

4.1. Regularity of summer blooms

Despite the long-held perception of the NPSG as an oceanic desert, summer phytoplankton blooms have been observed in these waters for as long as research vessels have frequented them (see the literature review in Table 1). However, what is termed a "bloom" depends on the eye of the beholder. For example, time-series measurements of primary production made in 1987–88 at 33°N, 139°W during the VERTEX project revealed strong summer maxima, yet the word "bloom" was not used to describe them (Knauer et al., 1990). Recurring summer maxima in primary productivity and particulate carbon at Station ALOHA have also been reported without being attributed to a bloom phenomenon (Karl et al., 1996; Hebel and Karl, 2001). Accumulations of phytoplankton biomass in the NPSG have only been termed blooms when some threshold of perception has been reached (e.g., Karl et al., 1992; Letelier et al., 2004). Satellite observations have made the detection and definition of summer blooms less ambiguous (Wilson, 2003), but satellites can only see what is present near the surface. For example, no blooms meeting the sustained surface chlorophyll $a > 0.15$ mg m^{-3} criterion were visible from space during 1998 and 2001 (Wilson, 2003), yet shipboard and mooring observations detected evidence of a strong bloom at Station ALOHA during 1998 and a weaker bloom during 2001 (Table 1; Figs. 2 and 8–10). Conversely, no evidence of a bloom was noted by shipboard observers at Station ALOHA in 1995, yet a passing research vessel detected a bloom farther to the north (Brzezinski et al., 1998), and bottom moored sediment traps near Station ALOHA collected an export pulse at 4000 m (Fig. 8d and e).

Summer blooms in the NPSG have often been termed "events" or "anomalies;" however, when all of the observations are considered, the summer bloom of phytoplankton in the upper 60 m of the eastern NPSG appears to be a recurring phenomenon. Its exact timing, intensity and spatial distribution vary interannually, presumably due to variability in physical and/or biological forcing. Although the accumulation of phytoplankton biomass in these blooms represents the net result of opposed production and loss terms (Longhurst, 1998), it is unlikely that the increase is due to a relaxation of grazing pressure, because the mesozooplankton populations are at, or are approaching, their annual maximum in early summer when the chlorophyll *a* is increasing (Landry et al., 2001; Sheridan and Landry, 2004). Increasing phytoplankton growth in excess of grazing is therefore implicated in summer bloom development. Satellite observations have shown that statistically, the most intense surface manifestation of the bloom occurs in a region to the northeast of Station ALOHA, from about 27–32°N and 130–155°W (Wilson et al., 2007; Fig. 1). Although the phytoplankton species composition may vary from year to year, the bloom appears always to be associated with at least one microorganism capable of N_2 fixation, judging from those occasions where direct observations have been made. The reliability of the bloom's annual development (at least since 1989), and its consistent association with N_2 fixation, are evident from a wealth of observations (Table 1). Yet as we will see below, the impacts of the bloom on bioelemental cycles may depend critically on the species composition of phytoplankton (including diazotrophs) present.

4.2. Horizontal, vertical and temporal variability and their effects on observations

Individual summer blooms in the NPSG display considerable spatiotemporal heterogeneity (Figs. 3–5). Because of this variability, there is little chance that the HOT program's quasi-monthly occupations of Station

ALOHA can reliably capture the rapid increase in production during the ramp-up of the bloom each year. Moreover, the HOT primary production measurements are made at a single site, at which the bloom may or may not develop to its full intensity in a given year. Satellite observations offer an opportunity for holistically capturing the large-scale areal extent of blooms as they develop and decay, especially with the 4 km resolution now available from MODIS (Wilson et al., 2007; also see Supplementary material herein). Relating the surface information from the satellite with measurements from ships, moorings and autonomous vehicles has the potential to improve our ability to capture the processes and dynamics beneath the surface, yet making the surface–subsurface connection is not straightforward. For example, the depth profiles of chlorophyll *a* from the July 1996 AC1 transect (Fig. 3b) reveal that at a location on the periphery of the bloom (Station 4), the surface chlorophyll *a* concentration could be assumed to be a valid estimate to a depth of about 40 m, while in the densest part of the bloom (Station 3), such an assumption would result in a large underestimate of total chlorophyll *a*, because of the subsurface maximum found between 25 m and 60 m. It is difficult to separate such spatial variability in the subsurface bloom manifestation from the temporal variability that results from the bloom's development and decay. The Station 3 chlorophyll *a* profile from July 1996 (Fig. 3b) is similar to the profile obtained at Station ALOHA during June 2000, while the Station 4 profile more closely resembles the conditions observed during July 2000 (Fig. 6a). We know from daily satellite observations that during the June 2000 HOT cruise, Station ALOHA was directly in the middle of a dense patch of the rapidly developing bloom. During the July 2000 HOT cruise, the station was occupied by a more diffuse part of the bloom, in its declining stage (Fig. 5). The subsurface distribution of chlorophyll *a* during a bloom may therefore be a function of both position within the bloom and of relative time in the bloom's progression.

