Temporal and Spatial Distribution of Phytoplankton Pigments in the Central Pacific Ocean along 175°E during the Boreal Summers of 1992 and 1993

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(Received 7 January 1997; in revised form 13 March 1997; accepted 20 March 1997)

The long meridional (175°E, 48°N–8°S) distribution of phytoplankton pigments was investigated in the central Pacific Ocean during the boreal summers of 1992 and 1993 by using high-performance liquid chromatography (HPLC). The sampling periods were under El Niño conditions. The distribution patterns of the chemotaxonomical pigments for eukaryotic phytoplankton were characterised: 19′-hexanoyloxyfucoxanthin (a prymnesiophyte marker) and 19′-butanoyloxyfucoxanthin (a pelagophyte marker) were detected throughout the whole study area, fucoxanthin (a diatom marker) was observed north of Kuroshio Extension, and peridinin (a dinoflagellate marker) was found at the stations both north of the Kuroshio Extension and the equatorial area, and the abundance of these pigments detected was not significantly changed (non-parametric one-way ANOVA, \( P > 0.05 \)) in the whole study area during the two sampling periods. However, the abundance of prokaryotic photoautotrophs (prochlorophytes and cyanobacteria) at the North Pacific subtropical gyre and the equatorial region during the boreal summers of 1993 was significantly higher (\( P < 0.001 \)) than that during the boreal summer of 1992 as estimated by their chemotaxonomical marker, zeaxanthin. The high prokaryotic phytoplankton biomass during the boreal summer of 1993 was also calculated by using the algorithm of Letelier et al. (1993) for partitioning total chlorophyll \( a \) biomass into contributions by major phytoplankton taxa. The North Pacific subtropical gyre has generally been thought to support a homogeneous, stable biological community, but our result suggests that the abundance of prokaryotic phytoplankton in this gyre may be spatially and temporally variable, and these change can affect primary production and zooplankton biomass.

1. Introduction

Small phytoplankton is well known to contribute significantly to phytoplankton biomass (e.g. Takahashi and Bienfang, 1983; Ishizaka et al., 1994) and primary production (e.g. Li, 1994) in the open ocean. In particular, two types of prokaryotic cells of <2 \( \mu m \) in size, cyanobacteria Synechococcus and prochlorophyte Prochlorococcus, were reported to be numerically dominant species in oligotrophic open waters within the last decade (Chisholm, 1992). Several advantages for survival of these small phytoplankton are considered: they could have higher nutrient acquisition rate per unit cell volume, and are probably capable of a higher photon absorption rate per unit cell volume in a given light field relative to larger cells (Raven, 1987). Some strains of Synechococcus can fix atmospheric nitrogen to survive in nitrate-depleted surface waters (Mitsui et al., 1986). Prochlorococcus cells also have a unique physiological characteristic, in that the cells require ammonia or urea and do not grow on nitrate substrates (Chisholm et al., 1992).

However, little is at present known of the whole community structure of phytoplankton including these small algae in the open ocean. Since many small eukaryotic cells often lack taxonomically useful morphological features for identification as observed by epifluorescence microscopy and conventional light microscopy (see Ishizaka et al., 1994). Although high-sensitive flow cytometry is often used for the observation of small algae such as Synechococcus and Prochlorococcus, this technique cannot determine the taxonomic composition of eukaryotic phytoplankton (see Binder et al., 1996; Landry et al., 1996).

Photosynthetic phytoplankton pigments have recently been used as chemotaxonomical markers for investigating
the composition of phytoplankton communities (e.g. Suzuki et al., 1995; Andersen et al., 1996; Suzuki et al., 1997). Suzuki et al. (1995), for example, showed that Prochlorococcus accounted for >50% of the total chlorophyll a (monovinyl (normal) chlorophyll a + divinyl chlorophyll a) above 1% isolume for most of the subtropical and tropical central Pacific along 175°E during the boreal summer of 1993. More recently, Andersen et al. (1996) make an attempt to compare the taxonomic composition basedon phytoplankton pigment signatures as measured by HPLC, with direct electron microscopic taxonomic identifications on eukaryotic algae in the oligotrophic open oceans. As a result, they found that electron microscopic observations and pigment data were reasonably similar in taxonomic composition, at least at the class level. Therefore, if it is considered that microscopic analysis requires a high level of taxonomic skill, may take considerable time, and can be variable among personnel (Millie et al., 1993), HPLC pigment data can provide a good first approximation concerning the taxonomic composition of phytoplankton, especially in small eukaryotic cells.

