

## Diurnal patterns of size-fractionated primary productivity across a coastal front

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### Abstract

In July 1985, diurnal patterns of photosynthesis and pigmentation were characterized for whole water ( $> 0.4 \mu\text{m}$ ) and size-fractionated ( $> 5 \mu\text{m}$  and  $0.4$  to  $5 \mu\text{m}$ ) communities from three light depths sampled across a coastal thermal front in the Southern California Bight. Samples were collected predawn and held for 20 h in deck incubators. Variations in chlorophyll *a* and accessory pigment-to-chlorophyll *a* ratios showed no obvious diurnal trends. Timing of peak photosynthetic potential ( $P_{\text{max}}$ ) and its coincidence with variations in light-limited rates of photosynthesis (alpha), as well as diurnal amplitudes in  $P_{\text{max}}$  and alpha, often differed between size fractions sampled within the same community. The same was true for identical size fractions collected from different depths and stations transecting the front. Primary productivity was 20-fold greater on the cold water side, where  $> 5 \mu\text{m}$  diatoms dominated the mixed layer and accounted for 80% of daytime productivity. Diatoms collected from the top and bottom of the upper mixed layer displayed nearly identical diurnal patterns in  $P_{\text{max}}$  and alpha, with midday peaks exceeding predawn values by four-fold and two-fold respectively. Above the pycnocline, the  $0.4$  to  $5 \mu\text{m}$  fraction had lower assimilation rates than the  $> 5 \mu\text{m}$  fraction and smaller diurnal amplitudes in  $P_{\text{max}}$  and/or alpha, with daytime patterns often characterized by two peaks interspersed by a short period of photoinhibition. Within the front, the  $0.4$  to  $5 \mu\text{m}$  fraction accounted for two-thirds of plant biomass and  $> 90\%$  of primary production. Pigment analyses by high-performance liquid chromatography revealed enrichment in 19'-hexanoyloxyfucoxanthin, indicative of enhanced numbers of prymnesiophytes. Photosynthetic activity in confined surface communities was susceptible to daytime photoinhibition, but subsurface communities exhibited midday  $P_{\text{max}}$  peaks that were three- to seven-fold predawn values. In the warm-water mass, both algal size fractions contributed equally to photosynthesis and chlorophyll *a* in surface waters, with the  $0.4$  to  $5 \mu\text{m}$  fraction becoming dominant at

the base of the euphotic zone. At all depths, peak  $P_{\text{max}}$  of the  $0.4$  to  $5 \mu\text{m}$  fraction occurred before noon, while  $P_{\text{max}}$  of the  $> 5 \mu\text{m}$  fraction was clearly evident in the afternoon. Elevated chlorophyll *b*-, 19'-hexanoyloxyfucoxanthin- and zeaxanthin-to-chlorophyll *a* ratios indicated a mixture of algal groups, including chlorophytes, cyanobacteria and prymnesiophytes.

### Introduction

The abundance, composition and photosynthetic capabilities of phytoplankton communities vary widely across frontal regions (Pingree *et al.*, 1975; Fournier, 1978; Pingree, 1978; Marra *et al.*, 1982; Richardson, 1985; Richardson *et al.*, 1985; Arnone *et al.*, 1986; Johnson *et al.*, 1987; Smith *et al.*, 1987). A previous study of the Santa Barbara frontal region (Johnson *et al.*, 1987) found greatest differences in phytoplankton ( $> 0.45 \mu\text{m}$ ) abundance and productivity across the thermal gradient during late summer months, when a strong association of the horizontal chlorophyll maximum with the cold side of the front was observed. At that time, several strong correlations were evident between algal productivity indices and the physical and chemical gradients measured across the front. Repeated *in situ* sampling of the water column over the day indicated that the large range of assimilation rates measured at the surface in the warm-water mass could be due to diel variation in photosynthetic potential. However, the sampling scheme of these earlier cruises was specifically designed to characterize seasonal variability in the nutrient and biological structure of the front, and could not adequately address and provide comparisons of temporal variations in photosynthetic physiology. Since the amplitude and timing of daily rates of photosynthesis are known to be influenced by algal composition and the hydrographic conditions particular to the sample location, differences in diel patterns would be likely occur across the front (Lorenzen, 1963;

Malone, 1971a; Fee, 1975; MacCaull and Platt, 1977; Prézelin and Ley, 1980; Malone, 1981, 1982; Harding *et al.*, 1982; Putt and Prézelin, 1985; Prézelin *et al.*, 1986; Putt *et al.*, in press). As a result, major errors could be introduced into attempts to characterize primary production with point measurements made at different times along frontal transect lines (Smith *et al.*, 1987).

The present study details the diurnal patterns of primary productivity in whole-water ( $> 0.4 \mu\text{m}$ ) and size-fractionated communities across the Santa Barbara front. Spatial netplankton-to-nanoplankton transitions can occur in response to transitions in temperature, water-column stability and/or nutrient availability and significantly impact algal photosynthetic responses (cf. Malone, 1981). The development of phytoplankton communities dominated by nano- and picoplankton-sized algae often are accompanied by a floristic shift from diatoms and dinoflagellates toward cyanobacteria and microflagellates (cf. Malone, 1981; Furnas, 1983; Glover *et al.*, 1986). Compared to netplankton, these smaller phytoplankton are reported to have increased assimilation rates, photosynthetic efficiencies and cell-division rates (cf. Malone, 1981; Geider *et al.*, 1986), as well as distinct accessory pigmentation which can affect wavelength-dependent scattering and/or attenuation coefficients (Kirk, 1983; Smith *et al.*, 1987; Bidigare *et al.*, 1987). Since there have been conflicting reports that the timing and amplitude of peak photosynthesis may be size-dependent in natural populations (Malone, 1971a, 1981, 1982; Paerl and Mackenzie, 1977), the present sampling regime was designed to allow detailed assessment of the diurnal patterns of photosynthesis in two algal size fractions collected from a wide variety of hydrographic communities. Sampling at three light depths across the front was based on realtime information about frontal structure, which was determined by intensive *in situ* vertical profiling (Smith *et al.*, 1987). Large shipboard incubators were used to hold phytoplankton communities under simulated *in situ* conditions without severely affecting community structure, thereby allowing replicate measurements of photosynthetic parameters and pigmentation over a day. The results illustrate the spatial variability that can develop, both in phytoplankton community structure and in diurnal patterns of size-fractionated photosynthesis in algal communities differentially distributed across a persistent frontal boundary. The following study in this issue (Smith *et al.*, 1987) illustrates how time-corrected *in situ* data can be generated from these diurnal studies and thereby provide an improved data base for analyzing the relationship between ocean optics and primary productivity across frontal boundaries.

## Materials and methods

The study was conducted between 13 July and 22 July, 1985 at four stations along a frontal transect (Fig. 1) in the Southern California Bight. Stations were distinguished on the basis of surface temperature ( $T_s$ ), with a cold-water

station ( $T_s = 15.4^\circ\text{C}$ ) at  $33^\circ 52.07'\text{N}$ ,  $120^\circ 27.9'\text{W}$ ; a frontal station ( $T_s = 17.0^\circ\text{C}$ ) at  $33^\circ 48.9'\text{N}$ ,  $120^\circ 05.20'\text{W}$ ; a warm-water station ( $T_s = 18.4^\circ\text{C}$ ) at  $33^\circ 48.8'\text{N}$ ,  $120^\circ 01.65'\text{W}$ ; and the warmest-water station ( $T_s = 20.2^\circ\text{C}$ ) at  $33^\circ 47.0'\text{N}$ ,  $118^\circ 50.40'\text{W}$ .

## Physical/chemical measurements and sample collection

Simultaneous vertical profiles of water temperature and *in vivo* chlorophyll fluorescence were determined using a pumping system previously described (Johnson *et al.*, 1987). Three sampling depths, approximating 80, 10 and 1% surface irradiance ( $I_0$ ), were determined on the basis of predawn vertical profiles compared with vertical profiles and *in situ* light readings obtained the previous day. Light profiles were constructed from downwelling irradiance data obtained with a Bio-Optical Profiling System (BOPS: Smith *et al.*, 1984) or with a deck-based Licor LI 185A light meter with 100 m of cable attached to an underwater quantum sensor.

