PHYTOPLANKTON PRODUCTION STUDIES IN THE COASTAL WATERS OFF THE CAPE PENINSULA, SOUTH AFRICA

by

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Submitted for the Degree
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- 1980 -

CONTENTS

TABLE OF FIGURES

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ABSTRACT

Procedures for measuring phytoplankton production in the southern Benguela upwelling region were investigated. A 125 mℓ incubation bottle is recommended for routine primary production measurements. Exposure of production samples to high light intensities during manipulations on deck was found to inhibit rates of production near the bottom of the euphotic zone particularly below a thermocline. Simulated *in situ* rates of oxygen production were only slightly higher than *in situ* rates. When ships time is limited, the simulated *in situ* method can safely be used in local waters. Definite diel periodicity in rates of production at the sea surface was demonstrated and appears to be linked to light levels and nutrient concentrations, as well as to the ratios of light to dark hours. Since diel variation probably decreases with depth, its effect on integrated daily production is reduced. Nevertheless, the time of incubation should be chosen to minimize the effect of periodicity on daily production estimates. The period spanning noon is recommended for local use.

Changes in phytoplankton production and biomass are linked with physical and chemical changes in the upwelling system off the Cape Peninsula. Extremely active upwelling was found to limit primary production and from these measurements the annual net primary production in the Cape Peninsula upwelling region is estimated for the first time to be approximately 1.13 $kg^{C}.m^{-3}.y^{-1}$.

CHAPTER 1

INTRODUCTION

In recent years upwelling ecosystems have received the close attention of many marine scientists, probably because the highest primary productivity is found in upwelling areas (Table 1.1). Changes in the intensity and duration of upwelling can be expected to affect the rate of primary production and therefore the supply of food for pelagic fish (Ryther 1969), particularly in the Benguela Current where anchovy and pilchard adults feed primarily on phytoplankton (King and Macleod 1976).

TABLE 1.1 Division of the ocean into provinces according to their level of primary organic production (Ryther 1969).

Province	% Ocean	Area (km^2)	Mean productivity ($gC.m^{-2}.y^{-1}$)	Total productivity (10^9 tons of $C.y^{-1}$)
Open Ocean	90.0	326.0×10^6	50	16.3
Coastal Zone*	9.9	36.0×10^6	100	3.6
Upwelling areas	0.1	3.6×10^5	300	0.1
Total				20.0

* Includes offshore areas of high productivity

The waters off the west coast of the Cape Peninsula contain a number of very active upwelling sites, including the main study site at Oudekraal. These form part of the southern Benguela upwelling system off the west coast of southern Africa (Andrews & Cram 1969, Bang 1973). Upwelling is generated by the strong southerly to south-easterly winds which predominate in summer. Upwelling north of the Cape Peninsula is generally less intense but more consistent than that found at Oudekraal (Andrews and Hutchings 1980).

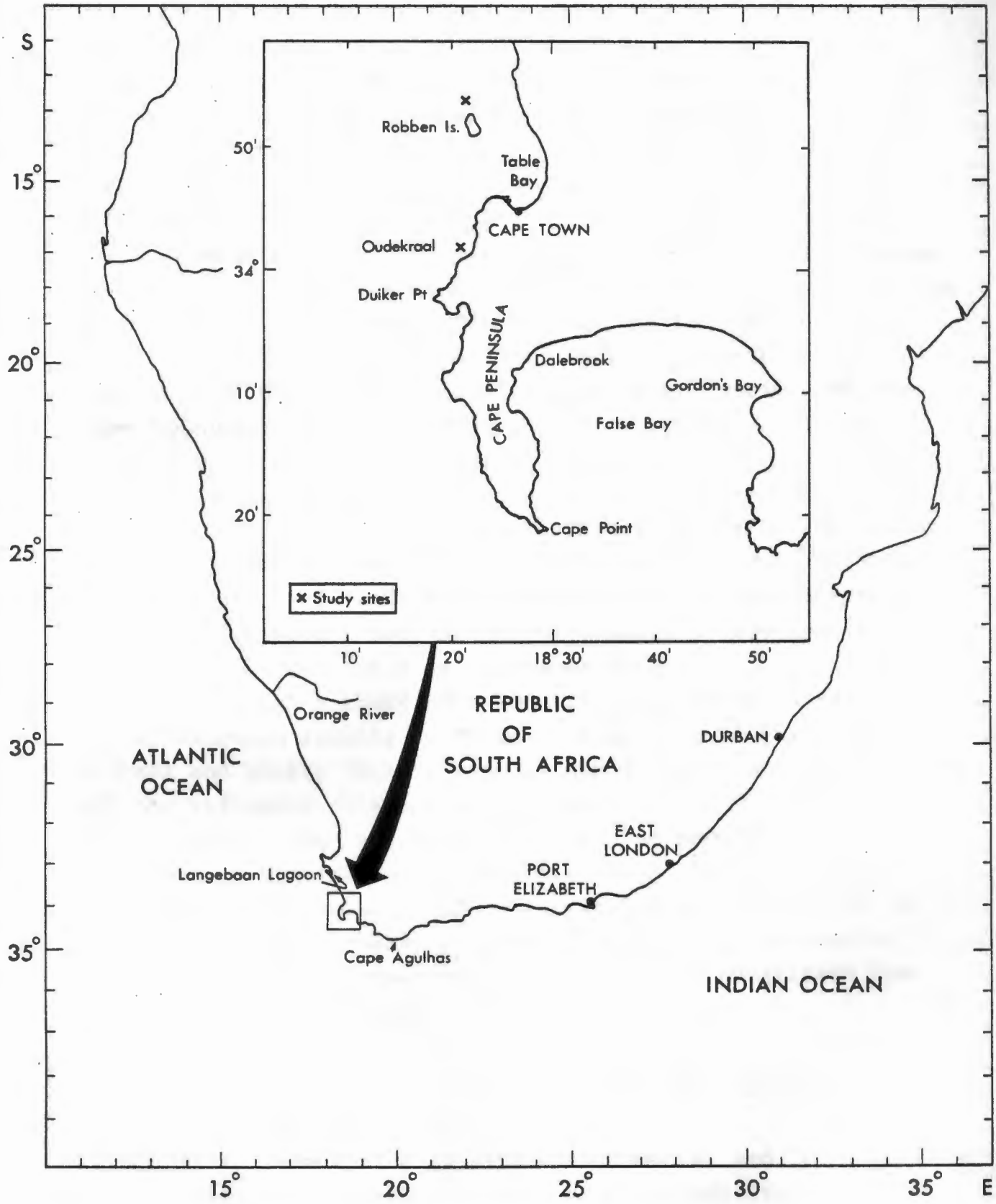

Fig. 1.1 Southern Africa showing the Cape Peninsula with study sites (x) at Oudekraal and Robben Island.

Relatively few phytoplankton production studies have been conducted in the coastal waters of South Africa. On the east coast Mitchell-Innes (1967) and Burchall (1968, 1968a) undertook ^{14}C primary production studies in the continental shelf region near Durban as part of the International Indian Ocean Expedition. On the west coast Henry *et al*. (1977) made *in situ* primary production measurements using the oxygen method, to assess the suitability of the Langebaan Lagoon area for commercial cultivation of the black mussel. Andrews and Hutchings (1980) measured potential gross production off the Cape Peninsula on a monthly basis for two years. In the north-east corner of False Bay, near Gordon's Bay, an attempt was made to assess the productivity of a dinoflagellate bloom (Brown *et al*. 1979), and in the north-west of False Bay, phytoplankton production was measured at Dalebrook during 1977-78 (Cliff 1979). R.A. Carter (unpublished data) and Borchers and Field (in press) measured phytoplankton production in 1978-79 in the kelp beds at Oudekraal (Fig. 1.1).

Several authors have identified problems in interpreting production results. These include differences between methods and biotic factors such as conditioning of phytoplankton and the influence of zooplankton grazing.

This study was aimed primarily at providing suitable procedures for measuring primary production locally, but the data collected have also led to a better understanding of the factors affecting primary production in the Cape Peninsula upwelling system. Experiments were made to investigate the effects on production rates of:

(i) size of incubation bottle;
(ii) temporary exposure to high light prior to *in situ* incubation;
(iii) simulating *in situ* measurements, and
(iv) diel variation or 24 hour periodicity.

CHAPTER 2

METHODS

A general description of the methods used is provided here. Specific procedures will be described for each chapter.

2.1 STUDY AREA

Experiments were conducted between September 1977 and March 1979 at two stations off the west coast of the Cape Peninsula (Fig. 1.1). The first was situated about two kilometres off Oudekraal and the second about two kilometres north of Robben Island.

Strong upwelling is common at Oudekraal particularly in summer. As a result, the state of the water ranges from cold, crystal clear, newly upwelled water with little trace of phytoplankton, to warmer, turbid, aged water with dense plankton blooms. Although strong south-easterly "blows" typically last for four to five days (Andrews and Hutchings 1980), intense upwelling may continue for up to two weeks as long as the south-east wind blows for a few hours each day. The clear, cold water constantly brought to the surface during upwelling moves offshore before it has a chance of being colonized by phytoplankton. Under these conditions phytoplankton production is negligible. An additional site of study was therefore chosen at Robben Island. This is not an active upwelling centre, and thus measurable concentrations of phytoplankton are found more consistently than at Oudekraal.

2.2 LIGHT

The euphotic zone is commonly known as that part of the ocean in which there is enough light for active photosynthesis. In practice it is taken to be the zone from the ocean surface to the depth at which 1% of the surface light penetrates (Steeman Nielsen 1975). The depths from which water samples were taken for primary production measurements were based on percentage light levels (rather than standard depths) to ensure that measurements covered the entire euphotic zone.

Light was measured using a Lamda LI-192S underwater quantum sensor and a LI-190S atmospheric quantum sensor as recommended by the SCOR Working Group 15 (SCOR 1965). The sensors measure radiation in the 400 - 700 nm band which approximates the photosynthetically active radiation (PAR) used by many algae. As photosynthesis is a photochemical reaction, PAR is measured in quanta as $\mu E.m^{-2}.s^{-1}$ (1 μE or microeinstein = $6{,}02 \times 10^{17}$ quanta) in preference to measurements of power such as Joules or Watts.

The depths of the required percentage light levels were estimated using the underwater sensor or, in a few cases, from the Secchi disc depth, D, where the following equation was applied (Poole and Atkins 1929):

$$L = \frac{\ln (I_L/I_o)}{-k}$$

I_L is the required percentage light, I_o is the percentage light at 0 metres (100%), k is the extinction coefficient ($k = 1.7/D$), and L is the required depth.

Incident light was monitored throughout most incubation periods using the atmospheric quantum sensor coupled to a LI-500 Integrator. Readings were taken every hour.

2.3 SAMPLING

Water samples were drawn from the required depths using 5ℓ or 7ℓ National Institute for Oceanography (NIO) bottles; for some surface samples a plastic bucket was used. Subsamples were taken for salinity, nutrient, chlorophyll *a*, and primary production analyses. A bathythermograph (BT) temperature profile was recorded.

NIO bottles were painted black to prevent exposing subsurface samples to bright sunlight as the samples were winched on board. Subsamples for primary production measurements were drawn (in the shade) into 125 mℓ glass reagent bottles and stored in small black bags at sea surface temperatures until the incubation was started.