4.3. Biomass and productivity: linking the surface and subsurface

Regardless of whether spatial or temporal dynamics are more important for relating surface chlorophyll *a* to subsurface distributions during summer, the combined ALOHA/AC1/WHOTS dataset reveals that a fairly robust relationship between the two does exist (Fig. 7a and b). However, total euphotic zone chlorophyll *a* in summer does not rise linearly with surface chlorophyll *a*. As surface values increase, the rate of increase of the total values declines, resulting in a logarithmic relationship between total and surface chlorophyll *a*. It is likely that this nonlinear relationship is at least partly due to the diminishing light available to subsurface populations as the near-surface phytoplankton bloom intensifies (Fig. 6b). The nonlinearity may also result in part from the physical concentration of buoyant phytoplankton within and (especially) just beneath the mixed layer (Figs. 2, 3b and 6a). An increase in grazing pressure during later stages of the bloom is also possible, yet primary productivity in summer appears to be similarly related to surface chlorophyll *a* (Fig. 7c and d), which suggests that the non-linearity is more a function of growth rather than of removal of the phytoplankton. The significant relationships between surface chlorophyll *a* and depth-integrated chlorophyll *a* and primary productivity revealed here are in stark contrast to the lack of such relationships in the NPSG that was reported by Hayward and Venrick (1982). Their data, collected in August–September 1980, included no chlorophyll *a* measurements >0.12 mg m^{-3}. The limited range of their dataset therefore prevented the underlying surface–subsurface relationships from being revealed. Even the chlorophyll *a* measurements reported by Venrick (1974) for "bloom" conditions in the summers of 1969 and 1972 contained no surface values >0.14 mg m^{-3}; the densest bloom conditions were therefore not present or not sampled. An important implication of the logarithmic curve fits in Fig. 7 is that the phytoplankton biomass accumulated during a summer bloom, relative to the background or pre-bloom condition, may be considerably less than would be expected from the relative increase in the surface chlorophyll *a* concentration. Our results suggest that a sixfold increase in surface chlorophyll *a* over "background" levels represents only a twofold increase in total euphotic zone chlorophyll *a* or primary production. While it is possible that our bottle sampling undercollects bloom organisms, we do not believe that the magnitude of such undercollection could be large enough to significantly bias the results, given the large number of samples collected and the repeated occupations of Station ALOHA. Also, if our bottle sampling were truly missing a large fraction of the surface chlorophyll *a* present during an individual station occupation, then satellite estimates of surface chlorophyll *a* during bloom events would consistently exceed the bottle estimates. To the contrary, the range of summer surface chlorophyll *a* values observed at Station ALOHA from SeaWiFS (about 0.05–0.25 mg m^{-3}; Fig. 4) is nearly identical to the range observed using bottle sampling (Figs. 4 and 7a).

We may estimate the carbon biomass produced during a summer bloom as follows. If we apply the logarithmic curve fit from Fig. 7b to each chlorophyll *a* value in the 45 m underway data from the July 1996 AC1 transect (Fig. 3a), we find that this bloom as a whole (200–440 km data) represented an average total euphotic zone chlorophyll *a* of 29.1 mg m^{-2}. This value is only 50% above the background condition (19.4 mg m^{-2}), due to the non-linearity of the curve fit and the inherent patchiness of the phytoplankton within the bloom. Applying a typical mixed layer phytoplankton carbon-to-chlorophyll *a* ratio of 50 g g^{-1} (Christian and Karl, 1994) to the "extra" 9.7 mg m^{-2} of chlorophyll *a* yields a net accumulation of 485 mg C m^{-2} over the pre-bloom condition. This figure does not include biomass that was removed by sinking or grazing during the period over which the production occurred. To account for this removal, we assume that the accumulation occurred over 30 days and that this 1-month increase represents some 50% of one day's worth of primary production (Longhurst, 1998). We approximate in this way a total 30-day carbon production of 29.1 g C m^{-2}, to which we assume the bloom organisms contribute 50% (scaling upon their relative contribution to total phytoplankton biomass). If 15–25% of the bloom organisms' carbon production is based on new nitrogen (i.e., $f = 0.15$–0.25), then the new production associated with the 1996 summer bloom is 2183–3638 mg C m^{-2}. A quasi-independent estimate of the biomass produced can be derived by similarly applying the productivity-chlorophyll *a* relationship in Fig. 7d to the same 45 m chlorophyll *a* dataset. The mean bloom primary productivity determined this way is 765 mg C m^{-2} d^{-1}, which is 52% higher than the background productivity of 504 mg C m^{-2} d^{-1}. If we assume the "extra" production of 261 mg C m^{-2} d^{-1} occurs continuously for a 30-day period, and assume that 15–25% of that primary production is based on new nitrogen, we obtain a total bloom new carbon production of 1175–1958 mg C m^{-2}. Both of the above approaches assume a total bloom development period of 30 days, but satellite observations suggest that the growth period may last as long as 8 weeks (Fig. 5), so the full range of these bloom new production estimates becomes 1175–6791 mg C m^{-2} per event.

A third, completely independent estimate of the summer bloom new production can be made by utilizing the data on the export flux resulting from the blooms. The 2002 bloom, although not directly sampled from a research vessel, was seen to be of moderate magnitude and duration at Station ALOHA by the SeaWiFS satellite ocean color sensor (Fig. 4). The evolution of export flux from this bloom was particularly well captured in the deep sea by sediment traps (Fig. 8d and e). If we integrate the POC flux at 4000 m (corrected for the "background" flux of 1 mg C m^{-2} d^{-1}) from 14 June to 6 November, we obtain a total bloom-associated POC flux of 337 mg C m^{-2}. Utilizing the previously described relationship between depth and carbon flux determined for Station ALOHA (Karl et al., 1996), we find that the POC flux at 4000 m should be approximately 6.8% of the flux leaving the euphotic zone at 150 m. Due to ballasting by silica in diatom-derived particles, the fraction of POC export reaching 4000 m in a summer bloom event could potentially be higher (Armstrong et al., 2002). Assuming that the actual fraction could be up to double the 6.8% derived above, we obtain a bloom-associated export from the euphotic zone of 2479–4956 mg C m^{-2} for the 2002 summer bloom at Station ALOHA. This estimate is well within the range we derived above for the 1996 bloom based on surface chlorophyll *a* and primary production considerations.

Given a long-term mean net community production of 102 mg C m^{-2} d^{-1} at Station ALOHA (Brix et al., 2006), the estimates of bloom new production above represent 3.2–18.2% of the annual new production at this site. This estimated range assumes that the 1996 and 2002 blooms were representative of the NPSG summer bloom phenomenon and that the bloom occurs annually. If we further assume that the new N requirements of the bloom are entirely met by N_2 fixation, and we accept that N_2 fixation at Station ALOHA supports, on average, 48% of new production (Dore et al., 2002), then the blooms could represent 6.6–38.0% of annual N_2 fixation at this site. Although these estimates involve a number of simplifying assumptions, the exercise does suggest that the summer blooms contribute significantly to new and export production where they occur, and may have important impacts on regional bioelemental cycling, as we will discuss below. The full biogeochemical impact of the blooms on the NPSG as a whole is less clear. The area that is known to be impacted by the blooms represents only about 10% of the area of the NPSG (Fig. 1). Thus the blooms, although likely representing net autotrophic systems, can probably account for only a fraction of the "missing" new production required to achieve metabolic balance in this biome. If the NPSG is really net autotrophic as a whole (Williams et al., 2004), then additional undersampled sources of production must exist and should be sought. Nevertheless, because of the relatively small number of direct shipboard bloom observations and the limitations of

remote sensing methods in characterizing the subsurface distributions and rate processes, the full extent of the summer bloom phenomenon across the NPSG has yet to be established.

