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PRODUCTIVITY OF DINOFLAGELLATE BLOOMS ON THE WEST COAST OF SOUTH AFRICA, AS MEASURED BY NATURAL FLUORESCENCE

B. A. MITCHELL-INNES, G. C. PITCHER* and T. A. PROBYN**

The biomass and productivity of phytoplankton populations inshore on the west coast of South Africa were investigated towards the end of the upwelling season, a period when high-biomass dinoflagellate blooms are common. Productivity was estimated from natural fluorescence measurements (P_{NF}), using photosynthesis (P) v. irradiance (E) relationships (P_E) and by means of the *in situ* ^{14}C-method (P_C). A linear regression of P_{NF} productivity against P_C and P_E productivities yielded a slope of 0.911 and an r^2 of 0.83 (n = 41). Physical and biological variability was high inshore, reflecting alternating periods of upwelling and quiescence. Mean chlorophyll inshore (within a 12 m water column) ranged from 0.7 to 57.8 (mean = 8.9) mg·m^{-3}, mean P_{NF} productivity ranged from 8.4 to 51.0 (mean = 24.6) mgC·m^{-3}·h^{-1} and daily integral P_{NF} productivity from 0.8 to 4.8 (mean = 2.3) gC·m^{-2}·day^{-1}. Transects sampled during active and relaxation phases of upwelling had different chlorophyll distributions. High chlorophyll concentrations (sometimes >50 mg·m^{-3}) were associated with surface blooms within the region of the upwelling front. Estimates of daily water-column P_{NF} productivity within these frontal blooms ranged from 4.0 to 5.6 gC·m^{-2}·day^{-1}. With relaxation of wind stress, blooms dominated by dinoflagellates flooded shorewards and often formed red tides. Chlorophyll concentrations of >175 mg·m^{-3} and productivity rates > 500 mgC·m^{-3}·h^{-1} and 12 gC·m^{-2}·day^{-1} were measured during a particularly intense red tide. Offshore, the water column was highly stratified with a well-defined subsurface chlorophyll maximum layer within the pycnocline region. Estimates of daily water-column P_{NF} productivity ranged from 2.4 to 4.0 gC·m^{-2}·day^{-1} offshore. The high productivity of shelf waters on the West Coast in late summer can be ascribed largely to dinoflagellate populations and their success in both upwelling systems and stratified conditions.

The west coast of South Africa is located within the southern part of the Benguela upwelling system (Fig. 1), one of the world's four major eastern boundary current systems (Nelson and Hutchings 1983, Shannon 1985). It constitutes the nursery and recruitment grounds for many commercially important fish, particularly anchovy *Engraulis capensis* and sardine *Sardinops sagax* (Hutchings 1992). The high primary productivity of the southern Benguela has been generally ascribed to diatoms (Shannon and Pillar 1986), which dominate in upwelling areas. However, there is increasing evidence to suggest that, in late summer, dinoflagellates form widespread and persistent subsurface populations in stratified midshelf waters on the West Coast (Pitcher *et al*. 1998). These populations form surface blooms nearshore, in the vicinity of the upwelling front. Periodically, following relaxation of upwelling, dinoflagellate populations accumulate inshore and form localized red tides (Pitcher and Boyd 1996, Pitcher *et al*. 1998, Probyn *et al*. 2000). Factors leading to the development, maintenance and decline of red tides in the southern Benguela upwelling system have been studied extensively (Pitcher *et al*. 1993, 1995, 1998, Pitcher and Boyd 1996, Probyn *et al*. 2000). Also, changes in dinoflagellate species composition and biomass have been studied over a broad range of spatial and temporal scales (Pitcher and Calder 2000). However, there is limited knowledge of the productivity of these populations, except from occasional measurements made by means of the traditional ^{14}C method.

The development of new technology has now made it possible to measure *in situ* primary productivity rapidly and easily by means of natural fluorescence (Kiefer *et al*. 1989, Chamberlin *et al*. 1990). Natural fluorescence is the solar-induced fluorescence of chlorophyll *a* and it provides an index of photosynthetic activity (Kiefer *et al*. 1989, Chamberlin *et al*. 1990, Kiefer and Reynolds 1992, Garcia-Mendoza and Maske 1996). Chlorophyll *a* in planktonic photoautotrophs fluoresces under excitation in a narrow spectral band centred at 683 nm. Natural fluorescence can be measured accurately within the euphotic zone, except just below the surface where scattering of red light is high (Kiefer *et al*. 1989). It is a passive measurement, unlike stimulated fluorescence that is used routinely to measure chlorophyll biomass. Several studies have compared natural fluorescence and radiocarbon measurements of primary productivity in environments ranging from coastal to mid-oceanic and equatorial to high-latitude waters, with encouraging results (Kiefer *et al*. 1989, Chamberlin *et al*. 1990, Stegmann *et al*. 1992, Lizotte and Priscu 1994, Garcia-Mendoza and Maske 1996, Stegmann and Lewis 1997). The relationship between photosynthesis and natural fluorescence depends on the ratio of the

* Marine & Coastal Management, Private Bag X2, Rogge Bay 8012, Cape Town, South Africa. E-mail: bminnes@sfri2.wcape.gov.za

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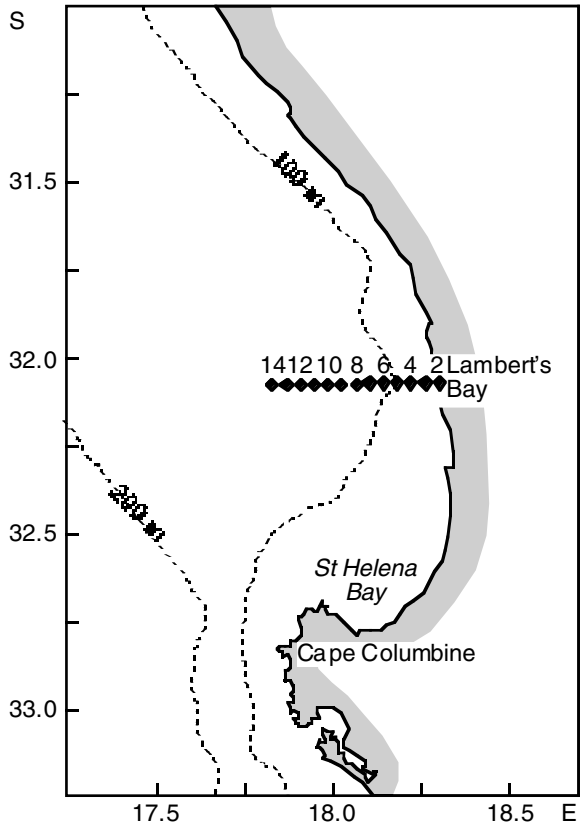

Fig. 1: Map of the west coast of South Africa showing the Lambert's Bay transect sampled during the study

quantum yields of these two processes. It is a function of incident irradiance (Kiefer *et al*. 1989, Chamberlin *et al*. 1990), but temperature (Chamberlin and Marra 1992) and nutrient status (Kiefer *et al*. 1989, Lizotte and Priscu 1994) may also affect the relationship (Garcia-Mendoza and Maske 1996).

