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Specific absorption coefficient and phytoplankton biomass in the southern region of the California Current

Eduardo Millán-Núñez[a,*], Michael E. Sieracki[b], Roberto Millán-Núñez[c], José Rubén Lara-Lara[a], Gilberto Gaxiola-Castro[a], Charles C. Trees[d,1]

[a]*Centro de Investigación Científica y de Educación Superior de Ensenada, Departamento de Ecología, Km 107 Carretera Tijuana-Ensenada, Baja California, México*

[b]*Bigelow Laboratory for Ocean Sciences, PO Box 475, 180 McKown Point, West Boothbay Harbor, ME 04575-0475, USA*

[c]*Facultad de Ciencias Marinas, Km 103 carretera Tijuana-Ensenada, Apartado Postal # 453 C.P. 22880, Ensenada, B.C., México*

[d]*Center for Hydro-Optics and Remote Sensing, San Diego State University, 605 Alvarado Road, Suite 206, San Diego, CA 92120-5005, USA*

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Abstract

In recent years, experts of optical hydrology have shown great interest in the variability of the specific absorption coefficient of light by phytoplankton (a^*_{ph}). This parameter is important and necessary for comparing in situ bio-optical and satellite optical measurements. Such comparisons are needed for detecting primary productivity at a mesoscale level. At present, however, the parameters used in algorithms for predicting productivity are global averages. To avoid this bias, we measured the spatial–temporal variability of a^*_{ph} as part of the Jan-01 Investigaciones Mexicanas de la Corriente de California cruise along the southern California Current. We observed median values of $0.041\,m^2$ (mg chlorophyll *a* (Chl *a*))$^{-1}$ at 440 nm and 0.015 at 674 nm, with significant differences between inshore and offshore stations. In general, the stations located in the area of Bahía Vizcaíno, with oceanographic conditions favorable for the growth of phytoplankton, showed lower values of the a^*_{ph}. The nano-microphytoplankton ($>5\,\mu m$) community comprised of 26 diatom genera with mean abundance values of the 19.5×10^3 cells l^{-1}. *Nitzschia closterium*, a pennate diatom, was almost uniform throughout the study region. Flow cytometry measurements indicated that the picoplankton ($<5\,\mu m$) community consisted of two prokaryotes, *Prochlorococcus* (mean 3.6×10^6 cells l^{-1}) and *Synechococcus* (mean 10.4×10^6 cells l^{-1}), and a mixture of picoeukaryotes (mean 6.5×10^6 cells l^{-1}). Analyses of Chl and carotenoid pigments determined by high-performance liquid chromatographic confirmed the presence of the divinyl Chl *a* characteristic of *Prochlorococcus*. The nano-micro- and picoplankton were 82% and 18% of total phytoplankton

*Corresponding author. Bigelow Laboratory for Ocean Sciences, PO Box 474, 180 McKown Point, West Boothbay Harbor, ME 04575-0475, USA.

E-mail addresses: emillan@cicese.mx, emillan@bigelow.org (E. Millán-Núñez).

[1]Now at NASA, Washington, DC.

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biomass (μg $C l^{-1}$), respectively. In general, we concluded that the phytoplankton community structure and biomass on this cruise showed conditions similar to oligotrophic systems.

1. Introduction

Light absorption in the ocean by particulate matter, including phytoplankton, is of great importance, since absorption and scattering of light bring about the color of the sea. The variability of particles gives us knowledge of light attenuation, primary productivity, and pigment biomass of phytoplankton. Likewise, some authors have shown that changes in the optical characteristics of water masses are associated with cellular biochemical processes inherent to the useable energy for photosynthesis (Yentsch, 1962; Bricaud et al., 1995). Light absorption by particles in seawater has been previously described (Yentsch and Phinney, 1989; Nelson et al., 1993; Cleveland, 1995). Most of these authors have concluded that there is a non-linear relationship between the coefficient of light absorption by phytoplankton and the concentration of chlorophyll (Chl). The relationship is complicated by the optical properties of phytoplankton, size and shape of the particles and accessory pigments (Morel and Bricaud, 1981; Spinrad and Brown, 1986).

Some mechanistic models have been used for predicting primary productivity as a function of the in vivo absorption capacity of cells (Kiefer and Mitchell, 1983; Platt and Sathyendranath, 1988). In these algorithms, the values of $^*a_{ph}$ are considered constants; however, recent studies have recorded variations from site to site, and with depth. These significant changes in $^*a_{ph}$ are caused mainly by taxonomic changes within the phytoplankton community as well as cell size and pigment composition (Mitchell and Kiefer, 1988; Millán-Núñez et al., 1998).