4.4. Diatoms, Trichodesmium and the fate of summer blooms

The NPSG summer bloom observations listed in Table 1 demonstrate that the dominant phytoplankton in these blooms are often *Trichodesmium* and diatoms of the genera *Hemiaulus* and *Rhizosolenia*. These organisms are relatively large and capable of some degree of buoyancy control, and are either able to fix N_2 themselves (*Trichodesmium*) or are frequently encountered in symbiotic association with diazotrophs such as *Richelia* (*Hemiaulus*, *Rhizosolenia*). The diatom *Mastogloia woodiana* is also frequently a bloom component (Scharek et al., 1999a,b; Table 1). Although this diatom is at times found in aggregates that also contain small coccoid cyanobacteria (Scharek et al., 1999b), it is not known to harbor diazotrophic endosymbionts. These observations suggest that *Mastogloia* cells may be able to obtain fixed nitrogen released into the seawater by other bloom organisms; such a transfer of dissolved fixed N from *Trichodesmium* to the dinoflagellate *Karenia brevis* has been documented in the Gulf of Mexico (Mulholland et al., 2004). All three of the major summer bloom-forming diatom genera are weakly silicified and have a high affinity for dissolved silicic acid, thus they are well suited to growth at the relatively low silicate concentrations observed in the NPSG (Brzezinski et al., 1998; Scharek et al., 1999a,b).

While the major summer bloom-forming organisms may have a capacity to fix N_2, we cannot assume that they are responsible for all of the new production occurring during a bloom. The diversity of N_2 fixing organisms in the NPSG appears to be much greater than previously believed (Zehr et al., 2000; Church et al., 2005), and small unicellular cyanobacteria may contribute significantly to oceanic N_2 fixation (Dore et al., 2002; Montoya et al., 2004; Grabowski, 2005). In addition, vertically migrating *Rhizosolenia* mats, which have the capacity to obtain nitrate at depth and "shuttle" it to the surface, may represent a significant source for new nitrogen in the surface waters of the NPSG (Villareal et al., 1999; Singler and Villareal, 2005). Nitrate brought up from depth this way bears a characteristic enriched stable ^{15}N isotopic signature (Villareal et al., 1993). At Station ALOHA, both suspended and sinking particulate matter during the summer have ^{15}N-depleted stable isotopic signatures characteristic of an N_2 fixation-derived N source (Dore et al., 2002), thus the diatom mat shuttle appears not to be a significant source of new N fueling bloom development at this site. Farther to the northeast, in the satellite bloom region (Fig. 1; Wilson et al., 2007), *Rhizosolenia* mats appear to be more common and may have a more significant role in new production (Pilskaln et al., 2005).

Although diatoms with diazotrophic endosymbionts and *Trichodesmium* are often seen in coexistence (Marumo and Asaoka, 1974; Scharek et al., 1999a,b), blooms may be heavily dominated by one or another genus. For example, *Trichodesmium* dominated the 1989 and 2001 blooms at Station ALOHA, while *Hemiaulus* was conspicuously abundant during the 2000 and 2003 blooms (Table 1 and references therein). The 1996 and 2005 blooms appeared to shipboard observers to be composed of a more balanced mix of diatoms and *Trichodesmium*. The factors that determine which species will dominate a summer bloom on a given year are not clear (Karl, 2002); it is even possible that different species dominate in different parts of the NPSG and at different times. Spatial variation in diazotroph species composition in the NPSG has been reported (Mague et al., 1974; Marumo and Asaoka, 1974), but this phenomenon has not been closely studied, and differentiating spatial from temporal variability is challenging. Recently, a model has been developed and implemented that utilizes satellite ocean color data to indicate the presence or absence of *Trichodesmium* blooms on a global scale (Westberry and Siegel, 2006). The results suggest that blooms of *Trichodesmium* are infrequent features near Station ALOHA, and that they are essentially absent farther north near the CLIMAX area and in the NPSG satellite bloom region. Also, shipboard observations have shown that although *Trichodesmium* occurs in the CLIMAX region, it does appear to be more prevalent at Station ALOHA (Venrick, 1997). It is therefore possible that diatoms are solely responsible for the blooms near 30°N, but that closer to Station ALOHA *Trichodesmium* is a more important contributor.

The fate of the organic matter produced during a bloom depends critically on whether diatoms or *Trichodesmium* are the dominant organisms. When diatoms dominate, the end of the bloom is characterized by aggregation and rapid sinking of biomass out of the euphotic zone to the deep sea (Scharek et al., 1999a,b). Such diatom-based export is clear during the 1998, 2000 and 2002 blooms at Station ALOHA

(Fig. 8). Mesozooplankton grazers reach their maximum total biomass during the summer months (Landry et al., 2001; Sheridan and Landry, 2004), hence their fecal pellets probably contribute significantly to this flux, yet much of this material reaches the sea floor as phytodetritus in a relatively undecomposed state, providing an important food source for benthic organisms (Smith et al., 2002). Because the bloom is largely supported by nitrogen fixation, this export represents true carbon sequestration (Karl et al., 2002b). *Trichodesmium*, however, tends to be decomposed by viral lysis or autolysis (Berman-Frank et al., 2004) or through inefficient feeding by the harpacticoid copepod *Macrosetella gracilis* (O'Neil et al., 1996), and appears to be lost from the sinking particulate flux rather quickly without making a significant direct contribution to particulate matter export (Scharek et al., 1999a,b). The 1999 bloom may be an example of this phenomenon. Elevated surface chlorophyll concentrations indicative of a bloom were observed in August–September (Table 1; Fig. 4), and a large export event was implicated by thorium/uranium isotopic disequilibrium in the euphotic zone in October (Benitez-Nelson et al., 2001), yet no corresponding export pulse reached the 4000 m sediment traps (Fig. 8d and e). Summer diatom blooms, therefore, represent a mechanism for rapidly exporting bioelements to the deep sea, while the fixed bioelements within summer *Trichodesmium* blooms are largely fueling the euphotic zone microbial assemblage through *in situ* regeneration (Karl, 1999; Mulholland, 2007). Shallow degradation of *Trichodesmium* biomass may, therefore, be at least partly responsible for the observed accumulation of N-rich dissolved organic matter at Station ALOHA (Church et al., 2002).

