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Long-term changes in plankton community structure and productivity in the North Pacific Subtropical Gyre: The domain shift hypothesis

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Abstract

Oceanic productivity, fishery yields and the net marine sequestration of atmospheric greenhouse gases are all controlled by the structure and function of planktonic communities. Detailed paleoceanographic studies have documented abrupt changes in these processes over timescales ranging from centuries to millennia. Most of these major shifts in oceanic productivity and biodiversity are attributable to changes in Earth's climate, manifested through large-scale ocean–atmosphere interactions. By comparison, contemporary biodiversity and plankton community dynamics are generally considered to be "static", in part due to the lack of a suitable time frame of reference, and the absence of oceanic data to document ecosystem change over relatively short timescales (decades to centuries). Here we show that the average concentrations of chlorophyll *a* (chl *a*) and the estimated rates of primary production in the surface waters of the North Pacific Subtropical Gyre (NPSG) off Hawaii have more than doubled while the concentrations of dissolved silicate and phosphate have decreased during the past three decades. These changes are accompanied by an increase in the concentration of chl *b*, suggesting a shift in phytoplankton community structure. We hypothesize that these observed ecosystem trends and other related biogeochemical processes in the upper portion of the NPSG are manifestations of plankton community succession in response to climate variations. The hypothesized photosynthetic population "domain shift" toward an ecosystem dominated by prokaryotes has altered nutrient flux pathways and affected food web structure, new and export production processes, and fishery yields. Further stratification of the surface ocean resulting from global warming could lead to even more enhanced selection pressures and additional changes in biogeochemical dynamics. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

In 1987, Venrick et al. reported that the average euphotic zone (0–200 m) chl *a* concentration in the oligotrophic North Pacific Ocean during summer (May–Oct.) had nearly doubled from 1968 to 1985. Their data set was collected in an area referred to as the "Climax region" (26.5°–31.0°N and 150.5°–158.0°W). The sampling frequency was insufficient to determine whether the chl *a* increase had been continuous over time or whether there had been a "step-function" increase between 1973 and 1980 (Venrick et al., 1987). The authors hypothesized that decade-scale changes in the open-ocean habitat, caused by large-scale atmosphere–ocean interactions, had resulted in significant long-term changes in the carrying capacity of the ecosystem.

Data from the ongoing Hawaii Ocean Time-series (HOT) program (Sta. ALOHA; 22.75°N, 158.00°W; Karl and Lukas, 1996), which also includes occasional sampling in the Climax region, extend this previous record of euphotic zone chl *a* concentrations for nearly another decade. The combined Climax-ALOHA data set documents that the mean euphotic zone chl *a* concentration from the period Oct. 1988 to Dec. 1997 (HOT program results) is also significantly greater than the average, pre-1976 Climax program chl *a* concentration. Other ecosystem changes, described herein, are also evident. We hypothesize that these changes in ecosystem structure and function are manifestations of climate-related variations in the stability of the gyre. Although changes in field methodology over the past three decades preclude a rigorous test of this hypothesis, we demonstrate a coherence in several independent data sets that is consistent with climate-related, long-term changes in plankton dynamics. Consequently, biogeochemical models and primary productivity algorithms based on historical or even contemporary data sets may not be accurate predictors of future trends.

2. Methods

Two primary data sets are presented in this study: (1) pigment determinations by fluorometric and high-performance liquid chromatographic (HPLC) methods, and (2) primary production by ^{14}C-bicarbonate incorporation. Although these methods are well documented in the oceanographic literature, it is critical to consider several features of the evolution of these methods over the period of consideration (1968 to present). These methodological considerations are important because we suggest herein that there has been a change in both microbial community structure and rates of photoautotrophic production over this time period.

2.1. Pigment determinations

Chlorophyll *a* (chl *a*) functions as the primary light-harvesting pigment for all prokaryotic and eukaryotic marine oxygenic photoautotrophs. Even though the chl *a*:carbon ratio of cells varies considerably as a function of environmental conditions and growth rate (Laws et al., 1983), measurements of chl *a* have been used extensively to estimate the biomass of photoautotrophic microorganisms in the sea. Typically cells are concentrated by filtration, extracted into an organic solvent (usually acetone), and pigments detected by fluorescence, sometimes after chromatographic separation.

2.1.1. Filtration

Contemporary microbial populations in the North Pacific Subtropical Gyre (NPSG) are dominated by photoautotrophic *bacteria* (picophytoplankton) with mean spherical diameters $\leqslant 1.0\,\mu m$ (e.g. *Prochlorococcus*). There are conflicting reports on the efficiency of Whatman microfine glass fiber filters (GF/F; nominal pore size $= 0.7\,\mu m$) for retaining *Prochlorococcus* cells. Goericke and Welschmeyer (1993) and Vaulot et al. (1990) reported $> 98\%$ collection efficiency, whereas Campbell et al. (1994) report an average 15% loss. Results from Sta. ALOHA, a site dominated by picophytoplankton, indicate that chl *a* measured using GF/F filters is not significantly different from chl *a* measured using $0.2\,\mu m$ porosity polycarbonate membrane filters (Chavez et al., 1995), suggesting negligible loss of *Prochlorococcus* cells. Prior to about 1980, most field studies employed Whatman GF/C filters rather than the now preferred GF/F grade. Direct field comparisons of chl *a* collected using Whatman GF/C (nominal pore size $= 1.2\,\mu m$) and millipore-HA ($0.45\,\mu m$) filters have shown that the Millipore filters retain an average of only 8.9% more chl *a* than GF/C filters for samples collected in the NPSG (Venrick et al., 1987), so glass fiber filters are more effective at trapping small cells than the manufacturer's specifications would predict. This result may have been influenced by the use of magnesium carbonate in the Climax sample processing, a step that is known to decrease the porosity of glass fiber filters (Garside and Riley, 1969). Our field comparisons of chl *a* retained by GF/C vs. GF/F filters for water samples collected at both the Climax and Sta. ALOHA reference sites (measured by fluorometry, but without magnesium carbonate) on cruises in July 1996 and July 1997 indicate a bias of similar magnitude: chl *a* (GF/C) $= 0.84$ [95% CI $= 0.72$–0.99] chl *a* (GF/F) $+ 0.004$ [95% CI $= -0.012$–0.020], ($r = 0.95$, $n = 28$; model 2 reduced major axis regression analysis).

2.1.2. Measurement

Historically, chl *a* concentrations in cell extracts have been measured using a sensitive, but relatively non-specific, fluorometric technique (Yentsch and Menzel, 1963; Holm-Hansen et al., 1965). In the fluorometric method, a sample acidification step is also included to convert chl *a* to its pheophytin derivative to detect the presence of chl degradation products in the non-acidified extract (Yentsch and Menzel, 1963; Holm-Hansen et al., 1965). In most field studies, both chl *a* and pheopigment (pheo) concentrations are reported. The term "pheo" is used here because the fluorometric method cannot distinguish the various chl *a* degradation products. In practice, the reported values of chl *a* from the fluorometric method (FL-chl) include both the monovinyl and divinyl forms of chl *a*. Furthermore, the accuracy of the estimates of both FL-chl and pheo (FL-pheo) is influenced by the presence of other fluorescent compounds. For example, when employing the standard broad-band chl *a* filter sets used in most oceanographic field programs (excitation: Corning CS-5-60 #5543, Kodak wratten #76, or equivalent and emission: Corning CS-2-60 #2408, Kodak wratten #26, or equivalent), the presence of chl *b* would cause a moderate negative bias on FL-chl estimation and a large positive bias on FL-pheo estimation (Loftus and Carpenter, 1971). Direct measurements of the mean chl *b*:*a* ratios (monovinyl plus divinyl derivatives) for samples collected at Sta. ALOHA for the period 1989–1997 using high-performance liquid chromatography (HPLC) are 0.07 (s.d. $= 0.03$, $n = 75$ cruises, cruise ranges $= 0.02$–0.15) and 0.56 (s.d. $= 0.15$, $n = 81$ cruises, cruise ranges $= 0.23$–1.04) for the 0–30 and 125–200 m portions of the water column, respectively. This assures chl *b* interference on fluorometric FL-chl determinations, especially in the lower portion of the euphotic zone. Furthermore, the presence of divinyl chl *a*

(DV-chl *a*) also will cause a positive bias on FL-pheo (Goericke and Repeta, 1993). Over four years (1994–1997) at Sta. ALOHA, the ratio of divinyl chl *a* to monovinyl chl *a* averaged 1.32 (s.d. = 0.41, $n = 37$ cruises) and 1.29 (s.d. = 0.51, $n = 37$ cruises) for the 5 and 125 m reference depths, respectively, so overestimation of FL-pheo is also assured.