Predawn, unfiltered water was collected from the pump effluent and held in 200-liter polypropylene deck incubators under simulated *in situ* conditions. The vats were prewashed with alcohol and air-dried to limit bacterial attachment and growth. Refrigeration units pumped cold, deionized water through 20 rows of heat-exchanging polypropylene coils lining the interior wall of each vat. The refrigerant flow was thermostatically controlled for each vat. A Plexiglas magnetic stirring device was situated at the incubator base and was hydraulically driven by circulating cooling-water. The three deck incubators were continuously stirred and maintained within  $1^\circ\text{C}$  of *in situ* temperature. Surface samples (2 m) were held at 80%  $I_0$ , sam-

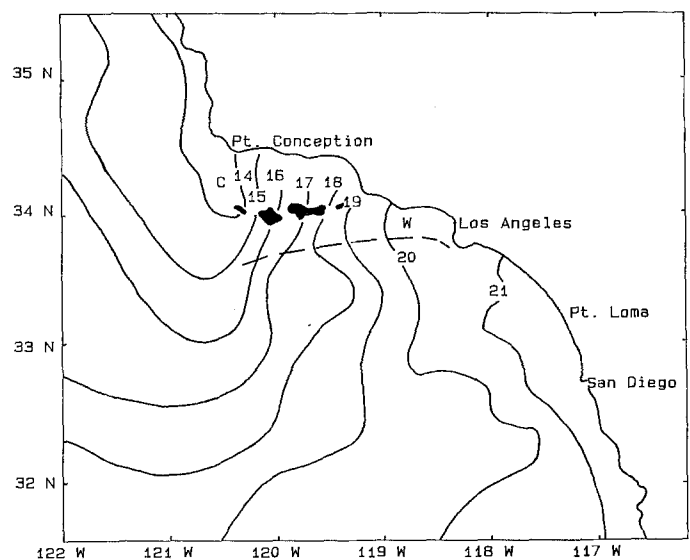


Fig. 1. Sea-surface temperatures ( $^\circ\text{C}$ ) in Southern California Bight, 30 July 1985; horizontal dashed line shows position of frontal transect. C, W: source water for cold and warm sides of front, respectively

ples from the subsurface chlorophyll maxima at 10%  $I_0$ , and samples from below the thermocline at 1%  $I_0$ . Irradiances were adjusted by wrapping the vats with neutral-density netting. Aliquots were taken from the vats at 2 to 4 h intervals for 20 h following collection and analysed for diurnal variations in photosynthetic activity and pigmentation.

#### Photosynthetic pigment analysis

Water samples (200 to 1 000 ml) were filtered through 0.4 and 5  $\mu\text{m}$  polyester Nuclepore filters, frozen (4°C) and transported on dry ice to Texas A&M University for analysis. The high-performance liquid chromatography (HPLC) methodology is described in the following studies in this issue (Smith *et al.*, 1987), and specific algal pigments quantified ( $\text{ng l}^{-1}$ ) included: chlorophylls *a*, *b*, and *c*; chlorophyllide *a*; peridinin, fucoxanthin; 19'-hexanoyloxyfucoxanthin; diadinoxanthin; zeaxanthin; and carotene. The concentration of pigments in the 0.4 to 5  $\mu\text{m}$  communities was determined by subtraction. The pigment:chlorophyll *a* ratios were only calculated for those samples which had detectable accessory pigment concentrations. Ratios were determined in this manner to avoid the possibility of calculating erroneous values when these pigments were below the limit of quantification.

#### Photosynthesis-irradiance ( $P$ - $I$ ) relationships

For each sample, 200 ml of seawater containing 0.2 mCi sodium  $^{14}\text{C}$ -bicarbonate ( $1 \mu\text{C ml}^{-1}$  final concentration) was dispensed as 10 ml aliquots into 16 scintillation vials which had been previously soaked sequentially with Nuclean (National Diagnostics) and 10% HCl and rinsed in deionized water. The vials were placed in three modified "photosynthetrons" (Lewis and Smith, 1983) which were water-cooled to near *in situ* temperature ( $\pm 2 \text{ C}^\circ$ ) and incubated for 1.5 to 2 h over an air-cooled 500 W quartz-halogen lamp (GTE Sylvania 500T3Q/CL-120V). Incubation light-intensities of 2 to 500  $\mu\text{E m}^{-2} \text{ s}^{-1}$  were obtained by placing neutral-density Plexiglas disks between the vials and the light source. Irradiance was measured twice a day with a Licor LI185A light meter. The attached underwater quantum sensor fitted into each sample chamber, so that light measurements were made at the chamber base without light leaks from above. Drift in mean irradiance measurements during incubation was less than 5%. After incubation, samples were filtered onto 25 mm Nuclepore filters of 0.4 or 5  $\mu\text{m}$  porosity, rinsed three times with filtered seawater, and placed in scintillation vials to which scintillation cocktail (Liquiscint) was later added. Earlier experiments showed no difference in  $^{14}\text{C}$  retention on Nuclepore filters rinsed with seawater or acidified with HCl. Radioactivity was determined on a Beckman LS1801 liquid scintillation counter. Quench was calculated and corrected using the external-standards methods.

Non-linear curve fits for the  $P$ - $I$  data were calculated using the Simplex method of Caceci and Cacheris (1984) on an Apple IIe microcomputer with an Enhancement Technology Corporation PDQ II 68000 coprocessor. Photosynthetic parameters were derived by fitting a series of widely accepted mathematical models to the data which describe photosynthesis as a continuous function of available light (cf. Platt and Gallegos, 1980). Since photoinhibition was not evident over the range of low to intermediate irradiances used in this study to increase accuracy of the estimates of light-limited rates of photosynthesis, Model 1 was used in all cases. Model 1 represents a hyperbolic tangent with no photoinhibition:

$$\text{Model 1: } P_s = P_{\max} \times \tanh(\alpha \times I / P_{\max}) + rb,$$

where  $P_s$  is the photosynthetic rate at some light intensity ( $I$ ),  $P_{\max}$  is the light-saturated photosynthetic rate,  $rb$  is the  $y$ -intercept, and  $\alpha$  is the slope of the light-limited region of the  $P$ - $I$  curve.  $I_k$  is  $P_{\max}:\alpha$ ,  $I_b$  is the light intensity beyond which photoinhibition occurs and  $\beta$  is the slope of the photoinhibited portion of the  $P$ - $I$  curve. This approach does not allow an independent assessment of the standard deviation of individual parameters. However, independent determinations of the mean  $P_{\max}$ , from averages of data points on the light-saturated portion of the  $P$ - $I$  curve, indicated that one standard deviation in  $P_{\max}$  was routinely less than 15% of the mean value ( $n=6$  to 14). The lower limit of detection for  $I_k$  was 10  $\mu\text{E m}^{-2} \text{ s}^{-1}$ . Rates of photosynthesis were determined directly for the  $> 0.4$  and  $> 5 \mu\text{m}$  populations and by deduction for the 0.4 to 5  $\mu\text{m}$  fraction.

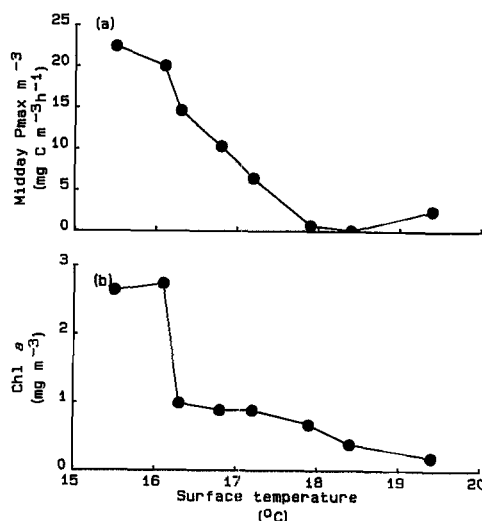


Fig. 2. Comparison of (a) midday light-saturated rates of volume-based photosynthesis and (b) extracted chlorophyll *a* biomass in surface (2 m) phytoplankton communities ( $> 0.4 \mu\text{m}$ ) collected across frontal region in July 1985. One standard deviation of peak photosynthetic potential ( $P_{\max}$ ) is less than 15% of the derived mean of 6 to 14 measurements