The aim of this study is to examine the biomass and productivity of dinoflagellate blooms on the West Coast and to assess the use of natural fluorescence as a measure of productivity under conditions of high chlorophyll biomass.

MATERIAL AND METHODS

Sampling approach

Sampling was off Lambert's Bay on South Africa's west coast in February and March 1996, in March 1997 and in April 1998. Sampling sites included an inshore monitoring station and an offshore transect (Fig. 1). The monitoring site was located at Station 2 on the offshore transect, in 12 m water depth. This station was sampled mid-morning for 24 consecutive days from 14 February to 8 March 1996. Samples were taken at 0.5, 2, 4 and 7 m using NIO bottles for extracted chlorophyll *a*, phytoplankton and nutrient analyses. Profiles of temperature and stimulated fluorescence were measured using a Chelsea Instruments Aquapack and profiles of natural fluorescence and underwater PAR, together with surface irradiance, were measured using a Biospherical Instruments Inc. Profiling Natural Fluorometer (PNF-300). On certain days, samples for ^{14}C productivity incubations were taken at the four sampling depths and photosynthesis v. irradiance (*P* v. *E*) relationships were investigated at 0.5 and 7 m. On two occasions, *P* v. *E* relationships were determined at three-hourly intervals during the day. Concomitant profiles of temperature, stimulated fluorescence and natural fluorescence were also recorded.

A transect, consisting of 14 stations each 2 miles (3.7 km) apart (Fig. 1), was sampled four times during February and March 1996, on 4 March 1997 and on 22 April 1998. Only on 16 February 1996 was it possible to sample all 14 stations. Temperature and stimulated fluorescence profiles were taken at all stations in 1996 and 1997, whereas natural fluorescence and underwater PAR profiles were measured to 20 m depth only at Stations 2, 5, 8, 11 and 14. Discrete samples were taken at 0.5, 5, 10 and 20 m for extracted chlorophyll *a*, phytoplankton and nutrient analyses. On 22 April 1998, temperature, stimulated fluorescence, natural fluorescence and underwater PAR were measured throughout the water column, to within a few metres of the bottom or to at least 50 m depth at Stations 2–10.

Sampling methods

Chlorophyll *a* was determined fluorometrically using a Turner Designs fluorometer. Water samples were filtered onto Whatman GF/F filters and extracted in 90% acetone for 24 hours at -10°C in the dark (Parsons *et al*. 1984). Extracted chlorophyll *a* data were used to calibrate Chelsea Instruments Aquapack stimulated-fluorescence readings. Comparison of chlorophyll profiles against extracted chlorophyll values revealed quenching in the upper 2 m. To compensate for this, data from the upper 2 m were calibrated separately from remaining water column data. Productivity was measured using the ^{14}C-method (Parsons *et al*. 1984). At each depth sampled, three light samples and one dark sample were inoculated with 7–10 μCi

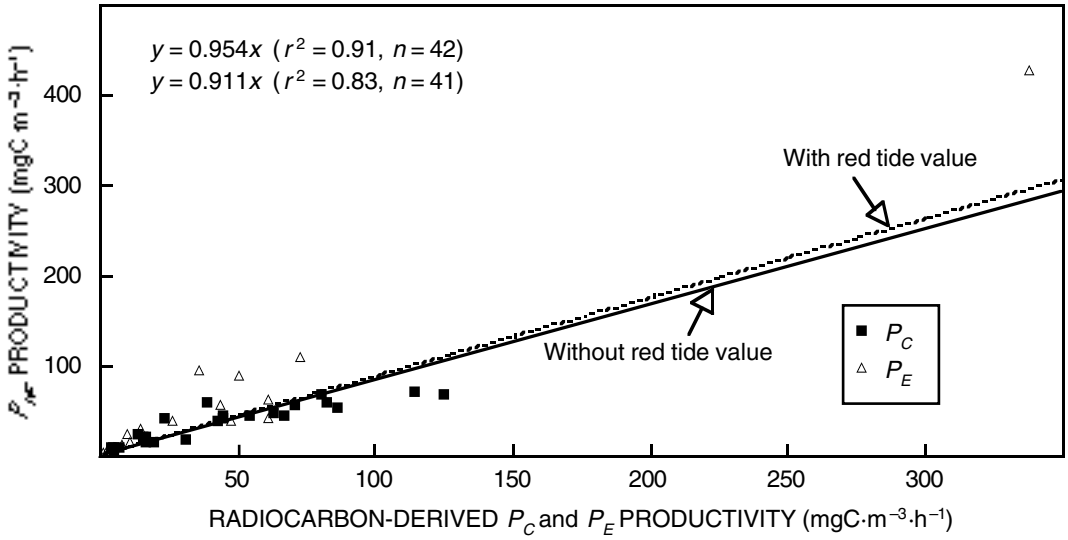

Fig. 2: Relationship between P_{NF} productivity and radiocarbon-derived P_C and P_E productivity. The regressions are given with and without the red tide value

$NaH^{14}CO_3$ and incubated *in situ* at their respective depths for 4 h over midday. A 24-h incubation from midday was carried out on 28/29 February. At the end of the incubation period, water samples were filtered onto Whatman GF/F filters, air-dried for 1.5 h and placed in scintillation vials to which 0.5 mℓ 1N HCl was added to remove any remaining inorganic ^{14}C. Vials were shaken vigorously after the addition of scintillation fluor (Instagel) and stored in the dark. The activity of filters was assayed by liquid scintillation counting using a Beckman LS1800. On occasions, parallel samples from 0.5 and 4 m were incubated for fractionation studies; post-incubation samples were pre-screened through 10-µm screens before filtering onto Whatman GF/F filters. Samples for nitrate analyses were frozen and later analysed using an autoanalyser (Mostert 1988). Samples for phytoplankton analyses were fixed in buffered 2% formalin and counted using an inverted microscope.

Natural fluorescence profiles were processed using software supplied with the PNF-300. Photosynthetic estimates were based on measured values of natural or upwelling fluorescence, scalar irradiance and diffuse attenuation coefficients for PAR, together with empirical constants ϕ_{rmax} and k_ϕ. These constants are the maximum value of the quantum yield ratio of photosynthesis to fluorescence, and the irradiance at which this ratio is equal to one-half of its maximum respectively (Chamberlin *et al*. 1990). Default values for these constants were taken to be 4 carbon atoms per photon and 133 µmol·m^{-2}·s^{-1} respectively. The diffuse attenuation coefficients for PAR were calculated as a running mean over 10–15 depth readings, obtained by regressing vertical profiles of log-transformed PAR values against depth. Photosynthetic rates in units of µmolC·m^{-3}·s^{-1} were converted to mgC·m^{-3}·h^{-1}.