In this study, we showed the long meridional distribution of algal chemotaxonomical pigments in the subarctic, transitional, subtropical and tropical waters of the central Pacific Ocean along 175°E in the boreal summers of 1992 and 1993. Such large-scale distribution of phytoplankton pigments in the open ocean has seldom been reported hitherto. Moreover, the contribution of different phytoplankton groups to total phytoplankton pigment-biomass in the water column (0–150 m) was estimated to infer between cruise-differences in their distributions. As a result, we found that the abundance of prokaryotic photoautotrophs varied significantly at the North Pacific subtropical gyre as estimated by the pigment analysis, although this gyre has generally been thought to support a homogeneous, stable biological community (e.g. McGowan and Hayward, 1978). Our study also offered an opportunity to examine the “consistent” habitation hypothesis, which specific phytoplankton groups placed within particular oceanic environment, suggested by Hobson and Lorenzen (1972).

2. Materials and Methods

2.1 Sample collections

Samples were collected in the central Pacific Ocean from 48°N to 8°S along 175°E during NH92-2 (August–September, 1992) and NH93-2 (August–September, 1993) cruises aboard the R/V Hakurei-Maru (Fig. 1). The sampling periods were during El Niño. Hydrographic measurements and sample collection for pigment analysis were undertaken according to Suzuki et al. (1995).

2.2 Pigment analysis

Samples of seawater (7–10 liters) were collected from several depths in the upper 200 m during NH92-2 and NH93-2 cruises. The water samples were pre-filtered through 100 μm nylon gauze mesh to remove large zooplankton and then filtered through 47 mm Whatman® GF/F filters. Pigment extraction was performed according to Suzuki et al. (1995). For NH92-2 samples, an aliquot (500 μl) of clear extract was mixed with 150 μl of ion-pairing solution P (Mantoura and Llewellyn, 1983), and 150 μl of the mixed solution was injected into a Shimadzu® HPLC system (SCL-6B system controller, SIL-6B autoinjector, dual LC-6AD pumps, SPD-M6A photodiode array UV-VIS detector) in incorporating a 5 μm Inertsil ODS-2 column (4.6 × 250 mm, GL Sciences®). The HPLC solvent system reported by Mantoura and Llewellyn (1983) was used with some modifications. Solvent A was 80% methanol, 10% ion-pairing solution P and 10% water, and solvent B was 60% methanol and 40% acetone by volume. A linear gradient from 100% solvent A to 100% solvent B for 12.5 min followed by an isocratic hold at 100% solvent B for 13.5 min was used at a flow rate of 1.3 ml min⁻¹. For NH93-2 samples, the analysis of phytoplankton pigments by HPLC was performed according to Suzuki et al. (1995), who used a C8-column HPLC method to separate monovinyl chlorophyll a from divinyl chlorophyll a. Pigments were identified on the basis of their relative retention times and by comparison of their on-line absorption spectra (380–670 nm) with reference to the commercial standards of zeaxanthin (Extrasyntehse®), monovinyl chlorophylls a and b, lutein, α-carotene and β-
carotene (Sigma Chemical Co.), and well-documented algal cultures: Thalassiosira sp., Tetraselmis sp. and Cyclotella closterium (Hokkaido National Institute of Fisheries, Japan), Heterocapsa triquetra (NIES; National Institute of Environmental Studies, Japan) and Emiliania huxleyi (Niigata University, Japan). Pigment standards for quantification were obtained from the commercial products, and from the extracts of both the algal cultures and suspended particles in seawater. The latter standards were purified by Waters C18 Sep-PAK cartridges (see Wright and Shearer, 1984) and a Shimadzu preparative-scale HPLC (LC-6AD system) equipped with a Gilson fraction collector (FC 203). Pigment standards were calibrated spectrophotometrically in the appropriate organic solvents, using published extinction coefficients listed in Bidigare (1991) or Goericke and Repeta (1993). Carotenoids were quantified from peak areas in absorbance at 440 nm and their calibration factors. Zeaxanthin and lutein coeluted in both the HPLC methods. Nevertheless, on-line diode array spectra on the samples in this study showed that lutein was virtually absent, so that zeaxanthin plus lutein peaks were quantified as zeaxanthin equivalent. As monovinyl chlorophyll a and divinyl chlorophyll a also coeluted in the HPLC method for NH92-2 samples, total chlorophyll a (monovinyl chlorophyll a plus divinyl chlorophyll a) was quantified on the basis of its peak area at 436 nm, which was halfway between the absorption maximum of chlorophyll a and divinyl chlorophyll a in the eluents of this study (data not shown), and by using the calibration factor of chlorophyll a at 436 nm (see Ondrusek et al., 1991).