More specific methods of chl *a* detection such as HPLC have largely replaced the fluorometric assay (Wright et al., 1991). In the HOT program, both fluorometric and HPLC methods are routinely employed, in part so that contemporary results can be compared to historical measurements from this region. Nevertheless even small interlaboratory differences in methodology can potentially confound the interpretation of data generated over long periods of time.

2.1.3. Interpretation

In the present study we use fluorometrically determined "chl" (FL-chl) and "pheo" (FL-pheo) as surrogates for chl *a* and *b*, respectively. To evaluate the validity of these proxies we made comparisons of fluorometric, chromatographic and flow cytometric measurements derived from the same seawater samples. HPLC-determined chl *a* (HPLC-chl *a*) was correlated linearly with FL-chl for HOT program data obtained during the period 1989–1997: HPLC-chl $a = 1.19$ (FL-chl) $- 0.01$ ($r = 0.84$, model 2 reduced major axis regression analysis). On average, HPLC-chl *a* was 19% higher than FL-chl, a result consistent with the reported negative bias of chl *b* on FL-chl determinations. By contrast, FL-pheo values are considerably higher than those determined by HPLC analyses, a result also consistent with the reported positive bias of chl *b* on FL-pheo determinations.

To assess the utility of FL-pheo as a proxy for *Prochlorococcus*-derived chl *b*, we compared: (1) FL-pheo to HPLC-chl *b* concentrations and (2) the flow cytometrically determined *Prochlorococcus*-derived red fluorescence signal (RFL_{Pro}) to HPLC-chl *b*. Our rationale for suggesting the latter relationship is that RFL_{Pro} is expected to co-vary with the cell quota of chl *b* (sum of monovinyl chl *b* plus divinyl chl *b*) because it is the primary agent responsible for light absorption and subsequent red fluorescence in the flow cytometric protocol employed in the HOT program (Bidigare et al., 1990). The analyses revealed that FL-pheo and chl *b* were positively correlated: HPLC-chl $b = 2.73$ [95% CI = 2.48–3.0] FL-pheo + 0.07 [95% CI = 0.05–0.09]; $r = 0.88$ (model 2 reduced major axis regression analysis) and that HPLC-chl *b* and RFL_{Pro} were also positively correlated: $RFL_{Pro} = 38.6$ [95% CI = 34.6–43.0] HPLC-chl $b + 0.38$ [95% CI = 0.08–0.70]; $r = 0.83$ (model 2 reduced major axis regression analysis). These results imply that *Prochlorococcus* cells are the major source of chl *b* in our study area, and that FL-pheo is an artifact caused by high concentrations of chl *b*, again derived from *Prochlorococcus*. Furthermore, these results are consistent with previous studies reporting that the deep FL-pheo maximum in the subtropical Pacific Ocean is a manifestation of chl *b* interference on the fluorometric assay rather than due to the presence of high concentrations of pheopigments (Vernet and Lorenzen, 1987; Ondrusek et al., 1991). We therefore conclude that FL-pheo, reported herein, is a good proxy for assessing secular changes in *Prochlorococcus*-derived chl *b* concentrations in plankton assemblages of the NPSG. As discussed later, there appears to be very little, if any, pheo in NPSG so the detection of FL-pheo by the standard fluorometric technique is an artifact of the presence of high chl *b* concentrations.

2.2. Primary production

Considerations of community structure that impact size spectra have been discussed above. There are at least two additional methodological procedures that need to be considered when evaluating the observed temporal trend of primary production (Fig. 1): (1) inadvertent contamination by toxic levels of trace metals (e.g. Zn and Cu), and (2) potential spectral mismatch of the light field during shipboard incubations of water samples. It is critical to emphasize that neither of these methodological considerations would likely create a bias of the magnitude required to eliminate the secular changes we report here.

2.2.1. Trace metal contamination

While there is no denying the potential negative bias of inadvertent contamination by toxic trace metals during ^{14}C-incubations, it is probably inappropriate to dismiss all pre-1983 plankton rate measurements as artifacts. First, while most of the pre-1983 rates are lower than most post-1983 "trace metal-free" determinations, there are numerous notable exceptions for both Climax and ALOHA data sets (Fig. 1). For example, ^{14}C-based primary production measurements made during expedition Fiona (Hayward and McGowan, 1985) and on Climax VII prior to the introduction of "clean" techniques yielded production estimates and assimilation numbers that were not significantly different from the mean values measured during the HOT program (Karl et al., 1998). Likewise, primary production rates measured on selected HOT cruises using "trace metal-clean" techniques were as low as the Climax program mean value (for full HOT program data set see http://hahana.soest.hawaii.edu). Furthermore, direct field comparisons of "trace metal-clean" vs. "dirty" incubations (Marra and Heinemann, 1984) or deliberate attempts to promote trace metal toxicity (Sharp et al., 1980) have failed to demonstrate the anticipated inhibition. Finally, it is illogical to assume that all water samples collected prior to 1983, regardless of sampling gear, research vessel or investigator, would be equally inhibited with identical sub-lethal doses of trace metals. The summarized data on assimilation number (available from DMK upon request) shows a relatively narrow range (1–5 g C (g chl h)$^{-1}$) of values for samples collected prior to 1983, including data from several experiments with specially designed plexiglass in situ incubation samplers (Bienfang and Gundersen, 1977) that would not have been subjected to the hypothesized trace metal inhibition. All of these observations indicate that the changes we observe cannot be attributed exclusively to a shift towards trace metal-free protocols.

2.2.2. Incubation

Ideally water samples for primary production rate measurements should be incubated under in situ conditions to reproduce the ambient temperature and light field. Theoretical calculations indicate that primary production could be underestimated by a factor $> 30\%$ and up to a factor of two in the open ocean if incubations are conducted using surface light attenuated with neutral density filters compared with a combination of neutral density and blue filters that also approximate the spectral characteristics of submarine light (Laws et al., 1990). However, direct comparisons of deck incubation techniques with and without proper spectral corrections have shown the effects to be much smaller, if not negligible (Doty et al., 1965; SIO, 1990). The actual measurement bias will depend on the species composition and other factors. Samples from the Climax study were generally incubated on deck using neutral density screens, and those from Sta. ALOHA were