2.4 PRIMARY PRODUCTION

2.4.1 Oxygen method

For the oxygen method (Gaarder and Gran 1927), six bottles, two initial (I), two light (L), and two dark (D), were filled with water taken from the appropriate depth. The oxygen in the initial bottles was fixed immediately. The light and dark bottles were incubated at the required light levels. The incubation period was usually four hours but ranged from three to six hours depending on the time taken for samples to become saturated as seen by the formation of bubbles. At the end of the incubation period, the oxygen in the production bottles was fixed and the samples stored underwater in the dark until the oxygen content was measured by the Winkler titration method. Two 50 (or 25) mℓ aliquots from each bottle were titrated using a Radiometer Autoburette (Model ABU-12) and the average value used to calculate the oxygen concentration in each bottle.

The range of production values was estimated using individual replicates.

Respiration (R) and net (NP) and gross (GP) production in terms of mℓ O_2/ℓ per incubation period were calculated as follows:

$$R = I - D$$
$$NP = L - I$$
$$GP = L - D$$

where I, D and L represent the oxygen concentrations in the initial, dark and light bottles respectively.

The oxygen evolved during photosynthesis was converted to carbon assimilated by assuming that 1 mℓ oxygen evolved was equivalent to 0.536 g carbon assimilated, and by using a photosynthetic quotient (PQ) of 1.2. The oxygen used during respiration was converted, in the same way, to carbon lost, except that a respiratory quotient of 1.0 was used (Strickland 1960), i.e.

Carbon assimilated by photosynthesis in mg per unit time = $m\ell$ O_2 evolved in unit time x $\frac{0.536}{PQ}$

and

Carbon lost by respiration in mg per unit time = $m\ell$ O_2 consumed in unit time x 0.536 x RQ.

2.4.2 ^{14}C method

For the ^{14}C method (modified from Strickland and Parsons 1972) two light bottles and one dark bottle were used. An ampoule of 5 μCi of $NaH^{14}CO_3$ was added to each sample. After a four (or occasionally two to three) hour incubation period, photosynthesis was arrested by placing the samples in the dark and filtering them immediately to remove the phytoplankton using cellulose nitrate filters (pore size 0.45 μm) at a vacuum of approximately 0.3 bar. The filters were fumed with concentrated HCl for one hour to remove inorganic ^{14}C. A Packard PL Liquid Scintillation Counter was used to measure the activity of the samples. The ^{14}C taken up in the dark bottle was subtracted from the mean uptake in the two light bottles to give net photosynthetic uptake of ^{14}C.

2.4.3 Incubation period

Variation in incubation period (two and a half to six hours), when using the oxygen method, was assumed to be of little consequence because McAllister *et al*. (1964) found that production rates measured by oxygen evolution remained constant for many hours. In contrast, they found that the rate of ^{14}C uptake with time was not constant. For cultures of *Dunaliella* and *Skeletonema* the mean rate of uptake decreased for about the first three to five hours and then increased to a fairly steady value. Variations increased at low light intensities and high nutrient concentrations. However, Savidge (1978) showed that the rate of ^{14}C uptake in some cases decreased after two hours, suggesting that the optimum incubation period should not be greater than two hours. Thus the ^{14}C incubation periods

in this study (two to four hours) might underestimate the production rate.

2.4.4 Methods of incubation

Water samples were incubated using one of three methods depending on the experiment in question.

(i) In situ incubation

Samples were suspended in the sea at the depths from which they were taken.

(ii) Simulated in situ incubation

Samples were incubated either on deck in a perspex box through which surface water was allowed to flow, or in holders suspended at the sea surface. The intensity of light at the depths from which samples were drawn (100%, 50%, 25%, 10% and 1%) was simulated by using light bottles coated with a spectrally neutral mixture of clear varnish and black polyeurethane paint. The required percentage transmission of light was attained by altering the proportions of paint and varnish in the mixture.

(iii) Constant light incubator

Samples were placed in an incubator through which surface water was pumped to maintain in situ temperatures. The incubating samples were rotated on a vertical wheel (to ensure a uniform light field) with a 400 Watt Mercury halide lamp providing a mean PAR level equivalent to that at about 07h00 in summer ($\sim$190 $\mu E.m^{-2}.s^{-1}$).

2.5 CHEMICAL ANALYSES

Salinity samples were stored at room temperature and analysed later in the laboratory using an inductively coupled salinometer.

Water samples for nutrient analysis were stored at -20^{o} until analysed on a Technicon Autoanalyser according to the methods of Grasshoff (1965) for silicate, and Armstrong et al. (1967) and Strickland and Parsons (1972) for phosphate

and nitrate (including nitrite).

One litre of water was filtered at a vacuum of approximately 0.3 bar for chlorophyll a determinations. When chlorophyll a levels were low, two litres of water were used. The water samples were filtered through Millipore membrane filters (0.45 um pore size) or GF-C filters coated with $MgCO_3$ both to increase the filtering capacity of the GF-C filter and to prevent acidification of the chlorophyll. The filters were stored in the dark at $-20^{\circ}C$ until they were analysed about one week later, according to the SCOR-UNESCO method (Strickland & Parsons 1972).

CHAPTER 3

THE EFFECT OF BOTTLE SIZE ON PRIMARY PRODUCTION MEASUREMENTS

3.1 INTRODUCTION

In the open ocean a dynamic equilibrium is maintained between phytoplankton production and zooplankton grazing. If the grazing effect is removed primary production can be measured by isolating a volume of water and subjecting it to conditions similar to those from where it was taken (e.g. light, temperature, agitation, etc.) (Sheldon *et al.* 1973). Although such a state of dynamic equilibrium is seldom found in the highly productive but unstable upwelling area off the Cape Peninsula, the grazing effect of zooplankton should ideally be removed for primary production measurements.

Sutcliffe *et al.* (1970) used a screen to remove particles greater than 200 µm, assuming these to be zooplankters but found that sometimes the phytoplankton that passed through the screen grew and other times it did not. Evidently phytoplankton cells and chains could be damaged or even retained by the mesh and, moreover, small zooplankters could pass through it.

Sheldon *et al.* (1973) suggested that instead of screening, one should isolate a small volume of water because the probability of including a zooplankter in a small sample is less than if one used a large volume of water. They found that the rate of particle production increased rapidly with a decrease in the size of the incubation bottle and attributed this to the elimination of grazers rather than to increased bacterial production, because growth took place at a relatively large particle size. The size of the bottle might therefore depend on zooplankton density. Bottles used by different institutes vary from 25 to 300 mℓ in volume.

The present study is aimed at measuring the effect of bottle size on primary production measurements in the coastal waters of the Cape Peninsula.

TABLE 3.2 Zooplankton species, numbers and densities in surface waters.

Experiment	Species	Number	Total	Volume filtered (litre)	Animals per litre
3	Centropages brachiatus	2	2	500	0.0
4	Oithona sp	9			
	Paracalanus parvus	4			
	P.crassirostris	1	14	200	0.1
	(Copepod nauplii)	(20)			
5	C.brachiatus	94			
	Oithona sp	5			
	P.crassirostris	1	100	200	0.5
	(Copepod nauplii)	(20)			
8	Oithona sp	271			
	P.parvus	3			
	Oncaea sp.	1			
	Calanid juvenile	5	280	200	1.4
	(Copepod nauplii)	(809)			
9	C.brachiatus	135			
	Oithona sp	132			
	P.parvus	30			
	Oncaea sp	9			
	Ctenocalanus sp	4			
	Clausocalanus sp	30			
	Microstella rosea	3			
	Calanid juvenile	153			
	Unrecognizable	167	663	200	3.3
	(Copepod nauplii)	(2660)			
10	No counts				
11	C.brachiatus	31			
	Oithona sp	65			
	P.parvus	19			
	P.crassirostris	1			
	Paracartia africana	1			
	Calanid juvenile	11			
	Unrecognizable	8	136	200	0.7
	(Copepod nauplii)	(451)			
12	C.brachiatus	118			
	Oithona sp	517			
	P.parvus	104			
	P.crassirostris	6			
	Calanoides carinatus	13			
	Clausocalanus sp	1			
	Oncaea sp	1			
	Calanid juvenile	60			
	Unrecognizable	1	821	200	4.1
	(Copepod nauplii)	(1811)			
13	No counts				
19	C.brachiatus	730			
	Oithona sp	195			
	P.parvus	148			
	P.crassirostris	18			
	Clausocalanus sp	9			
	Nannocalanus minor	8			
	Paracartia africana	75			
	Calanid juveniles	27			
	Unrecognizable	72	1282	200	6.4
	(Copepod nauplii)	(43)			

3.2 PROCEDURE

Water drawn from the sea surface using either a plastic bucket or NIO bottle was mixed in a large container. The oxygen method was used to measure primary production. Sub-samples were siphoned into two light and two dark 1000 mℓ, 500 mℓ, 250 mℓ, 125 mℓ and 60 mℓ incubation bottles. An initial bottle was drawn before and after each set of incubation bottles was filled.

The effect of the size of the incubation bottles on gross production was investigated using the non-parametric Wilcoxon signed-ranks test (Dixon, 1977).

Zooplankton densities at the sea surface were established by pumping either 200 or 500 litres of water from just below the surface, using a pump with an inlet diameter of 7.6 cm. The water was cascaded through 200 µm and 37 µm mesh nets. Both fractions were retained for identifying and counting zooplankton.

3.3 RESULTS AND DISCUSSION

In the 19 experiments conducted, phytoplankton biomass ranged from 0 to 20 mg.Chl1 a.m^{-3}. In only ten experiments (Appendix 1) were gross production measurements within the limits of precision of the oxygen method. Of these, no significant differences in gross production were found among the 1000 mℓ, 500 mℓ, 250 mℓ and 125 mℓ incubation bottles (Table 3.1). This agrees with findings published by UNESCO (1973).

However, gross production in the 60 mℓ bottles was significantly lower (prob. < 5%) than in the other bottle sizes. The rate of production did not increase with a decrease in bottle size as was found by Sheldon et al. (1973).

Zooplankton species and numbers are listed in Table 3.2. Most of the species are either herbivorous or omnivorous (Lazarus 1975).

Zooplankton densities at the surface ranged between 0 and 6.4 animals per litre. Large numbers of very small copepod nauplii were retained by the 37 µm mesh net. These were not included in the density estimates. WP-2 net (200 µm mesh) samples collected 5 km off Duiker Point in midsummer in 1969

(Hutchings 1979) independently estimated zooplankton densities at between 0.2 and 3.5 animals per litre. These estimates are lower because only a 200 µm mesh net was used. At the maximum density encountered (6.4 animals per litre in experiment 19), the chance of a zooplankter occurring in a 1000 mℓ incubation bottle is high. However, oxygen levels gave no indication of the presence of zooplankton in the incubation bottles.

TABLE 3.1 A comparison of gross production as measured in five different sized incubation bottles using the Wilcoxon signed ranks test. (* = different at a level of significance ⩽ 5%, NS = not significantly different).

BOTTLE SIZE	100 mℓ	500 mℓ	250 mℓ	125 mℓ	60 mℓ
1000 mℓ					
500 mℓ	NS				
250 mℓ	NS	NS			
125 mℓ	NS	NS	NS		
60 mℓ	*	*	*	*	

In experiment 11, however, a zooplankter was noticed in a 500 mℓ light bottle. Gross production calculated using this bottle was 80% less than in the other (Appendix 1). This confirms that the presence of zooplankton in an incubation bottle can, by respiration and grazing, cause an underestimation of primary production. No marked differences in gross production in the duplicate light bottles were observed in other cases, despite fairly high zooplankton densities (Table 3.2). This may be due to the difference in methods of sampling for zooplankton and for water for primary production measurements. Zooplankton probably have less chance of avoiding the end of a pipe drawing water at a rate of 100 litres per minute, than they would a bucket or NIO bottle. Consequently zooplankton densities as estimated by the pump are probably greater than those obtained by sampling with a bucket or NIO bottle. Using the latter samplers one apparently excludes a large proportion

of the zooplankton.