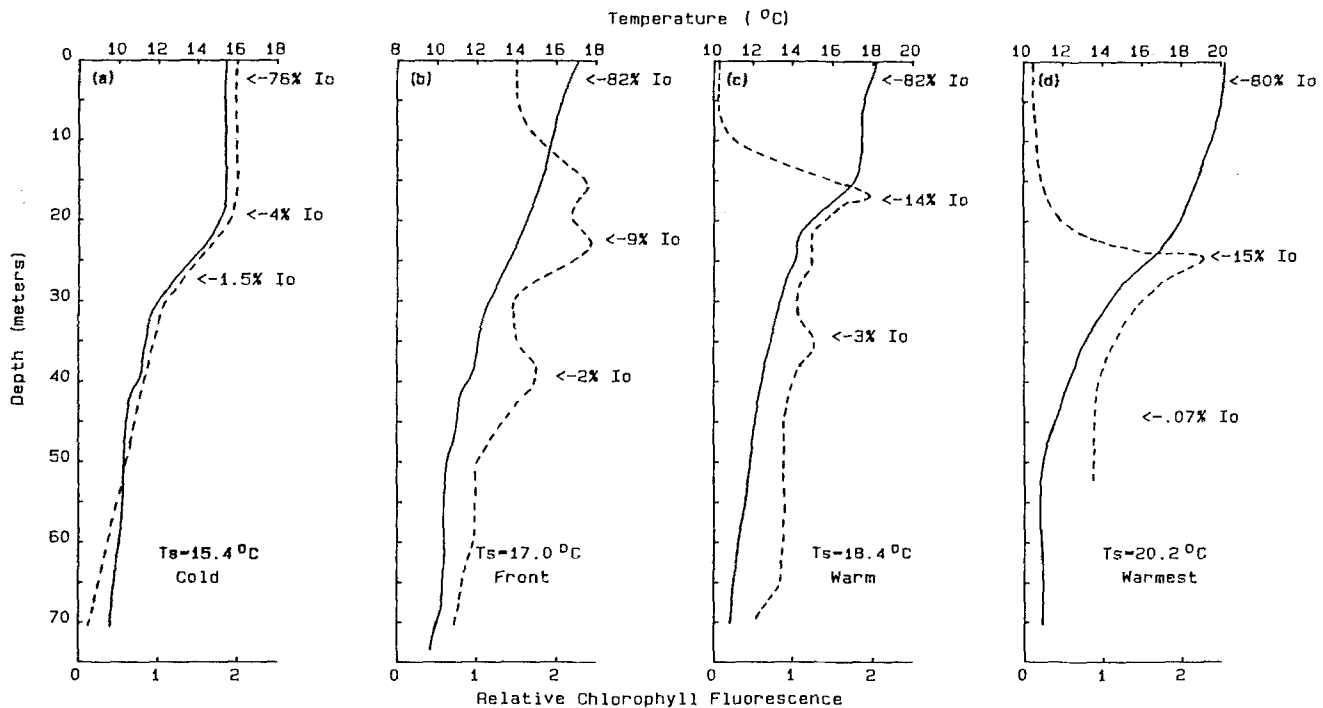


Fig. 3. Comparison of depth profiles of water temperature (continuous lines) and *in vivo* chlorophyll fluorescence (dashed lines) at cold, front, warm and warmest-water stations across frontal region in July 1985. Sampling depths and corresponding light levels (as % surface irradiance,  $I_0$ ) indicated by horizontal arrows.  $T_s$ : surface temperature

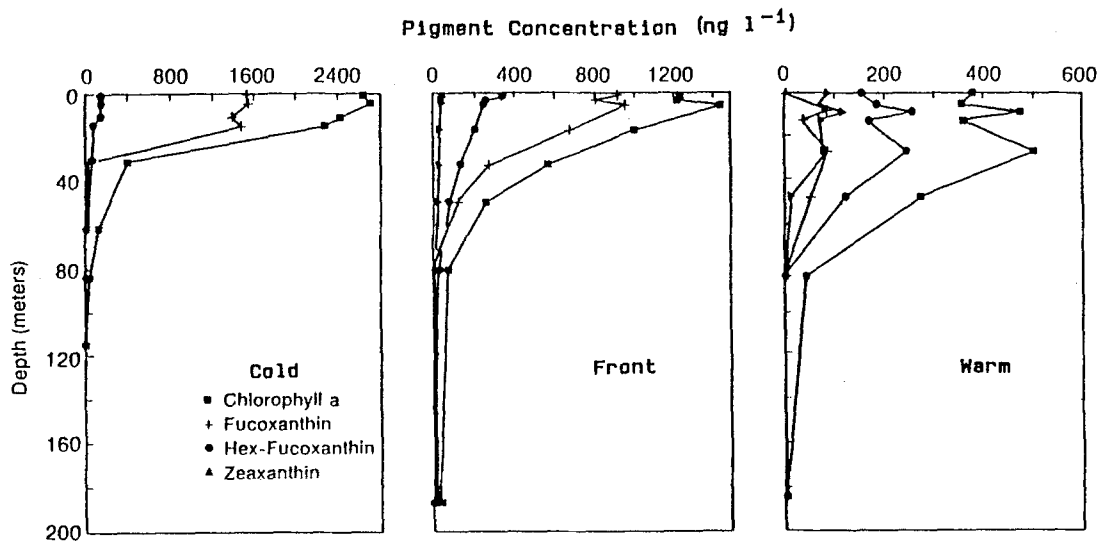


Fig. 4. Comparison of depth profile of extracted chlorophyll *a*, fucoxanthin, 19'-hexanoyloxyfucoxanthin, and zeaxanthin for  $>0.4 \mu\text{m}$  phytoplankton communities across frontal region in July 1985

## Results

The frontal region was identified during the cruise by measuring near-surface temperatures along the axis of the Santa Barbara Channel Islands. The sampling transect is shown in Fig. 1, where it is superimposed on a remotely-sensed sea-surface thermal map of coastal California obtained on 30 July 1985. The water-mass structure of the water column was resolved in an accompanying study (see following paper in this issue: Smith *et al.*, 1987) by examining the salinity and temperature data measured at transect stations across the front. At the surface (2 m), primary productivity and chlorophyll *a* biomass increased more than

20-fold across the front, being greatest on the cold-water front where surface temperatures ( $T_s$ ) were less than  $16^{\circ}\text{C}$  (Fig. 2). Primary productivity and chlorophyll *a* levels declined sharply in surface samples collected within the frontal region ( $T_s = 16.5^{\circ}$  to  $17.5^{\circ}\text{C}$ ), reaching lowest values on the warm side of the front ( $T_s = 18^{\circ}$  to  $19^{\circ}\text{C}$ ). Warmest surface temperatures ( $T_s > 20^{\circ}\text{C}$ ) occurred nearshore, in Santa Monica Bay (Fig. 1), where surface chlorophyll was about  $0.2 \text{ mg m}^{-3}$  and midday rates of  $P_{\text{max}}$  were less than  $1 \text{ mg C m}^{-3} \text{ h}^{-1}$ .

The distinctive physical and biological features of the four sampling stations are presented in Figs. 3 and 4. Light availability to phytoplankton communities at the ther-

mocline increased from 4%  $I_0$  on the cold-water side to 15%  $I_0$  on the warm-water side of the front (Smith *et al.*, 1987). On the cold-water side, *in vivo* chlorophyll-fluorescence intensity was uniformly high within the mixed layer, while subsurface chlorophyll-fluorescence maxima were dominant near the thermocline on the warm-water side (Fig. 3). Measurements of extracted chlorophyll *a* (Fig. 4) in the  $>0.4 \mu\text{m}$  fraction indicated that the depth of the chlorophyll maximum was not necessarily the site of maximum *in vivo* chlorophyll fluorescence, especially on the warm-water side of the front where near surface secondary maxima were evident. Distribution of accessory pigmentation also varied across the front, with fucoxanthin concentrations uniformly high within the mixed layers of the cold-water side of the front, 19'-hexanoylfucoxanthin concentrations highest within surface waters of the frontal boundary and declining with depth, and zeaxanthin content elevated within the upper mixed layers on the warm-water side of the front.

Depth-dependent changes in the timing and amplitude of light-saturated (Fig. 5) and light-limited (Fig. 6) rates of chlorophyll-based photosynthesis were compared in whole-water ( $>0.4 \mu\text{m}$ ) phytoplankton communities col-

lected at the four stations. At the warmest-water station ( $T_s=20.2^\circ\text{C}$ ), surface phytoplankton displayed coincident daytime fluctuations in chlorophyll-based  $P_{\text{max}}$  and chlorophyll-based alpha which included an apparent midday suppression of photosynthetic activity (Figs. 5a, 6a). The  $I_k$  for photosynthesis for these samples declined temporarily to  $28 \mu\text{E m}^{-2} \text{s}^{-1}$  at midday, compared to a mean value of  $269 \pm 73 \mu\text{E m}^{-2} \text{s}^{-1}$  for all other daytime measurements.