4.5. Sverdrup's critical depth, nutrient limitation and N_2 fixation

The spring phytoplankton bloom in temperate seas is a result of release from energy limitation of net growth, as the water column stabilizes sufficiently to allow phytoplankton to capture more light energy than they lose through respiration, death and grazing. Sverdrup (1953) hypothesized that there must be a critical depth where integrated photosynthetic energy capture equals integrated energy losses; once the mixed layer shoals above this critical depth, net growth of phytoplankton becomes possible and a bloom can ensue (until the grazing zooplankton populations catch up). One of the key assumptions in Sverdrup's model is that the euphotic layer must have sufficiency of all potentially growth-limiting nutrients for a bloom to develop. In temperate waters, deep winter mixing often ensures that this is indeed the case as spring approaches. In the NPSG, however, the near absence in the upper layer of nutrients (especially fixed nitrogen) would appear to preclude a surface spring bloom. But what about these summer blooms that appear to be recurring features of this ecosystem?

We suggest that the summer bloom in the NPSG is quite analogous to the temperate spring bloom, but with some important differences. We submit that when diazotrophs are a major component of the seed population, N cannot be a growth-limiting bioelement in its own right. There is always an abundant, practically limitless supply of dissolved N_2 in the ocean. Although non-photosynthetic organisms capable of N_2 fixation exist in the sea (Karl et al., 2002b), the restriction of significant N_2 fixation rates to the upper 80 m at Station ALOHA suggests that cyanobacteria are responsible for most of the diazotrophy in this system (Dore et al., 2002). Prominent cyanobacterial diazotrophs found in the NPSG are capable not only of meeting their own N demands through fixation of N_2, but also appear to support the N demands of associated phytoplankton through symbioses or via excretion of NH_4^+ and DON (Villareal, 1988; Carpenter et al., 1999; Mulholland et al., 2004, 2006). When considering factors limiting bloom development, therefore, we may look beyond the low concentrations of fixed N and instead consider other factors that may limit the growth of large phytoplankton and the fixation of N_2 by cyanobacteria. Barring limitation by some as-yet unappreciated micro-element or vitamin (Karl, 2002; Panzeca et al., 2006), it is likely that availability of P and Fe is a key determining factor as to whether or not nutrient sufficiency exists in the surface waters of the NPSG. As long as there is sufficient P and Fe to support a bloom as the water column stratifies, a bloom should occur, provided that the mixed layer shoals above the critical depth for a sufficiently long time.

But what is the critical depth in this diazotrophy-supported system? We must consider that Sverdrup's critical depth model effectively balances energy, not elements. The energy input to the ecosystem is that associated with phototrophy. The losses include respiration by both autotrophs and heterotrophs, and loss of the energy stored in both particulate and dissolved matter that are exported from the system. The capacity of phytoplankton cells for harvesting available light may itself be initially energy-limited, due to the energetic costs

associated with chlorophyll synthesis and with the assimilation of new inorganic N required for such synthesis (Pahlow, 2005; Smith and Yamanaka, 2007). Because chlorophyll synthesis takes time as well as energy and fixed N, the onset of bloom conditions may lag the onset of stratification, therefore the condition of a shallow mixed layer must remain for a sufficiently long period in order for a bloom to develop. In a diazotrophy-supported system, an additional sink term is the considerable energy required to break the N≡N triple bond in the process of dinitrogen fixation. Given that the diazotrophs are cyanobacterial, this additional energy requirement must also be met from solar radiation. We expect, therefore, that the "N_2-critical depth" will be substantially shallower than the classical critical depth of Sverdrup. This concept is consistent with the strong and frequent association of blooms of diazotrophs with very shallow mixed layers within tropical and subtropical waters of high insolation (Karl et al., 2002b). An additional important point here is that phytoplankton blooms can occur without stratification under certain conditions of turbulence (Huisman et al., 1999, 2002). Sverdrup himself stated "a phytoplankton population may increase independently of the thickness of the mixed layer if the turbulence is moderate," and "a similar development may take place even with strong turbulence if the phytoplankton displays a positive phototaxis" (Sverdrup, 1953). Thus, shoaling of the mixed layer above the critical depth is not necessarily required for bloom formation, as long as phytoplankton populations remain in the upper layer of net energy capture for a sufficiently long period to build up biomass (Smetacek and Passow, 1990). We therefore consider that there may be an N_2-critical turbulence and an N_2-critical period as well as an N_2-critical depth.

We can examine the Station ALOHA data set for such a link between the depth of the mixed layer and the development of summer blooms (Fig. 9). During summer station occupations with high chlorophyll *a* in the upper (0–80 m) euphotic zone, the total chlorophyll *a* present is inversely proportional to the mixed layer depth, suggesting that there is some energy limitation to the growth of the phytoplankton during these "bloom" events. During low summer chlorophyll *a* ("non-bloom") periods, we see no relationship between chlorophyll *a* and mixed layer depth. Mixed layers at Station ALOHA seldom exceed 60 m during summer, and indeed, the intersection of the bloom and non-bloom regression lines in Fig. 9a near 80 m suggests that there would be insufficient light energy for bloom development in deeper mixed layers. This is approximately the depth where measured N_2 fixation rates at Station ALOHA reach near zero values (Dore et al., 2002; Grabowski, 2005); these data are therefore roughly consistent with our N_2-critical depth concept. Importantly, however, there is a lack of bloom development noted during many summer observations, despite the presence of mixed layers sufficiently shallow for such net growth. These results imply that a shallow mixed layer (= a high energy supply) is a *necessary* but not a *sufficient* condition for bloom initiation. It is possible that insufficient P and/or Fe prevent bloom initiation during these high-energy, low chlorophyll summer months at Station ALOHA.