At present, remote-sensing instruments allow us to obtain large amounts of bio-optical information. Knowledge of the in situ variability of $^*a_{ph}$ is needed to develop better models and algorithms. The results obtained in this study could be extrapolated to the southern region of the California Current from the average values ($^*a_{ph}$), leading to improved synoptic maps of the primary productivity.

2. Materials and methods

2.1. Samples collection

Water samples were collected in the southern region of the California Current in the Investigaciones Mexicanas de la Corriente de California (IMECOCAL) project between 16 January and 5 February 2001 aboard the R./V. *Francisco de Ulloa*. Samples were taken from a depth of 10 m with 51 Niskin polyethylene bottles and Tygon tubing. Particulate matter was collected on Whatman GF/F filters. The samples collected for high-performance liquid chromatographic (HPLC) were also used in the measurement of Chl *a* extracted with 90% acetone by fluorometric analysis. The filters were immediately frozen and stored in liquid nitrogen until analysis in the laboratory. Pigments and carotenoids were separated using HPLC (Bidigare et al., 1990; Wright et al., 1991) at the Center Hidro-Optic Research Science (CHORS) with Radial-Pak C_{18} (Spherisorb, 25 μm, 25 cm), using three solvents (A = 80:20 methanol:ammonium acetate; B = 90:10 acetonitrile:H_2O of HPLC water omnisolv; C = ethyl acetate). A sample volume was injected with 1050 μl at a rate of 1 ml min^{-1}. Canthaxanthin was used as an internal standard for correcting changes in volume during the extraction process. Samples for flow cytometry were preserved with glutaraldehyde (0.1% final concentration) and stored in liquid nitrogen until analysis. Samples were processed through a FACScan (Becton-Dickinson) benchtop flow cytometer with an air-cooled argon (488 nm) laser at a high flow rate (ca. 60 μl min^{-1}) for 5 min or until 10^6 events had been recorded. Data were acquired triggering on Chl fluorescence (FL3) in log mode. As an

internal standard, we added 10 µl per 600 µl sample of a $10^5\,ml^{-1}$ solution of yellow–green 0.92 µm diameter polysciences latex beads. *Synechococcus* cells were detected by their signature in a plot of orange fluorescence of phycoerythrin (FL2) versus red Chl fluorescence (FL3). *Prochlorococcus* have a lower FL3 signal and no FL2 signal. Autotrophic picoeukaryotes have higher FL3 and scatter signals and low or no FL2 signal. Taxonomic enumeration of the large phytoplankton was performed using a microscope Zeiss inverted at 160× and 400× magnification. Subsamples of 250 ml of water for diatoms was fixed with formalin-borate solution (0.4% final concentration) and stored in amber high-density polyethylene bottles. Within two months after sampling, 50 ml of water was settled in a composite chamber and was examined using the inverted microscope technique (Utermöhl, 1958). The observed diatoms were classified into the lowest possible taxonomic level.

2.2. Analysis of the absorption coefficients

The samples for light absorption by phytoplankton were collected on Whatman GF/F filters and stored in liquid nitrogen. Blank filters were saturated with filtered seawater through 0.2 µm Nuclepore filters. Absorption of sample and blank filters was measured on a Spectrophotometer Integrate Lasphera Perkin-Elmer Lambda 10, following the procedure of Cleveland and Weidemann (1993). The wavelength scanning of absorption was done between 400 and 750 nm with a resolution of 2 nm before and after rinsing the filters with warm methanol (Kishino et al., 1985). Phytoplankton absorption $a_{ph}(\lambda)$ was determined by the difference between total particulate matter absorption $a_p(\lambda)$ and non-pigmented material $a_d(\lambda)$:

$$a_{ph}(\lambda) = a_p(\lambda) - a_d(\lambda). \quad (1)$$

The specific absorption coefficient by phytoplankton (m^2 (mg Chl a)$^{-1}$) was obtained by standardizing the phytoplankton absorption (m^{-1}) with the concentration of Chl a ($\mu g\,l^{-1}$) measured with a Turner Designs model 10-005 Fluorometer, using the US joint global ocean flux study (JGOFS) standard protocol. The absorption spectra were corrected for light scattering (β) by adjusting the optical density of the filtered samples $OD_{filt}(\lambda)$ to the optical density of samples in suspension $OD_{sus}(\lambda)$:

$$OD_{sus} = 0.3038\,OD_{filt} + 0.4086(OD_{filt})^2. \quad (2)$$

2.3. Phytoplankton biomass and taxonomic composition

With the inverted microscope, diatoms (>5 µm) were analyzed and their identifications were based on Cupp (1943), Hasle and Syvertsen (1996), and Hallegraeff (1986). Typically, cell lengths and widths of diatoms were measured with an ocular micrometer. These measurements were converted to biovolume assuming the steriometric shapes suggested by Edler (1979) and Strathmann (1967). The biomass of the cell populations was calculated as

$$B_p = C_p V_p F_p, \quad (3)$$

where B_p is the biomass of cell population (µg C l^{-1}), C_p is the cell concentration (cells l^{-1}), V_p is the mean cell biovolume ($\mu m^3\,cell^{-1}$), and F_p is a biovolume-to-carbon conversion factor. The equation pg C cell^{-1} = 0.433 × (µm^3)$^{0.863}$ (Verity et al., 1992) was adapted for cyanobacteria, picoeukaryotes, and prochlorophytes using mean cell biovolumes of 0.52, 3.05, and 0.27 μm^3, respectively.

3. Results

3.1. Specific absorption phytoplankton coefficient ($^*a_{ph}$)

The variability of the $^*a_{ph}$ (440 nm) on this cruise showed a range of 0.008–0.102 m^2 (mg Chl a)$^{-1}$, while at 674 nm it was 0.001–0.038 (Table 1). The spectral curves with lower $^*a_{ph}$ (440 nm) were located at the inshore areas of line 113.30 (station 28) at the north Bahía Vizcaíno, and 120.45 (station 50) located in Punta Eugenia. A similar pattern was seen on lines 123.42 (station 62) at south Bahía Vizcaíno, and 133.25 (station 74) at south Punta Eugenia (Fig. 1). In general, we

Table 1
Values of the specific absorption coefficient phytoplankton ($^*a_{ph}$) at 440 and 674 nm (m^2 (mg Chl a)$^{-1}$)) from 10-m samples collected on the IMECOCAL cruise 01/2001

Lines	Sta.	$^*a_{ph}$ (440 nm)	$^*a_{ph}$ (674 nm)	Lines	Sta.	$^*a_{ph}$ (440 nm)	$^*a_{ph}$ (674 nm)
100.30	1	0.059	0.027	120.30	47	0.044	0.022
100.35	2	0.043	0.018	120.35	48	0.047	0.020
100.40	3	0.034	0.015	120.39	49	0.024	0.012
100.45	4	—	—	120.45	50	0.008	0.009
100.50	5	—	—	120.50	51	0.031	0.013
100.55	6	0.057	0.020	120.55	52	0.013	0.004
100.60	7	0.061	0.021	120.60	53	0.046	0.017
103.60	8	0.059	0.020	120.65	54	0.023	0.010
103.55	9	0.048	0.018	120.70	55	0.047	0.019
103.50	10	0.066	0.022	120.75	56	0.039	0.014
103.45	11	0.072	0.022	120.80	57	0.084	0.028
103.40	12	0.059	0.019	123.60	58	0.064	0.023
103.35	13	0.035	0.015	123.55	59	0.030	0.012
103.30	14	0.032	0.015	123.50	60	0.029	0.011
107.32	15	0.033	0.014	123.45	61	—	—
107.35	16	0.059	0.025	123.42	62	0.013	0.007
107.40	17	0.060	0.021	127.35	63	0.047	0.018
107.45	18	0.038	0.012	127.40	64	0.019	0.010
107.50	19	0.042	0.013	127.45	65	0.020	0.011
107.55	20	0.046	0.016	127.50	66	0.034	0.011
107.60	21	0.045	0.015	127.55	67	0.061	0.024
110.60	22	0.038	0.012	127.60	68	0.037	0.014
110.55	23	0.041	0.012	130.60	69	0.071	0.025
110.50	24	0.082	0.026	130.55	70	0.037	0.015
110.45	25	0.032	0.013	130.50	71	0.053	0.020
110.40	26	0.063	0.023	130.45	72	0.038	0.015
110.35	27	0.057	0.020	130.40	73	0.026	0.014
113.30	28	0.020	0.009	133.25	74	0.022	0.010
113.35	29	0.023	0.007	133.30	75	0.027	0.011
113.40	30	0.037	0.013	133.35	76	0.028	0.012
113.45	31	0.056	0.019	133.40	77	0.034	0.011
113.50	32	0.051	0.014	133.50	78	0.021	0.009
113.55	33	0.037	0.013	133.60	79	—	—
113.60	34	0.049	0.015	137.40	80	0.102	0.038
117.80	35	0.098	0.027	137.35	81	0.078	0.027
117.75	36	0.060	0.019	137.30	82	0.035	0.013
119.33	46	0.019	0.001	137.25	83	—	—

Note: The system of numbering lines follows the CalCOFI grid.

observed that $^*a_{ph}$ decreased southward along the Baja California coast.