Even though there are no significant differences in production estimates in the 1000 mℓ, 500 mℓ, 250 mℓ and 125 mℓ bottles, it is expedient to use the smallest bottle for ease of handling and for the reasons mentioned previously. The relatively lower estimate of gross production in the 60 mℓ bottle appears not to be related to the presence of zooplankton and remains unexplained.

CHAPTER 4

THE EFFECT OF TEMPORARY EXPOSURE TO SURFACE IRRADIANCE

4.1 INTRODUCTION

It is well known that light intensity affects the photosynthetic rate of marine phytoplankton. The photosynthesis/light (P. vs. I) curve (Fig. 4.1) reflects the general response of phytoplankton to an increase in light intensity. Photosynthesis increases linearly with increasing light intensity but phytoplankton become light saturated and the curve flattens out at an asymptotic value, P_{max}. Further increase in light intensity eventually results in a decrease in the photosynthetic rate. This photo-inhibition has been attributed to various factors including enzyme inactivation, light damage to either light or dark reactions and photorespiration (Harris and Piccinin 1977). Generalizations regarding photosynthesis-rate depressions at high light intensities are difficult because the rate depends on experiment duration, adaptation time, temperature, light spectral composition, etc. (Finenko 1978).

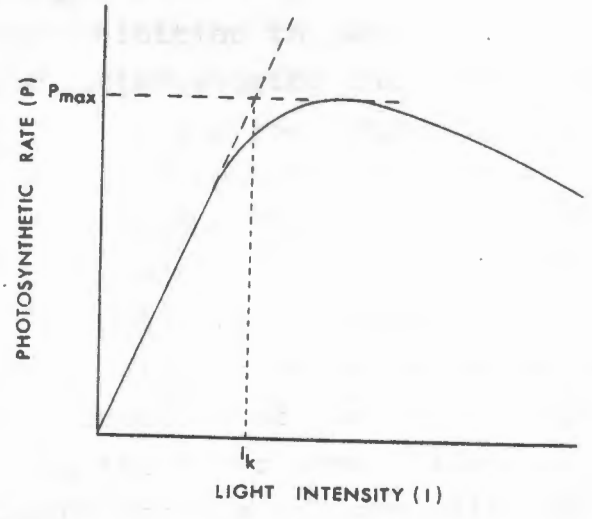

Fig. 4.1 Diagrammatic photosynthetic/light (P. vs. I) relationship. P_{max} = photosynthetic maximum (after Parsons *et al.* 1977).

A practical problem associated with the phenomenon of photo-inhibition is that of exposure of deep water samples (used for photosynthetic measurements in the euphotic zone) to surface light levels during manipulation on deck. Light levels may reach 2000 to 3000 $\mu E.m^{-2}.s^{-1}$ at noon in summer off Cape Town. Thus phytoplankton from the 1% light depth are exposed to several times more light in a few minutes than they are over the whole day under normal conditions. Although precautions are normally taken to shade water samples from the light at the surface, they are inevitably exposed when lowered from a ship for *in situ* incubation.

Dyson *et al.* (1965) and Watt (1965) independently devised incubation systems to avoid this problem. Sample bottles were filled, automatically innoculated with ^{14}C, and allowed to incubate *in situ*, thereby not being exposed to surface light prior to incubation. A problem with this method is that another sampler has to be used to retrieve water samples for measuring the usual accessory parameters (e.g. chlorophyll *a*, nutrients, oxygen). Due to "patchiness" in phytoplankton distribution one could not be sure of sampling the same "patch" and for this reason Dyson *et al.* (1965) discontinued the method.

There are some inconsistencies in the literature concerning light intensity and the period of exposure necessary for photo-inhibition to take effect. Goldman *et al.* (1963) found that after storing lake water under dim light (50 ft-c$\approx$ 3.5 $\mu E.m^{-2}.s^{-1}$) and low temperature (4°C), and then exposing it to direct sunlight for 5 minutes, ^{14}C assimilation was reduced by between 17% and 31%. It took about 4 hours for the water to recover to the same level as that of the control samples. Exposure to direct sunlight for one hour increased the recovery time to 20 hours and suggested that the recovery time was a function of the exposure period.

On the other hand, Takahashi *et al.* (1971) found that photo-inhibition was not generally observed over short periods (e.g. 10 minutes) but might be caused by longer exposures and increase in magnitude with time.

Falkowski and Owens (1978) found that for 6 species of phytoplankton, inhibition of oxygen production commenced after only 6 minutes exposure to light levels ranging between 2000 and 6000 $\mu E.m^{-2}.s^{-1}$ and that inhibition was completely reversible. These experiments were done with cultures grown at 250 $\mu E.m^{-2}.s^{-1}$. Had the stock cultures been acclimatized to a different light level, the light intensity at which inhibition occurred may have been different. It is possible that the light intensity used by Takahashi was not high enough to cause inhibition after short exposures. Doty et al. (1965) found that exposing natural phytoplankton populations to bright sunlight for even a few minutes caused a strong depression in photosynthetic rates.

The present experiment was designed to investigate the effect of surface light intensities, normally encountered during sampling, on phytoplankton photosynthetic rates in the euphotic zone off the Cape Peninsula.

4.2 PROCEDURE

Water samples were taken from a series of depths ranging from the surface to the bottom of the euphotic zone. Owing to problems with the light metering system, light depths were calculated only approximately at the time of measurement and corrections were made later. Consequently percentage light levels were grouped into the following classes:

100%
~43% (30-57%),
~22% (18-28%),
~8.4% (3-13%), and
~0.8% (0.4-1.4%).

The oxygen method was used for primary production measurements except for experiment 3 when the ^{14}C method was used. Instead of the usual two light bottles, there were six for each incubation level. Two were completely unprotected (i.e. exposed to surface irradiance from the time the samples were taken until they were suspended in the sea for in situ incubation). Two more were semi-protected (i.e. placed in small black bags which were removed immediately before the

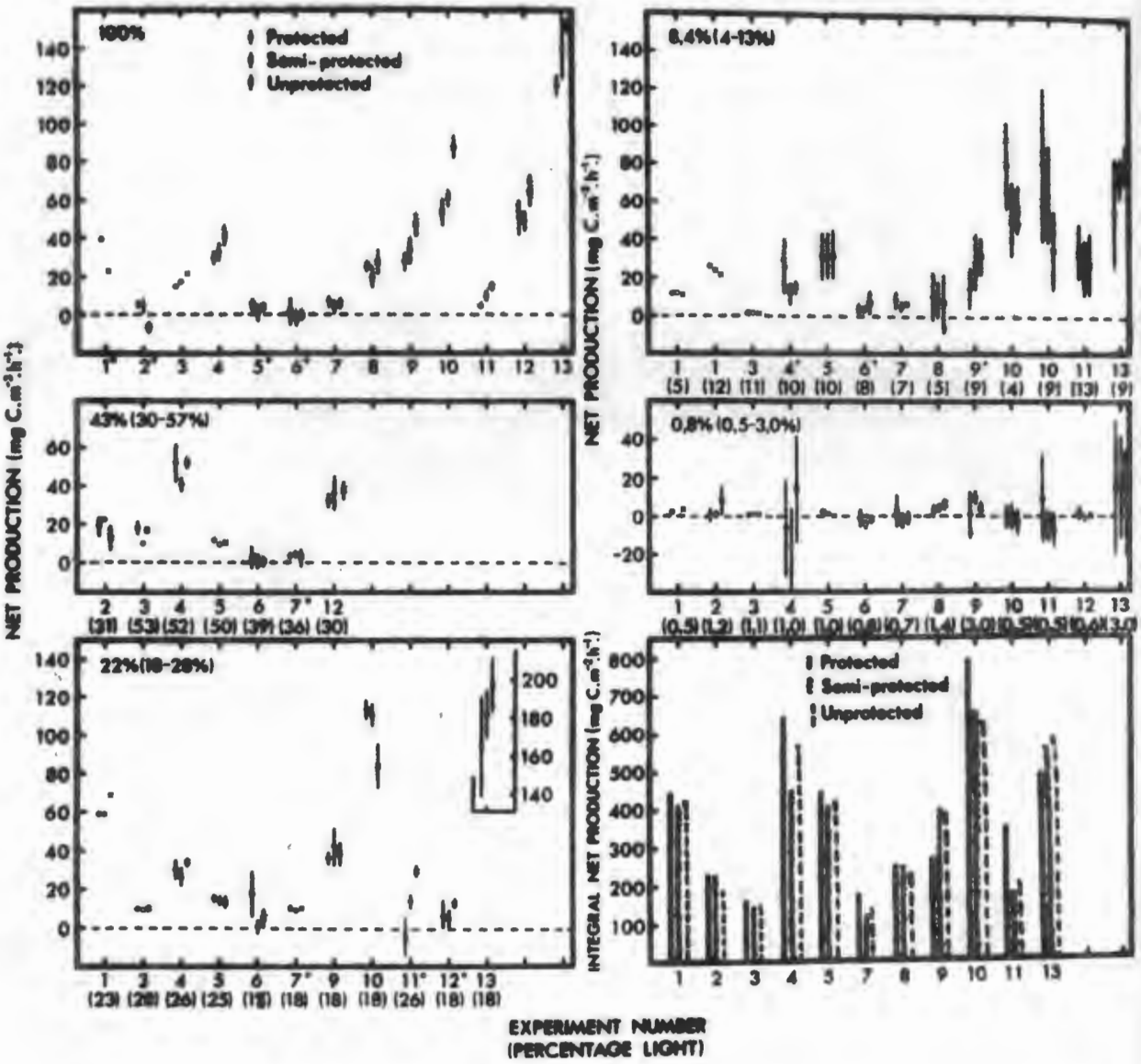

Fig. 4.2

The effect of exposure of primary production samples to surface light prior to incubation at the 100%, ~43%, ~22%, ~8.4% and~0.8% light depths is shown. Integrated net production estimates are also presented. Samples were protected (P), semiprotected (S) or unprotected (U) from surface light (see text). Error bar is range of production estimate.

bottles were lowered into the sea). The last two were completely protected from surface irradiance (i.e. the black bags were taken off by scuba divers immediately the bottles reached their incubation depths in the sea).

The net production values obtained from the protected samples were assumed to be the true values. The experiment was replicated thirteen times under a wide range of chlorophyll and nutrient levels.

The effects of the three conditions (unprotected, semi-protected and protected) on net production were compared separately for each range of light levels using the Wilcoxon signed ranks test (Dixon, 1977). The overall effect in the euphotic zone was ascertained by comparing integrated values, i.e. production per square metre. Production values from the 0.8% light level were all below the limits of precision of the oxygen method of measuring production and, therefore, could not be used in the comparison. The mean 0.8% production estimate for each experiment was used in the calculation of production per square metres so as not to bias the results.

Mean S/P (semi-protected/protected), U/P (unprotected/protected) and U/S (unprotected/semi-protected) ratios were calculated. Unreliable production estimates or those which were below the limits of precision of the method of measuring production were marked with an asterisk and were not used in the computations.

4.3 RESULTS AND DISCUSSION

Production estimates under the three conditions (protected, semi-protected and unprotected) are given in Fig 4.2. Table 4.1 presents the mean S/P, U/P and U/S ratios along with the results of the Wilcoxon signed ranks test which compares numerator and denominator values.

TABLE 4.1 Ratios comparing the unprotected (U), semi-protected (S) and protected (P) net production estimates at different mean light intensities (see text). Results of the Wilcoxon signed ranks test comparing numerator and denominator values are given in parenthesis (** = probability $\leq$1%, * = probability $\leq$ 5%, NS = not significantly different, n = number of replicates).