2.3 Chemotaxonomic pigments and the contribution of selected phytoplankton groups to total chlorophyll a biomass

Chlorophyll a contributions provided by the major eukaryotic phytoplankton groups (i.e. prymnesiophytes, pelagophytes, dinoflagellates and diatoms) were calculated by the method of Bidigare and Ondrusek (1996), which used integrated pigment concentrations in the water column (trapezoidal rule; 0–150 m) and the algorithms given in Table 1 (after Letelier et al., 1993). The chlorophyll a associated with eukaryotic photoautotrophs was calculated by summing the contributions of prymnesiophytes, pelagophytes (sensu Andersen et al. (1993) referred to chrysophytes in Letelier et al. (1993)), diatoms and dinoflagellates. The chlorophyll a associated with prokaryotic autotrophs (Prochlorococcus and cyanobacteria) was calculated as the difference between total chlorophyll a and that contributed by eukaryotic photoautotrophs. The low level of prasinoxanthin and alloxanthin detected indicate that prasinophytes and cryptophytes were not major phytoplankton components (described below), and their contributions were ignored in the chlorophyll biomass calculations. Non-parametric one-way analysis of variance (ANOVA) was used to test for significant differences in pigment concentrations.

3. Results and Discussion

3.1 Hydrographic conditions along 175°E

The intermediate cold layer, which is a characteristic feature of the western subarctic gyre in summer, appeared at 70–190 m between 48°N and 46°N during both NH92-2 and NH93-2 (Fig. 2). The subarctic front was located around 42°N during the two cruises. The degree of salinity north of the subarctic front increased with depth. The low surface salinities (<33.0 psu) indicated that the precipitation was much higher than the evaporation. Nutrients (nitrate plus nitrite) concentrations north of the subarctic front were generally high, but their surface concentrations decreased rapidly toward the south (Fig. 3). At south of the subarctic front, the Kuroshio Extension regions were located between