3.2. Phytoplankton taxonomic composition

The taxonomic analyses of nano-microphytoplankton (>5 μm) revealed a total of 26 diatom genera. The most important diatom genera in relation to niche width index (Levins, 1978) were *Nitzschia* spp., *Chaetoceros* spp., *Thalassionema* sp., and *Coscinodiscus* spp. The diatom abundances showed three main areas along Baja California. The inshore line 123.42 (station 62) and line 127 (stations 64 and 65) located at south Punta Eugenia showed major abundances of diatoms with a range ($2.7–173.5 \times 10^3$ cells l^{-1}). The second area of high diatoms was on line 119.33 (station 46), line 120 (stations 49 and 50),

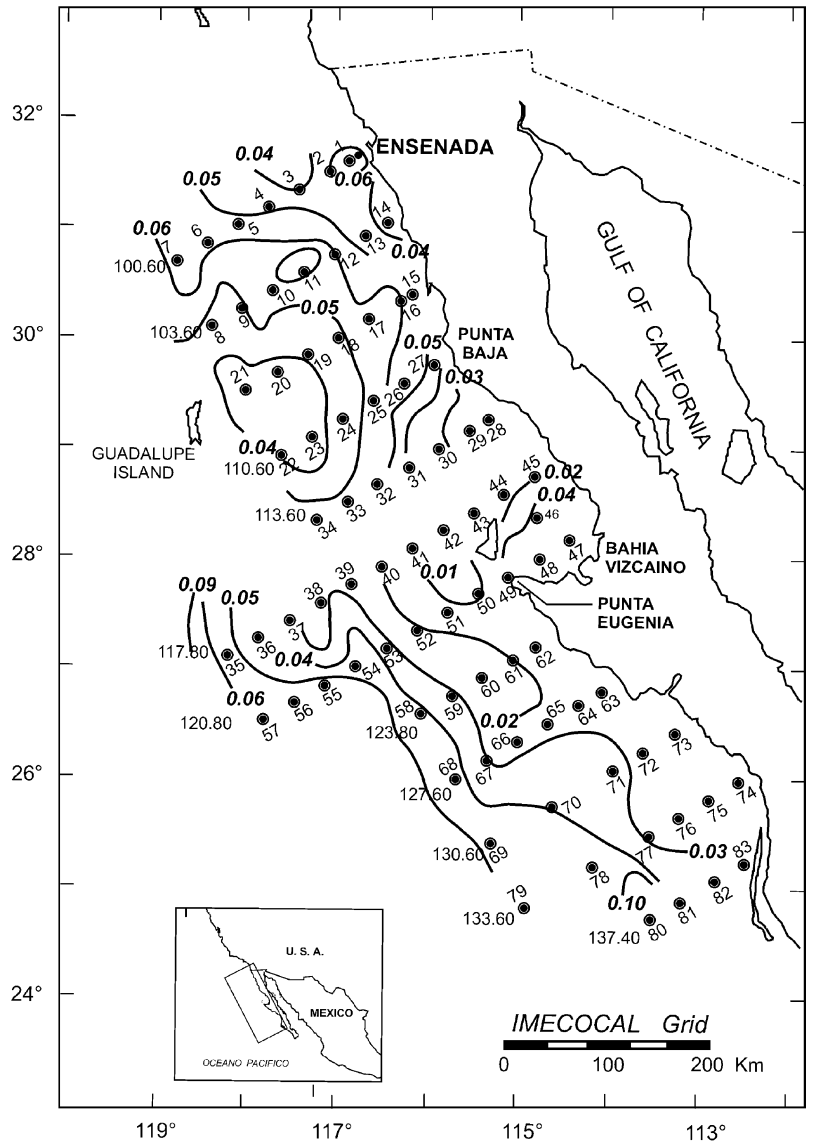

Fig. 1. Map of the study area showing a subset of the original CalCOFI grid. Solid circles indicate station positions. The contour lines show the distribution of the specific absorption phytoplankton (m^2 (mg Chl a)$^{-1}$) at 10 m depth and 440 nm during the IMECOCAL cruise 01/2001. The line 119.33 contains only station 46.

and the offshore stations of line 123 (stations 59, 60, and 62), where values ranged from 1.1 to 70.5×10^3 cells l^{-1} (near Bahía Vizcaíno and Punta Eugenia). The third area of high diatoms was between Ensenada to Punta Baja with values ranging from 2.3 to 28.4×10^3 cells l^{-1}.