At the warm-water station ( $T_s=18.4^\circ\text{C}$ ), a midday maximum in assimilation rates was evident in both 80%  $I_0$  and 10%  $I_0$  communities, with peak  $P_{\text{max}}$  values at levels six and four times the respective minimum values measured predawn or postdusk (Fig. 5b). In the 1%  $I_0$  community, assimilation rates were several-fold lower than those measured in the upper mixed layer, and the daily variation in photosynthesis was less apparent. However, the daily amplitude in  $P_{\text{max}}$  was 7.5, ranging from a low value of  $0.20 \text{ mg C mg chlorophyll } a^{-1} \text{ h}^{-1}$  measured from 03.00 to 04.30 hrs and a high value of  $1.5 \text{ mg C mg chlorophyll } a^{-1} \text{ h}^{-1}$  measured from 12.00 to 14.00 hrs. Only subsurface 10 and 1%  $I_0$  communities exhibited coincident daytime changes in  $P_{\text{max}}$  and alpha (Figs. 5b, 6b), resulting in generally constant  $I_k$  values over the day, i.e.,  $135 \pm 24$  and

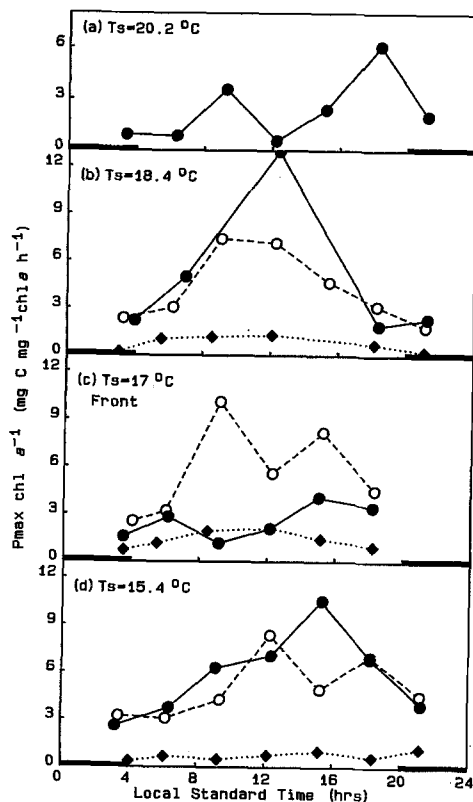


Fig. 5. Diurnal changes in light-saturated chlorophyll *a*-based photosynthesis measured for  $>0.4 \mu\text{m}$  phytoplankton communities collected at surface, 80%  $I_0$  (2 m, continuous line), subsurface, 10%  $I_0$ , chlorophyll maximum (dashed line) and depth of 1% light level ( $\blacklozenge$ ) at (a) warmest, (b) warm, (c) front, and (d) cold-water stations across frontal regions in July 1985. One standard deviation of  $P_{\text{max}}$  is less than 15% of derived mean of 6 to 14 measurements

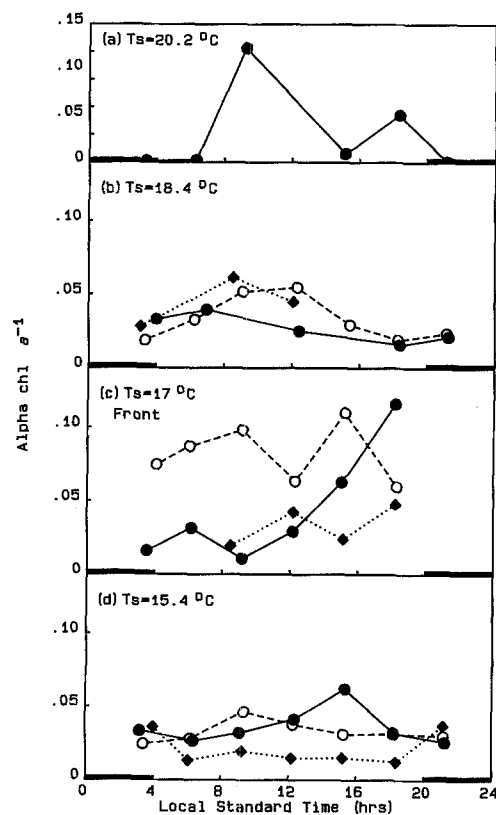


Fig. 6. Diurnal changes in chlorophyll *a*-based light-limited slope ( $\alpha \text{ chl } a^{-1}$ ) of photosynthesis-irradiance relationships measured for  $>0.5 \mu\text{m}$  phytoplankton communities collected at surface, 80%  $I_0$  (2 m, continuous line), subsurface, 10%  $I_0$ , chlorophyll maximum (dashed line) and depth of 1% light level ( $\blacklozenge$ ) at (a) warmest, (b) warm, (c) front, and (d) cold-water stations across frontal region in July 1985

$18 \pm 9 \mu\text{E m}^{-2} \text{s}^{-1}$ , respectively. In contrast, chlorophyll-based alpha changed little during the day in surface samples and caused  $I_k$  values for the 80%  $I_0$  community to closely parallel diurnal changes in  $P_{\text{max}}$ , i.e., increasing almost ten-fold from a predawn minimum of  $66 \mu\text{E m}^{-2} \text{s}^{-1}$  to a maximum value of  $518 \mu\text{E m}^{-2} \text{s}^{-1}$  at midday (data not shown).

Within the frontal boundary, the phytoplankton community collected from the subsurface chlorophyll maximum (10%  $I_0$ ) displayed the largest daily variations in assimilation rates, with a maximum:minimum ratio of 5 (Figs. 5c, 6c). Daytime photosynthetic rates were much lower in both the surface and 1%  $I_0$  communities, but daytime peaks in  $P_{\text{max}}$  were evident and day:night amplitudes of 2.6 and 3.0 were measured, respectively. Within all three frontal communities, daily fluctuations in chlorophyll-based alpha were evident, but no clear pattern was observed and the alpha changes were not coincident with changes in  $P_{\text{max}}$ . Therefore,  $I_k$  values altered over the day for each community, declining from 100 to  $30 \mu\text{E m}^{-2} \text{s}^{-1}$  between dawn and dusk in both 80 and 1%  $I_0$  communities, while increasing from 35 to  $75 \mu\text{E m}^{-2} \text{s}^{-1}$  in the 10%  $I_0$  community.

On the cold-water side of the front, surface and 10%  $I_0$  communities displayed nearly identical diel patterns in both  $P_{\text{max}}$  and alpha (Figs. 5d, 6d). About four-fold changes in  $P_{\text{max}}$  occurred over the day, while diel variations in alpha were smaller in amplitude. The 1%  $I_0$  community had assimilation rates which never exceeded  $1 \text{ mg C chlorophyll } a^{-1} \text{ h}^{-1}$ , however a day/night amplitude in photosynthesis of 2.2 was detected (Fig. 5d). Since light-limited rates of photosynthesis for the 1%  $I_0$  community showed no detectable variation over the day, a daily vari-

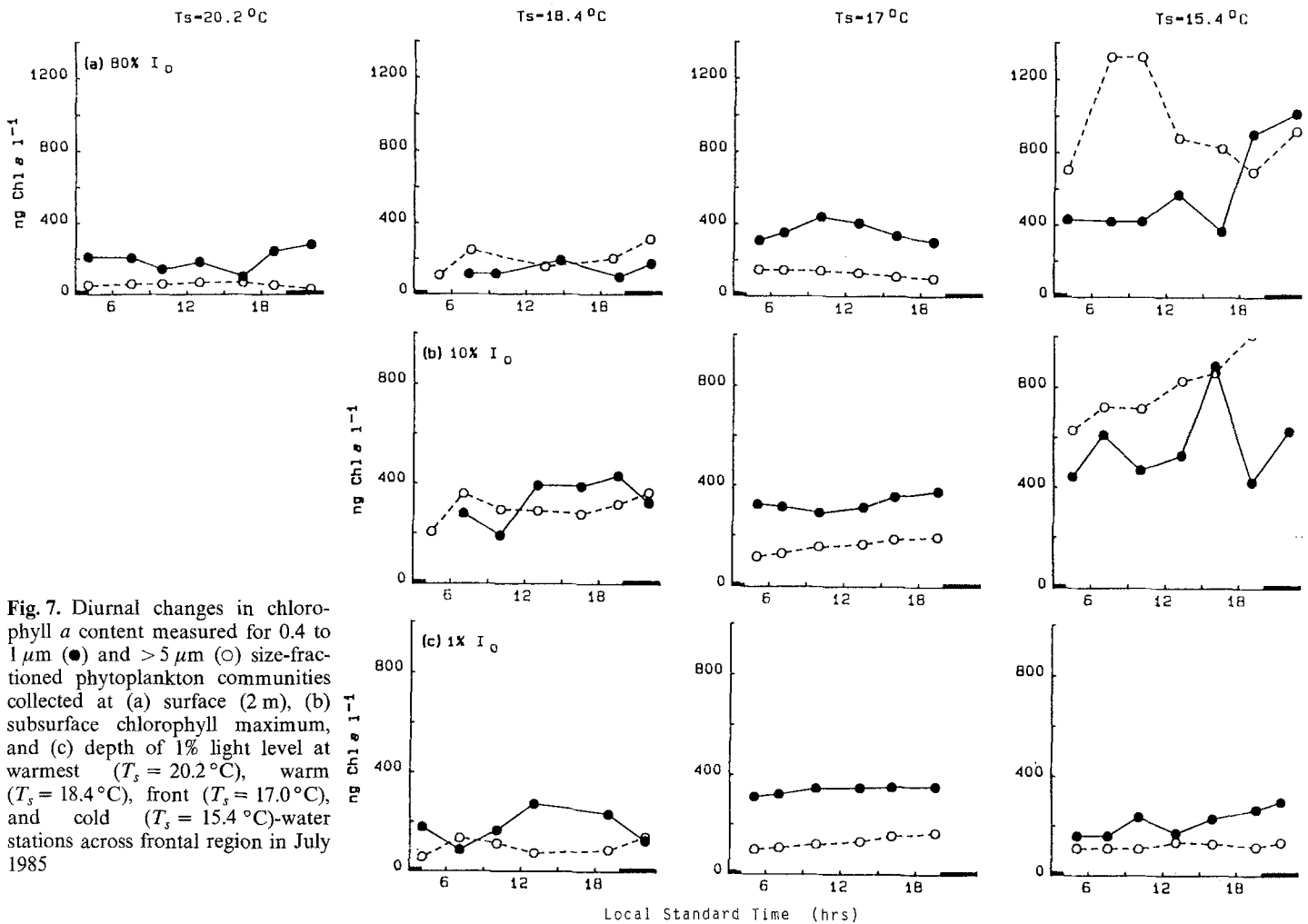
ation in  $I_k$  ranging between  $\leq 10$  to  $50 \mu\text{E m}^{-2} \text{s}^{-1}$  was evident (data not shown).