<table>
<thead>
<tr>
<th>Algal group</th>
<th>Equation</th>
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<tbody>
<tr>
<td>Prymnesiophytes</td>
<td>[Chl a] Prym = 1.3 × [19'-hex] Prym</td>
</tr>
<tr>
<td>Pelagophytes</td>
<td>[Chl a] Pel = 0.9 × [19'-but] Pel</td>
</tr>
<tr>
<td>Dinoflagellates</td>
<td>[Chl a] Dino = 1.5 × [Peridinin]</td>
</tr>
<tr>
<td>Diatoms</td>
<td>[Chl a] Diat = 0.8 [(Fucos) – (0.02[19'-hex] Prym + 0.14 [19'-but] Pel)]</td>
</tr>
<tr>
<td></td>
<td>where</td>
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<tr>
<td></td>
<td>[19'-hex] Prym = (P/P – C) × ([19'-hex] Total – ([19'-but] Total × C))</td>
</tr>
<tr>
<td></td>
<td>[19'-but] Pel = (P/P – C) × ([19'-but] Total – ([19'-hex] Total × 1/P))</td>
</tr>
<tr>
<td></td>
<td>P = [19'-hex] Prym/[19'-but] Prym = 54.27</td>
</tr>
<tr>
<td></td>
<td>C = [19'-hex] Pel/[19'-but] Pel = 0.14</td>
</tr>
<tr>
<td>Eukaryotic phytoplankton</td>
<td>[Chl a] Euk = [Chl a] Prym + Ple + Dino + Diat</td>
</tr>
<tr>
<td>Prokaryotic phytoplankton</td>
<td>[Chl a] Prok = [Chl a] Total – [Chl a] Euk</td>
</tr>
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42°N and 30°N during NH92-2, and between 42°N and 35°N during NH93-2. Surface temperatures were high (>27°C) in the subtropical gyre extending from 30°N to 12°N during NH92-2, and from 35°N to 12°N during NH93-2, and their isolines deepened with depth. Surface nutrient concentrations were below detection limits (0.1 µM) south of the Kuroshio Extension during the two survey cruises. These are probably due to the strong pycnocline which restricted the vertical mixing of nutrients. During NH93-2, a pronounced doming of the isotherms was observed near 19°N. This indicates that the subtropical front was formed near 19°N, and the subtropical counter current existed around there. An upwelling between the North Equatorial Current and the North Equatorial Counter Current was also observed near 8°N from both the distributions of nutrients and temperature. The equatorial divergence during NH93-2 was almost same as that during NH92-2 as estimated from the temperature and nutrients distributions. However, the water temperature at the equator during NH93-2 is slightly higher than that during NH92-2. According to the monthly mean SST data of NOAA, which were obtained from the World Wide Web (http://www.pmel.noaa.gov/toga-tao/el-nino-story.html), in the equatorial Pacific ranged from 2°N to 2°S, the SST anomalies in the area of 175°E during NH92-2 and NH93-2 were 1–1.5°C and 1.5–2°C, respectively. The temperature data indicate that the El Niño during NH93-2 was stronger than that during NH92-2.

3.2 Pigment distributions along 175°E

The dominant pigments detected during NH92-2 and NH93-2 cruises were total chlorophyll a (monovinyl chlorophyll a plus divinyl chlorophyll a), total chlorophyll b (monovinyl chlorophyll b plus divinyl chlorophyll b), chlorophylls c_{1+2}, chlorophyll c_{3}, 19′-butanoyloxyfucoxanthin, 19′-hexanoyloxyfucoxanthin, fucoxanthin, zeaxanthin, diadinoxanthin and carotenes (α-carotene and β-carotene). On the samples of NH93-2, total chlorophyll a was separated monovinyl chlorophyll a from divinyl chlorophyll a (Suzuki et al., 1995). Prasinoxanthin and alloxanthin were detected only north of the subarctic front, but their concentrations were less than 0.005 µg l^{-1}. Distributions of total chlorophyll a concentration, which
is a phytoplankton biomass index, are shown in Fig. 4. Relatively high concentrations (>0.4 µg l⁻¹) of total chlorophyll a appeared only near the subarctic front during NH92-2, and were observed both near the subarctic front and at subsurface layer on the equator during NH93-2. Chlorophyll maximum layers were deeper (~100 m) at the subtropical gyre, and their concentrations were consistently lower (<0.2 µg l⁻¹).