Picoplankton ($<5\,\mu m$) were divided into three groups: prochlorophytes, picoeukaryotes, and cyanobacteria (Fig. 2). The most abundant group was the cyanobacteria, with a range of $0.19–76.7 \times 10^6$ cells l^{-1}, the second group was the picoeukaryotes with a range of $0.76–40.7 \times 10^6$

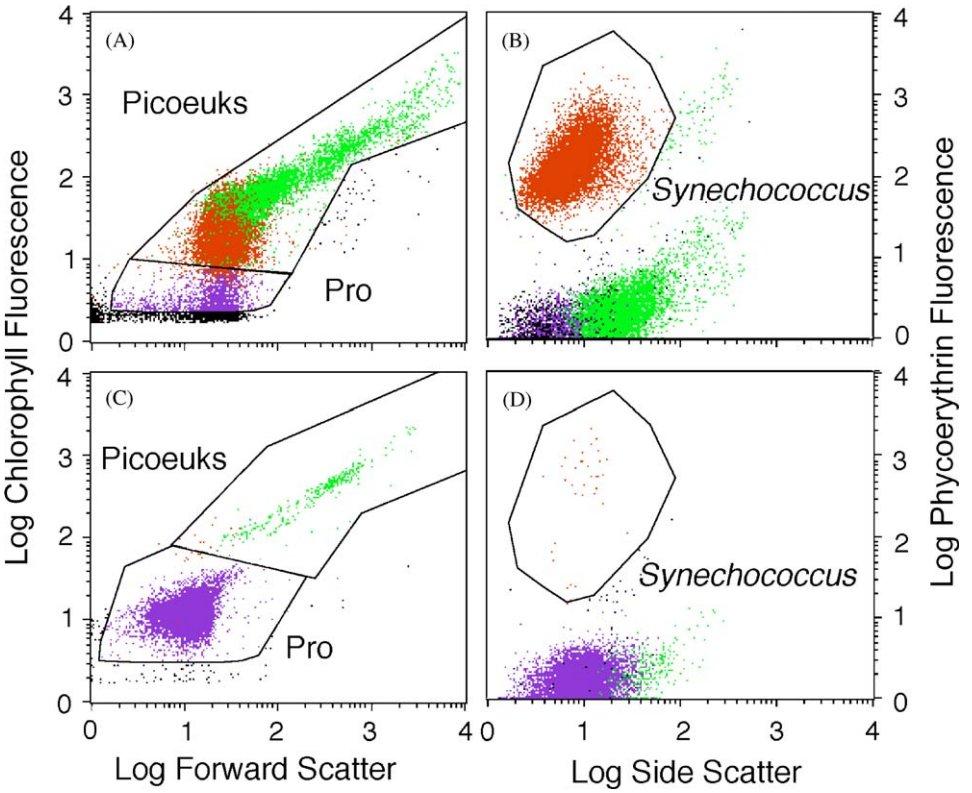

Fig. 2. Flow cytometric signature at 10 m samples of station 14 (a and b) and station 57 (c and d) during IMECOCAL 01/2001. Note the 90° side scatter of the particles and, forward light scatter relate to cell size, and the orange and red fluorescence identify the *Synechococcus*, picoeukaryotes, and *Prochlorococcus*.

cells l^{-1}, while the prochlorophytes ranged from 0.30 to 36.9×10^6 cells l^{-1}. Prochlorophytes were mainly detected in places where diatom abundances were lower. This occurred on the inshore stations 14 and 82 and the offshore station 57 (Fig. 3).