During years when blooms are observed, the decline of the bloom following its peak expression often tracks the deepening mixed layer (Fig. 9b). Chlorophyll *a* levels in the upper 80 m fall to near pre-bloom levels as the mixed layer deepens to 60–80 m in October. This correlation could be spurious, for available P and/or Fe supplies may be running out during this time period, independent of mixed layer depth. However, the decline may occur as energy becomes insufficient to support growth (and/or N_2 fixation that provides N for growth) in excess of the rate of grazing and cell death. Interestingly, the decrease in chlorophyll *a* with increasing mixed layer depth was steeper during 1998, 2000 and 2005 than it was during 1989 and 1999 (Fig. 9b). The former three blooms are believed to have been dominated by diatoms, and the latter two by *Trichodesmium*. The differences in slope may indicate that N_2 fixation by *Trichodesmium* is more energy-efficient than N_2 fixation in the diatom–diazotroph symbioses. Alternatively, the result may indicate that *Trichodesmium* is less desirable than diatoms as a food source to grazing zooplankton.

4.6. Phosphorus and iron requirements and supply mechanisms

Because sufficiently low turbulence/shallow mixing conditions for bloom development appear to occur every summer throughout the NPSG, we need to look to the sources of potentially growth-limiting bioelements (Fe and P) in order to gain further insight into the spatiotemporal distributions of summer blooms. While iron is potentially growth limiting, its levels appear to be sufficient to support production in the near-surface waters at Station ALOHA (Johnson et al., 2003; Boyle et al., 2005). Inputs of iron to the NPSG

are associated with Asian dust deposition, hence they are somewhat patchy in time and space (Boyle et al., 2005; Brown et al., 2005), and the process of N_2 fixation has a fairly high Fe requirement (Karl et al., 2002b). Thus, Fe may at times limit growth and/or N_2 fixation in an instantaneous physiological sense, such as in a bottle incubation. However, because of the fairly consistent aeolian supply, iron is unlikely to be a *systemic* limiting factor for controlling the cumulative biomass accumulation in those parts of the NPSG that receive this supply. The situation may be considered similar to that observed in the SW Pacific, where phosphate was found to be responsible for systemic limitation of *Trichodesmium* biomass, while inputs of iron served to drive the system to a more or less rapid consumption of available phosphate (Moutin et al., 2005). Where Fe supply does not limit N_2 fixation, the delivery of sufficient supplies of new P to the phytoplankton community in the upper layer of the euphotic zone may well be a key factor in determining the spatiotemporal variability of the appearance of summer blooms.

The phosphorus requirement of a summer bloom may be estimated from the biomass carbon production estimates we made above for the 1996 bloom. We found that this bloom produced new biomass of 1175-6791 mg C m^{-2}. We can calculate the maximum P that would be required to produce this biomass by using the larger carbon figure and a minimum molar C:P ratio of 106, indicative of nutrient-sufficient growth in Redfield proportion. We can similarly calculate a minimum P estimate by using the lower carbon estimate and a maximum C:P ratio of 290 observed for natural populations of *Trichodesmium* (White et al., 2006a). The results reveal that the 1996 bloom is likely to have required between 337 and 5334 μmol P m^{-2}. If the new production associated with the bloom all occurred in the upper 60 m (Fig. 3b), then the average concentration of new P over this depth range that would need to be assimilated to support the observed growth would have been 6–89 μmol P m^{-3}. At Station ALOHA, most of the phosphate measurements in this part of the water column lie between 10 and 100 μmol m^{-3} (Karl et al., 2001a). If, as we suggest below, the bloom organisms rely mainly on phosphate for their P demands, then variability in phosphate at this site has the potential to control both whether a bloom may develop and the maximum extent of the developing bloom. We can estimate the Fe demands of a bloom by applying an appropriate P:Fe ratio to the P demands derived above. We use a mean P:Fe ratio of 244 mol mol^{-1}, based on tabulated bioelemental measurements of phytoplankton collected by net in the oligotrophic North Pacific (Ho et al., 2003). The resulting bloom Fe demands are 1.4–21.9 μmol Fe m^{-2} in the upper 60 m, implying a required mean Fe concentration of 0.02–0.37 μmol Fe m^{-3} over this depth range. Dissolved iron concentrations at Station ALOHA are usually above the higher figure (Boyle et al., 2005), even in summer and fall, suggesting that iron is unlikely to be a primary factor limiting bloom development at this site.

How may phosphate be delivered to the bloom-forming organisms in and just beneath the shallow summer mixed layer? Mixing to the depth of the phosphacline is not observed during summer in the NPSG. P deposition from the atmosphere occurs, but is thought to be a very minor flux; moreover, this atmospheric P is typically accompanied by fixed nitrogen in a high N:P ratio, especially in areas far from potential volcanic sources (Karl and Tien, 1997). Significant horizontal transport of phosphate is unlikely due to the low inorganic phosphorus surface concentrations across the gyre.

Three additional potential source mechanisms for P must be considered. First, the relatively large pool of dissolved organic phosphorus (DOP) includes compounds that may be made available to phytoplankton via enzymatic hydrolysis and subsequent uptake of the liberated phosphate. Because of this lability of part of the DOP pool, the truly bioavailable P in the surface waters at Station ALOHA has been estimated to be 1.4–2.8 times larger than the pool of phosphate (measured as soluble reactive phosphorus) alone (Björkman and Karl, 2003). In addition, low-density particulate organic matter containing phospholipids may passively float upwards from deeper in the euphotic zone, becoming concentrated, and eventually solubilized, near the surface (Karl and Tien, 1997). DOP, however, represents a regenerated source of phosphorus, hence over the long term it cannot support the new biomass associated with summer blooms unless replenished from a remote source (see Abell et al., 2000). Moreover, it is likely that bloom-forming phytoplankton (especially large diatoms) rely on inorganic phosphate for much or most of their P demands. Diatoms are seldom plentiful in oligotrophic surface waters, despite the presence of bioavailable DOP, yet they multiply rapidly when exposed to new inorganic nutrients (Goldman, 1993). Bioassay experiments at Station ALOHA have shown that when deep, nutrient-rich seawater is added to surface water, large diatoms grow rapidly and draw the ambient phosphate concentrations down to lower levels than were present in the initial surface water sample (McAndrew

et al., 2007). Therefore, summer phytoplankton blooms (at least those dominated by diatoms) may rely to a large extent on phosphate for meeting their P requirements, while the utilization of labile DOP may be more important for regenerated production by background picophytoplankton communities.