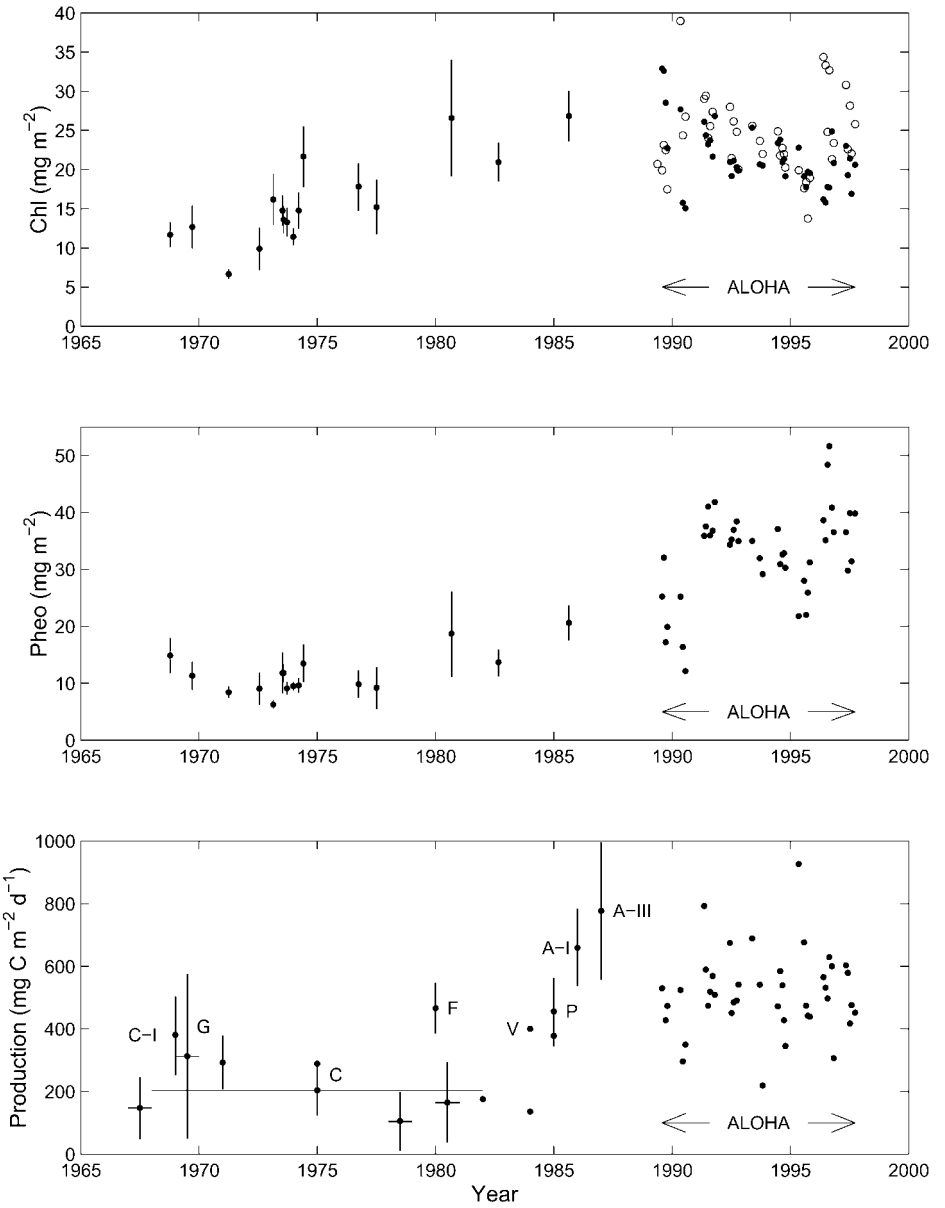


Fig. 1. Composite time-series analysis of phytoplankton community parameters for samples collected in the NPSG during the period May–October. See Section 2. Measurements include: [TOP] euphotic zone depth-integrated chlorophyll concentrations as determined by FL (●) and HPLC (○), [MIDDLE] euphotic zone depth-integrated pheopigment (FL-pheo) concentrations, and [BOTTOM] euphotic zone depth-integrated rates of primary production obtained from numerous sources and locations but derived largely from oceanographic investigations at or near the Climax region and Sta. ALOHA. Where appropriate, mean values are presented $\pm$ 1 s.d. for multiple observations for a given cruise, season or study. Where shown, horizontal bars indicate the duration of multi-cruise data sets. Data sets (see Karl and Lukas, 1996) from selected expeditions are noted by the following abbreviations: AI/AIII = Asian Dust Inputs to Oligotrophic Seas (ADIOS) I and III cruises, C = Climax time-series, C-I = Climax-I and F = FIONA (two separate cruises in the Climax region), G = GOLLUM, P = Planktonic Rate Processes in Oligotrophic OceanS (PRPOOS) cruise, V = Vertical Transport and Exchange (VERTEX-5) cruise. These data, relevant metadata and data source credits are available from DMK upon request.

incubated under in situ conditions. Direct comparisons indicate a much smaller systematic bias than would be needed to explain the results summarized herein (Letelier et al., 1996).

2.3. Nutrient determinations

Seawater for soluble reactive phosphorus (SRP) and dissolved silicate (Si) determinations at Sta. ALOHA was collected in polyvinyl chloride (PVC) water bottles attached to a 24-place rosette sampler. As our intent here was to compare contemporary and historical nutrient inventories, we report the standard autoanalyzer SRP, not the more modern high-sensitivity phosphate determinations (see Karl and Tien, 1997). Dissolved silicate also was measured using standard autoanalyzer methods (Strickland and Parsons, 1972). The complete Sta. ALOHA data sets are available at http://hahana.soest.hawaii.edu. The Sta. ALOHA data were binned by year and presented as annual mean $\pm$ 1 s.d. for each period. The historical (pre-1988) SRP and Si data sets were obtained from the World Ocean Database 1998 (WOD-98; M. E. Conkright, S. Levitus, T. O'Brien, T. P. Boyer, C. Stephens, D. Johnson, L. Stathoplos, O. Baranova, J. Antonov, R. Gelfeld, J. Burney, J. Rochester, C. Forgy, *National Oceanographic Data Center*, *U.S. Department of Commerce*) within the region 20–30°N, 140–170°W. Unedited concentration vs. depth profiles were integrated (0–100 m depth interval), then binned by calendar year. The data are presented as the mean $\pm$ 1 s.d. inventories for each year. The number of profiles for a given year ranged from 1 to >20. Years where less than 3 profiles were used include: 1956, 1977, 1979, 1983 for SRP and 1958, 1977, 1979, 1983 for Si.

3. Results and discussion

3.1. Changes in pigment inventories in the NPSG

The nearly monthly, decade-long Hawaii Ocean Time-series (HOT) program data set reveals a dynamic ecosystem with relatively large ($>75\%$), high-frequency (monthly) changes in pigment inventories (Fig. 1). Furthermore, there is a time-variable disparity between FL-chl and HPLC-chl, which is especially pronounced in the periods 1991–1993 and 1996–1997 (Fig. 1). Examination of the Climax and ALOHA depth profiles of FL-chl and FL-pheo concentrations reveals secular increases in both FL-chl and in FL-pheo concentrations since 1968, especially within the deep chlorophyll-maximum layer (DCML) centered at about 100–120 m (Figs. 1 and 2, Table 1). The largest differences between FL-chl and HPLC-chl generally coincide with elevated FL-pheo (Fig. 1).

It is now recognized that the standard fluorometric method used for pigment determinations does not provide an accurate measurement of pheo, and more reliable determinations using HPLC have generally failed to detect any significant concentrations of pheo in the water column (Ondrusek et al., 1991). Recently we have used an improved multiple wavelength protocol (Turner Designs; based on Welschmeyer, 1994) to apportion the total fluorescence into chl *a*–*c* and pheo components. For samples collected during 10 separate HOT cruises in 1998, we were unable to detect any significant amount of pheo for samples collected in the euphotic zone.