% Light	S/P (Prob)	U/S (Prob)	U/S (Prob)	n
100	1.17 *	1.60 **	1.36 **	9
43	1.08 (NS)	0.97 (NS)	0.93 (NS)	6
22	0.98 (NS)	1.02 (NS)	1.06 (NS)	9
8.4	0.84 (NS)	0.85 (*)	1.10 (NS)	10
0.8	Values below the limits of precision of the method.			
Euphotic zone	0.95 (NS)	0.95 (NS)	1.06 (NS)	11

At the 100% light level (0 metres) semi-protected (S) and unprotected (U) production estimates were significantly higher than the protected (P) ones, and unprotected estimates were higher than semi-protected ones. At the 43% and 22% light levels, no significant differences were observed amongst the three conditions, whereas at the 8.4% level unprotected were significantly lower than protected estimates. No significant differences were observed amongst integrated production estimates.

Results show that exposing water samples to surface irradiance prior to their incubation at the correct light level

affects production rates in two ways. It may act either to stimulate production in populations adapted to high light levels, or to inhibit production in populations conditioned to low light levels.

At the 100% light level, exposure to surface irradiance merely served to increase the incubation time, thereby effectively increasing production. The slightly longer (at most five minutes) incubation period of the 100% semi-protected samples (compared with the protected ones) appears to be too brief to cause the significant increase in production.

At the 43% and 22% light levels the increase in production due to increased light was probably countered by the inhibitory effect, with the result that no significant differences were observed. At the 8.4% light level, however, the inhibitory effect out-weighed any possible increase in production due to increased light so that the unprotected result was lower than the protected. Even though the semi-protected and protected values were not significantly different, the mean S/P ratio (0.84) suggests that even the relatively short (approximately one minute) exposure to surface irradiance may have an inhibitory effect on production. Therefore, the period of exposure to surface light should be kept as short as possible.

At the 0.8% light level, one would expect results similar to those found at the 8.4% light level but the oxygen method is not sensitive enough to detect significant differences at such low levels of production. However, even if the method of measurement was more sensitive, it is unlikely that the differences in production at the bottom of the euphotic zone would be large enough to contribute significantly to the total production in the euphotic zone.

No significant differences were found with integrated production estimates; apparently the over-estimates near the sea surface compensate for the underestimates deeper down.

Work by Platt *et al.* (in press) on natural diatom populations supports these findings, particularly since diatoms dominate in local waters (Sea Fisheries Institute, unpublished data). Their P vs. I curves show little inhibition on samples taken from the 50% light level, but intense inhibition on those from the 1% light level thus supporting the widely held view

that the light history of a phytoplankton population plays an important role in the response of phytoplankton to different light levels.

Savidge (1979) demonstrated that phytoplankton populations from a mixed water column show a different response to those from a stratified water column. In the former, mixing ensured that the long term light histories of samples from different depths were similar, with the result that P_{max} values were comparable. In stratified water, however, little mixing occurred between the two phytoplankton populations separated by the thermocline. The light histories were considerably different, the shallower population receiving more light than the deeper one. The P vs. I curve of shallow samples taken in the late morning and afternoon showed no inhibition at the higher light levels (linear response), whereas samples from below the thermocline showed a definite levelling off in the rate of photosynthesis with an increase in the intensity of incubating light. This strongly suggests that the two populations were conditioned to different light levels.

In the present series of experiments the water column was sometimes completely mixed and at other times a shallow thermocline was present. Results in Table 4.2 show little inhibition in samples above the thermocline, whereas those below or in the thermocline zone tend to be inhibited by exposure to surface light levels prior to incubation. In mixed water the results are variable and no definite trends are evident.

Strong winds and intense upwelling characterise the coastal waters of the south-west Cape in summer and stratification, if present, is usually poorly developed. The water column is more strongly stratified further offshore away from the upwelling zone, and on the south coast, particularly over the Agulhas Bank. Conditioning of phytoplankton can be expected to be of greater significance in these areas.

TABLE 4.2 The effect of exposing primary production samples to high surface light levels prior to incubation is shown for phytoplankton populations taken from mixed and stratified water bodies.
U/P = unprotected/protected net production estimates.

No thermocline			Thermocline present (stratified)					
			Above thermocline			In or below thermocline		
Expt	% Light	U/P	Expt	% Light	U/P	Expt	% Light	U/P
5	50	1.35	3	57	0.97	1	23	1.17
	25	0.83	4	52	1.00		12	0.82
	10	1.04		24	1.13		5	0.92
7	36	0.70	9	18	1.07	2	31	0.67
	18	1.40	12	30	1.15	3	28	1.01
	7	0.73	13	18	1.20		11	1.00
8	24	0.97		9	1.45	8	24	0.97
	5	0.63		Mean =	1.14		5	0.63
	Mean =	0.96				10	18	0.73
							9	0.44
						11	13	0.81
							Mean =	0.83

4.4 CONCLUSIONS

Exposing water samples from the euphotic zone to surface light levels prior to *in situ* incubation appears to have both a stimulatory and an inhibitory effect on production. The stimulatory effect decreases with depth, whereas the inhibitory effect increases. Consequently surface production estimates (at the 100% light depth) were increased by the additional light, whereas deep production estimates (at the 8.4% and possibly the 0.8% light depths) were inhibited by it. Production estimates midway in the euphotic zone (at the 43%

and the 22% light depths) were not significantly altered by the excess light, the stimulatory effect apparently being countered by the inhibitory effect. Integrated production estimates for the euphotic zone also appear to be unchanged by temporary exposure to bright light.

Results indicate that water samples taken from the euphotic zone for production measurements should be shaded from surface light as much as is practically possible during operations on deck. However, when samples are lowered into the water for *in situ* incubation, the short exposure (less than one minute) to surface light does not affect production measurements significantly. The additional complication of trying to shade the samples until they are at the *in situ* light levels is, therefore, not justified.

CHAPTER 5

PRIMARY PRODUCTION *IN SITU* AND UNDER SIMULATED *IN SITU* CONDITIONS

5.1 INTRODUCTION

Phytoplankton productivity is commonly measured directly by incubating water samples in the sea at the depths from which they came (the *in situ* method), or in an incubator on deck under natural light filtered to simulate conditions in the sea (the simulated *in situ* method), or in an incubator in the laboratory with a constant artificial light source (incubator method). Indirectly production is often estimated from measurements of such correlated features as the concentration of chlorophyll *a* and natural irradiance (modelling method).

These methods have inherent sources of error (Finenko 1978). *In situ* measurements have long been considered the simplest and most reliable for estimating total primary production in the euphotic zone (Strickland 1960, Finenko 1978). However, this time consuming method is often avoided because the prolonged delays severely limit the area of ocean that can be sampled. The variability of natural sunlight also makes it difficult to estimate the average production of an area from one measurement, and to compare the productivity of two bodies of water measured under different weather conditions. Steeman Nielsen (1952) partly overcame these problems by incubating water samples on board ship in a constant light incubator. Variations on this method have been used extensively but most measure potential production rather than the production that would occur naturally. Better understanding of the responses of phytoplankton to different environmental factors subsequently enabled workers to use incubator production values to estimate actual daily production with a reasonable amount of confidence (Gargas *et al.* 1976, Jitts *et al.* 1976, Fee 1977). Nevertheless, *in situ* measurements remain the most realistic until artificial light more closely approximates natural submarine light. Another practical constraint favouring *in situ* measurements is that the equipment necessary for constant light experiments is expensive.

As a compromise, the simulated *in situ* method is often used. However, the simulation of submarine light for production measurements is difficult (Jerlov and Nygaard 1969, Yentsch 1974, Steeman Nielsen 1975, Jitts *et al.* 1976 and Parsons *et al.* 1977). The spectral composition of light in sea water changes with depth due to preferential absorption of different wavelengths. The longest wavelengths (infra red and red) and, to a lesser extent, the shortest wavelengths (violet and ultraviolet) are absorbed first, leaving the short and intermediate wavelengths (blue or green) to penetrate deepest. The colour that penetrates the deepest depends mainly on the turbidity of the water. In general blue light penetrates deepest in clear oceanic water, whereas green or green-yellow light penetrates deepest in turbid coastal water. The natural density filters used by many workers simulate light intensity at different depths without changing light quality. Jitts (1963) therefore fitted his deck incubators with blue glass filters to approximate the quality of light at a depth of ten metres in clear water. He found good correlation between simulated and actual *in situ* measurements to about the 25% light level. Below this depth, light limited the photosynthetic rate so that certain errors in measurement were accentuated, viz.:

(i) the action spectrum of a phytoplankton species or population may be quite different from the spectral response of the sensor, and

(ii) the optical filters in incubators do not necessarily duplicate the transmission characteristics of the water.

Ideally the spectral response of a sensor for measuring photosynthetically active radiation (PAR) in the sea should be the same as the action spectrum of the phytoplankton. However the action spectrum varies for different groups of algae depending on the accessory pigments (Steeman Nielsen 1975, Parsons *et al.* 1977). Consequently no single sensor would be generally suitable. On considering these problems the Scientific Committee on Oceanic Research (SCOR)

Working Group 15 reluctantly gave up the idea of the "equivalent" sensor because of the inherent difficulties associated with the measurement of utilized energy (Burt et al. 1969). Instead, Working Group 15 made the alternative recommendation that the total number of quanta (or total energy if a quantum sensor was not available) in the PAR waveband, be measured (SCOR 1965).

When simulating in situ incubations, the second important consideration is what filters can best be used in incubators to simulate the effect of depth on light quality in different types of seawater. Kiefer and Strickland (1970) found that if the intensities of light through blue and neutral filters were matched, using a quantum sensor, photosynthesis was higher under the blue filter. This suggests that sampling depths cannot be set by matching the in situ quantum sensor readings with the readings for deck incubators fitted with neutral filters. Consequently they recommended that deck incubators should simulate not only the intensity but also the spectral composition of submarine light. Jerlov (1951) described three optical types of oceanic water and nine types of coastal water, ranging from clearest oceanic water where blue light penetrates the deepest to the most turbid coastal waters where yellow light penetrates furthest. To simulate submarine light spectrally, one should determine the water type first and then choose filters with the appropriate spectral transmission characteristics. In coastal waters, particularly in upwelling areas, the water type is far more variable than in oceanic waters so that one set of filters would hardly be adequate. The practical difficulties involved led Ryther & Yentsch (1970) to recommend the use of spectrally neutral filters for general use.

Another source of error in simulating in situ production was encountered by Jitts et al. (1976). The inhibitory effect of ultraviolet light on photosynthesis in the surface waters of the ocean was excluded from the simulated in situ samples by a thick sheet of glass on the incubator, but not from the in situ samples at the sea surface because the thin pyrex glass of the incubation bottles was largely transparent to ultraviolet light. The thick glass bottles used by Jitts

(1963) in previous studies excluded ultraviolet light from both simulated and *in situ* incubations, and could result in a 40% over-estimate of surface production. This phenomenon has also been reported by Steeman Nielsen (1964).

The present study was designed to compare *in situ* primary production measurements with simulated *in situ* measurements in the highly productive coastal upwelling area off the Cape Peninsula.