A second mechanism for phosphate delivery is associated with the vertical migrations of phytoplankton in conjunction with shoaling of the phosphacline due to the passage of mesoscale features. In cyclonic eddies, such as the one that passed through Station ALOHA during the summer of 1998, waters that would be typically found in the lower euphotic zone are found at shallower depths, where there is more available light (Fig. 10). However, at Station ALOHA the doming waters are highly deficient in nitrate relative to phosphate (Fig. 11). Very intense eddies may bring waters from sufficient depth to represent significant nitrate inputs (Seki et al., 2001), and within these features N_2-fixing organisms may be inhibited (Vaillancourt et al., 2003). However, such intense features in the NPSG are known to occur only in a relatively small area subjected to unusual wind stresses in the lee of the Hawaiian Islands (Falkowski et al., 1991; Seki et al., 2001). While the frequent, less intense eddies of the NPSG (Niiler and Hall, 1988) may impact bloom development, their influence may be more through the delivery of phosphate to phytoplankton communities in the upper layer of the euphotic zone rather than through delivery of nitrate. Doming of isotherms within cyclonic eddies reduces the length scale over which vertically migrating organisms need to travel in order to obtain phosphate. For example, Villareal and Carpenter (2002) have estimated that *Trichodesmium* should not be capable of vertical migrations of greater than 70 m, far less than needed to reach the nutricline under normal conditions. However, there is some evidence that *Trichodesmium* does in fact bring new phosphorus into the upper euphotic zone through this mechanism (Karl et al., 1992; Letelier and Karl, 1998; White et al., 2006b). Eddies such as the one observed at Station ALOHA in 1998 (Fig. 10) reduce the phosphacline depth, making a round trip to it more manageable for vertical migrators. The timing and magnitude of the 1998 summer bloom at Station ALOHA may have been influenced by the passage of this mesoscale feature. A similar feature, attributed to a first baroclinic mode Rossby wave, passed through the site in late July 1999, and appears to have influenced productivity and community structure in the lower euphotic zone (Sakamoto et al., 2004). There may have been an influence of this feature on the upper layer as well, since enhanced surface chlorophyll *a* was detected in August (Table 1) and a large ^{234}Th deficit in the upper 100 m was noted in October (Benitez-Nelson et al., 2001). An eddy also was associated with the 2005 summer bloom sampled during the WHOTS transect; this mesoscale feature appears to have been anticyclonic (Fong, 2006), hence it is not clear whether or how it may have influenced the bloom's development. In addition to phosphacline doming caused by eddies, shading of the lower euphotic zone by the bloom organisms themselves (Fig. 6) may result in shoaling of the nutricline as growth of the deeper populations slows (Letelier et al., 2004), which again allows for a reduced round-trip distance for successful vertical migrations to obtain P. Such a mechanism may act as a positive feedback on bloom development, with the potential for phosphate delivery increasing as surface biomass accumulates.

A third mechanism for phosphate delivery is via the legacy of seasonal mixing. Because P can cycle rapidly through particulate and dissolved organic and inorganic phases (Björkman et al., 2000; Karl et al., 2001a), inputs of phosphate need not occur contemporaneously with the onset of stratification in order for the P to be available for summer growth. The system may be ''recharged'' with phosphate delivery via mixing and entrainment during winter (Karl et al., 2001a), and this P cycled many times through the DOP pool via microbial activity before it is eventually utilized as phosphate by the summer phytoplankton. At Station ALOHA, the mixing does not penetrate deeply into the nutricline. Due to very low nutricline N:P ratios (Fig. 11), what little nitrate that is delivered in such cases will be rapidly utilized in the lower euphotic zone, leaving excess phosphate to be delivered to the upper euphotic zone.

Time-series phosphate measurements at Station ALOHA reveal evidence for both the winter legacy and summer eddy mechanisms of phosphate delivery to surface phytoplankton (Fig. 12). During 1998 and 2000, increases in phosphate just below the mixed layer (60–80 m) heralded the blooms in both years. In 1998, the phosphate increase occurred in association with the passing cyclonic eddy, during the period of greatest water column stratification. In 2000, the increase occurred during the winter/spring transition. In both years, the subsequent bloom resulted in a drawdown of phosphate in this 20 m thick layer of roughly 80 μmol m^{-3} (Fig. 12); this amount of net P uptake (1600 μmol m^{-2}) represents from 30% to >100% of the 1996 bloom total P requirements estimated earlier from biomass and productivity considerations. Although these figures are approximate, the comparison does suggest that the amount of phosphate immediately

beneath the mixed layer that is potentially utilized by buoyancy-controlling phytoplankton is of sufficient magnitude to explain the extent of phytoplankton biomass accumulation within a summer bloom. In 2000, the 60–80 m phosphate was drawn down to <10 μmol m^{-3} by the end of July; this value is remarkably close to the critical phosphate concentration of 9 μmol m^{-3} estimated for net biomass production by *Trichodesmium* in the SW Pacific (Moutin et al., 2005). It is conceivable, therefore, that exhaustion of available phosphate supplies influenced the termination of the 2000 bloom.