Variations in the accessory pigment-to-chlorophyll *a* (P:chl) ratios for the  $> 0.4 \mu\text{m}$  phytoplankton component of each community showed no obvious diurnal trends. For this reason, mean ( $\pm$  SD) daily P:chl ratios were calculated and are summarized in Table 1; the coefficient of variation (mean:SD $\times$ 100%) for the individual pigment ratios averaged 41% ( $n=58$ ) and changes in P:chl ratios across the thermal front were considerably greater than diurnal variations in the vats. Concentrations of chlorophyll *b*, 19'-hexanoyloxyfucoxanthin and zeaxanthin (relative to chlorophyll *a*) were elevated two- to eight-fold on the warm side of the front ( $T_s=18.4$  and  $20.2^\circ\text{C}$ ), reflecting the presence of chlorophytes, prymnesiophytes and cyanobacteria, respectively. Conversely, fucoxanthin-to-chlorophyll *a* ratios on the cold side of the front ( $T_s=15.4^\circ\text{C}$ ) were approximately two-fold greater than those measured on the warm side of the front, indicating the dominance of diatoms. When stations on either side of the front are compared, the frontal zone waters ( $T_s=17.0^\circ\text{C}$ ) were "enriched" in 19'-hexanoyloxyfucoxanthin and depleted in fucoxanthin, relative to chlorophyll *a*. Chlorophyll *c*- and diadinoxanthin-to-chlorophyll *a* ratios were highest in the warmest water sampled ( $T_s=20.2^\circ\text{C}$ ). A consistent depth pattern was only observed with the chlorophyll *b*-to-chlorophyll *a* ratios, which generally increased with decreasing irradiance (Table 1).

Diurnal patterns of size-fractionated chlorophyll *a* samples collected at the surface (Fig. 7a) indicated a switch from communities dominated by the 0.4 to  $5 \mu\text{m}$  size fraction to those dominated by  $> 5 \mu\text{m}$  phytoplankton when crossing from the warm to the cold side of the front

**Table 1.** Mean ( $\pm$ SD) accessory pigment-to-chlorophyll (Chl) *a* ratios (w:w) for phytoplankton ( $> 0.4 \mu\text{m}$ ) collected at four stations across a thermal front in coastal waters off California (July 1985). Populations were collected pre-dawn and maintained in vats under simulated *in situ* conditions; five to seven replicate measurements were made at periodic intervals (3 to 4 h) over the day, and tabulated as a function of light depth. Elevated ratios are boxed.  $T_s$ : surface temperature; %  $I_0$ : % surface irradiance. Fucox: fucoxanthin; H-fuc: 19'-hexanoyloxyfucoxanthin; Diad: diadinoxanthin; Zeax: zeaxanthin. nd: accessory pigment not detectable

Thermal station	Chl <i>b</i> Chl <i>a</i>	Chl <i>c</i> Chl <i>a</i>	Fucox Chl <i>a</i>	H-fuc Chl <i>a</i>	Diad Chl <i>a</i>	Zeax Chl <i>a</i>
$T_s=20.2^\circ\text{C}$ 80% $I_0$	0.41 $\pm$ 0.22	0.27 $\pm$ 0.09	0.32 $\pm$ 0.20	0.38 $\pm$ 0.02	0.31 $\pm$ 0.12	0.30 $\pm$ 0.07
$T_s=18.4^\circ\text{C}$ 80% $I_0$	nd	0.20 $\pm$ 0.14	0.32 $\pm$ 0.16	0.16 $\pm$ 0.07	0.10 $\pm$ 0.02	0.10 $\pm$ 0.05
10% $I_0$	0.29 $\pm$ 0.14	0.05 $\pm$ 0.02	0.36 $\pm$ 0.09	0.13 $\pm$ 0.04	0.11 $\pm$ 0.05	0.08 $\pm$ 0.04
1% $I_0$	0.40 $\pm$ 0.20	nd	0.27 $\pm$ 0.10	0.23 $\pm$ 0.10	0.12 $\pm$ 0.02	0.08 $\pm$ 0.02
$T_s=17.0^\circ\text{C}$ 80% $I_0$	0.22 $\pm$ 0.07	0.08 $\pm$ 0.02	0.14 $\pm$ 0.06	0.29 $\pm$ 0.26	0.10 $\pm$ 0.01	0.16 $\pm$ 0.08
10% $I_0$	0.32 $\pm$ 0.12	0.08 $\pm$ 0.03	0.14 $\pm$ 0.07	0.18 $\pm$ 0.05	0.08 $\pm$ 0.03	0.11 $\pm$ 0.07
1% $I_0$	0.36 $\pm$ 0.11	0.06 $\pm$ 0.03	0.24 $\pm$ 0.10	0.23 $\pm$ 0.06	0.09 $\pm$ 0.06	0.05 $\pm$ 0.02
$T_s=15.4^\circ\text{C}$ 80% $I_0$	0.18 $\pm$ 0.08	0.09 $\pm$ 0.02	0.62 $\pm$ 0.05	0.06 $\pm$ 0.02	0.13 $\pm$ 0.08	0.04 $\pm$ 0.01
10% $I_0$	0.11 $\pm$ 0.05	0.08 $\pm$ 0.03	0.58 $\pm$ 0.08	0.04 $\pm$ 0.02	0.13 $\pm$ 0.12	0.03 $\pm$ 0.02
1% $I_0$	0.27 $\pm$ 0.11	0.13 $\pm$ 0.09	0.23 $\pm$ 0.11	0.12 $\pm$ 0.05	0.15 $\pm$ 0.03	0.06 $\pm$ 0.03