5.2 PROCEDURE

Water samples were taken from the 100%, 50%, 25%, 10% and 1% light depths established using an underwater quantum sensor. Primary production was measured by either the oxygen (twelve experiments) of ^{14}C (seven experiments) methods. Replicate production samples from each depth were incubated both *in situ* and in a deck incubator where *in situ* light levels were simulated using light bottles coated with a spectrally neutral mixture of varnish and polyurethane paint (see Chapter 2). Because the clarity of the water in the study was variable, neutral density filters were used rather than the blue glass filters that Jitts *et al*. (1976) used in oceanic water. In several experiments a third set of samples was incubated in similar neutral density bottles. These were suspended at the sea surface, away from the ship and alongside the *in situ* set, in order to investigate any "ship effect" on the deck incubator.

When enough data were available, *in situ* production estimates (P_i) and simulated *in situ* production estimates in the deck incubator (P_d) and on the sea surface (P_s) were compared, using the Wilcoxon signed ranks test (Dixon 1977). The mean P_d/P_i, P_s/P_i and P_d/P_s ratios were calculated (negative production values were not used). The overall effect of the different incubation methods on production estimates in the euphotic zone as a whole, was ascertained by comparing the integrated production estimates, $\int P_i$, $\int P_d$ and $\int P_s$ ($mgC.m^{-2}$). Measurements at the 1% light level were mostly below the limits of precision of the oxygen production method so were not used in the comparison. The mean production estimate at the 1% light level was used to calculate integrated production for each experiment.

TABLE 5.1 Oxygen method. Ratios comparing *in situ* production estimates (P_i), and simulated *in situ* production estimates in a deck incubator (P_d) and at the sea surface (P_s) at different light intensities (see text). Results of the Wilcoxon signed ranks test comparing numerator and denominator values are given in parenthesis (** = probability ⩽ 1%, * = probability ⩽ 5%, NS = not significantly different, - = test not done, n = number of replicates).

Sample Group	Mean P_d/P_i (Prob)	n	Mean P_s/P_i (Prob)	n	Mean P_d/P_s (Prob)	n
100%	1.34		0.98		1.49	
	(NS)	8	(NS)	6	(-)	3
50%	1.35		1.12		1.17	
	(*)	9	(-)	3	(-)	3
25%	1.48		0.94		1.38	
	(**)	9	(NS)	5	(-)	3
10%	1.42		1.16		1.11	
	(*)	9	(NS)	5	(-)	3
1%	Production levels were below the limits of precision					
All values (100%-10%)	1.36		1.03		1.23	
	(**)	35	(NS)	21	(**)	12
$\int P$ (m^{-2})	1.20		1.06		1.13	
	(**)	9	(NS)	5	(-)	3

5.3 RESULTS AND DISCUSSION

Production estimates are presented in Appendix 2 (oxygen method) and Appendix 3 (^{14}C uptake). Tables 5.1 and 5.2 give the mean P_d/P_i, P_s/P_i and P_d/P_s ratios along with the results of the Wilcoxon test (which compares numerator and denominator values) for experiments using the oxygen and ^{14}C methods respectively.

Oxygen production

Simulated *in situ* production estimates on deck (P_d) were significantly higher than *in situ* estimates (P_i) at each light level except at the sea surface (100% light level) where there was no significant difference, although the mean P_d estimate was 34% greater than the mean P_i one.

Although there were not enough data to state unequivocally that there is no difference between simulated *in situ* production estimates at the sea surface (P_s) and *in situ* estimates (P_i), the mean ratios of both $\int P_s / \int P_i$ and P_s/P_i for individual light levels are close to unity. In addition, when all the valves were lumped together (n = 18), P_s and P_i were not significantly different.

In only three experiments was production measured using all three incubation methods simultaneously. Although not conclusive, results suggest that simulated *in situ* production estimates on deck (P_d) were greater than those at the sea surface (P_s).

It appears that P_d over-estimates P_i, whereas P_s is similar to P_i. This suggests that the spectral composition of the incubation light (which would have been the same in the deck incubator and at the sea surface) is not responsible for the difference between the simulated *in situ* production estimates on deck and the *in situ* estimates. The disagreement between the two sets of measurements is more likely to be related to differences in light intensity and/or temperature. Because thick glass-walled incubation bottles were used, ultraviolet light was excluded from all samples so was unlikely to influence production rates.

Reflection from the white superstructure of the ship may have caused the light incident on the deck incubator to be

greater than on the sea surface. An increase in light generally causes an increase in production until the phytoplankton becomes light saturated (Parsons et al. 1977).

Production rates of populations at the 100% and 50% light levels were unlikely to be limited by lack of light. However, deeper populations were probably not light saturated so could be expected to show higher production rates when incubated at slightly higher light levels on deck. In fact this was the case for samples at the 25% and 10% levels.

The other factor which might affect production rates is temperature. Temperature decreased with depth so that the simulated in situ samples from low light levels were incubated at higher temperatures than in situ samples. The effect of temperature on the rate of photosynthesis is not well understood, but is thought to manifest itself only after light saturation (Gessner 1970 quoted by Finenko 1978). Consequently phytoplankton subjected to the greatest changes in temperature (i.e. the deep samples) were least likely to be affected by an increase in temperature as they were incubated at low light levels. Furthermore, the temperature difference between the 100% and 1% light levels is usually less than $2^{\circ}C$ because strong thermoclines are seldom established in such a dynamic upwelling system. Even in those cases when the temperature difference was greater than $2^{\circ}C$, the simulated production measurements on the sea surface were not noticeably higher at the low light levels (1%, 10% and even 25%). For the shallow samples at saturating light levels (100% and 50%), the temperature difference between samples incubating in situ and at the sea surface was negligible and production measurements were not significantly different. The temperature in the deck incubator was usually about 1 - $2^{\circ}C$ higher than at the sea surface. This increase was unlikely to affect rates of production at low light levels (for reasons discussed above) but may have been responsible for the higher production rates at the 100% and 50% light levels on deck.

It appears that the increase in production on deck at high light levels (100% and 50%) was due to the slightly higher temperature in the deck incubator, whereas at low light levels (25% and 10%) increased production was due to an increase

TABLE 5.2 ^{14}C method. Ratios comparing *in situ* production estimates (P_i), and simulated *in situ* production estimates in a deck incubator (P_d) and at the sea surface (P_s) at different light intensities (see text). Results of the Wilcoxon signed ranks test comparing numerator and denominator values are given in parenthesis (** = probability $\leq$ 1%, * = probability $\leq$ 5%, NS = not significantly different, - = test not done, n = number of replicates).

SAMPLE GROUP	EXPT 13-19		EXPERIMENTS 15-17					
	Mean P_d/P_i (Prob)	n	Mean P_d/P_i (Prob)	n	Mean P_s/P_i (Prob)	n	Mean P_d/P_s (Prob)	n
100%	0.96		1.07		0.97		1.13	
	(NS)	7	(-)	3	(-)	3	(-)	3
50%	0.98		1.23		1.16		1.08	
	(NS)	7	(-)	3	(-)	3	(-)	3
25%	1.10		1.30		0.78		2.01	
	(NS)	6	(-)	3	(-)	3	(-)	3
10%	1.33		2.24		2.29		1.24	
	(NS)	6	(-)	3	(-)	2	(-)	2
1%	Data few and very variable							
All values (100%-10%)	1.08		1.46		1.21		1.38	
	(NS)	26	(*)	12	(NS)	11	(*)	11
$\int P$ (m^{-2})	0.98		1.39		1.12		1.29	
	(NS)	7	(-)	3	(-)	3	(-)	3

in incubating light. It is possible that both the increased light and temperature on deck simultaneously affected the rate of production (Platt et al. 1977) but that the effect of light dominated at limiting light levels whereas that of temperature dominated at saturating light levels.

^{14}C uptake

Of the seven ^{14}C experiments, only three (number 15-17) included production estimates at the sea surface (P_s). These experiments show results (Table 5.2) similar to those obtained using the oxygen method (Table 5.1). That is, when all the values are grouped, simulated in situ production estimates on deck (P_d) are higher than those at the sea surface (P_s) and higher than in situ estimates (P_i). However, in experiments 13, 14, 18 and 19 (Appendix 2) the simulated in situ production measurements on deck (P_d) underestimate the in situ measurements (P_i) and tend to cancel out the opposite trends in experiments 15-17, so when all the experiments are grouped (numbers 13-19) no significant differences between production estimates on deck and in situ are observed (Table 5.2, column 2). The reason for the different trends is not known. However, too much significance should not be placed on these differences as there are few data.

MacIsaacs and Dugdale (1976) using ^{15}N uptake to estimate production, found that in situ estimates were generally higher than simulated ones on deck in the north-west African upwelling region, whereas in the oligotrophic western Mediterranean no significant differences were observed. They gave no satisfactory explanation for the observations but recommended that the simulated in situ incubation technique be continued.

The error in any single ^{14}C production measurement is at least 30%, even if all precautions are taken (Steeman Nielsen 1975). The method of incubation may increase this error considerably. For example, production samples are usually incubated at fixed light depths, whereas under natural conditions, phytoplankton populations may experience a far more variable light regime due to vertical movement in the water column. Marra (1978) found that simulating the latter conditions gave estimates of integrated photosynthesis 19-87% higher than

estimates calculated from measurements at fixed light depths, suggesting that the variations between simulated and in situ measurements is relatively small. Therefore, it seems acceptable to use the simulated in situ technique for measuring production rates off the Cape Peninsula. As our understanding of the physiology and ecology of phytoplankton improves, the reasons for differences between the two techniques may become clearer.

5.4 SUMMARY

Simulated in situ primary production measurements are compared with actual in situ measurements in an upwelling area off the Cape Peninsula, using the oxygen and ^{14}C methods separately.

When oxygen production was simulated in a deck incubator measurements over-estimated in situ production at discrete depths by $\sim$ 40% and in the whole euphotic zone (integrated production) by $\sim$ 20%. It appears that higher light levels on deck (caused by reflection from the white super-structure of the vessel) may be responsible for the increase in production at light limiting levels (10% and 25%), whereas at saturating light levels (50% and 100%) the slightly higher temperatures (1-2^{o}C) in the deck incubator seem responsible for the increased rate of production.

Data obtained using the ^{14}C method are fewer and do not show significant differences. More measurements are required to draw firm conclusions.

The differences observed between in situ and simulated in situ production measurements are small, compared with experimental errors. It is therefore suggested that the convenient simulated in situ incubation technique be employed to measure primary production off the Cape Peninsula when ship's time is limited.

CHAPTER 6

DIEL VARIATION IN PRIMARY PRODUCTION

6.1 INTRODUCTION

Variation in the quality and intensity of light during the day is likely to cause fluctuations in the photosynthetic rate of phytoplankton. The existence of a diel rhythm in the photosynthetic capacity (i.e. potential photosynthesis under constant saturating light) of natural populations and cultures of phytoplankton has been established by a number of different workers using a variety of methods (Sournia 1974). Although there is general agreement about the existence of such a rhythm findings differ as to:

(i) the cause(s) of variation

(ii) the extent of variation, and

(iii) the times during the 24 hours period at which the peaks in production occur.

Changes in photosynthetic capacity are important practically because when short term primary production measurements are used for estimating daily rates of production, the conversion factor will depend on the time at which the incubation was carried out. Better understanding of daily periodicities will lead to improved estimates of daily or annual production.

The main aim of this study is to investigate the diel variations in photosynthetic potential (i.e. under constant bright light) and actual photosynthesis (under natural light) of photoplankton populations off the Cape Peninsula. The ultimate objective is to use short term measurements of primary production to estimate daily, monthly or annual production values.

6.2 PROCEDURE

Four diel experiments were conducted in 1978 : 4-6 January (summer), 20-23 March, 24-28 April and 24-27 October.

Experiments in January and April were carried out at Robben Island and those in March and October at Oudekraal (Fig. 1.1).