4.7. Distribution of NPSG blooms – does P mark the spot?

Wilson et al. (2007) have determined from satellite observations that the NPSG summer bloom is most likely to produce a surface manifestation of >0.15 mg m^{-3} chlorophyll *a* in an area to the northeast of Station ALOHA, from about 27–32°N and 130–155°W (Fig. 1). Summer blooms can develop almost anywhere within a larger area of the eastern half of the NPSG on any given year, which includes both the CLIMAX area and Station ALOHA. Curiously, however, the blooms do not appear to develop in the western half of the gyre (Wilson et al., 2007). Thus to explain the distribution of the summer bloom phenomenon we must look to a mechanism that is: (1) at work at least some of the time across much of the eastern NPSG, (2) not at work in the western NPSG and (3) enhanced within the area where satellites have observed the highest frequency of blooms. Wilson et al. (2007) have suggested that the area of highest bloom frequency may be unusually calm in summer, due to the convergence of weak surface currents there, allowing for accumulation of buoyant organisms. However, we can see from the Station ALOHA record that the summer bloom represents both rapid growth of phytoplankton and accumulation of their biomass near the surface. Furthermore, exceedingly calm conditions can occur for long periods of time in summer over most of the gyre. It is difficult, therefore, to accept excessive calmness as a mechanism for bloom initiation unique to this area, although persistently shallow mixed layers may relieve the bloom-forming organisms from energy limitation (Fig. 9), and the surface accumulation of chlorophyll *a* seen by satellites may well be enhanced by particularly calm seas (Karl et al., 1992).

We hypothesize that the peculiar spatial distribution of the NPSG summer blooms may be related to the relative amounts of phosphate delivered to the upper euphotic zone in different locations across the gyre. If we look throughout the NPSG to the waters immediately below the depth of greatest winter mixing at Station ALOHA (150 m), from which new P is ultimately delivered to the euphotic zone, we see that the entire gyre is characterized by low phosphate, and the central portions of both the western and eastern portions of the gyre are characterized by low nitrate:phosphate ratios (Fig. 13a and b). However, the bloom region of the eastern NPSG has considerably higher phosphate concentrations than the western NPSG at this depth. If we look to the depth to which mixing must penetrate in order to entrain substantial amounts of phosphate, we see that much deeper mixing is required in the western NPSG than in the eastern NPSG (Fig. 13c). An examination of the climatology of mixed layer depths indicates that such deep mixed layers are never achieved in the western NPSG (Fig. 13d). However, winter mixed layers in the satellite bloom region tend to be sufficiently deep to reach into the deep phosphate pool. We hypothesize that summer blooms in the NPSG occur where they do because the supply of phosphate in that region is sufficient to support them, while in the western NPSG, chronic P limitation is seldom if ever relieved.

The correspondence between bloom observations and potential phosphate supply suggested by Fig. 13 is not perfect. For example, at Station ALOHA, the phosphate $= 0.5$ μmol m^{-3} level appears deeper, and the winter mixed layer depth appears considerably shallower, than those within the satellite bloom region (Fig. 13c and d). We caution that climatological mapping in any specific area may be based on relatively few observations, and in particular, these climatological mixed layer depths do not include HOT program results. HOT program observations from 1988 to 2005 have revealed that winter mixed layer depths at Station ALOHA actually exceed 100 m in most years (Fig. 11), and that the phosphate $= 0.5$ μmol m^{-3} level can be as shallow as 200 m. The main point here is that the conditions in the northeastern section of the NPSG, where blooms are observed, are much more favorable for phosphate delivery to the upper water column than are conditions in the rest of the gyre, especially the region west of the Hawaiian Islands, where summer blooms are not observed.

Another enigma in the phosphate supply – summer bloom correspondence is the "lobe" to the southeast of the satellite bloom region, centered at about 27°N, 130°W, where winter mixed layers are relatively deep and