3.3. Variability of the specific absorption of phytoplankton ($^*a_{ph}$) with respect to biomass and pigments

The specific phytoplankton absorption at 440 nm showed a significant inverse correlation ($r = -0.42$, $p < 0.05$ and $r = -0.57$, $p < 0.05$) with respect to phytoplankton biomass (μg C l^{-1}) and Chl *a* (μg l^{-1}), respectively, while zeaxanthin and divinyl Chl *a* showed a significant positive correlation ($r = 0.52$, $p < 0.05$, and $r = 0.51$, $p < 0.05$, respectively) with respect to the specific absorption phytoplankton. Likewise, zeaxanthin carotenoid showed a significant inverse correlation ($r = -0.52$, $p < 0.05$) with respect to phytoplankton cell biovolume (μm^3). The variability of the $^*a_{ph}$ was along the offshore to inshore gradient of the Baja California (Fig. 1). Nevertheless, the statistical data for all stations showed no significant differences with respect to latitude. The variability of the specific absorption of phytoplankton with respect to offshore and inshore stations did show significant differences ($f = 2.41$, $p = 0.029$).

4. Discussion

During our study, the $^*a_{ph}$ showed significant spatial variability between the stations sampled,

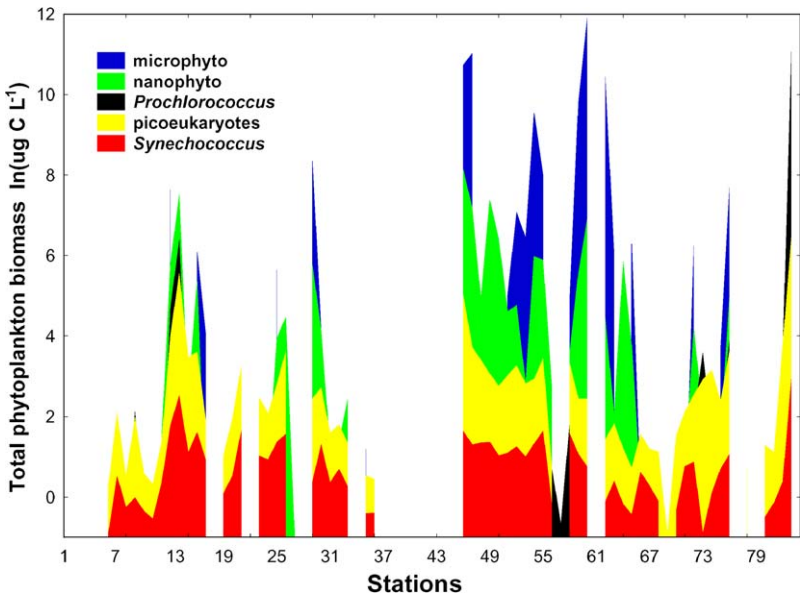

Fig. 3. Contribution of each phytoplankton group: microphytoplankton, nano-phytoplankton, *Prochlorococcus*, picoeukaryotes, *Synechococcus* to total phytoplankton biomass (μg Cl^{-1}) during the IMECOCAL cruise 01/2001. Carbon biomass estimated by microscopy and flow cytometry.

with greater variability in the blue band (440 nm) than in the red band (674 nm). A high blue–red (b/r) peak ratio (a_{ph} (440):a_{ph} (674)) was associated with phytoplankton communities dominated by small organisms such as cyanobacteria and prochlorophytes. In this cruise, we showed a b/r peak ratio range of 1.75–3.66, values similar to those shown by Sosik and Mitchell (1995) for the California Current. Recent work on cyanobacteria and marine prochlorophytes (Kana et al., 1988; Moore et al., 1995) has shown that these small prokaryotes can exhibit very high values of $^{*}a_{ph}$ at 440 nm, and blue–red ratios that are typically greater than 2.5 (and even >8 at very high light intensities). In general, the stations of this cruise showed high abundance of small cells (Fig. 2). Nevertheless, their contribution to total biomass (μg Cl^{-1}) was lower than the nano-microphytoplankton group (Fig. 3).

The average contributions to total phytoplankton biomass for cyanobacteria, picoeukaryotes, prochlorophytes, nano-phytoplankton, and microphytoplankton were 4%, 12%, 3%, 36%, and 45%, respectively. In general, the highest phytoplankton abundances are located between Bahía Vizcaíno and Punta Eugenia. Discounting the three stations with the highest abundance cells (stations 62, 64, and 65) the percentages of phytoplankton biomass were 17% (cyanobacteria), 46% (picoeukaryotes), 3% (prochlorophytes), 31% (nano-phytoplankton), and 3% (microphytoplankton). These values are different from those presented by Blanchot et al. (2001) for September–October 1994 for the western warm pool region, and Mackey et al. (2002) for the high-nutrient low-Chl region of the equatorial Pacific. These authors showed an average 63% for *Prochlorococcus,* 5% for *Synechococcus*, and 32% of phytoplankton biomass for picoeukaryotes, while our data showed 18%, 21%, and 61%, respectively.