In each case 150 litres of surface water was siphoned into eight 20 litre plastic containers and suspended at the sea surface. Every three hours subsamples were taken for nutrient, chlorophyll a and primary production measurements. In situ and incubating temperatures were recorded. Light (PAR) was integrated continuously during each experiment and read hourly.

Primary production was measured by the oxygen method. Two light and two dark bottles were incubated under natural light conditions either in situ (January) or in the simulated in situ incubator on deck (March, April and October). A similar set of samples was incubated simultaneously in the constant light incubator.

Missing net production values were estimated from gross production results when possible.

6.3 RESULTS

6.3.1 Light

Fig. 6.1 presents incident light levels during each experiment. Maximum levels were highest in the January and October experiments ($\sim$ 2000 $\mu E.m^{-2}.s^{-1}$) and lowest in April ($\sim$1400 $\mu E.m^{-2}.s^{-1}$) with intermediate levels in the March experiment ($\sim$ 1650 $\mu E.m^{-2}.s^{-1}$). Cloud cover caused occasional minor variations in intensity particularly on day 2 in January and day 2 in October.

6.3.2 Temperature

Fig 6.2 summarizes the temperature results. In the January, March and April experiments the in situ temperature at which the bulk water sample was stored, showed slight diel fluctuations ($\leq 2^{\circ}C$) due to sun warming. In the October experiment temperature variation was greater ($\sim 3.2^{\circ}C$) because cold water upwelled shortly after the experiment commenced and gradually warmed up.

In the first experiment (January) the difference

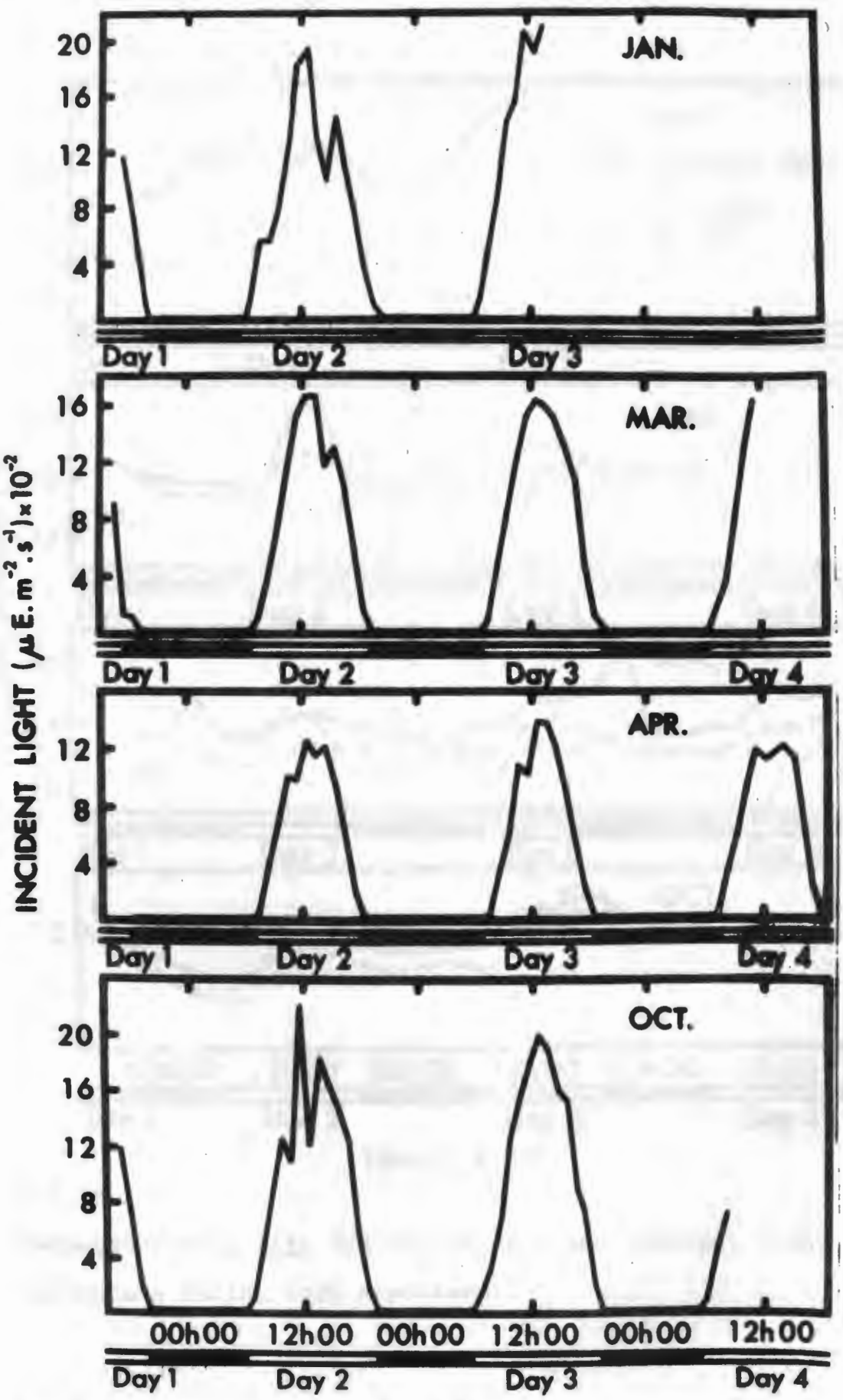

Fig. 6.1

Hourly incident light levels during each experiment.

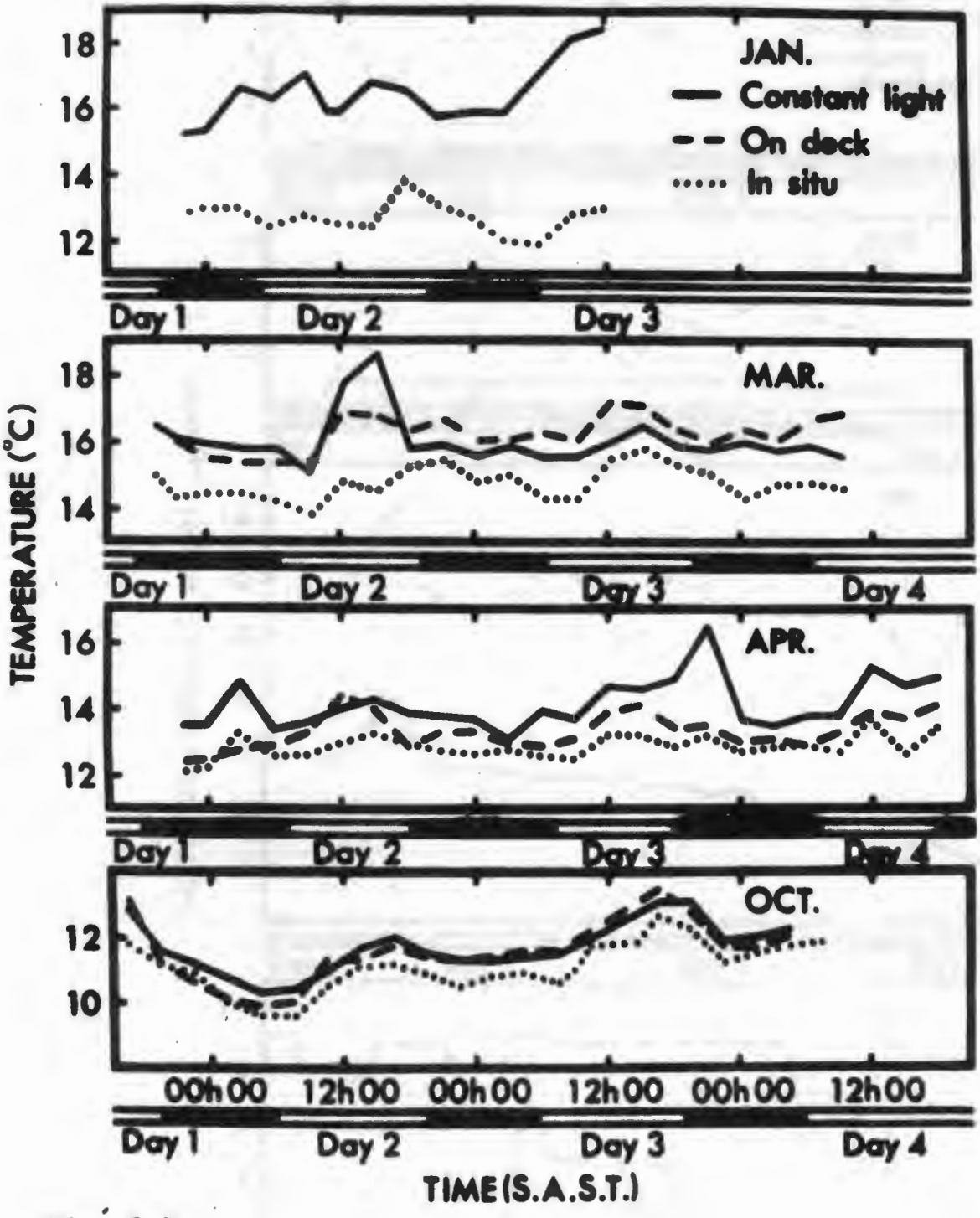

Fig. 6.2

Temperatures *in situ* and in the deck and constant light incubators during each experiment.

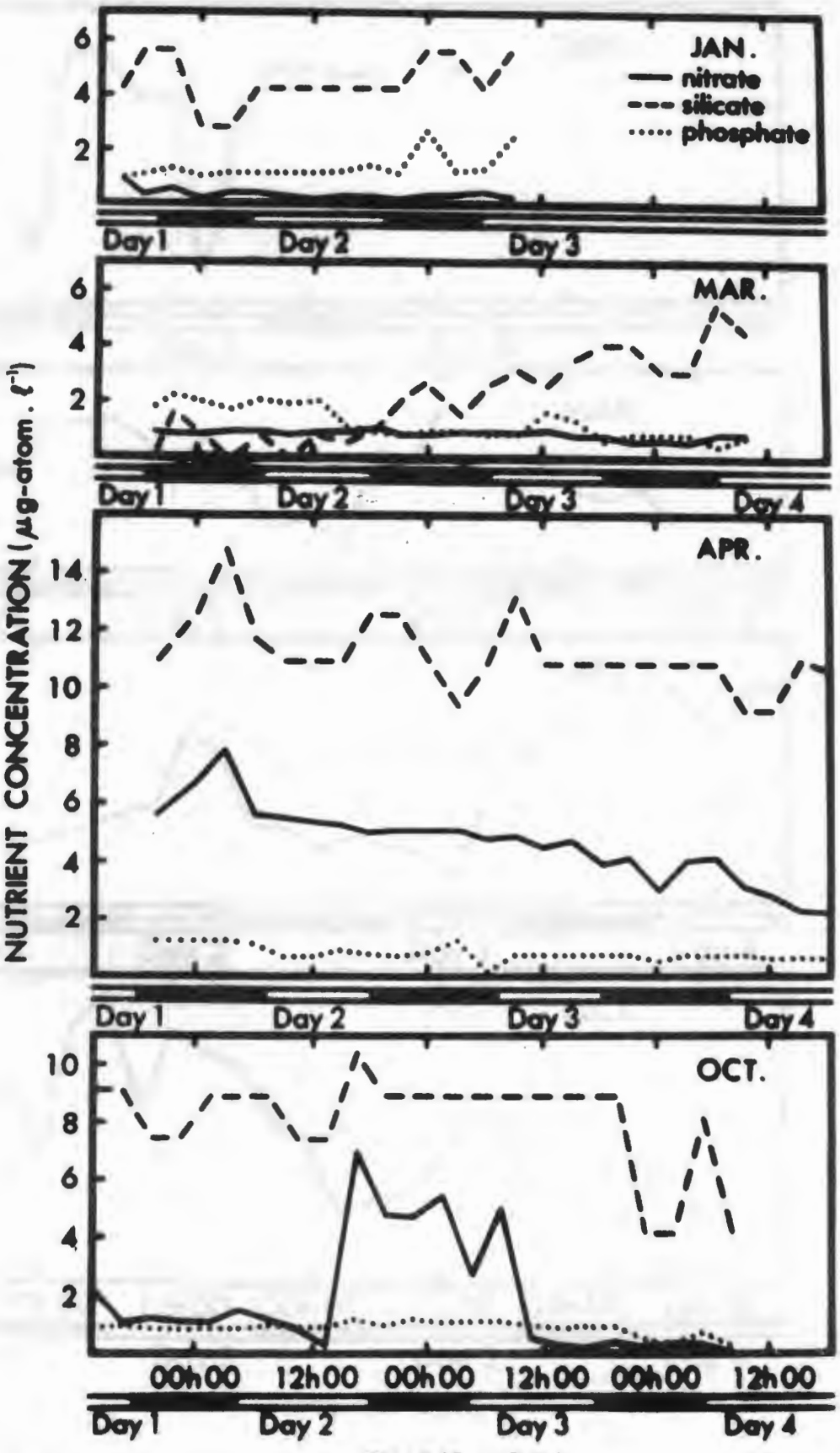

Fig. 6.3

Nitrate, silicate and phosphate concentrations during each experiment.