P v. *E* determinations were carried out in a photosynthetron (Lewis and Smith 1983). Samples were inoculated with ^{14}C-bicarbonate to yield a final activity of about 1.0 µCi·mℓ$^{-1}$. Aliquots of 1 mℓ were dispensed into 39 glass scintillation vials (20 mℓ) in a temperature-controlled water bath. Irradiances from 0 to 2 600 µmol·m^{-2}·s^{-1} were provided by a tungsten-halogen lamp. Incubations were terminated after 20 minutes. Samples were counted in a Beckman LS1800 scintillation counter, after the addition of Hionic fluor. Biomass-normalized productivities (P^*) over the range of irradiances (E) were used to calculate photosynthetic parameters according to the photosynthesis-irradiance model of Platt *et al*. (1980):

$$P^*(E) = P^*_m\,[1-\exp(-\alpha^* E/P^*_m)]\,\exp(-\beta^* E/P^*_m) \qquad (1)$$

where P^*_m (mgC·mgChl^{-1}·h^{-1}) is the light-saturated rate of photosynthesis normalized to chlorophyll, α^* (mgC·mgChl^{-1}·h^{-1}·[µmol m^{-2}·s^{-1}]$^{-1}$) is the initial slope of the P v. E curve and β^* (mgC·mgChl^{-1}·h^{-1}·[µmol m^{-2}·s^{-1}]$^{-1}$) is the parameter characterizing photoinhibition at high light intensities. Curve fitting was carried out using a nonlinear estimation routine (STATSOFT 1992). The light saturation index (E_k) was calculated from P^*_m/α^* (Platt *et al*. 1980).

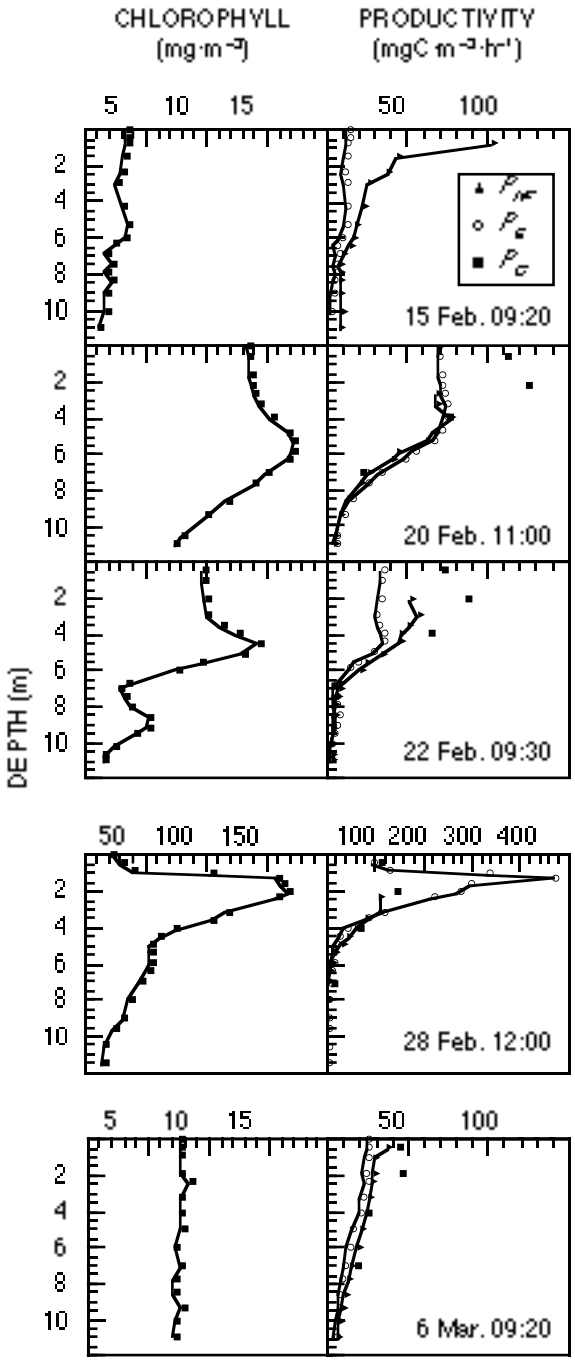

Fig. 3: Profiles of chlorophyll, P_{NF} and P_E productivity and P_C productivity at discrete depths. P_E productivity was based on measured *P* v. *E* parameters and *in situ* PAR and chlorophyll. There is no P_C productivity data for 15 February 1996

RESULTS

Validation of natural fluorescence measurements of productivity

Figure 2 shows the comparison between natural fluorescence-derived primary productivity (P_{NF}) estimates with those calculated from the standard ^{14}C bottle incubations (P_C) and with those derived from *P* v. *E* relationships (P_E). P_{NF} values from profiles at the beginning of the *in situ* ^{14}C incubation period were compared with P_C rates measured at discrete sampling depths. *P* v. *E* relationships established at 0.5 and 7 m were also used to verify P_{NF} estimates. P_E productivity was calculated from measured *P* v. *E* parameters and *in situ* PAR and chlorophyll measurements using the photosynthesis-irradiance model of Platt *et al*. (1980). P_{NF} measurements slightly underestimated P_C measurements and overestimated P_E measurements at high values. One set of *P* v. *E* determinations was done during a red tide event, when chlorophyll concentrations and productivities were high. By excluding the red tide value from the regression, the slope decreased from 0.954 to 0.911 and the r^2 was reduced from 0.91 to 0.83. It should be noted that the regressions were forced through the origin.

Vertical profiles of chlorophyll, of P_E and P_{NF} productivity and discrete ^{14}C measurements of productivity are shown for the five occasions when *P* v. *E* parameters were measured (Fig. 3). For P_E profiles, parameters measured at the surface were assumed constant throughout the upper mixed layer and those measured at 7 m were applied to the remainder of the water column. P_E productivity was lower than P_{NF} and P_C estimates in the upper few metres, except on 28 February during a red tide (Fig. 3). There was close correspondence between the three measures of productivity below the upper few metres. The shape of the chlorophyll profiles below 6 m had little influence on the productivity profile, which was most likely determined by decreasing irradiance.