At our most oceanic line 120.80 (station 57), however, we observed a picoplankton group composition of *Synechococcus* 1%, picoeukaryotes 5%, and *Prochlorococcus* 94%. These percentages were similar to those presented by Blanchot et al. (2001) for the equatorial Pacific. Likewise, Goericke et al. (2000) showed in cells and biovolume

per liter higher values for May 1997 in the Eastern Tropical North Pacific along a transect off Manzanillo, Mexico. At 10 m depths they found 160×10^6 cells l^{-1} with $35 \times 10^6\,\mu m^3\,l^{-1}$ for *Prochlorococcus*, 5×10^6 cells l^{-1} with $3 \times 10^6\,\mu m^3\,l^{-1}$ for *Synechococcus*, and 3×10^6 cells l^{-1} for picoeukaryotes. In this study, we observed 37×10^6 cells l^{-1} and $9.9 \times 10^6\,\mu m^3\,l^{-1}$ for *Prochlorococcus*, 0.1×10^6 cells l^{-1} and $0.1 \times 10^6\,\mu m^3\,l^{-1}$ for *Synechococcus*, and 1.7×10^6 cells l^{-1} for picoeukaryotes.

The physical oceanography for this cruise was characterized by Durazo and Baumgartner (2002). In common with other oligotrophic environments, the euphotic zone of the California Current has a two-layer structure thought to result from differential adaptation of phytoplankton to gradients of light and nutrients (Venrick, 2000). Punta Eugenia was where the nano-microphytoplankton showed the largest contribution of diatoms. The dominant genera were *Nitzschia* spp., *Chaetoceros* spp., *Thalassionema* spp., and *Coscinodiscus* spp. The characteristic of this group is the high concentration of Chl *a* and fucoxanthin, primarily associated with the inshore stations (Fig. 4a) while the dinoflagellates contain peridinin (Fig. 4b). The pigment divinyl Chl *a* (highest concentrations in offshore stations) characteristic of *Prochlorococcus* showed an inverse correlation with Chl *a*. Likewise, Goericke et al. (2000) showed the highest abundances of *Prochlorococcus* in the top portion of the oxygen minimum zones or below the bottom of the euphotic zone (1% surface irradiance, E_0). The photoprotecting pigments such as zeaxanthin, characteristic of *Synechococcus*, showed increased concentrations where the Chl *a* was lower.

Zeaxanthin has a maximum absorption between 454 and 480 nm wavelength (Jeffrey et al., 1997) typical of carotenoids, high in the blue band with a decline in the blue–green band. When zeaxanthin is present, its absorption at 440 nm artificially increases the $^*a_{ph}$ 440 nm, since this coefficient is normalized only by the Chl *a* concentration. Indeed, in this study we observed that the $^*a_{ph}$ 440 nm tends to be high when the pigment group of the photoprotectors is high. In this study, we demonstrate a positive tendency between the $^*a_{ph}$ 440 nm and zeaxanthin, and a significant inverse