Table 1
A comparison of chl *a* (FL-chl) and pheopigment (FL-pheo) concentrations and related phytoplankton parameters for samples collected in the North Pacific Subtropical Gyre before and after the 1976 Pacific climate step[a]

Parameter (units)	Pre-1976	Location	Post-1988	Location
Depth-integrated FL-chl (mg m^{-2})				
0–25 m	1.3[b] ($\pm$ 0.8)	Climax	2.0 ($\pm$ 0.7)	ALOHA
75–200 m	8.0 ($\pm$ 2.1)	Climax	14.8 ($\pm$ 3.0)	ALOHA
0–200 m	12.7 ($\pm$ 3.4)	Climax	22.5 ($\pm$ 4.6)	ALOHA
Depth-integrated FL-pheo (mg m^{-2})				
0–25 m	0.4 ($\pm$ 0.3)	Climax	1.4 ($\pm$ 0.7)	ALOHA
75–200 m	8.5 ($\pm$ 2.6)	Climax	25.2 ($\pm$ 7.1)	ALOHA
0–200 m	10.3 ($\pm$ 3.0)	Climax	30.8 ($\pm$ 8.2)	ALOHA
FL-pheo : FL-chl (mg : mg)				
0–25 m	0.36 ($\pm$ 0.19)	Climax	0.71 ($\pm$ 0.38)	ALOHA
75–200 m	1.11 ($\pm$ 0.30)	Climax	1.74 ($\pm$ 0.52)	ALOHA
0–200 m	0.86 ($\pm$ 0.26)	Climax	1.41 ($\pm$ 0.46)	ALOHA
Parameter (units)	**Pre-1976**	**Location**	**Post-1988**	**Location**
Euphotic zone (0–200 m) biomass carbon (g m^{-2})				
Phototrophs based on microscopy	1.2 ($\pm$ 0.3)	Climax	—	—
Phototrophs based on flow cytometry	—	—	1.5 ($\pm$ 0.4)	ALOHA
Particulate carbon (g m^{-2}) 0–50 m	0.96 ($\pm$ 0.22)	GOLLUM	1.32 ($\pm$ 0.32)	ALOHA
Particulate nitrogen (g m^{-2}) 0–50 m	0.13 ($\pm$ 0.03)	GOLLUM	0.23 ($\pm$ 0.07)	ALOHA
Dominant phytoplankton species (domain assignment)	Monads, flagellates and non-thecate dinoflagellates (*Eukarya*)	Climax	*Prochlorococcus*, *Synechococcus* (*Bacteria*)	ALOHA

[a]Data from various sources: Climax site chl *a* (FL-chl) and pheopigment (FL-pheo) concentrations from Scripps Institution of Oceanography Data Reports # 74-20, 75-6, 90-3, 90-4, 91-28, 93-17 and several unpublished cruise reports; Climax biomass carbon estimation and species composition data from Beers et al. (1982); GOLLUM particulate carbon and nitrogen from Gordon (1971). ALOHA biomass carbon by flow cytometry and species composition data from Campbell et al. (1994) and Karl and Dobbs (1998). ALOHA particulate carbon and nitrogen data from HOT program data set (http://hahana.soest.hawaii.edu).

[b]Values throughout are mean values $\pm$ 1 s.d. where appropriate.

We suggest that the apparent increases in FL-pheo and in the FL-pheo : FL-chl ratios (Table 1) for samples collected in the NPSG during the past three decades reflect an increase in the relative abundance of chl *b* resulting from temporal variations in phytoplankton community structure. If our interpretation is correct, then the DCML FL-chl concentrations reported for the period after 1976 are actually underestimates (depending upon the chl *b* : *a* ratios) of the true chl concentrations, suggesting that the actual chl concentration step increase may be greater than the reported factor of two (Venrick et al., 1987). This contention is consistent with the observed FL-chl vs. HPLC-chl data from Sta. ALOHA (Fig. 1) where methods have remained consistent over the past decade.

The separate chronologies of the changes in FL-chl and FL-pheo concentrations indicate a decoupled system with antecedent FL-chl concentration increases (Figs. 1 and 2). The greatest increase in FL-chl was between 1976 and 1985, whereas the major step in FL-pheo occurred after 1985 (Figs. 1 and 2). Furthermore, FL-pheo concentration appears to be still on the rise in the NPSG (Fig. 1).

As one component of the HOT core measurement program, FL-chl and FL-pheo are also measured at an inshore station off Kahe Point, Oahu (Sta. Kahe; 21°20.6′N, 158°16.4′W). This location was the site of a previous 6-cruise time-series study conducted from May 1980 to May 1981 (Bienfang et al., 1984). Identical to the results presented for the open-ocean station, FL-chl and FL-pheo concentrations in the DCML (100–125 m) at Sta. Kahe are greater now than they were approximately a decade prior to the start of the HOT program (all values, $mg\,m^{-3}$): FL-chl *a* (1980–1981) = 0.16 (s.d. = 0.09, $n = 49$) vs. FL-chl *a* (1989–1997) = 0.21 (s.d. = 0.08, $n = 167$) and FL-pheo (1980–1981) = 0.19 (s.d. = 0.14, $n = 49$) vs. FL-pheo (1989–1997) = 0.37 (s.d. = 0.14, $n = 168$). These observed increases in FL-chl and FL-pheo are both highly significant. Furthermore, within the Kahe data set (Jan 1989–Dec 1997), a significant increase in FL-pheo ($mg\,m^{-3}$) is observed: (FL-pheo = 0.08 + 0.56 times years since 1 Jan 1989). The contemporary FL-pheo : FL-chl ratio for the DCML at Sta. Kahe (mean = 1.75) is similar to that observed at Sta. ALOHA (Table 1).

3.2. Changes in biodiversity and productivity in the NPSG

In 1988, *Prochlorococcus* was first reported as a cosmopolitan and abundant member of the marine plankton (Chisholm et al., 1988). *Prochlorococcus* is now recognized as a group of fairly diverse photosynthetic prokaryotes within the cyanobacterial lineage that are closely related to *Synechococcus*, another member of the photosynthetic marine picophytoplankton (Urbach et al., 1998; Moore et al., 1998). The type species, *Prochlorococcus marinus*, has a novel but variable pigment composition, including high chl *b* : *a* ratios and the presence of "red-shifted" divinyl chl *a* (DV-chl *a*) as a diagnostic characteristic (Table 2; Chisholm et al., 1992; Goericke and Repeta, 1992). The presence of chl *b* and DV-chl *a* both interfere with measurements of FL-chl and FL-pheo. The magnitude of this error depends critically on pigment concentration ratios and on the spectral characteristics of the filters used to measure sample fluorescence.

We hypothesize that the dramatic temporal increase in FL-pheo, especially for samples collected at the DCML (Figs. 1 and 2, Table 1), is a manifestation of a phylogenic domain shift from a phytoplankton population dominated by eukaryotic cells to one dominated by DV-chl *a* and chl *b*-containing prokaryotes (domain *Bacteria*). The large, nearly two-fold increase in FL-pheo concentration in the lower portion of the euphotic zone (75–200 m) in 1991 (Fig. 1) may have been