Inshore monitoring station

DAILY HYDROGRAPHIC AND BIOLOGICAL CHANGES

Daily surface temperature and mean chlorophyll and P_{NF} productivity in the water column are presented for the period 14 February–8 March 1996 (Fig. 4). On several occasions, cold water of 11–12°C was advected into the study area. These upwelling periods varied in duration from 1 to 3 days and were followed by incursions of warmer water. The cold water

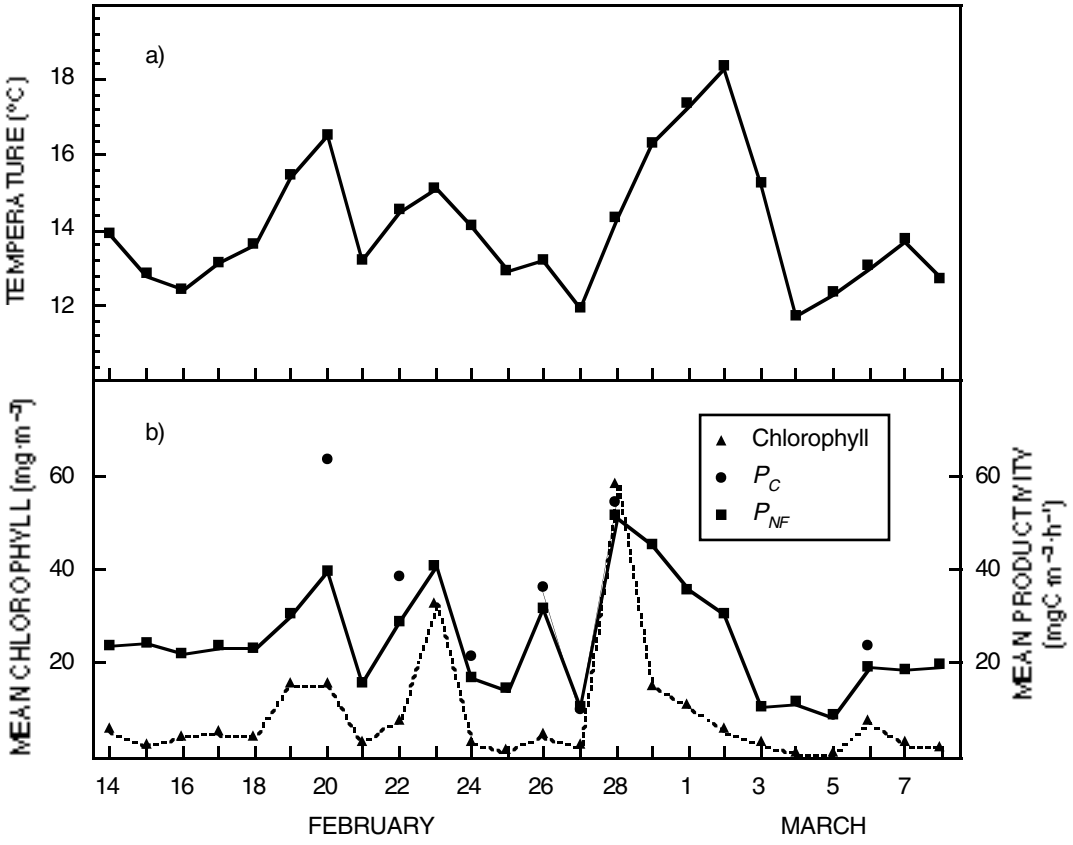

Fig. 4: Daily changes in (a) SST and (b) mean chlorophyll and mean P_C and P_{NF} productivity within the water column (12 m) at the Lambert's Bay monitoring station from 14 February to 8 March 1996

was low in chlorophyll but high in nutrients, whereas the warm water was high in chlorophyll, with concentrations >75 mg·m^{-3} on two occasions. Mean chlorophyll in the water column varied from 0.7 to 57.8 (mean = 8.9) mg·m^{-3} (Fig. 4b); the highest values were associated with red tide events on 23 and 28 February. Mean water-column P_{NF} productivity mirrored the variability in chlorophyll, ranging from 8.4 to 51.0 (mean = 24.6) mgC·m^{-3}·h^{-1}. Peak productivities were associated with the red tide events (Fig. 4b), in which P_{NF} values exceeded 180 mgC·m^{-3}·h^{-1} in near-surface waters. P_{NF}* (mean productivity / mean chlorophyll) values for the water column ranged from 0.9 to 14.1 (mean = 5.5) mgC·mgChl^{-1}·h^{-1}, low values coinciding with chlorophyll peaks and high values with low chlorophyll concentrations.

Mean water-column P_C values ranged from 9.6 to 62.7 mgC·m^{-3}·h^{-1} and closely matched P_{NF} productivity, except on 20 February (Fig. 4b). A water-column P_C productivity of 6.6 gC·m^{-2}·day^{-1} was measured over 24 h on 28/29 February during a red tide. Productivity of the <10 µm size fraction, measured at 0.5 and 4 m, ranged from 1.2 to 34.0 mgC·m^{-3}·h^{-1} and accounted for 4.8-32.7% of total P_C. Productivity of the <10 µm fraction was highest in warm water and lowest in cool water, when diatoms were dominant.

INTENSIVE STUDIES

Profiles taken three-hourly during the day at the monitoring station on 20 February illustrate changes in chlorophyll concentration, P_{NF} productivity and PAR within the water column (Fig. 5). Chlorophyll was initially highest near the surface, then became concentrated in a subsurface layer by mid-morning (Fig. 5a). Irradiance and P_{NF} productivity increased steadily from sunrise, attaining maximum values between 11:00 and 16:00 (Fig. 5b, c). The greatest variation in productivity was within the upper 4 m of the water column. Integrated water-column P_{NF} pro-

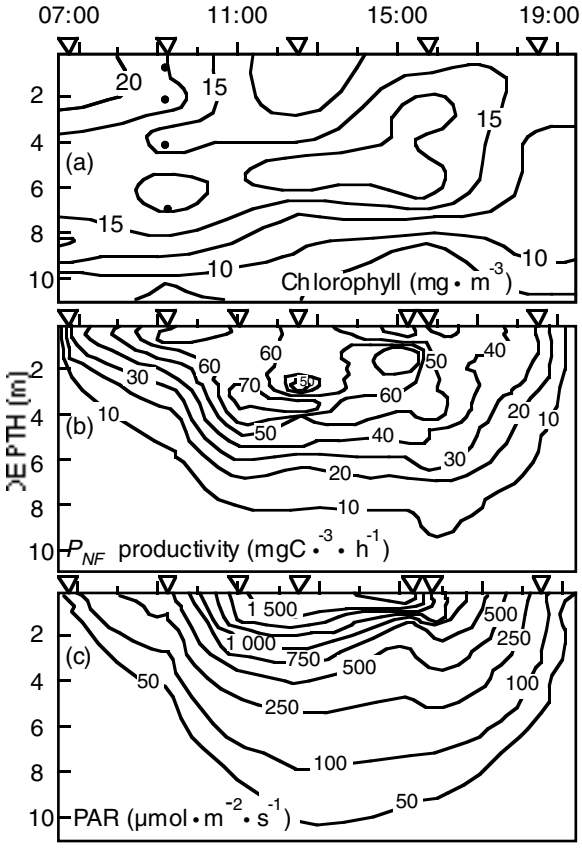

Fig. 5: Changes in (a) chlorophyll, (b) P_{NF} productivity and (c) PAR at the monitoring station on 20 February 1996. Sampling times and depths are indicated

ductivity increased from early morning, remained relatively constant (ranging from 364 to 434 mgC·m^{-2}·h^{-1}) between 11:00 and 16:00 and declined thereafter. The mean P_{NF} productivity of 390 mgC·m^{-2}·h^{-1} over the incubation period was lower than the P_C productivity of 690 mgC·m^{-2}·h^{-1}. This can be ascribed in part to lower *in situ* biomass near the surface over the incubation period from 11:00 to 16:00 than that encapsulated within the incubation bottles earlier at 09:15 (Fig. 5a).