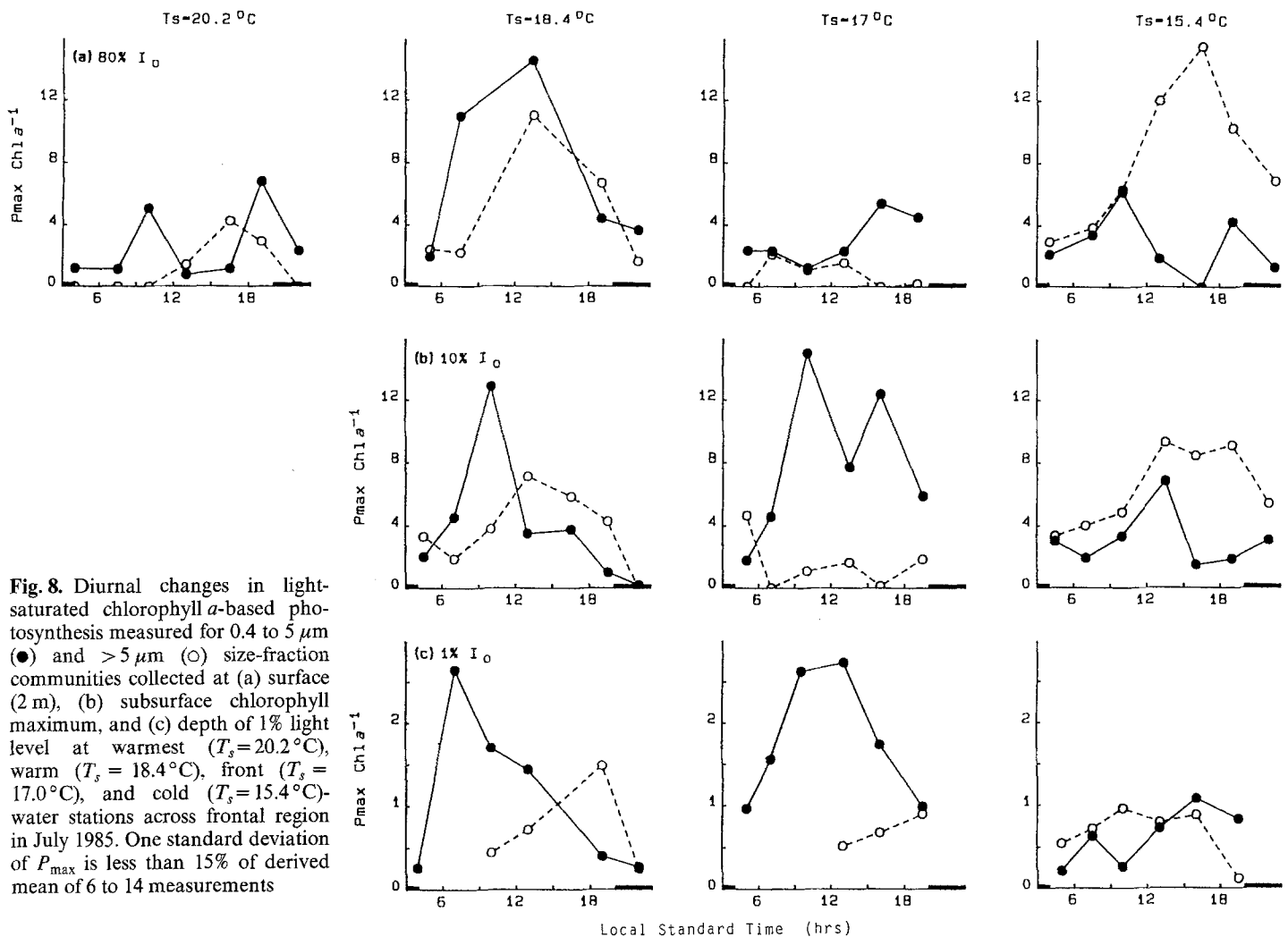
**Fig. 7.** Diurnal changes in chlorophyll *a* content measured for 0.4 to 5  $\mu\text{m}$  (●) and > 5  $\mu\text{m}$  (○) size-fractionated phytoplankton communities collected at (a) surface (2 m), (b) subsurface chlorophyll maximum, and (c) depth of 1% light level at warmest ( $T_s = 20.2^\circ\text{C}$ ), warm ( $T_s = 18.4^\circ\text{C}$ ), front ( $T_s = 17.0^\circ\text{C}$ ), and cold ( $T_s = 15.4^\circ\text{C}$ )-water stations across frontal region in July 1985

**Table 2.** Mean ( $\pm$ SD) percent contribution of 0.4 to 5  $\mu\text{m}$  and  $\geq 5 \mu\text{m}$  algal size fractions to chlorophyll *a* biomass and volume-based light-saturated rates of photosynthesis ( $P_{\text{max}}:V$ ) within phytoplankton communities collected at four stations across a thermal front off coastal California in July 1985. Populations were collected pre-dawn and maintained in 200-liter vats under simulated *in situ* conditions; five to seven replicate measurements were made at periodic intervals (3 to 4 h) over the day, and tabulated as a function of light depth

Thermal station	Chlorophyll <i>a</i>		$P_{\text{max}}:V$	
	0.4 to 5 $\mu\text{m}$	$\geq 5 \mu\text{m}$	0.4 to 5 $\mu\text{m}$	$\geq 5 \mu\text{m}$
$T_s = 20.2^\circ\text{C}$				
80% $I_0$	76 $\pm$ 10	24 $\pm$ 10	79 $\pm$ 33	21 $\pm$ 33
$T_s = 18.4^\circ\text{C}$				
80% $I_0$	41 $\pm$ 11	59 $\pm$ 15	55 $\pm$ 15	45 $\pm$ 11
10% $I_0$	54 $\pm$ 12	46 $\pm$ 12	57 $\pm$ 15	43 $\pm$ 15
1% $I_0$	64 $\pm$ 18	36 $\pm$ 16	77 $\pm$ 26	23 $\pm$ 26
$T_s = 17.0^\circ\text{C}$				
80% $I_0$	73 $\pm$ 3	27 $\pm$ 3	90 $\pm$ 11	10 $\pm$ 11
10% $I_0$	68 $\pm$ 3	32 $\pm$ 3	87 $\pm$ 18	13 $\pm$ 18
1% $I_0$	72 $\pm$ 3	28 $\pm$ 3	91 $\pm$ 12	9 $\pm$ 12
$T_s = 15.4^\circ\text{C}$				
80% $I_0$	38 $\pm$ 13	62 $\pm$ 13	18 $\pm$ 14	82 $\pm$ 14
10% $I_0$	40 $\pm$ 9	60 $\pm$ 7	24 $\pm$ 11	76 $\pm$ 11
1% $I_0$	64 $\pm$ 6	36 $\pm$ 6	49 $\pm$ 14	51 $\pm$ 14

( $T_s = 15.4^\circ\text{C}$ ; Table 2). The greatest biomass of 0.4 to 5  $\mu\text{m}$  chlorophyll was in the front itself ( $T_s = 17.0^\circ\text{C}$ ) and at the base of the euphotic zone (1%  $I_0$ ) at three stations, where this size fraction accounted for more than 64% of the chlorophyll biomass (Table 2). With the exception of samples collected within the upper mixed layer (80 and 10%  $I_0$ ) on the cold-water side, negligible daily variations in chlorophyll content of the vat communities were observed (Fig. 7). In cold-water surface communities (80%  $I_0$ ), the > 5  $\mu\text{m}$  community had a midmorning peak in chlorophyll content that was about two-fold greater than that at dawn and dusk (Fig. 7a). Within this same community, the chlorophyll *a* content of the 0.4 to 5.0  $\mu\text{m}$  community was stable during the first 15 h of incubation and then doubled abruptly near the end of the day. Daytime increases in chlorophyll content of the 10%  $I_0$  cold-water vat were around 50% for both phytoplankton size fractions (Fig. 7b).

Diurnal patterns of size-fractionated photosynthesis revealed that the timing of peak activity, as well as the amplitude of daily change, often differed between the two size fractions sampled within the same community (Fig. 8). For example, the surface 0.4 to 5  $\mu\text{m}$  fraction of the warmest-water mass showed two daytime peaks in  $P_{\text{max}}$ , inter-