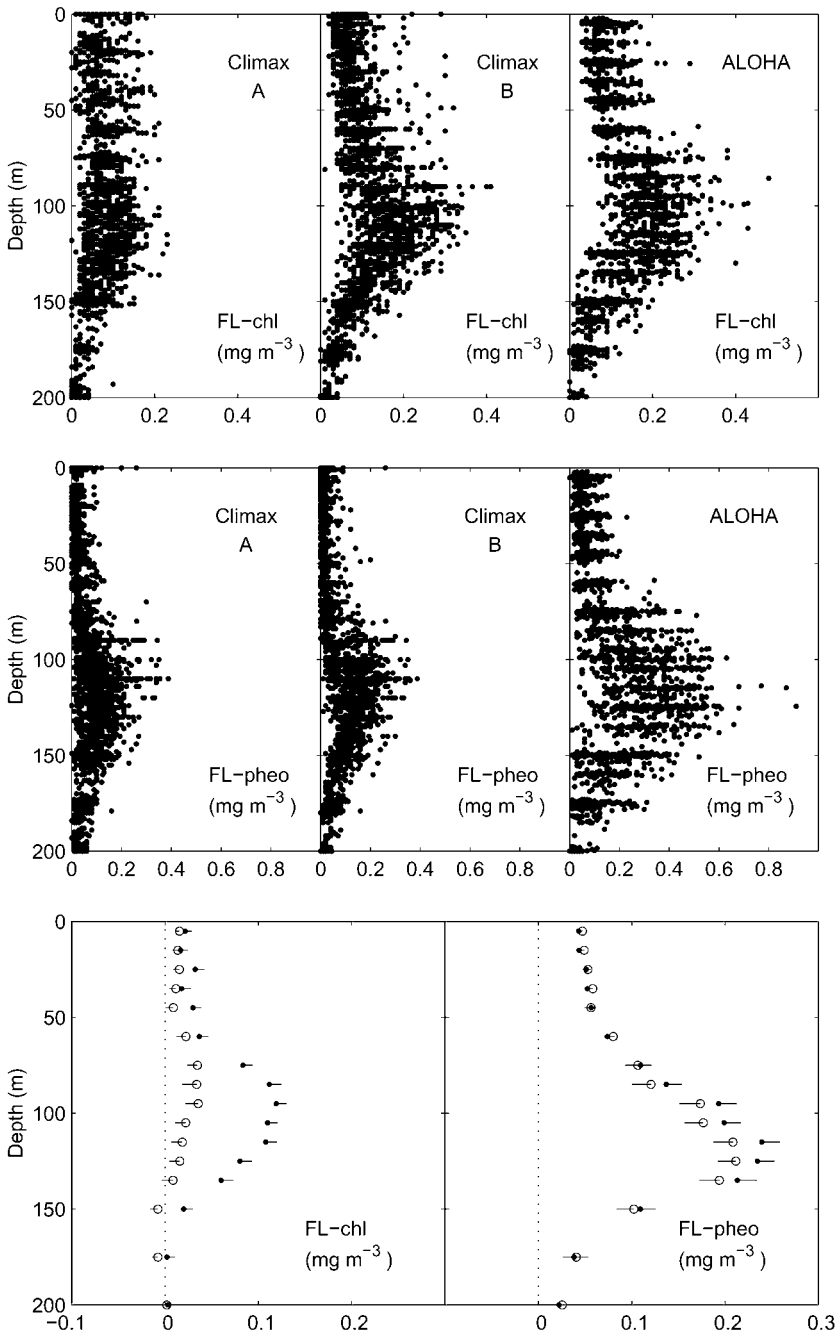


Fig. 2. Comparisons of the concentration vs. depth profiles for FL-chl [TOP] and FL-pheo [CENTER] in the NPSG for the periods 1968–1975 (Climax A), 1976–1986 (Climax B) and 1988–1997 (ALOHA). Each data set displays all samples collected during the respective time period. Both Climax region and Sta. ALOHA data sets, relevant metadata and data source credits are available from DMK upon request. [BOTTOM] Mean ($\pm$ 1 s.d., as shown) differences for FL-chl (left) and FL-pheo (right) calculated as: ALOHA minus Climax A (●) and ALOHA minus Climax B (○).

a result of enhanced stratification of the water column resulting from the onset of El Niño (Karl et al., 1995). This enhanced stratification has led to decreased inorganic nutrient availability (see Section 3.5) and, perhaps, greater reliance on the much larger pools of dissolved organic nitrogen and phosphorus. Both of these conditions would tend to favor the growth and accumulation of *Prochlorococcus*. Direct measurements of chl *b* in samples collected from the NPSG (Table 2) and other data reported herein are all consistent with this domain-shift hypothesis.

These results, suggesting a fundamental change in phytoplankton biomass and community structure, are also supported by several independent lines of evidence. Beers et al. (1982) reported that the total biomass (expressed in terms of carbon) of photosynthetic organisms ranged from 16 to 59% of the total particulate organic carbon (POC) for five cruises to the Climax region between 1973 and 1974, and these estimates did not include *Prochlorococcus* or other picoautotrophs. Integrated POC for the 0–50 m depth interval was approximately 1.0 g $C\,m^{-2}$ compared to 1.3 g $C\,m^{-2}$ today (Table 1). Furthermore, in the contemporaneous subtropical gyre, *Prochlorococcus* accounts for $> 75\%$ of the photoautotrophic biomass in the upper portion of the water column. It is hard to ascribe these major apparent differences in biomass and community structure to anything but ecosystem change.

In addition to chl *a* and pheo (chl *b*) variability, we also present a 30-year chronology for primary production. Compared to the 17-year Climax program mean of about 200 mg $C\,m^{-2}\,d^{-1}$, the average rate of primary production measured during the HOT program (473 ± 123 mg $C\,m^{-2}\,d^{-1}$; $n = 74$) is more than twice as high (Fig. 1). While it is impossible to estimate the consequences of methodological improvements over this 30-year period, we believe that these plankton rate processes, along with the pigment data discussed previously, result from fundamental changes in phytoplankton community structure that ultimately derive from habitat variations. This shift towards a more efficient and rapidly growing phytoplankton assemblage is consistent with the hypothesized domain shift, and the timing of the productivity step is consistent with the FL-pheo (chl *b*) inventories.

3.3. Phytoplankton succession and climate change

Theoretically, the implied increase in the chl *b* : *a* ratio of the DCML phytoplankton populations could be a result of either an increased number of *Prochlorococcus* cells relative to total phytoplankton biomass or to long-term photoadaptation of a static population, or a combination of both. Neither process would proceed without an antecedent change in the physical and chemical structure of the habitat. If the historical measurements of phytoplankton community structure and biomass are valid, then one must conclude that *Prochlorococcus* has become more abundant over the past few decades. *Prochlorococcus* cell enumeration data, which will be presented elsewhere (R. Bidigare et al., in preparation), support this conclusion. We are not suggesting that *Prochlorococcus* was totally absent from the water column prior to 1976, or that it is exclusive in the contemporary ocean. We do maintain, however, that environmental changes have occurred since 1976 that were conducive for the selection and succession of *Prochlorococcus* as the dominant marine phytoplankton group in the NPSG. This has resulted in an overprinting of *Prochlorococcus* biomass onto the background photosynthetic eukaryote assemblages, resulting in the domain shift we presently describe.

Table 2
Chronology of chlorophyll *a* and *b* concentrations and chlorophyll *b* : *a* concentration ratios for water samples collected in the subtropical North Pacific Ocean[a] and selected laboratory data from *Prochlorococcus* isolates

Station location and sampling date(s)	Depth or depth range (m)	Chl *a* ($mg\,m^{-3}$)	Chl *b* ($mg\,m^{-3}$)	*b*/*a* ratio ($mg\,mg^{-1}$)	Method[b]	Comments	References
20.7°N, 156.9°W (June 1972)	0–250	—	—[c]	< 0.05	Absorption spectrophotometry	Chl *c* : chl *a* in and above DCML was 0.5–2.0	Gundersen et al. (1976)
13–18°N, 157°W (Mar 1982)	25 DCML	0.07 0.28	0.003 0.076	0.04 0.27	reverse-phase HPLC	Chl *b* was found in 32 of 45 water samples and was always present at depths > 100 m	Vernet and Lorenzen (1987)
24°N, 140°W	25 DCML	0.035 0.120	0.003 0.030	< 0.05 0.3	GF/F filters; reverse-phase	Chl *c* undetectable in surface waters; chl *c* : chl *a* in DCML	Ondrusek et al. (1991)
24°N, 160°W (Mar–Apr 1985)	25 DCML	0.040 0.130	0.003 0.075	< 0.05 < 0.6	HPLC	was < 0.1	
ADIOS I 26°N, 155°W (Mar–Apr 1986)	25	0.03–0.08	0.002–0.009	0.09 (± 0.03)	GF/F filters; reverse-phase	Observed a 5-fold storm-induced increase in chl *b* at 150 m; chl *c* : chl *a* ratio in DCML < 0.1	DiTullio and Laws (1991)
	150	0.03–0.23	0.02–0.10	0.42 (± 0.05)	HPLC		
Sta. ALOHA 22.75°N, 158°W (26 cruises from Feb 1989–Oct 1991)	5 DCML	0.078 (± 0.021) 0.258 (± 0.059)	—[d] 0.123 (± 0.044)	< 0.1 0.48	GF/F filters; reverse-phase HPLC	Chl *c* ($c_1 + c_2 + c_3$) : chl *a* ratio in DCML < 0.2	Letelier et al. (1993)
Sta. ALOHA 22.75°N, 158°W 78 cruises (1989–1997)	5 DCML	0.076 (± 0.024) 0.234 (± 0.063)	0.006 (± 0.004) 0.109 (± 0.095)	0.08 0.47	GF/F filters; reverse-phase HPLC	Divinyl chl *a* : monovinyl chl *a* ratio was 1.32 (± 0.41; 5 m) and 1.29 (± 0.51; DCML) for period 1994–1997	This study