A daily water column P_{NF} productivity under clear condition can be roughly estimated by assuming that water column productivity is relatively constant over the 4-h midday period and increases and declines steadily before and after that time respectively, viz:

$$\text{Daily productivity (mgC·m}^{-2}\text{·day}^{-1}) = (P_{NF} \times 4) + (P_{NF} \times [\text{daylight hours} - 4])/2 \quad ,$$

where P_{NF} is the mean integral productivity between 11:00 and 16:00.

Using this formula, a value of 3.3 gC·m^{-2}·day^{-1} is computed for 20 February. A similar value of 3.5 gC·m^{-2}·day^{-1} is obtained for that day by integrating P_{NF} productivity within the water column between sunrise (06:30) and sunset (19:30 – Fig. 5b).

P v. *E* determinations at three-hourly intervals throughout the day on 20 February, when diatoms were dominant, and on 28/29 February during a red tide event, demonstrated a diurnal response to increasing irradiance (Fig. 6). P^*_m values were lowest early in the morning, increased to a maximum at midday or early afternoon and declined thereafter (Fig. 7a). Diurnal variation in α^* and E_k differed between the two studies (Fig. 7b, c). When dinoflagellates were dominant, α^* increased over the midday period, whereas E_k, an index of photoadaptation, declined. Conversely, in diatom-dominated populations, α^* declined and E_k increased during that period. Photo-inhibition was most pronounced in the early morning and evening populations. In surface samples, the photosynthetic parameters (P^*_m, α^* and E_k) were higher in diatom-dominated than in dinoflagellate-dominated populations (Table I). The mean values of these parameters from surface samples were higher than those at 7 m depth. When photosynthetic parameters from the 09:00 station were plotted against the ratio of dinoflagellate:diatom cell counts, the only trend was a decline in the index of light saturation (E_k) with increasing dinoflagellate dominance (Fig. 7f).

OFFSHORE TRANSECTS

Two transects were chosen to show contrasting hydrographic conditions under different wind conditions and subsequent changes in chlorophyll and productivity over the shelf (Fig. 8). The transect on 16 February 1996 was sampled after several days of moderate upwelling winds, whereas the transect on 22 April 1998 was sampled soon after relaxation of upwelling winds. There was a pronounced thermocline over the shelf on both occasions. On 16 February 1996, the thermocline deepened from 10 m inshore to 20 m offshore and surface temperature increased from cool (12.4°C), upwelled water inshore to warmer (15.5°C) water offshore (Fig. 8a). On 22 April 1998, the thermocline depth was between 11 and 12 m along the entire transect, with higher surface temperature inshore than offshore (Fig. 8d).

The chlorophyll distribution on 16 February 1996 changed from a broad, near-surface maximum within the frontal zone to a narrow subsurface maximum layer in the vicinity of the pycnocline in stratified waters farther offshore. The frontal bloom was dominated by *Ceratium furca*, in 13–14°C water. Chloro-

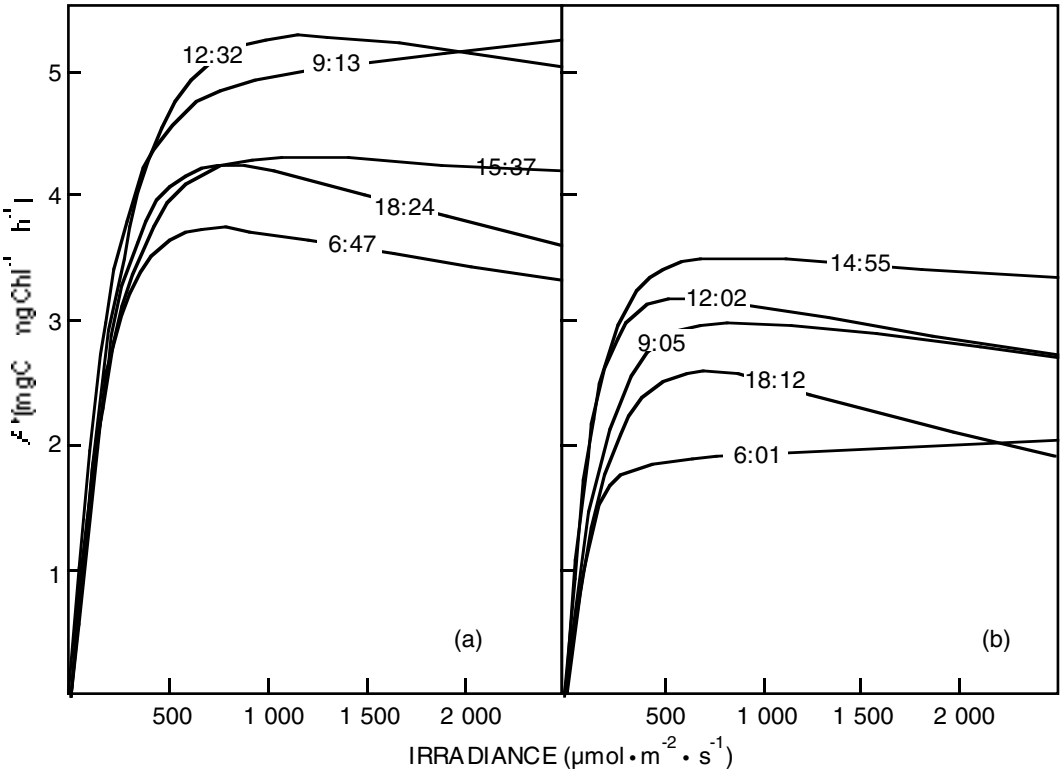

Fig. 6: *P* v. *E* studies on (a) 20 February 1996, when diatoms were dominant, and (b) 28/29 February 1996, when dinoflagellates were dominant

phyll concentrations ranged from 20 to 40 mg·m^{-3} and P_{NF} productivity exceeded 50 mgC·m^{-3}·h^{-1} (Fig. 8b, c). Offshore, the subsurface chlorophyll maximum of 15–45 mg·m^{-3} ranged between 15 and 23 m depth. At Station 11, the light level at the productivity peak (20 mgC·m^{-3}·h^{-1}) at 17 m was 45 µmol·m^{-2}·s^{-1}; the productivity peak was about 5 m above the chlorophyll peak. At other offshore stations where the subsurface chlorophyll maximum was deeper, light levels were <10 µmol·m^{-2}·s^{-1}, and no corresponding productivity maximum was apparent.