Diagnostic pigment markers for prymnesiophytes, 19′-hexanoyloxyfucoxanthin (Fig. 5), and for pelagophytes, 19′-butanoyloxyfucoxanthin (Fig. 6), were consistently present at all the stations for both NH92-2 and NH93-2, suggesting that these flagellates may be the most ubiquitous phytoplankton groups in the central Pacific Ocean. This speculation is supported by Okada and Honjo (1973), who showed that the 19′-hexanoyloxyfucoxanthin-containing coccolithophorid, *Emiliania huxelyi*, was ubiquitously present in the north Pacific from 50°N to 15°S along 155°W. The 19′-butanoyloxyfucoxanthin-containing pelagophyte *Pelagococcus subviridis*, which was previously classified in chrysophyte (see Andersen et al., 1993), was also observed all around the Pacific (Vesk and Jeffrey, 1987). The 19′-hexanoyloxyfucoxanthin prymnesiophytes and 19′-butanoyloxyfucoxanthin pelagophytes might also correspond to the autotrophic microflagellates (AMF) in Ishizaka et al. (1994), which were widely distributed in the central Pacific along 175°E during northern summer 1990. However, distribution patterns of these chemotaxonomical pigments were different from each other at the stations north of the Kuroshio Extension during the two cruises. 19′-hexanoyloxyfucoxanthin showed a maximum concentration at 40 m depth of 44°N during NH92-2 and NH93-2, and these distributions were very similar to those of total chlorophyll a in the whole study area. On the other hand, the highest concentration of 19′-butanoyloxyfucoxanthin was observed at 50 m depth of 40°N in the Kuroshio Extension region during the two cruises. According to Venrick (1971), the transition regions such as Kuroshio Extension between subarctic and subtropical gyres were often zones of maximum abundance for species and occasionally harbor a few endemic species, although the regions were non-conservative environments, which are characterized by zonal currents.

![Fig. 3. Distributions of nitrate plus nitrite concentration (µM) measured along 175°E during (a) NH92-2 and (b) NH93-2.](image)
and strong meridional gradients of physical and chemical properties. Therefore, 19′-butanoyloxyfucoxanthin-containing pelagophytes were the diagnostic phytoplankton group in the region.

Distributions of fucoxanthin (a diatom marker) determined in this study are shown in Fig. 7. Fucoxanthin concentrations north of the Kuroshio Extension above 100 m depth exceeded by 0.01 µg l⁻¹ during the cruises, but those in the other areas were very low. These data indicate that diatoms were relatively abundant north of the Kuroshio Extension during the survey cruises, and perhaps prefer the lower temperature and higher nutrient concentrations. Ishizaka et al. (1994) showed that the 3–20 µm chlorophyll a fraction contributed a relatively high percentage (30–50%) of total chlorophyll a at stations north of the Kuroshio Extension compared to the other stations along 175°E during August and October 1990. The 3–20 µm fraction of Ishizaka et al. (1994) may be partly derived from diatoms.

Peridinin (a dinoflagellates marker) was found at low concentrations (<0.1 µg l⁻¹) both north of the Kuroshio Extension (except a station at 48°N during NH93-2), and the equatorial region during the two cruises (Fig. 8). However, peridinin at the subtropical gyre during NH93-2 was not detected. According to the microscopic analysis of Kiyosawa et al. (unpublished data), autotrophic dinoflagellates Gymnodiniales, which was 20–30 µm in size, contributed to >90% for NH92-2 and >60% for NH93-2 of the carbon biomass for autotrophic dinoflagellates in the whole study area, suggesting that most of the peridinin detected might be derived from the Gymnodiniales group. Chavez et al. (1990) also reported that most autotrophic dinoflagellates collected from equatorial waters were gymnodinoid in shape.

A chemotaxonomical pigment for prokaryotic photo-autotrophs (prochlorophytes and cyanobacteria), zeaxanthin, was ubiquitously present south of the subarctic front during the two cruises (Fig. 9). Zeaxanthin is also contained in prasinophytes and chlorophytes, but these phytoplankton groups were considered to be minor in this study because their chemotaxonomical markers, prasinoxanthin and lutein, were not detected with high concentrations. Although the concentrations of the other chemotaxonomical pigments described above were enhanced at the subsurface layer.
Temporal and Spatial Distribution of Phytoplankton Pigments in the Central Pacific Ocean along 175°E during the Boreal Summers (Kiyosawa, unpublished data). This discrepancy between pigment analysis and microscopic observation was also found in a case of Barlow et al. (1993) in the north eastern Atlantic. In this manner, the presence of non-zeaxanthin-containing cyanobacteria could be confirmed in the open ocean.