Prochlorococcus marinus culture	—	—	1.15	GF/F filters; reverse-phase HPLC and NMR-mass spectrometer	Major pigment was 8-desethyl, 8-divinyl chl *a* and major accessory pigment was 8-desethyl, 8-divinyl chl *b*, "normal" chl *a* and chl *b* are not present	Goericke and Repeta (1992)
Prochlorococcus strains	—	—			Divinyl chl *a* only; ratio of divinyl chl *b* : total chl *b* ranged from 100% in MED to 40–96% in SARG to 17–94% in NATL1 with highest values under low light conditions	Partensky et al. (1993)
MED (low light)[e]	—	—	0.12			
MED (high light)	—	—	0.08			
SARG (low light)	—	—	0.75			
SARG (high light)	—	—	0.52			
NATL1 (low light)	—	—	0.88			
NATL1 (high light)	—	—	0.40			
Prochlorococcus strains — PAC (low light)	—	—	1.53	GF/F filters; reverse phase HPLC	Ratio of divinyl chl *b* : total chl *b* = 100%	R. Bidigare and L. Campbell (unpubl.)

[a] Jeffrey (1976) and Lorenzen (1981) have also reported the presence of chl *b* in samples collected in the subtropical North Pacific Ocean. Jeffrey (1976) used sucrose thin-layer chromatography of large volume (60-*l*) water sample extracts to measure chl *b*, but reported only "approximate" chl *b* : *a* ratios. Lorenzen (1981) reported detecting chl *b* in 72% of the water samples analyzed (using reverse-phase HPLC) but the total chl *b* was low relative to chl *a* (*b* : *a* ratios were < 0.02, 0.06 and 0.09 in 51, 79 and 95% of the samples). Unfortunately, he does not provide the station coordinates or sampling dates other than "eastern North Pacific Ocean".

[b] GF/F = Whatman GF/F glass fiber filters; HPLC = high-performance liquid chromatography.

[c] Reports "very little chl *b* was present in our samples" which we conservatively assume to be $< 1\,\text{mg chl } b\,\text{m}^{-2}$.

[d] Chlorophyll *b* "sporadically detected" with values ranging from < 0.001 to $0.012\,\text{mg m}^{-3}$.

[e] Low light conditions were blue (475 ± 50 nm) light at 3.8–6.0 μmol quanta $\text{m}^{-2}\,\text{s}^{-1}$; high light conditions were white light at 133 μmol quanta $\text{m}^{-2}\,\text{s}^{-1}$.

Recent studies in the Gulf of Aqaba and the Arabian Sea have documented an annual succession of phytoplankton from eukaryotic cells to *Prochlorococcus* as the water column stratified and nutrients were depleted (Lindell and Post, 1995; Latasa and Bidigare, 1998). For the Arabian Sea study, Latasa and Bidigare (1998) noted a mutual exclusion of diatoms and *Prochlorococcus*. The contemporaneous phytoplankton community structure at Sta. ALOHA, with a dominance of *Prochlorococcus* throughout the entire euphotic zone (Campbell and Vaulot, 1993; Campbell et al., 1994), may be the oligotrophic ocean end-member in picophytoplankton succession. Evidence presented elsewhere (Karl et al., 1995, 1997; Karl and Tien, 1997; Karl, 1999) has documented a significant change in the NPSG habitat over the past decade, with a trend towards increasing water column stratification and increasing nutrient limitation. Under these conditions, there would be strong selection for small cells with enhanced nutrient uptake and light absorption capabilities as well as photosynthetic diazotrophs. This prolonged "endless summer" in the NPSG provides the selection pressure necessary for a several decade-long succession of *Prochlorococcus* to have taken place under generally stratified, nutrient-depleted conditions.

Both Venrick et al. (1987) and Polovina et al. (1994) suggested that the increase in photosynthetic microbial biomass (i.e. chl *a*) in the NPSG following the 1976–1977 climate step (Ebbesmeyer et al., 1991) was the result of an increased frequency of deep mixing events due to an intensification of the Aleutian low-pressure system in late winter. This vigorous mixing, they argued, would enhance nutrient input to the euphotic zone and stimulate ecosystem productivity. While these effects may certainly be important to ecosystem dynamics, they would neither select for *Prochlorococcus* (Lindell and Post, 1995) nor for the co-occurring N_2-fixing cyanobacterium, *Trichodesmium* (Karl et al., 1995, 1997; Karl, 1999), nor would they necessarily lead to the additional ecosystem changes that we describe herein.

Wind stress, heat and water exchange in addition to gyre circulation tempo and mode are all biogeochemically relevant physical determinants. The pathways and rates of supply of nutrients, including trace elements, ultimately control community structure, ecosystem carrying capacity and productivity. Climate variability is a result of both ordered forcing and chaotic behavior (Rind, 1999). This provides for a potentially complex ecosystem response with multiple levels of interaction, including threshold and feedback phenomena. Add to that the vagaries of biology, especially microbiology, and it should be no surprise that a simple and predictable cause-and-effect mechanistic understanding of the role of climate variability on ecosystem function is not presently available. Understanding these complex climate variations and their atmospheric and oceanic teleconnections is a major contemporary challenge in earth science (Miller et al., 1994; Graham, 1994; Mantua et al., 1997).

3.4. Spatial vs. temporal variations

The comparison of two Eulerian time-series data sets collected from different regions in the NPSG assumes that the Climax region and Sta. ALOHA are reasonably similar and representative of the subtropical biome as a whole. To test the former assumption for the contemporaneous ocean, water samples were collected during summer 1996 and 1997 at both Climax and ALOHA. Analyses of selected eukaryotic phytoplankton revealed that the composition of shallow, mid-level and deep species at Climax and ALOHA were not statistically different (July 1996), and were indistinguishable from the historical 1973–1985 summer data for the Climax region (Venrick,

1997). Furthermore, the abundances of shallow "key species" at Climax were not statistically different from those determined for Sta. ALOHA. In contrast, the abundances of selected mid-level and deep "key species" were significantly higher at Climax than at Sta. ALOHA during July 1996 (Venrick, 1999).

Pigment samples (FL and HPLC) also were collected from both stations (Fig. 3). Concentrations of FL-chl, FL-pheo, DV-chl *a* (*Prochlorococcus* biomarker) and chl *b* (*Prochlorococcus* biomarker) measured at both stations are in good agreement with historical summertime measurements at Sta. ALOHA (1988–1997). These results indicate that total chl *a* and *Prochlorococcus* pigment concentrations are nearly identical during summertime for Climax and ALOHA (Fig. 3). The same is true for the majority of analyses performed for the eukaryotic marker pigments 19′-hexanoyloxyfucoxanthin (19′-hex, prymnesiophyte biomarker) and fucoxanthin (fuco, diatom biomarker). However, there are three samples from the Climax region where 19′-hex (100 and 125 m) and fuco (125 m) concentrations were $\sim 50\%$ greater than Sta. ALOHA climatology (Fig. 3). This finding is consistent with the observation of enhanced mid-level and deep species counts at Climax (Venrick, 1999) because these pigments are associated with representatives found in these "key species" groups (i.e. diatoms and coccolithophores). The higher biomass of deeper-living eukaryotic phytoplankton for the Climax region may be a vestige of the southward migration of the "subsurface front" during wintertime. While there appear to be significant differences in the abundances of some of the relatively rare, deeper-living phytoplankton species (Venrick, 1999), total chl *a* and concentrations of the *Prochlorococcus* marker pigments are remarkably similar at both study sites during summertime.