There was a pronounced red tide inshore on 22 April 1998. Chlorophyll concentrations exceeded 40 mg·m^{-3} and P_{NF} productivity was 90 mgC·m^{-3}·h^{-1} in near-surface water at Station 2, in the core of the red tide. Farther offshore, the chlorophyll maximum layer was 5–11 m deep. P_{NF} productivity (40–60 mgC·m^{-3}·h^{-1}) was more than double that measured in the deeper subsurface layer on 16 February 1996 (Fig 8c, f). Light levels were higher, ranging from 140 to 365 µmol·m^{-2}·s^{-1} at the productivity maximum and from 50 to 120 µmol·m^{-2}·s^{-1} at the deeper chlorophyll maximum.

The present results and those from other transects showed that the distribution of chlorophyll and productivity varied spatially, depending on the wind conditions prior to sampling. For example, on 4 March 1997, following onshore winds, an intense red tide developed inshore, where near-surface P_{NF} productivity exceeded 500 mgC·m^{-3}·h^{-1} and chlorophyll concentrations were between 100 and 180 mg·m^{-3} at its core (Stations 2 and 3). However, after active upwelling, the offshore extent of the frontal bloom varied, depending on the displacement of the front offshore. Beyond the upwelling front, in stratified shelf water, temporal and spatial variability in chlorophyll and productivity was reduced.

DISCUSSION

Validation of natural fluorescence productivity

The close relationship (r^2 = 0.83) found between

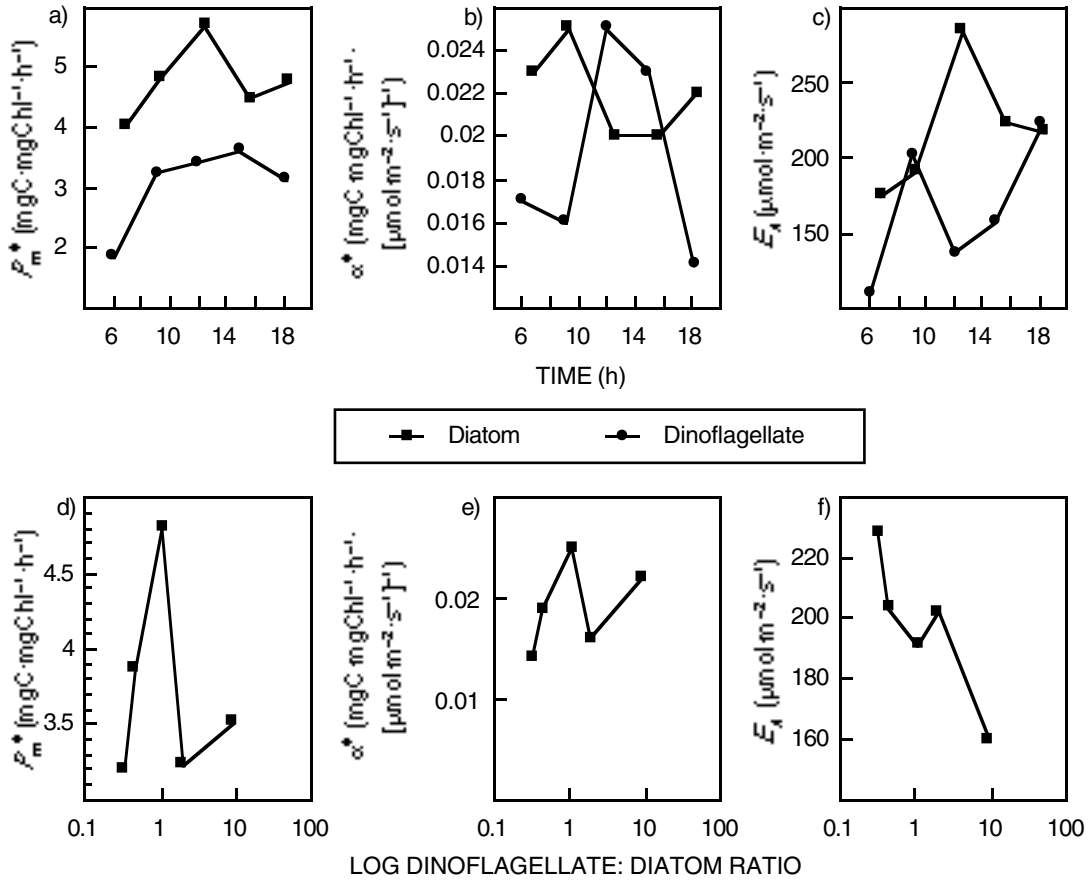

Fig. 7: Diurnal changes in photosynthetic parameters (a) P^*_m, (b) α^* and (c) E_k in diatom- and dinoflagellate-dominated assemblages, and (d, e, f) changes in the same parameters in morning populations with increasing dinoflagellate dominance

P_{NF} productivity and P_C and P_E productivities in the southern Benguela (Fig. 2) has been obtained elsewhere from a wide variety of environments (Garcia-Mendoza and Maske 1996). Part of the variance between the three sets of measurements can be related to changes in *in situ* biomass and ambient light when sampling took place, as illustrated by the 20 February study (Fig. 5). The P_{NF} profiles taken at the start of the incubation period at 11:00 neither reflected the biomass at the time of sample collection (09:00) nor the light regime over the midday incubation period. The profiles gave an instantaneous measurement of gross productivity, whereas ^{14}C productivity provided a time-integrated response to ambient irradiance changes, including photoinhibition in surface incubation bottles, coupled with respiratory carbon losses during the incubation period (Kiefer and Reynolds 1992). Nevertheless, there was a close correspondence between the three sets of productivity measurements below about 4 m depth (Fig. 3).