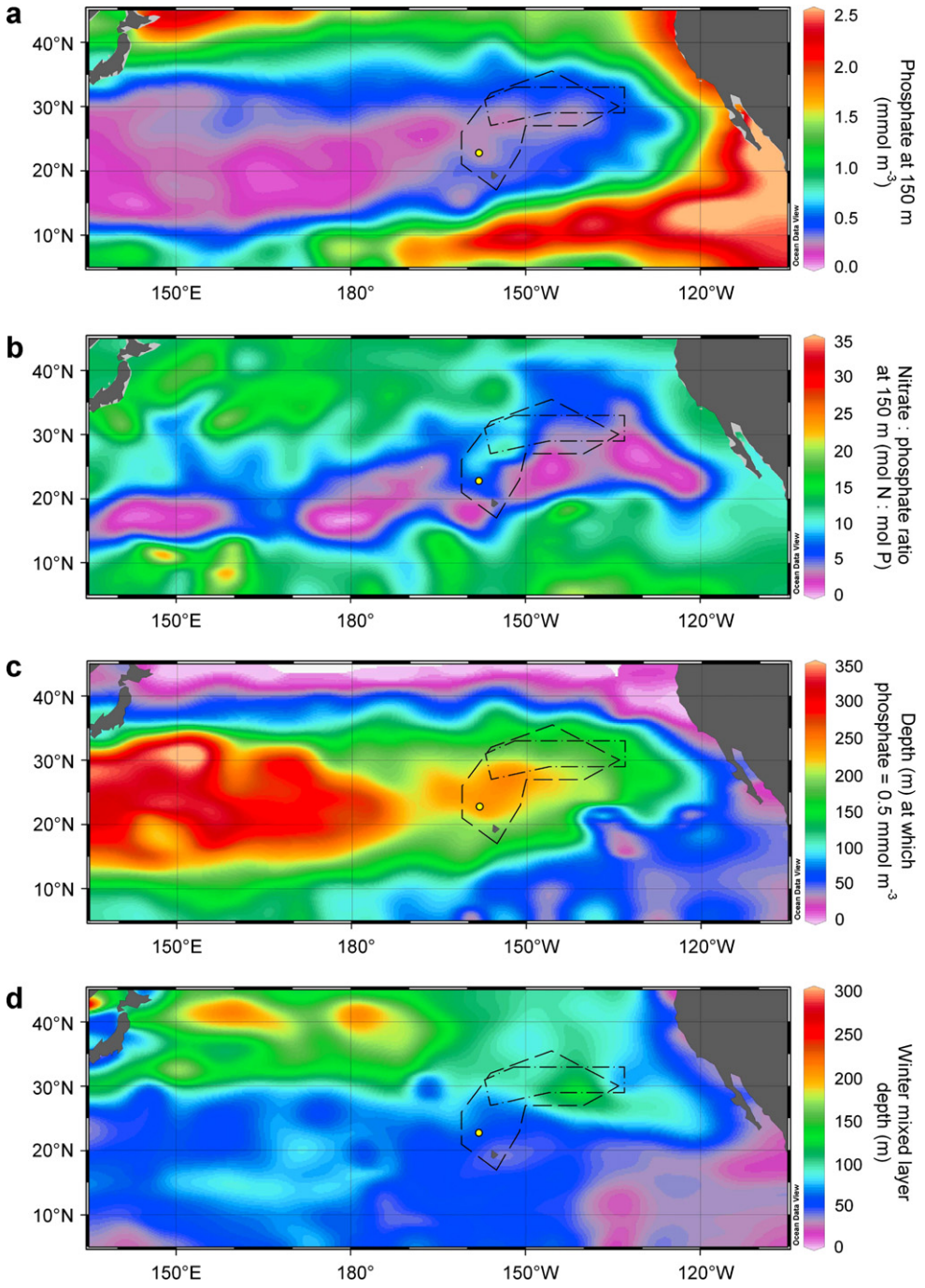


Fig. 13. Climatological maps of selected parameters in the North Pacific Subtropical Gyre. (a) Mean phosphate concentration at a depth of 150 m during July–September. (b) Mean molar ratio of nitrate:phosphate at 150 m during July–September. (c) Mean depth at which phosphate concentration reaches 0.5 mmol m^{-3} during July–September. (d) Mean mixed layer depth during January–March. The position of Station ALOHA is indicated by the filled yellow circle. The dashed and dot-dashed lines indicate the historical bloom observation area and the satellite high-frequency bloom detection area, respectively, as presented in Fig. 1.

phosphate at 150 m is relatively high, yet bloom observations are lacking (Fig. 13). We do find evidence from satellite imagery that a bloom extended into this area during at least one summer (1999), but apparently no other bloom observations have been made here. To explain this enigma, we suggest that a difference in bio-

available iron supply may in this case be an additional underlying control on the spatiotemporal distribution of NPSG summer bloom development. The deposition of Asian dust appears to be similar at Station ALOHA and in the satellite bloom region, but is low in this southeastern lobe (Moore et al., 2004; Boyle et al., 2005). Consistent with these dust deposition patterns, the surface dissolved Fe concentrations are relatively high at Station ALOHA but they decline with distance to the east (Boyle et al., 2005). Insufficient Fe to support N_2 fixation may be a persistent feature of this area, preventing bloom development during most summers despite an adequate P supply.

Measurements of surface iron made on an east–west transect in 2002 revealed lower concentrations in the western NPSG than at Station ALOHA (Brown et al., 2005). However, dust deposition observations and model results suggest that the annual iron input from the atmosphere is just as large, if not larger, in the western NPSG than in the northeastern NPSG (Moore et al., 2004; Boyle et al., 2005; Jickells et al., 2005). Biogeochemical model results also suggest that N_2 fixation rates should be higher in the west than in the east (Deutsch et al., 2001, 2007; Moore et al., 2004). Ironically, it may be that a higher iron supply in the western NPSG has allowed diazotrophs to sequester, export, and ultimately draw down bioavailable P to extremely low levels; because of this lack of phosphate, the P demands of potentially bloom-forming organisms with limited capability for DOP utilization (such as diatoms) are not met. The northeastern NPSG may be on its way to becoming more like the west in this regard. Continued export of organic matter with high N:P ratios, both in dissolved (Church et al., 2002) and particulate (Karl et al., 1997) form has resulted in declining euphotic zone inventories of phosphate at Station ALOHA since the HOT program began in 1988 (Karl et al., 2001a; Karl, 2002, 2007; McAndrew et al., 2007). However, over sufficiently long timescales, the N:P of mesopelagic nutrient inventories should increase as this organic matter is remineralized. The nutrient flux from below the euphotic zone should become less N-depleted, which should ultimately select against N_2-fixing organisms. Karl (2002) has suggested that such a feedback mechanism may result in an alternation between P-controlled and N-controlled ecosystem states on a time scale of 20–40 years. The vertical length scale of remineralization may influence the period of this oscillation, however, because rapid export of diatom biomass to the deep sea could remove excess N from the upper ocean for centuries. Net phosphate (relative to nitrate) delivery from the low N:P denitrified waters of the eastern tropical North Pacific (Castro et al., 2001; Lukas and Santiago-Mandujano, 2001; Deutsch et al., 2007) may also impact the cycle and may be a key factor in preventing the eastern NPSG from reaching the same extreme level of P deficiency observed in the west.

5. Conclusions

The summer bloom appears to be a recurring, possibly seasonal, phenomenon in the northeastern NPSG. The spatial distribution and evolution of summer blooms can be visualized from satellite remote sensing; however, direct observations are needed in order to determine the ecosystem dynamics within, and the potential biogeochemical impacts of, these enigmatic accumulations of phytoplankton biomass. From numerous observations at Station ALOHA and other encounters in the region, we are beginning to resolve a clearer picture of summer bloom dynamics. The blooms appear to be supported largely by N_2 fixation, and their development appears to be controlled mainly by the availability of phosphorus, radiant energy and iron. The dominant phototrophs in the blooms are diatoms and/or *Trichodesmium*; the reasons for dominance by one or the other in a given bloom are still unclear. We are beginning to connect the surface and subsurface manifestations of the summer blooms; our results suggest that they can be ecologically and biogeochemically important locally, yet due to the limited area over which they appear to occur, their contribution to new production and net autotrophy in the NPSG as a whole may not be substantial. When *Trichodesmium* dominates, the bloom biomass is largely recycled in the upper ocean, while diatom blooms sink out rapidly and fuel deep sea and benthic ecosystems. The blooms may occur in the northeastern but not the western NPSG because of a greater supply of phosphate to the former than the latter area, while insufficient iron may preclude bloom development in the southeastern NPSG. Additional direct observations are needed, especially to the northeast of Station ALOHA, where the frequency of surface chlorophyll *a* accumulations in summer is greatest and biogeochemical and ecological data are sparse.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.pocean.2007.10.002.

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