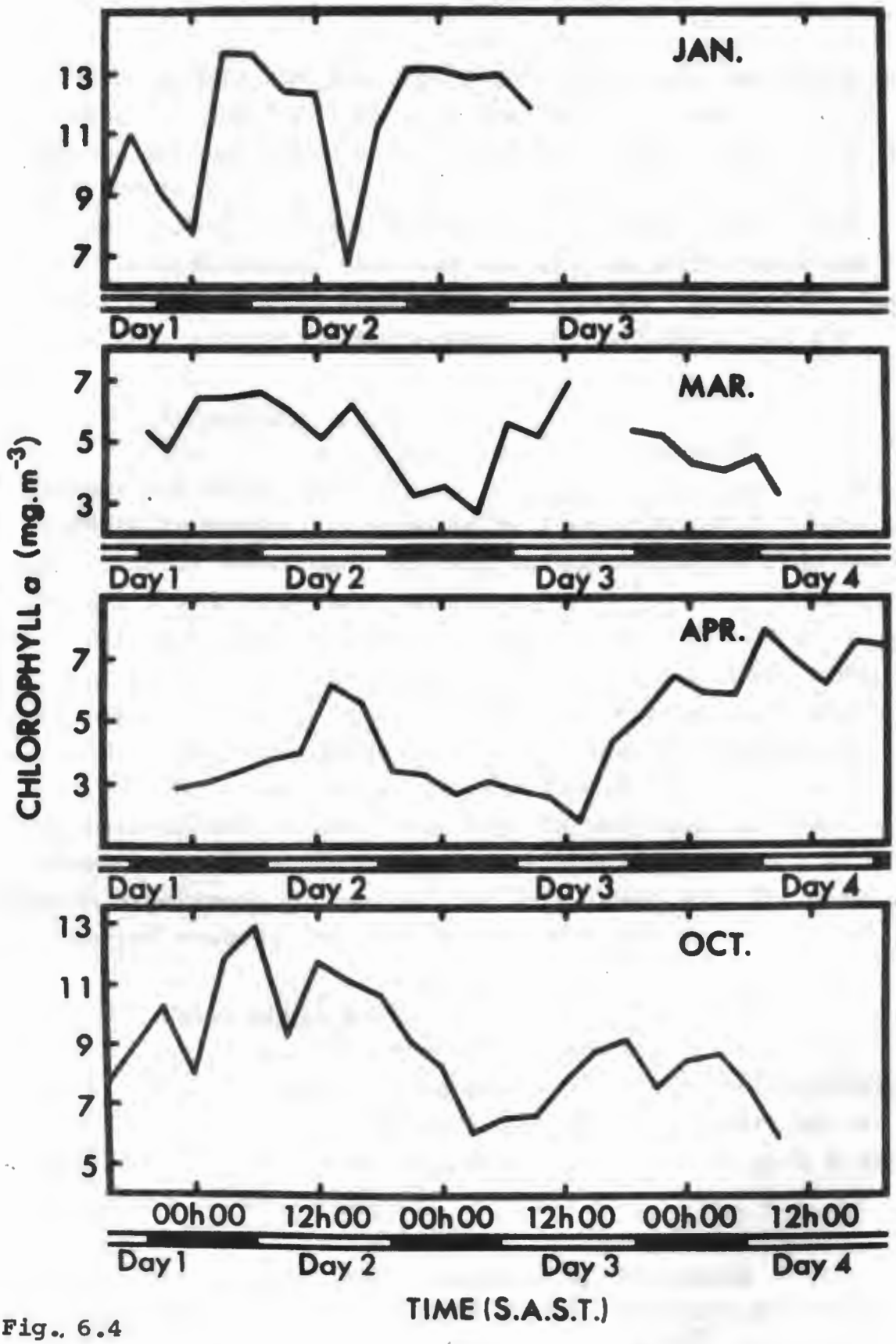

Fig. 6.4

Chlorophyll a concentrations during each experiment.

between natural and constant light incubation temperatures was between 3.0 and 5.2°C because insufficient water could be circulated through the constant light incubator to maintain *in situ* temperatures. However, after increasing the flow rate in the constant light incubator in the March, April and October experiments, the mean temperature difference was less than 1°C. In most cases *in situ* storage temperatures were lower than incubating temperatures by between 0 and 4°C.

6.3.3 Nutrients

Fig. 6.3 summarizes the nutrient results. In the January and March experiments, nitrate concentrations showed no definite trends but were below 1 μg-at NO_3-N.ℓ^{-1}, whereas in the April experiment concentrations decreased from between 5.6 and 7.3 at the start to 2.2 μg-at.ℓ^{-1}. In the October experiment nitrate concentrations decreased from 2 to 0 μg-at.ℓ^{-1} except for a set of inexplicably high values in the middle of the experiment. Although the containers had been thoroughly rinsed, it appears that one may have been contaminated.

Phosphate concentrations showed little variation. Silicate concentrations were high in the January, April and October experiments and showed no definite trends. In the March experiment concentrations were lower and, for some reason, increased towards the end of the experiment.

6.3.4 Chlorophyll a

Chlorophyll a data are summarized in Fig. 6.4. Concentrations showed little evidence of diel periodicity. No trends were evident in January, March and October, but a distinct increase in April appears to correlate with a decrease in nitrate concentration.

6.3.5 Production under a natural light regime

Under a natural light regime, both net production (P_i) and net production per unit chlorophyll *a* (P_i^B) peaked during the day, then decreased steadily to an overnight minimum (Fig. 6.5). The times at which P_i and P_i^B peaked varied (Table 6.1).

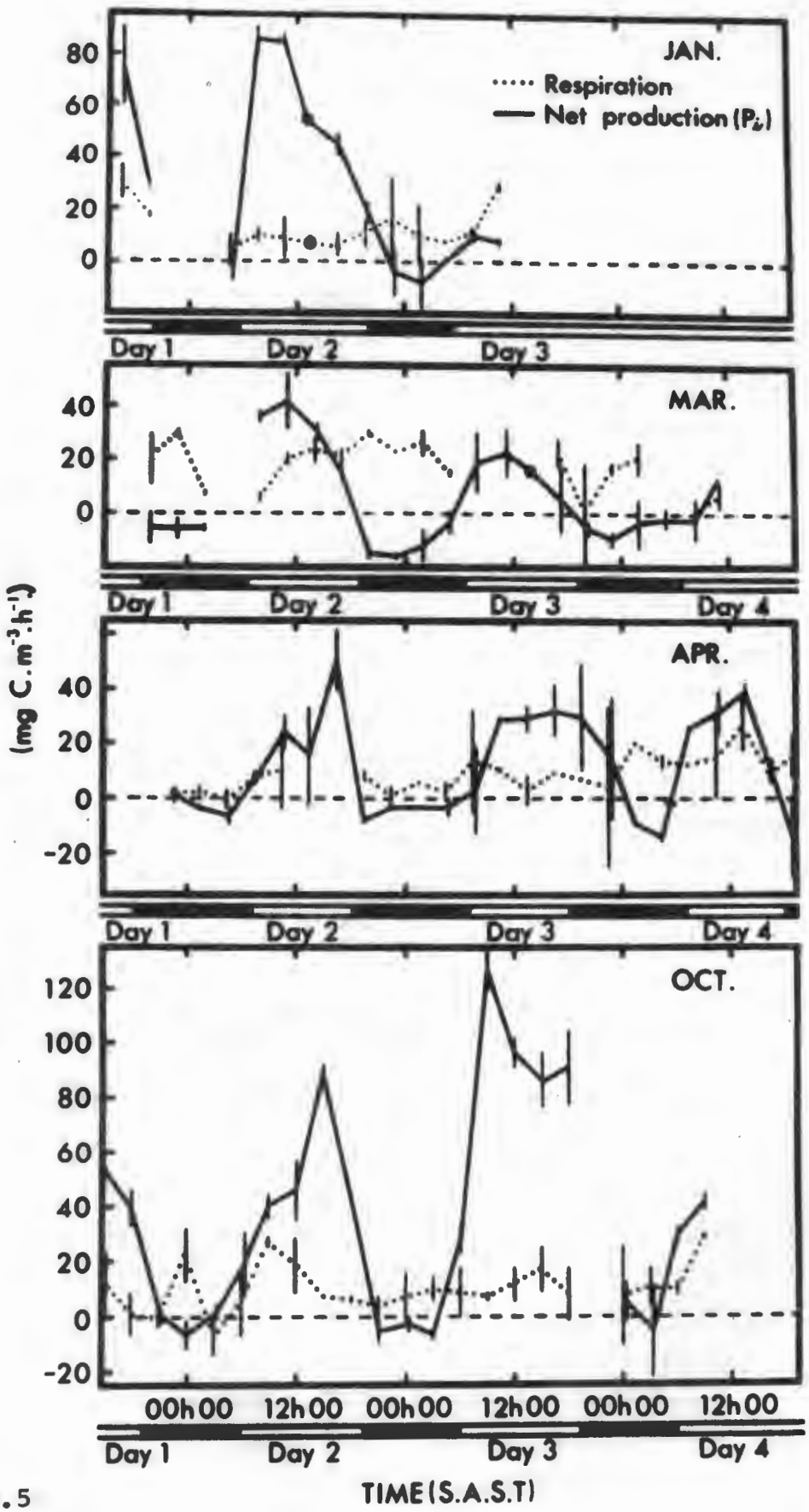

Fig. 6.5

Net production and respiration under natural light during each experiment. ⊙ = value estimated from gross production measurement; error bar = range.