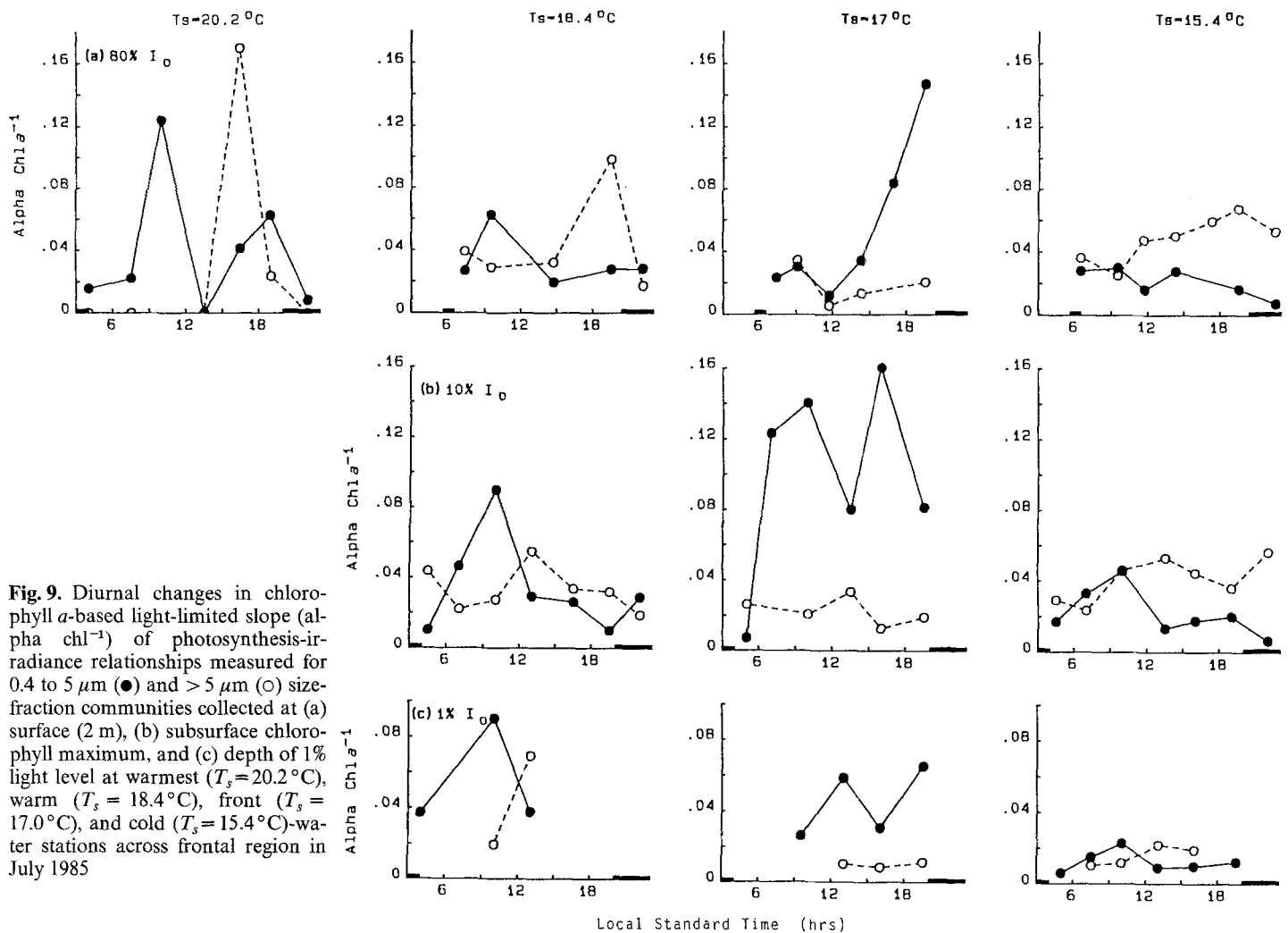
**Fig. 8.** Diurnal changes in light-saturated chlorophyll *a*-based photosynthesis measured for 0.4 to 5  $\mu m$  (●) and >5  $\mu m$  (○) size-fraction communities collected at (a) surface (2 m), (b) subsurface chlorophyll maximum, and (c) depth of 1% light level at warmest ( $T_s = 20.2^\circ C$ ), warm ( $T_s = 18.4^\circ C$ ), front ( $T_s = 17.0^\circ C$ ), and cold ( $T_s = 15.4^\circ C$ ) water stations across frontal region in July 1985. One standard deviation of  $P_{max}$  is less than 15% of derived mean of 6 to 14 measurements

spersed by a strong photosuppression of  $P_{max}$  during the afternoon when  $P_{max}$  of the >5  $\mu m$  fraction was highest. In the other water masses examined, differences in timing of peak  $P_{max}$  observed in the two size fractions at one depth appeared to be conserved generally throughout the water column at any given station. On the warm side of the front, nanoplankton throughout the water column had a peak in  $P_{max}$  occurring before noon, while netplankton peak  $P_{max}$  was clearly in the afternoon. Photosynthetic activity in surface frontal communities appeared to be photosuppressed throughout the day when confined to surface irradiance, but subsurface 0.4 to 5  $\mu m$  communities exhibited strong midday peaks in  $P_{max}$  while photosynthetic activity of the >5  $\mu m$  fraction was often negligible over the day. Conversely, it was the larger phytoplankton communities in cold water which exhibited greatest diurnal variations in  $P_{max}$ . Above the pycnocline, the 0.4 to 5  $\mu m$  fraction had lower assimilation rates than the >5  $\mu m$  fraction and smaller diurnal amplitudes in  $P_{max}$  and/or  $\alpha$ , with daytime patterns often characterized by two peaks interspersed by a short period of apparent photoinhibition.

Generally, light-limited rates of photosynthesis covaried with  $P_{max}$  over the day in both size fractions (Fig. 9). But major diurnal oscillations in  $I_k$  were sometimes observed within some size-fractionated communities (Fig. 10), indicating either that  $P_{max}$  and  $\alpha$  did not covary over the day and/or that the amplitude of daily variation in covarying  $P_{max}$  and  $\alpha$  was not the same.

When diurnal patterns of photosynthesis were considered, it appeared that the 0.4 to 5  $\mu m$  fraction accounted for >90% of the total primary production in the front and >50% in the warm-water mass of the front, as well as at the base of the euphotic zone in the cold-water mass (Table 2). Only above the pycnocline or in the cold-water mass was more than >75% of total primary production attributable to >5  $\mu m$  communities, which were dominated by very abundant diatom populations. The relative distribution of size-fractionated chlorophyll *a* biomass followed that described for size-fractionated photosynthesis in the warm-water mass for both algal size fractions. However, chlorophyll biomass underestimated and overestimated the photosynthetic potential of the 0.4 to 5  $\mu m$  fraction at all





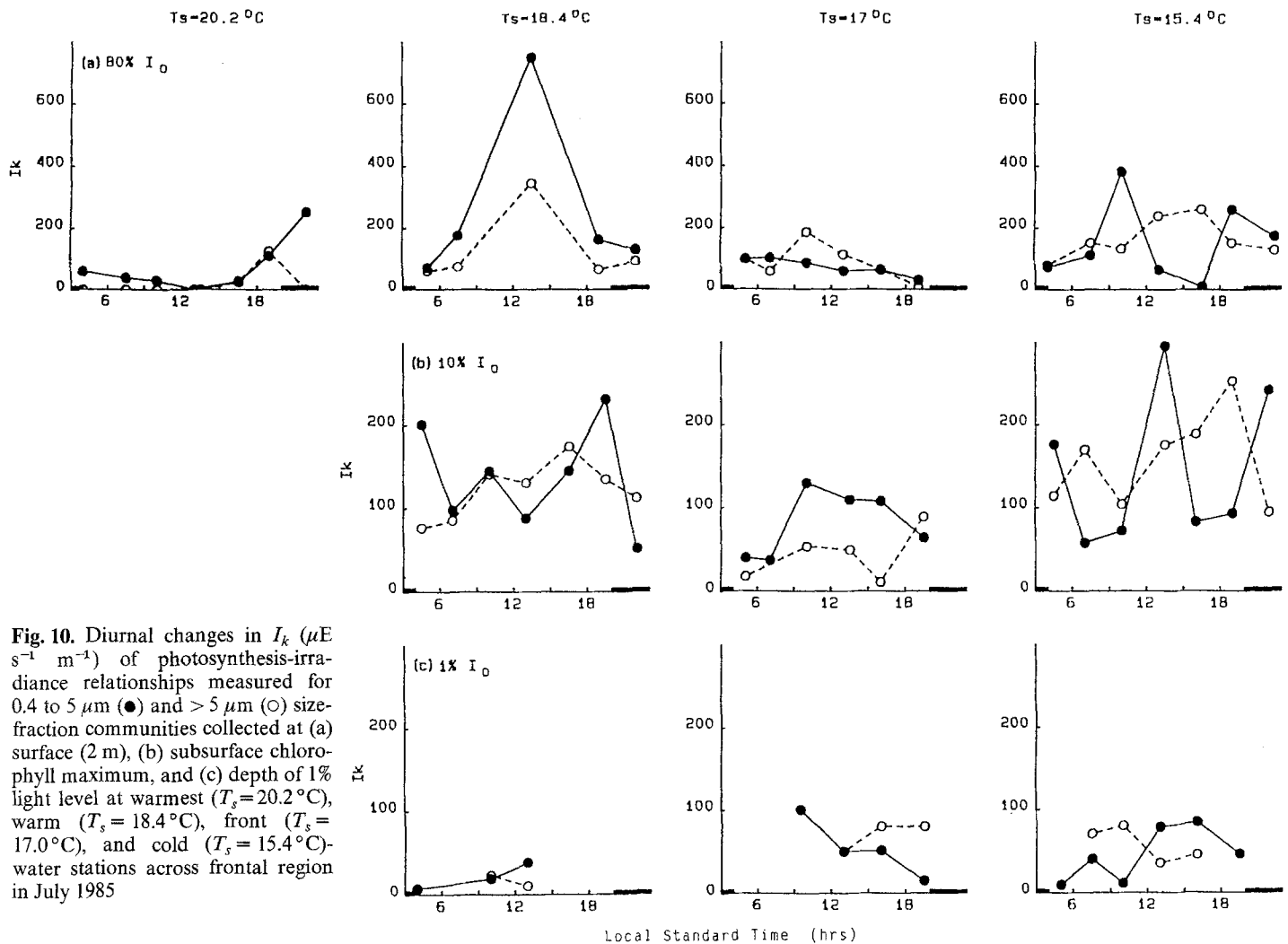
**Fig. 9.** Diurnal changes in chlorophyll *a*-based light-limited slope ( $\alpha$  chl<sup>-1</sup>) of photosynthesis-irradiance relationships measured for 0.4 to 5  $\mu$ m (●) and > 5  $\mu$ m (○) size-fraction communities collected at (a) surface (2 m), (b) subsurface chlorophyll maximum, and (c) depth of 1% light level at warmest ( $T_s = 20.2^\circ\text{C}$ ), warm ( $T_s = 18.4^\circ\text{C}$ ), front ( $T_s = 17.0^\circ\text{C}$ ), and cold ( $T_s = 15.4^\circ\text{C}$ )-water stations across frontal region in July 1985

depths within the front and cold-water masses, respectively (Table 2).