Repeated sampling during the day suggest that water-column productivity remains relatively constant between 11:00 and 16:00 on clear days (Fig. 5b). As light intensities increase after 11:00 to beyond saturation level in near-surface water, there is little corresponding increase in photosynthetic rate of *in situ* phytoplankton, and photoinhibition may even occur. As observed in the *P* v. *E* studies, and confirmed by similar studies (e.g. Cullen *et al*. 1992), P^*_m increases from morning to early afternoon as photoadaptation to increasing ambient irradiance occurs (Table I). There is also a corresponding increase in irradiance at the onset of saturation of photosynthetic activity (Figs 6, 7c). In the current study, saturation intensities were

Table I: Summary of photosynthetic parameters from all *P* v. *E* studies at the Lambert's Bay monitoring station

Date	Time	Depth	Photosynthetic parameters			
			P^*_m (mgC·Chl^{-1}·h^{-1})	α* (mgC·Chl^{-1}·h^{-1}·[µmol·m^{-2}·s^{-1}]$^{-1}$)	β*	E_k (µmol·m^{-2}·s^{-1})
15 Feb. 1996	9:20	Surface	3.86	0.019	0.00004	203
		7 m	4.05	0.020	0.00024	203
20 Feb. 1996	6:45	Surface	4.02	0.023	0.00032	175
	9:15	Surface	4.80	0.025	−0.00016	192
	12:30	Surface	5.69	0.020	0.00029	285
	15:35	Surface	4.47	0.020	0.00011	224
	18:25	Surface	4.77	0.022	0.00056	217
Mean			4.75	0.022	0.00022	218
22 Feb. 1996	9:34	Surface	3.20	0.014	−0.00011	229
		7 m	3.60	0.016	0.00085	225
28–29 Feb. 1996	12:00	Surface	3.42	0.025	0.00033	137
	14:55	Surface	3.61	0.023	0.00012	157
	18:10	Surface	3.12	0.014	0.00064	223
	6:00	Surface	1.86	0.017	−0.00005	109
	9:05	Surface	3.23	0.016	0.00024	202
Mean			3.05	0.019	0.00026	166
28–29 Feb. 1996	12:00	7 m	2.97	0.018	0.00017	165
	14:55	7 m	4.21	0.025	0.00008	168
	18:10	7 m	1.94	0.019	0.00005	102
	6:00	7 m	2.20	0.016	−0.00001	138
	9:05	7 m	2.92	0.017	0.00008	172
Mean			2.85	0.019	0.00007	149
6 Mar 1996	9:50	Surface	3.51	0.022	0.00030	160
		7 m	3.36	0.017	0.00035	198

<1 000 µmol·m^{-2}·s^{-1} in diatom-dominated communities and <750 µmol·m^{-2}·s^{-1} in dinoflagellate communities (Fig. 6). This is about 50% or less of summer sunlight in the study area. Therefore, for several hours over the midday period, ambient irradiances exceed saturating irradiances. The relative constancy of water-column productivity over the midday period permits a rough calculation of daily productivity based on the mean water-column productivity over the midday period and daylength in hours.

Cross-shelf changes in chlorophyll and productivity

Large-scale oceanographic processes as well as local physical forcing influence the hydrographic conditions on the West Coast. Cold bottom water of 10–11°C blankets over the broad continental shelf during summer and autumn (Probyn *et al*. 2000), sometimes raising the thermocline to within 10–15 m of the surface, as observed on 22 April 1998. In response to local wind forcing, cold bottom water upwells to the surface inshore and forms a narrow belt of coastal upwelling between broader upwelling centres at Cape Columbine and Hondeklip Bay on the West Coast (Fig. 1).

Inshore, hydrographic and biological characteristics within the water column can change within hours of wind forcing events (Pitcher *et al*. 1998). This is shown for Station 2, which exhibited large temporal variability in thermal and biological characteristics (Fig. 4). Conservative estimates of integral P_{NF} productivity ranged from 0.8 gC·m^{-2}·day^{-1} for newly upwelled water to 12.3 gC·m^{-2}·day^{-1} for a red tide event. Apart from changes in biomass, different phytoplankton life-forms are also associated with changes in water temperature. Diatoms tended to predominate in cool (<13°C), nutrient-rich upwelled water, dinoflagellates in water of 13–15°C and micro-flagellates in warmer (>16°C) water (Pitcher *et al*. 1998). *C. furca* dominated the dinoflagellate blooms, except in 1998 when *C. dens* co-dominated. During quiescent periods, physical factors in combination with the swimming behaviour of dinoflagellates concentrated dinoflagellate populations inshore, forming red tides (Pitcher *et al*.

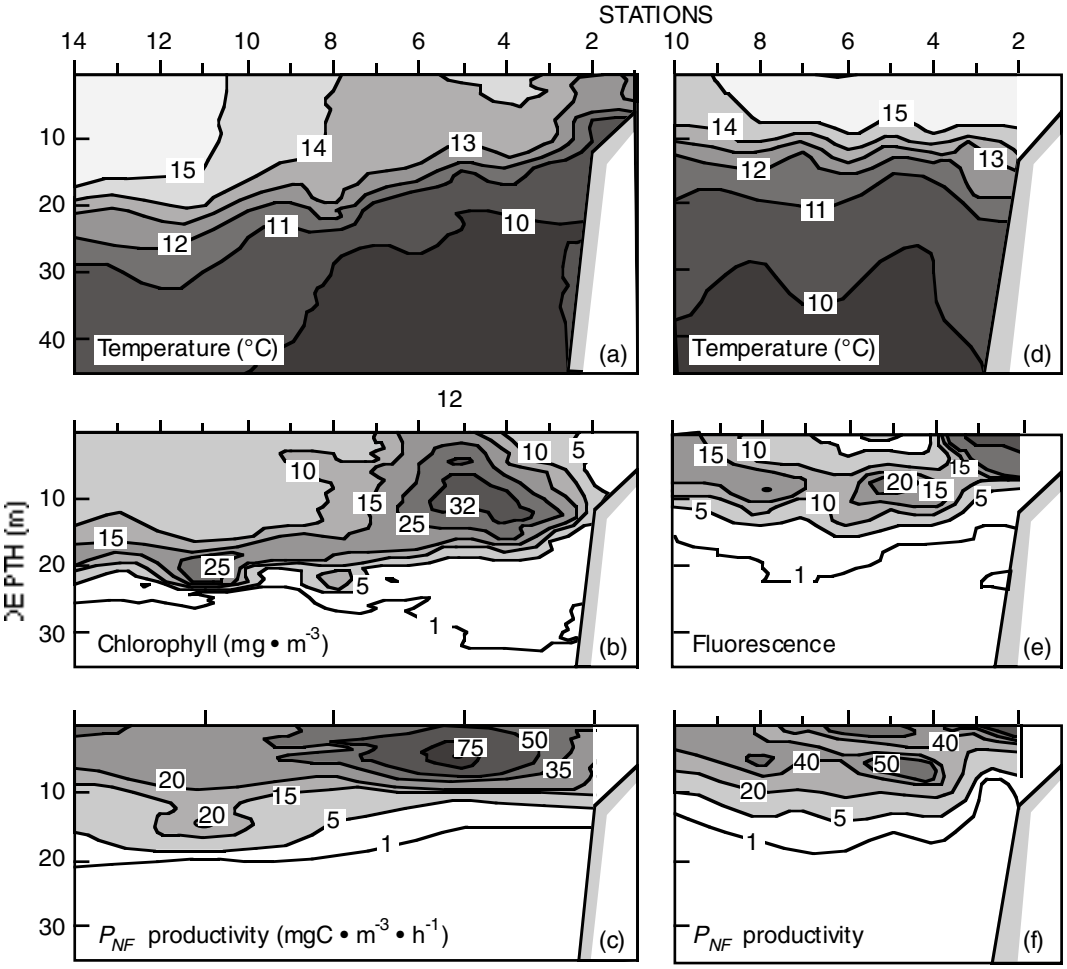

Fig. 8: Vertical sections of (a and d) temperature, (b and e) chlorophyll and (c and f) P_{NF} productivity along the Lambert's Bay transect on 16 February 1996 and 22 April 1998 respectively