3.3 Specific pigment-biomass of phytoplankton in the central Pacific along 175°E

Previous studies have demonstrated the utility of pigment algorithms for partitioning total chlorophyll a biomass into contributions by major phytoplankton group in the open Pacific (e.g. Letelier et al., 1993; Bidigare and Ondrusek, 1996) and in the open Atlantic (e.g. Claustre and Marty, 1995). In this study, this approach was carried out to infer between cruise-differences in taxon-specific phytoplankton distributions along 175°E using the algorithm of Letelier et al. (1993). In order to make the algorithm, Letelier et al. (1993) obtained the ratios of chlorophyll a to accessory pigments of each phytoplankton group from the analysis of pigments extracted from phytoplankton cultures, which were because of photo-adaptation, zeaxanthin concentration in surface waters was generally almost same as that in subsurface waters. This is most likely related to the fact that the amount of zeaxanthin per cell on the prokaryotes is little changed by light intensity (Kana et al., 1988; Cailliau et al., 1996). Zeaxanthin concentrations during NH93-2 were about 1.5-fold higher than those during NH92-2, suggesting that cyanobacteria and prochlorophytes during NH93-2 were probably more abundant than those during NH92-2. In particular, zeaxanthin concentration shows a maximum in the subsurface layer at the equator, where divinyl chlorophyll a concentration was the highest in the study area (Suzuki et al., 1995), during NH93-2. Zeaxanthin-containing cyanobacteria and prochlorophytes are well-recognized as major contributors to the phytoplankton biomass and primary productivity in the subtropical and tropical Pacific (e.g. Ishizaka et al., 1994; Landry et al., 1996). Nevertheless, zeaxanthin was not detected north of 44°N during NH92-2, a cyanobacteria Synechococcus was counted at more than 1×10⁴ cells ml⁻¹ north of the subarctic front by epifluorescent microscopy in 1990 (Ishizaka et al., 1994), 1992 and 1993 (Kiyosawa, unpublished data). This discrepancy between pigment analysis and microscopic observation was also found in a case of Barlow et al. (1993) in the north eastern Atlantic. In this manner, the presence of non-zeaxanthin-containing cyanobacteria could be confirmed in the open ocean.

Fig. 5. As for Fig. 4 except for the prymnesiophyte marker, 19′-hexanoyloxyfucoxanthin.
shade-adapted. Therefore, they used only samples collected from subsurface layers in the subtropical Pacific (Station ALOHA). However, Andersen et al. (1996) found that taxonomic partitioning based on the algorithm of Letelier et al. (1993) agreed with electron microscopic observations in the upper water-column samples at sites in the Atlantic and Pacific Oceans (Hydrostation S and Station ALOHA, respectively), but there was increasing disagreement between the two methods in deeper water samples. Goericke (1990) showed that photosynthetically active carotenoids/chlorophyll a ratios were independent of irradiance. Therefore, the algorithm of Letelier et al. (1993) was used on depth-integrated pigment concentrations in this study to minimize potential biases. However, since the algorithm of Letelier et al. (1993) was created for pigment samples from the station ALOHA, the application of the algorithm to this study may be inadequate, especially in the stations north of the subarctic front. However, this technique can be used sufficiently to infer between cruise-differences in taxon-specific phytoplankton distributions in this study. Bidigare and Ondrusek (1996) also applied the algorithm of Letelier et al. (1993) to pigment samples from the equatorial Pacific (12°N–12°S, 135°–140°W) to infer between cruise-differences in phytoplankton assemblages.

The chlorophyll biomass above 150 m depth during NH92-2 were not significantly different ($P > 0.05$) from that during NH93-2 in the whole study area (Fig. 10). The ANOVA differences between the chlorophyll biomass associated with eukaryotic phytoplankton (prymnesiophytes, pelagophytes, diatoms and dinoflagellates) during NH92-2 and NH93-2 were not also significant ($P > 0.05$) in the whole study area, suggesting that the variations of eukaryotic phytoplankton abundance may be small in the central Pacific along 175°E during El Niño condition. The contribution of prymnesiophytes to the chlorophyll biomass was relatively high (>40%) north of the subarctic front, and was relatively constant (30 ± 10%) south of the subarctic front during the two cruises. Pelagophytes in the Kuroshio Extension region contributed significantly (~25%) to the chlorophyll biomass, but their contributions in the other areas were ~10% during NH92-2 and NH93-2. Contribution of diatoms to the chlorophyll biomass was only high (10–20%) north of