Independent evidence for decadal-scale variations in pigment biomass and phytoplankton community structure has recently been reported for the western subtropical Pacific (Sugimoto and Tadokoro, 1998). Measurements of FL-chl (using Climax protocols; see Methods) were determined during summer and winter cruises to the subtropical front region (21–23°N) along 137°E for the period 1972–1993. During 1972–1980, integrated FL-chl concentrations for summer and winter cruises averaged about $30\,mg\,m^{-2}$. After 1980, chl *a* inventories decreased dramatically to a level of $\sim 20\,mg\,m^{-2}$. This pattern was observed for both summer and winter cruises, and the decrease in FL-chl was attributed to increases in wind speed and decreases in stratification of the western subtropical Pacific (Sugimoto and Tadokoro, 1998). It was further noted that the FL-chl reductions were associated with increases in diatom abundance. Interestingly, the secular changes in FL-chl and community composition changes reported for this western Pacific site, located at the frontal boundary of the subtropical gyre, are exactly opposite to those observed for the eastern subtropical North Pacific gyre, as reported herein.

3.5. Nutrient–phytoplankton interactions

Historically, biomass production in the subtropical gyre was thought to be limited by available inorganic nitrogen or simultaneously by nitrogen and phosphorus (Eppley et al., 1973; Eppley et al., 1977). However, following enhanced stratification and decreased inorganic nutrient availability, there has been a selection for N_2-fixing cyanobacteria, including *Trichodesmium*, and a shift to a phosphorus-limited or iron-limited state with attendant changes in biogeochemical cycling rates and processes (Karl et al., 1995, 1997; Karl and Tien, 1997).

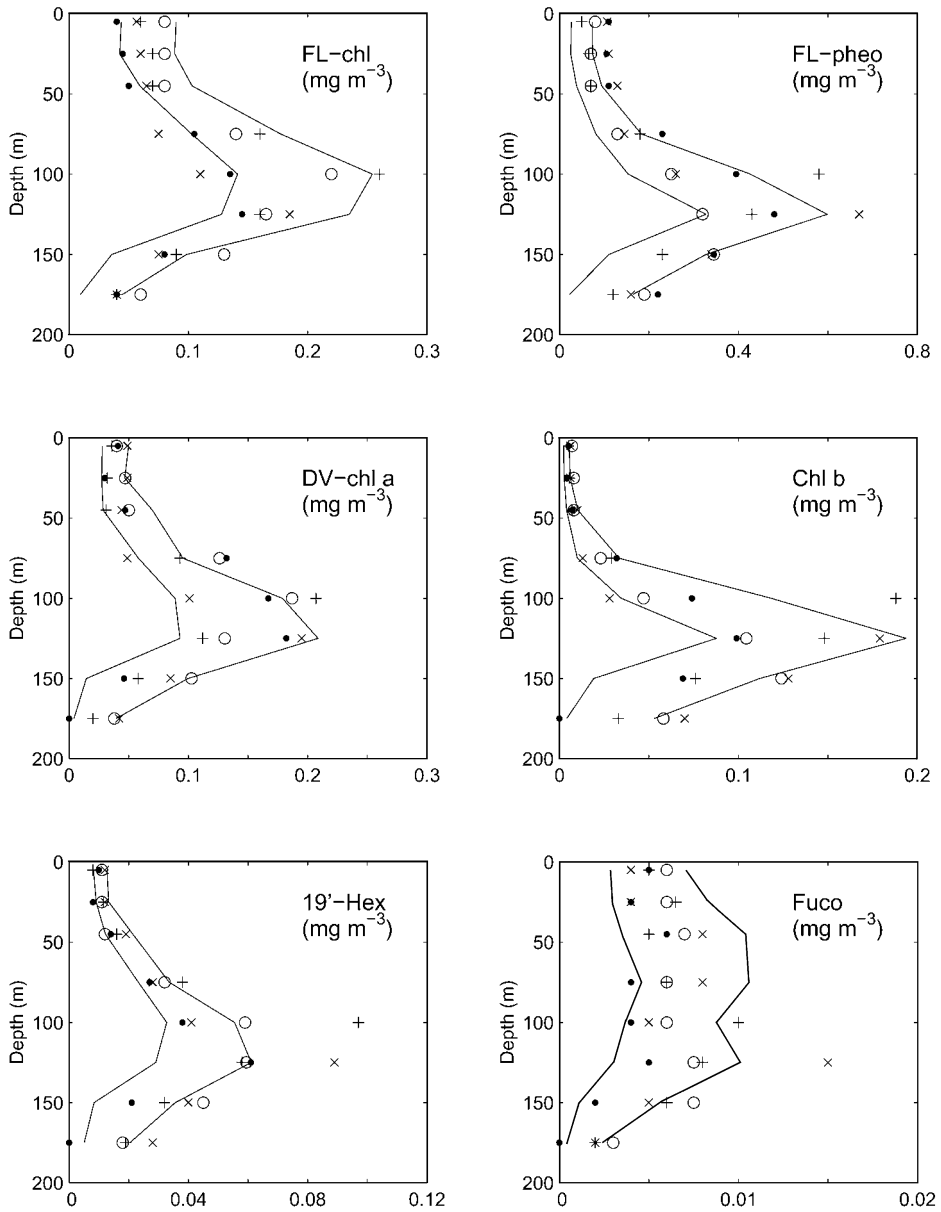


Fig. 3. Vertical distributions of phytoplankton pigment concentrations (mg m^{-3}) determined at Sta. ALOHA and Climax: FL-chl, FL-pheo, DV-chl *a* (divinyl chl *a*; *Prochlorococcus* marker), chl *b* (*Prochlorococcus* marker), 19′-Hex (19′-hexanoyloxyfucoxanthin; prymnesiophyte marker), and Fuco (fucoxanthin; diatom marker). Symbols represent samples collected at Sta. ALOHA during 1996 (●) and 1997 (○), and Sta. Climax during 1996 (×) and 1997 (+). Solid lines represent the summertime (Jun–Aug) climatological mean (± 1 s.d.) data envelope for each pigment established for Sta. ALOHA (1988–1997).

The Pacific (inter) Decadal Oscillation, or PDO, is a pan-Pacific phenomenon with significant ecological impact on marine and terrestrial habitats (Mantua et al., 1997). The PDO characteristics (e.g. sign and amplitude) are correlated with the Southern Oscillation Index (SOI) such that warm (or cold) phase ENSO-like conditions tend to coincide with years of positive (or negative) polarity in the PDO; however, ENSO-like conditions can develop regardless of PDO polarity. Significant PDO polarity reversals, the so-called regime shifts, occurred in 1925, 1947 and 1977 (Mantua et al., 1997) so the coupled ENSO–PDO interactions (both positive and negative) vary depending upon PDO polarity. Other climate cycles with different periodicities and consequences also may interact.

During the past several decades, the upper water column (0–100 m) inventories of Si and SRP in the NPSG have declined significantly (Fig. 4). These changes also coincide with a period of an unprecedented and sustained El Niño-favorable condition, as depicted by the SOI (Fig. 4). These extended periods are most likely the cause of the domain shifts that we report herein. The Si concentrations might be expected to select against diatoms and other Si-containing plankton, and the low SRP would select for picophytoplankton capable of growing at reduced nutrient concentrations and *bacteria* with the ability to fix N_2. Both selection pressures are consistent with the observed domain shift, and both would be expected to alter food web structure, carbon export and sequestration. Secular warming trends, due to greenhouse emissions, would comprise a new climate-forcing process and could act to enhance natural oceanic habitat variability.

The North Pacific gyre may oscillate, on multi-decadal time scales, between sink and source habitats for eukaryotic vs. prokaryotic photoautotrophic populations. The relative fitness of each subpopulation would be determined by the habitat, which is ultimately under climate control. In this regard, the NPSG probably represents a two-state phototrophic system, with permanent eukaryote and prokaryote presence, but periodic prokaryote dominance. One intriguing potential consequence of these decade-scale habitat changes might be the tendency to promote spatial and temporal biological heterogeneity as a result of vertical mixing via non-linear interactions between mesoscale eddies and the local wind-forced currents (Letelier et al., 2000). These event-scale phenomena could provide a short-lived source of new inorganic nutrients, allowing the ecosystem structure to temporarily revert back to one where eukaryotic phytoplankton and herbivorous crustacean zooplankton are selected. Particulate matter export from the euphotic zone and other biogeochemical processes may be more dependent on these short-term shifts in plankton species composition than on the mean ecosystem state. These stochastic biodiversity "flashbacks" also might help to explain why the $> 5\,\mu m$ phytoplankton species list and species rank order abundance have remained relatively constant over the past several decades (Venrick, 1997, 1999), despite the major ecosystem changes that we describe in this report.