1998, Probyn *et al*. 2000). Chlorophyll concentrations >175 mg·m^{-3} and P_{NF} productivities >500 mgC·m^{-3}·h^{-1} were measured in the core of a nearshore bloom on 4 March 1997. Similar chlorophyll concentrations and productivity values have been reported for other dinoflagellate red tides in South African coastal waters and elsewhere. Brown *et al*. (1979) measured a net productivity of 405 mgC·m^{-3}·h^{-1} for a *Gymnodinium* bloom in False Bay on the Cape south coast; the daily surface productivity was 3.74 gC·m^{-3}·day^{-1}. In a *C. furca* bloom in St Helena Bay (Fig. 1), Walker and Pitcher (1991) measured a productivity of 520 mgC·m^{-3}·h^{-1} and a chlorophyll concentration of 139 mg·m^{-3} at the surface; the daily integral productivity was 22.8 mgC·m^{-2}·day^{-1}. A chlorophyll concentration of 280 mg·m^{-3} was reported by Blasco (1979) for a *Gymnodinium splendens* bloom off the coast of Peru. Off Baja California, a daily integral productivity of 25 gC·m^{-2}·day^{-1} was reported for a nearshore dinoflagellate bloom of *Lingulodinium* (*Gonyaulax*) *polyedra* (Walsh *et al*. 1974). In the present study, a P_C productivity of 6.6 gC·m^{-2}·day^{-1} was measured for a red tide dominated by *C. furca*. Conservative estimates of daily water-column P_{NF} productivity of red tides at Station 2 on 28 February 1996 and at Station 3 on 4 March 1997 were 9.4 and 12.3 gC·m^{-2}·day^{-1} respectively.

The nearshore zone is subject to alternating off-

shore movement of cold upwelled water in response to wind forcing and the subsequent onshore movement of warmer, maturing upwelled water during relaxation phases (Pitcher *et al*. 1998). Chlorophyll concentrations sometimes exceeded 50 $mg \cdot m^{-3}$ in frontal blooms, in populations dominated by dinoflagellates, particularly *C. furca* (Pitcher *et al*. 1998). Conservative estimates of water-column P_{NF} productivity within frontal blooms ranged from 4.0 to 5.6 $gC \cdot m^{-2} \cdot day^{-1}$. Farther offshore, beyond the upwelling front, a narrow and well-defined subsurface chlorophyll maximum layer (dominated by dinoflagellates) within the pycnocline region is typical of the midshelf in late summer (Pitcher *et al*. 1998). In the current study, chlorophyll maxima ranged between 15 and 45 $mg \cdot m^{-3}$, with P_{NF} productivities of 20–50 $mgC \cdot m^{-3} \cdot h^{-1}$, depending on the depth of the subsurface layer. As the chlorophyll maximum layer deepened, there was no corresponding subsurface production maximum, despite high chlorophyll concentrations. Conservative estimates of water-column P_{NF} productivity ranged from 2.4 to 4.0 $gC \cdot m^{-2} \cdot day^{-1}$ for offshore waters.

Late summer dominance of dinoflagellate populations

In late summer and autumn, subsurface dinoflagellate populations are widespread in stratified midshelf waters on the West Coast (Pitcher and Boyd 1996, Pitcher *et al*. 1998). Under these low energy, stratified conditions, dinoflagellates are able to position themselves within the water column with respect to the light and nutrient environment, whether by tactic (Blasco 1978, Pitcher *et al*. 1998, Smayda 1997, 2000) or by metabolic-directed swimming behaviour (Kamykowski and Yamazaki 1997). Their motility enables them to exploit nutrient and light gradients within the pycnocline or even the upper mixed layer, affording them a competitive advantage in such an environment (Smayda 2000). The present *P* v. *E* studies show a marked decline in the light saturation index with increasing dinoflagellate dominance (Fig. 6f). This is consistent with the finding by Richardson *et al*. (1983) that dinoflagellates have lower saturation irradiances than diatoms. Dinoflagellates tend to grow well at low irradiances (<50 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and typically have compensation points of <10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Richardson *et al*. 1983). Assimilation values (P_{NF}*) of 3.0–4.5 $mgC \cdot mgChl^{-1} \cdot h^{-1}$ measured in shallow subsurface layers on 22 April 1998 (Fig. 8e) suggest good growth. In deeper subsurface maxima at the base of the euphotic zone on 16 February 1996 (Fig. 8b), assimilation values of < 0.2 $mgC \cdot mgChl^{-1} \cdot h^{-1}$ imply poor growth. However, subsurface populations periodically undergo vertical displacements by internal waves that are well developed in this region in autumn (Probyn *et al*. 2000), which increase both the average light intensity experienced by phytoplankton and their critical depth (Lande and Yentsch 1988). This enhancement of productivity is most pronounced in water with moderate to high attenuation coefficients of PAR, and the increase in productivity in the lower euphotic zone can be substantial (Lande and Yentsch 1988). An additional factor that increases productivity in subsurface layers is the movement of cold water onto the shelf in response to oceanic forcing (Probyn *et al*. 2000), which raises the thermocline closer to the surface. The present study demonstrates that the depth of the subsurface chlorophyll maximum layer had a pronounced effect on productivity within that layer (Fig. 8a, f).

Dinoflagellates have developed various strategies and behavioural patterns (Pitcher *et al*. 1998, Kamykowski and Yamazaki 1997, Smayda 1997, 2000), which enable them to take advantage of both coastal upwelling and the stratified conditions that are typically found over the shelf in late summer and autumn on the West Coast. In the coastal upwelling regions, they bloom within the upwelling front, periodically forming red tides inshore; daily P_{NF} productivities within these high-biomass dinoflagellate blooms exceeded 12 $gC \cdot m^{-2} \cdot day^{-1}$. Over the midshelf, dinoflagellates dominate subsurface populations, contributing to daily P_{NF} productivities of 2–4 $gC \cdot m^{-2} \cdot day^{-1}$. Collectively, they make a major contribution to a relatively stable, highly productive shelf environment on the West Coast, which rivals that in diatom-dominated upwelling plumes (Pitcher *et al*. 1992).

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