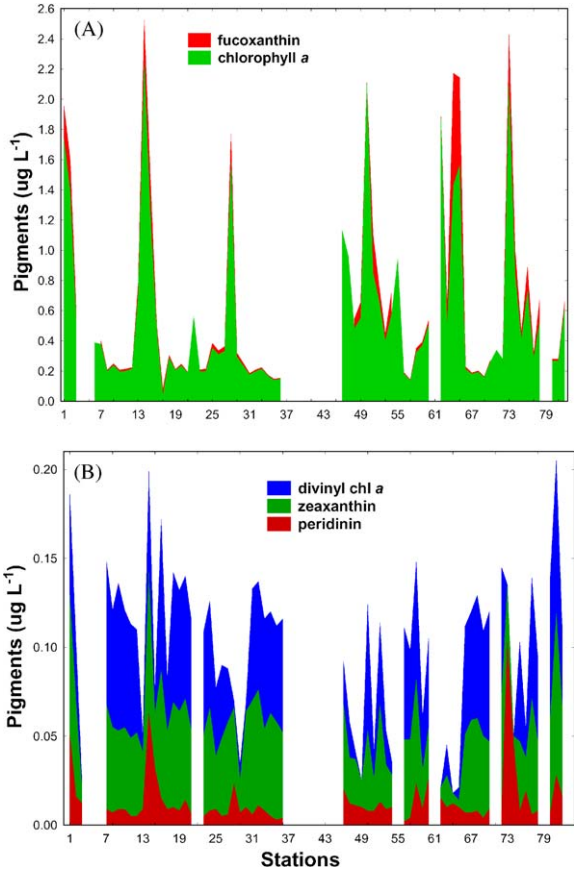

Fig. 4. Contribution of phytoplankton pigments: (a) Chl *a* and fucoxanthin, (b) divinyl Chl *a*, zeaxanthin, peridinin to total Chl biomass (μg $C\,l^{-1}$) during the IMECOCAL 01/2001.

correlation with phytoplankton biomass. These results suggest that biomass and Chl *a* were involved in the variability of the $^*a_{ph}$ (440 nm). This means that the stations with lower biomass and Chl will have higher values of the specific absorption coefficient by phytoplankton at 440 nm and vice versa.

The highest values of zeaxanthin were observed in lines 100.30 (station 1), 117.80 (station 35), and 137.35 (station 81), with a mean value of $0.074\,\mu g\,l^{-3}$ corresponding to the highest values of the specific absorption by phytoplankton. This was probably due to the high irradiance in the sea surface ($\approx 1500\,\mu E\,m^{-2}\,s^{-1}$) which commonly causes an increase in photoprotecting carotenoids. These pigments function to reduce or prevent

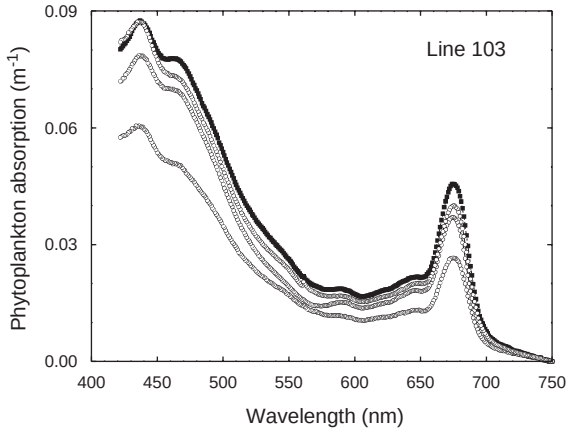

Fig. 5. Phytoplankton absorption spectra from 10-m samples collected on IMECOCAL cruise 01/2001 with one spectrum plotted for the line 103, stations 9, 12, 13, and 14.

photoinhibition and/or whitening of the cell. This physiological mechanism causes a decrease in the photosynthetically active carotenoids. From Fig. 2, we can observe the presence of two prokaryotes, *Prochlorococcus* and *Synechococcus*, and a high abundance of picoeukaryotes. Likewise, we can observe the typical signature of cyanobacteria in the spectral shoulder range of 480–540 nm (Fig. 5) characteristic of phycoerythrin (Kana et al., 1988; Falkowski and LaRoche, 1991; Moore et al., 1995).

The magnitude of the spectral $^*a_{ph}$ for the inshore stations of lines 120, 123, and 127 was similar to that reported by Roesler and Perry (1995) for estuarine and fjord environments. Likewise, the rest of our stations were similar to the spectral curves reported by Roesler and Perry (1995) for the coastal water and oceanic waters off Oregon. Sosik and Mitchell (1995) reported mean values of 0.057 $^*a_{ph}$ (440) for the CalCOFI 9202 cruise in the California Current. This compares to the mean value of 0.044 $^*a_{ph}$ (440) that we observed farther south in the California Current.

Our results of the specific absorption coefficient phytoplankton for January 2001 in the southern California Current demonstrate a spatial variability in relation to the coast (inshore and offshore). Latitudinal variations did not show significant differences. These variations of the $^*a_{ph}$ were mainly due to the different abundances of the diatom genera, *Synechococcus*, *Prochlorococcus*, and their characteristic pigment concentrations. Likewise, the absorption coefficients a_p and a_{ph} were highly correlated ($r^2 = 0.93$, data not shown), indicating that about 90% of the variability of the particulate spectral absorption coefficient was caused by biogenic matter. Our results support the suggestions by Sosik and Mitchell (1995) and Marra et al. (2000), who have proposed including not only Chl *a*, but the sum of the photosynthetically active pigments for obtaining an $^*a_{ph}$ closer to reality.

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