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Fig. 6. As for Fig. 4 except for the pelagophyte marker, 19'-butanoyloxyfucoxanthin.
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Although the eukaryotic phytoplankton abundances in the central Pacific along 175°E during NH92-2 and NH93-2 were not significantly different, as described above, the abundance of the prokaryotic phytoplankton (prochlorophytes and cyanobacteria) during NH93-2 was generally higher ($P < 0.05$) than that during NH92-2. The ANOVA differences were significant ($P < 0.005$) particularly in the stations south of the subarctic front (<40°N). The estimation using the algorithm of Letelier et al. (1993) coincided with the data that the integrated (0–150 m) concentrations of zeaxanthin, which was the biomarker for prokaryotic phytoplankton, south of the subarctic front during NH93-2 were significantly higher ($P < 0.001$) than those during NH92-2 (Fig. 9). These data suggest that the abundance of prokaryotic cells may change significantly at the North Pacific subtropical gyre and the equatorial region during El Niño conditions.

The North Pacific subtropical gyre has generally been thought to support a homogeneous, stable biological community (e.g. McGowan and Hayward, 1978), but recent observations have indicated that this region can undergo significant shifts in community structure and abundance, particularly during La Niña events. These changes are likely driven by shifts in the physical environment, such as changes in upwelling and temperature, which can significantly impact the growth and distribution of phytoplankton species. The presence of prokaryotic phytoplankton in these regions can also have significant implications for the carbon and nutrient cycling in the ocean.

Fig. 7. As for Fig. 4 except for the diatom marker, fucoxanthin.
investigations (Venrick, 1990a, 1990b; Karl et al., 1995) have suggested that the ecosystem of this gyre is temporally and spatially variable. Recently, Karl et al. (1995) showed evidence of a major change in the structure and productivity of the pelagic ecosystem in the subtropical North Pacific Ocean (station ALOHA off Hawaii), and an effect that the authors attribute to the 1991–92 El Niño-southern Oscillation event. In their report they found that decreased upper-ocean mixing and a change in ocean circulation resulted in an increased abundance (from ~8% to ~17% of total chlorophyll biomass) of nitrogen-fixing cyanobacterium *Trichodesmium*.

In this study, however, the total chlorophyll *a* abundances (mg m<sup>−2</sup>) for the prokaryotic phytoplankton in the North Pacific subtropical gyre and the equatorial region during NH93-2 cruise were very close to the integrated concentrations of divinyl chlorophyll *a* (the chemotaxonomical marker for *Prochlorococcus*) obtained from the data set of Suzuki et al. (1995) for NH93-2 (Table 2). This indicates that most prokaryotic photoautotrophs in the subtropical and tropical areas during NH93-2 were presumably *Prochlorococcus*. This speculation is supported by the microscopic data of Kiyosawa et al. (unpublished data), who have counted cyanobacteria (mostly *Synechococcus*) abundances ranging from ~10<sup>2</sup> to 5 × 10<sup>3</sup> cells ml<sup>−1</sup> above 150 m depth in the subtropical and tropical Pacific during NH93-2 cruise. If the cell numbers are converted to chlorophyll *a* concentrations by using the cellular content of chlorophyll *a* from 1 to 5 fg cell<sup>−1</sup> for *Synechococcus* (Kana et al., 1988; Goericke, 1990), chlorophyll *a* concentrations are estimated to range from ~0.1 to 1 ng l<sup>−1</sup>. Since the chlorophyll *a* concentrations estimated in this manner are extremely low compared to the total chlorophyll *a* concentrations in the subtropical and tropical areas during NH93-2 (Fig. 4), the contributions of cyanobacteria to the total chlorophyll *a* biomass seem to be insignificant.