3.6. Ecological implications and future prospects

There are several major ecological implications of our hypothesized domain shift in plankton community structure and productivity that could have potential impacts on oceanic C, N and P cycles. Although the standing stock of phytoplankton in the sea is less than 1% of the total global plant carbon, these microscopic organisms are responsible for the production of an estimated 45–50 petagrams ($Pg = 10^{15}$ g) of organic carbon annually, nearly half of the total global photosynthesis (Field et al., 1998). Within the marine environment, a majority of total primary production

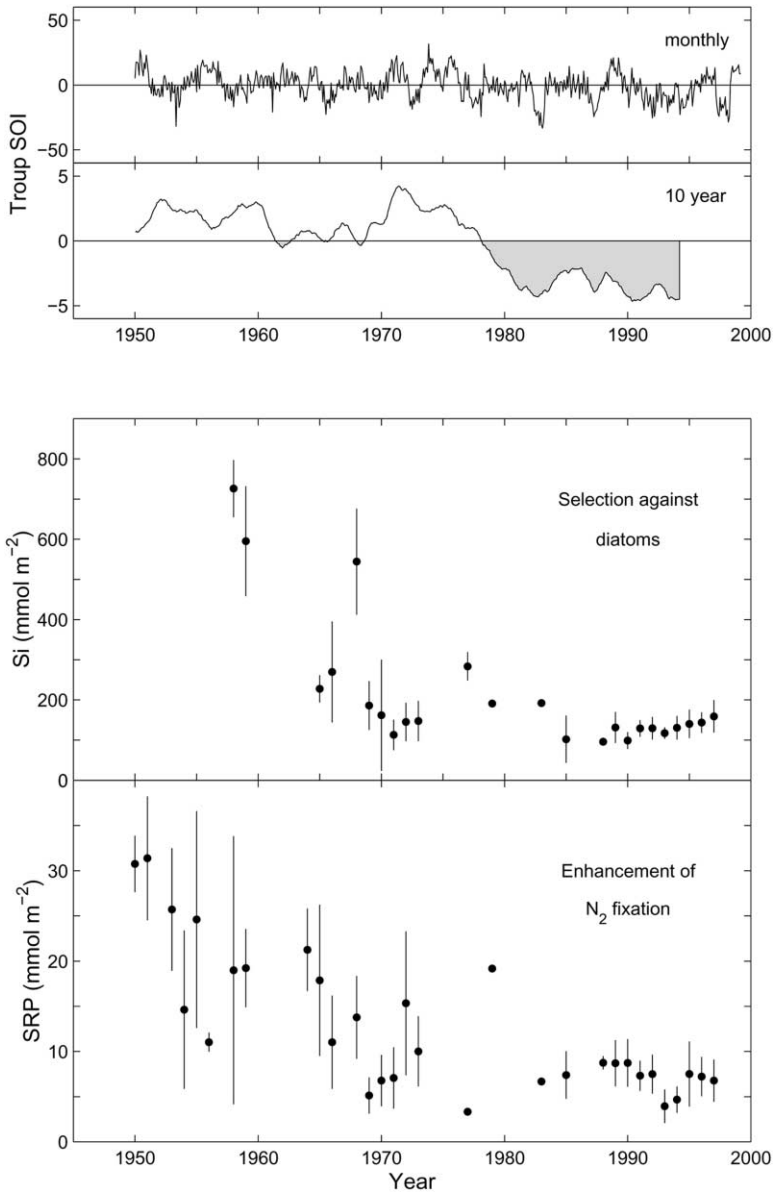


Fig. 4. [TOP] The Troup Southern Oscillation Index (SOI) defined as: [dP(Tahiti) –dP(Darwin)]/s.d., where dP(Tahiti) and dP(Darwin) are the monthly pressure anomalies (monthly mean minus the 1882–1997 mean) at Tahiti and Darwin, respectively, and s.d. is the monthly standard deviation of the difference. Low SOI values generally indicate El Niño-favorable conditions. [BOTTOM] Upper water column (0–100 m) inventories (mmol m^{-2}) of dissolved silicate (Si; upper) and soluble reactive phosphorus (SRP; lower) for samples collected within the region 20–30°N, 140–170°W (see Section 2 for more details).

occurs in open-ocean habitats, which are characterized by low nutrient and low chl *a* concentrations. However, because of the spatial dominance of these biomes on the Earth, small variations in the productivity of these "biological deserts" can cause major changes in the global carbon cycle. Furthermore, *Prochlorococcus* is the smallest known marine oxyphototroph, so a greater reliance on these prokaryote-based food webs would result in fundamental changes in the structure and function of the NPSG ecosystem. For example, a shift downward in the size distribution of the herbivore population from small crustaceans to protozooplankton would lead to a more complex food web and a reduction in the flow of carbon and energy to the top level predators of the subtropical ocean. Consequently, even though the rates of primary production may be enhanced (Fig. 1), fish production could decrease as a result of food-web interactions. The less important ecological role of herbivorous crustaceans also would lead to a reduction in the export of particulate organic matter from the euphotic zone, and eventually to a longer residence time for C, N and P in the upper ocean due to enhanced rates of dissolved organic matter production and regeneration. Bacterial processes would dominate in the surface waters, as they clearly do at the present time, and the delivery of carbon and energy to the mesopelagic zone would be curtailed compared to those in eukaryote-dominated ecosystems of comparable productivity. These complex, cascading trophic interactions need to be fully described and understood before the oligotrophic ocean ecosystem can be modeled with any degree of accuracy.

It is important to emphasize that the contemporary NPSG ecosystem is almost entirely microbial in composition; both standing stocks and fluxes of carbon and energy are dependent upon small ($< 20\,\mu m$) organisms. These microorganisms, especially prokaryotes (*Bacteria* and *Archaea*), are truly the "unseen majority"; it has been estimated that there are more than 10^{29} prokaryotes in the world ocean (Whitman et al., 1998). In addition to this sheer number, global ocean microbial biomass is also substantial, accounting for $0.6–1.9 \times 10^{15}$ g of carbon (Karl and Dobbs, 1998). During the past decade major progress has been made in the detection of sophisticated signal transduction networks among bacteria (Shapiro, 1998), and it now appears almost certain that unicells derive adaptive benefit from multicellular organization and integration. It is intriguing to contemplate this potential connectivity between Earth's climate, North Pacific population structure, and oceanic biogeochemical cycles.

Finally, if our model of climate-induced variations in NPSG community structure and biogeochemical processes is valid, then one might speculate further on the ultimate cause. A change, beginning in 1976, towards more frequent El Niño and fewer La Niña events may be crucial (Fig. 4). It has been suggested that this unprecedented warming may be, at least in part, related to the anticipated greenhouse climate effect of increased atmospheric carbon dioxide concentrations (Trenberth and Hoar, 1996, 1997). Recent results from a high-resolution global climate model suggest that an increasing burden of atmospheric greenhouse gases will lead to more frequent El Niño-like events as well as stronger La Niña events (Timmermann et al., 1999) and therefore, could enhance the ecosystem domain shifts described herein. The second report of the Intergovernmental Panel on Climate Change (Houghton et al., 1995) concludes that "the balance of evidence suggests a discernible human influence on climate". If the fundamental domain shift that we hypothesize here is a result of enhanced upper water-column stratification in response to global warming, then we might anticipate selection for similar processes in other subtropical regions of the world ocean as stratification is further enhanced and inorganic nutrients become depleted.

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