## Discussion

Our study documents the range of variability possible in diurnal patterns of size-fractionated photosynthesis and illustrates that a general view of the size-dependency in assimilation rates and diurnal patterns of photosynthesis cannot be supported. The results were achieved with a unique sampling regime that allowed a detailed comparison of daytime changes in photosynthesis in algal communities collected within a few days of one another across the hydrographic gradients characterizing the Santa Barbara frontal boundary (Smith *et al.*, 1987). First, it is apparent that either nanoplankton or netplankton can dominate natural phytoplankton assemblages in coastal frontal regions. Second, in both the >5  $\mu$ m and 0.4 to 5  $\mu$ m size fractions, large diurnal variations in  $P_{\max}$  and  $\alpha$  were discernable. However, the timing of peak photosynthetic

potential ( $P_{\max}$ ), its coincidence with variations in light-limited rates of photosynthesis ( $\alpha$ ), as well as diel amplitudes in  $P_{\max}$  and  $\alpha$ , often differed between nano- and netplankton fractions sampled within the same community and between identical size fractions collected from different depths and stations. Third, the present study was designed to examine the physiology of phytoplankton at the base of euphotic zone and below the thermocline. Like the earlier Atlantic study (Prézélin *et al.*, 1986), there was a general dampening in the amplitude of diurnal variations in  $P_{\max}$  below the thermocline; but, unlike the previous study, no depth-dependent shift in the time of peak  $P_{\max}$  was noted in algal communities sampled anywhere across the front. Fourth, like previous efforts where chlorophyll was also measured in studies of diurnal patterns of size-fractionated photosynthesis (Putt and Prézélin, 1985; Prézélin *et al.*, 1986), diurnal variations in photosynthesis occurred independently of pigmentation and indicate that chlorophyll biomass estimates alone are poor measures of photosynthetic performance. Lastly, HPLC analyses of accessory pigmentation:chlorophyll *a* ratios were used to de-



**Fig. 10.** Diurnal changes in  $I_k$  ( $\mu\text{E s}^{-1} \text{m}^{-1}$ ) of photosynthesis-irradiance relationships measured for 0.4 to  $5 \mu\text{m}$  ( $\bullet$ ) and  $> 5 \mu\text{m}$  ( $\circ$ ) size-fraction communities collected at (a) surface (2 m), (b) subsurface chlorophyll maximum, and (c) depth of 1% light level at warmest ( $T_s = 20.2^\circ\text{C}$ ), warm ( $T_s = 18.4^\circ\text{C}$ ), front ( $T_s = 17.0^\circ\text{C}$ ), and cold ( $T_s = 15.4^\circ\text{C}$ )-water stations across frontal region in July 1985

termine floristic changes in community structure across the Santa Barbara front and showed that variations in pigment ratios do not underlie diurnal changes in rates of photosynthesis in natural populations.

Consistent with views that larger phytoplankton dominate in colder waters along coastal California following an upwelling event (cf. Malone, 1971 b, 1981),  $> 5 \mu\text{m}$  diatoms were abundant in the mixed layer and these netphytoplankton accounted for 80% of potential daytime productivity in the cold-water mass (Table 2) thought to be locally upwelled near Point Conception (cf. Johnson *et al.*, 1987; Smith *et al.*, 1987). Nearly identical diurnal patterns in  $P_{\text{max}}$  and alpha were displayed in cold-water samples collected at the surface (2 m) and at the depth of 10%  $I_0$ , with midday peak  $P_{\text{max}}$  about four-fold greater than predawn values. In cold-water communities, the  $> 5 \mu\text{m}$  fraction exhibited greater diurnal variations in photosynthesis than smaller phytoplankton, which had lower assimilation rates and less distinct diurnal patterns in photosynthesis.

Contrary to previous reports of netplankton flagellates dominating frontal boundaries (Pingree *et al.*, 1975; Hol-

ligan, 1979; Seliger *et al.*, 1979; Incze and Yentsch, 1981), we found that the 0.4 to  $5 \mu\text{m}$  fraction accounted for two-thirds of the plant biomass and  $> 90\%$  of primary production at all three sampling depths (Table 2). HPLC pigment analyses showed enrichment in 19'-hexanoyloxyfucoxanthin, indicative of enhanced numbers of prymnesiophytes. This algal group is comprised mostly of nanoplankton-sized phytoflagellates, the most notable of which are the coccolithophorids (Hibberd, 1980). Photosynthetic activity in confined surface communities appeared photosuppressed over the day, but subsurface (10 and 1%  $I_0$ ) 0.4 to  $5 \mu\text{m}$  phytoplankton exhibited midday peaks in  $P_{\text{max}}$  that were several-fold predawn values.

In the warm-water mass thought to represent the northward movement of the Southern California Counter Current, both algal size fractions contributed equally to  $P_{\text{max}}$  activity and chlorophyll *a* biomass. Throughout the water column, the 0.4 to  $5 \mu\text{m}$  fraction had a peak in  $P_{\text{max}}$  occurring before noon, while peak  $P_{\text{max}}$  in the  $> 5 \mu\text{m}$  fraction was clearly evident in the afternoon. Elevated chlorophyll *b*-, 19'-hexanoyloxyfucoxanthin- and zeaxanthin-to-chloro-

phyll *a* ratios indicated a mixture of algal groups, including chlorophytes, cyanobacteria and prymnesiophytes. Large dinoflagellates ( $> 35 \mu\text{m}$ ) were microscopically observed within warm-water communities (Putt *et al.*, in press), but pigment analyses indicate that they dominated at no location across the front. While the lack of dinoflagellates contrasts findings in other frontal regions (Pingree *et al.*, 1975; Holligan, 1979; Seliger *et al.*, 1979; Incze and Yentsch, 1981), they have been found to be seasonal components of the Santa Barbara Front during previous studies in this region (Harding *et al.*, 1982; Johnson *et al.*, 1987).

Our observations on mixed algal populations in the warm-water mass supported the earlier conclusions of Malone (1971a, b, 1981, 1982) and others (Paerl and Mackenzie, 1977) indicating that nanoplankton ( $< 22 \mu\text{m}$ ) assimilation rates are generally higher than netplankton ( $> 22 \mu\text{m}$ ) and that peak  $P_{\text{max}}$  is reached earlier in the day for nanoplankton than for netplankton. However, this pattern was not observed in either the frontal boundary where nanoplankton dominated populations, or in the cold-water mass where  $> 5 \mu\text{m}$  diatom-dominated populations accounted for  $> 80\%$  of total algal biomass (Table 2). Neither was a separation in timing of nanoplankton and netplankton photosynthesis observed when in the Santa Barbara Channel during "el Niño" conditions (Putt and Prézélin, 1985), when nanoplankton (0.2 to  $5 \mu\text{m}$ )-dominated populations accounted for  $> 90\%$  of algal biomass and displayed lower assimilation rates than netplankton. Similar results were observed in water masses in the northwest Atlantic Ocean, where  $< 5 \mu\text{m}$  algal size fractions accounted for about 90% of total chlorophyll *a* and the coccoid cyanobacteria *Synechococcus* spp. accounted for  $> 90\%$  of the phytoplankton cells in the 0.6 to  $5 \mu\text{m}$  size range (Glover *et al.*, 1986). In both a warm-core eddy and at Wilkinson's Basin in the Gulf of Maine, three size categories of phytoplankton (0.6 to 1, 1 to 5, and  $> 5 \mu\text{m}$ ) displayed identical depth-dependent diurnal patterns of chlorophyll-based and cell-based  $P_{\text{max}}$ . In contrast, in a single community in the Antarctic, two species of net diatoms ranging in size from 50 to  $300 \mu\text{m}$  displayed differences in the timing of peak  $P_{\text{max}}$  (Putt *et al.*, in press). As has been concluded for the size-dependence of photosynthetic rates in diatoms (cf. Geider *et al.*, 1986), it may also be true that the size-dependency of the timing/amplitude of peak  $P_{\text{max}}$  is only apparent when the phytoplankton community represent a large range of algal sizes and/or taxonomic groups.

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