*Prochlorococcus* cells are generally numerous in nitrate-depleted near-surface waters in the open ocean, although the abundances of *Synechococcus* and eukaryotic phytoplankton are high when nitrate is present near surface waters (e.g. Olson et al., 1990; Binder et al., 1996; Landry et al., 1996). Landry et al. (1996) suggested that *Prochlorococcus* was a superior competitor for remineralized

![Fig. 8. As for Fig. 4 except for the dinotlagellate marker, peridinin.](image-url)
nutrients such as ammonium, compared to the other phytoplankton groups. In this study, nitracline at the North Pacific subtropical gyre for NH93-2 was deeper than that for NH92-2 (Fig. 3). This indicated that the oligotrophic environment, which was probably suitable for the growth of Prochlorococcus, for NH93-2 was spread, compared to that for NH92-2.

Nevertheless, nitracline at the equatorial region for NH93-2 was not clearly deeper than that for NH92-2, the prokaryotic phytoplankton during NH93-2 was more abundant than that during NH92-2. The causes of this variability are not clear, but it should be noted that the abundance of heterotrophic nanoflagellates, which is the predator for the prokaryotic photoautotrophs, at the equator during NH93-2 (42 mgC m\(^{-2}\)) was about 2-fold lower than that during NH92-2 (105 mgC m\(^{-2}\)) (Ishizaka et al., 1997). This suggests that the variability in the standing stocks of nanoflagellates at the equatorial region during the two cruises might not be able to maintain the constant levels of the prokaryotic phytoplankton.

Because our sampling periods were during El Niño, the driving force of equatorial upwelling would be weaker than if there were no El Niño event. In fact, concentrations of nitrate plus nitrite in the surface layer of the equatorial region were completely depleted during the two cruises. According to Ishizaka et al. (1997), the biomass of cyanobacteria, diatoms, and dinoflagellates at the equator of 175°E during non-El Niño type mesotrophic condition of April, 1994 were larger than that during non-El Niño periods such as NH92-2 and NH93-2. Murray et al. (1994) and Bidigare and Ondrusek (1996) also showed that the abundance of eukaryotic phytoplankton (especially in diatoms) and their chemotaxonomical pigments were increased in the equatorial central Pacific along 135–140°W during non-El Niño conditions, in which nitrate existed in surface waters. These data including our study suggest that both the abundance and the composition of phytoplankton in the central Pacific near the equator would change largely, and the change can affect primary production and zooplankton biomass.
4. Summary and Conclusion

We investigated the large-scale distribution of phytoplankton pigments in the central Pacific along 175°E during the boreal summers of 1992 and 1993, when El Niño occurred. Although both the distribution patterns and the abundances of the chemotaxonomical pigments for eukaryotic phytoplankton were not changed significantly in the whole study area during the two cruises, the abundances of prokaryotic pico-phytoplankton at the subtropical and tropical Pacific during the boreal summer of 1993 were significantly increased, as estimated by the algorithm of Letelier et al. (1993) and by the zeaxanthin concentrations. When the size of the dominant phytoplankton is small, the food chain is lengthened. In such situations, marine protozoans like zooflagellates and ciliates become important intermediary links; they may consume a major fraction of the primary production, and in turn they constitute an abundant dietary source for suspension-feeding copepods or other zooplankton that are incapable of feeding directly on very small phytoplankton (e.g. Landry et al., 1995).

Acknowledgements

The Northwest Pacific Carbon Cycle Study (NOPACCS) was supported by the New Energy and Industry Development Organization (NEDO). This study was partly supported by a grant-in-aid for the JSPS Fellows (K. Suzuki; No. 00000128) of the Ministry of Education, Science and Culture, Japan.

We thank the captain and crew of the R/V Hakurei-maru for their support during both the NH92-2 and NH93-2 cruises. We are indebted to the members of Kansai Environmental Engineering Corp. for technical support. We wish to thank Drs. S. Taguchi (Hokkaido National Institute of Fisheries, Japan (Soka University at present)) and Y. Shiraiwa (Niigata University) for providing the algal cultures. We also thank two anonymous referees for their beneficial suggestions to improve our manuscript.

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