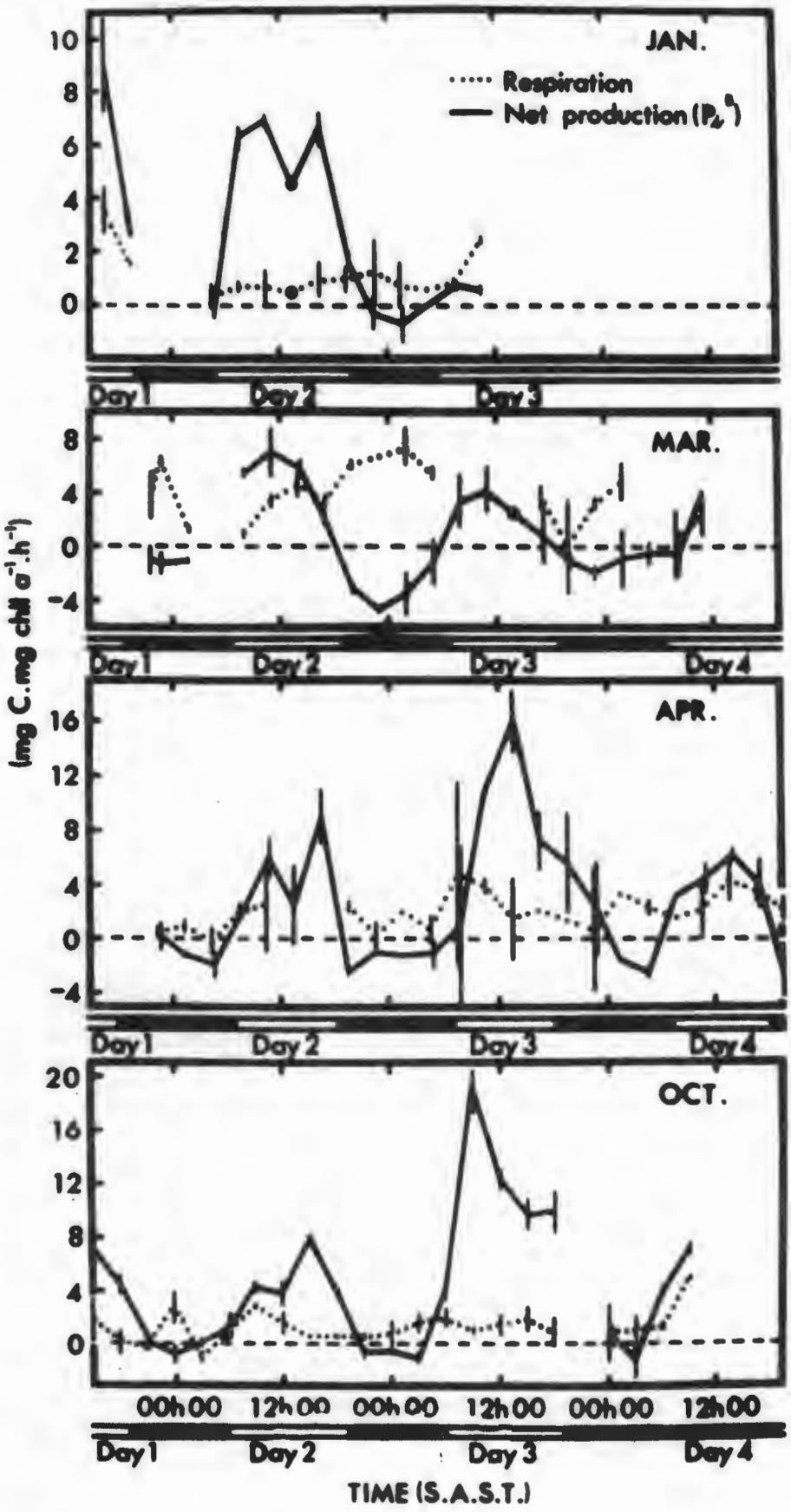

Fig. 6.5 continued ...

Net production and respiration per unit chlorophyll a under natural light.

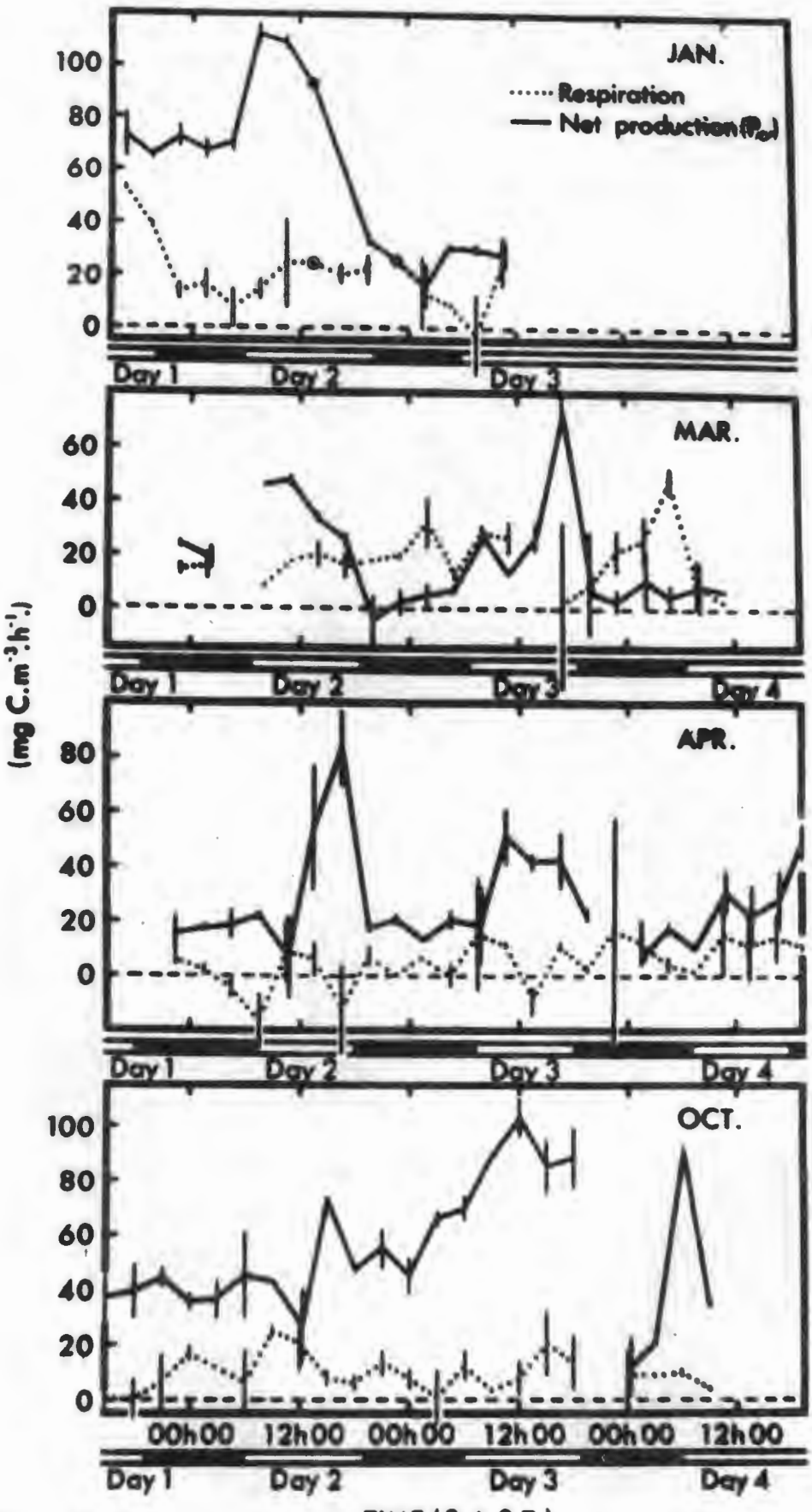

Fig. 6.6

Net production and respiration under constant light during each experiment. ⊙ = value estimated from gross production measurement; error bar = range.

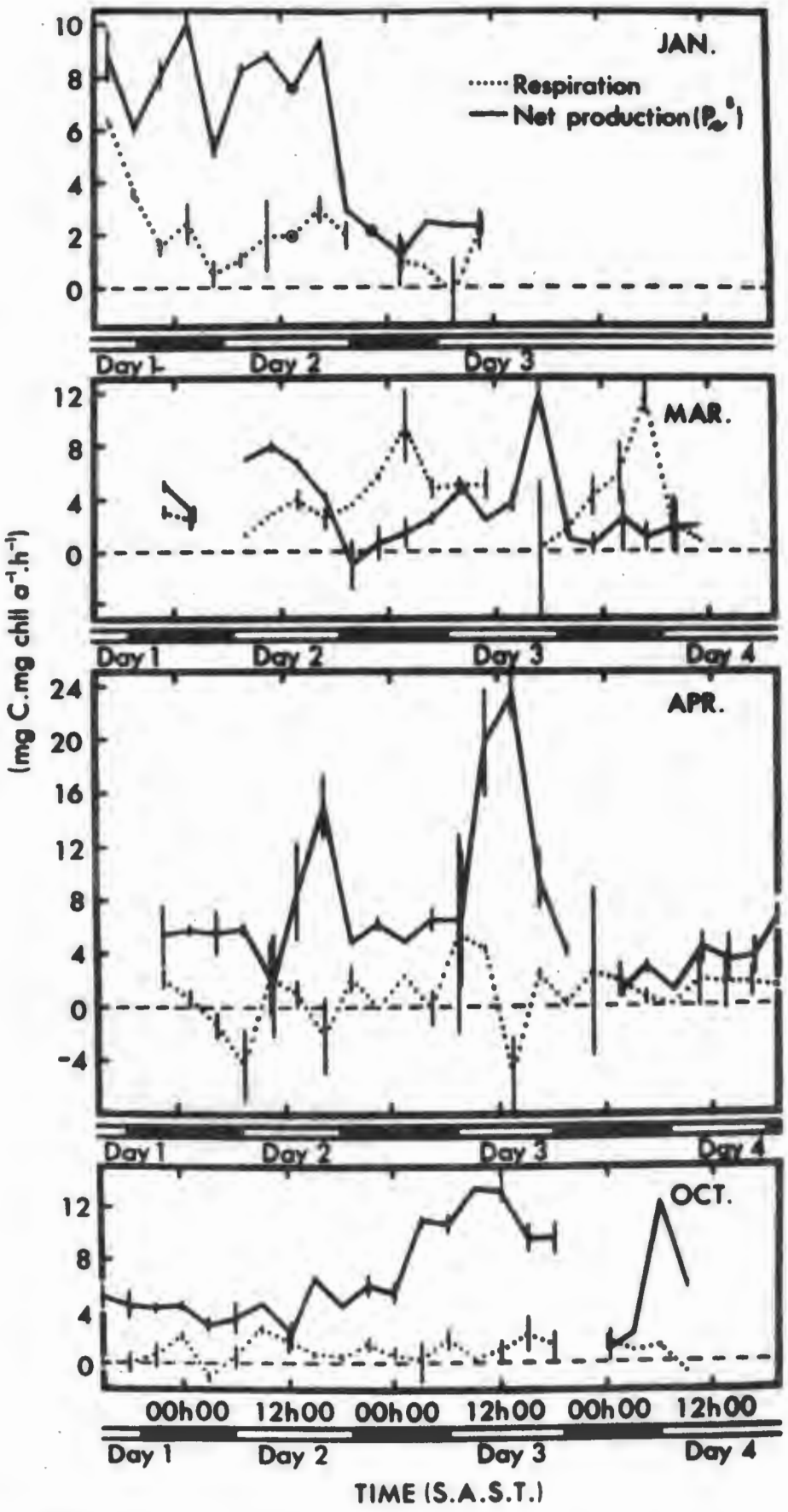

Fig. 6.6 continued ...
Net production and respiration per unit chlorophyll a under constant light.

TABLE 6.1 Times of peak net production and net production per unit chlorophyll a under natural light (P_i and P_i^B) and constant artificial light (P_c and P_c^B) for phytoplankton populations at the sea surface. Times of sunrise (SR) and sunset (SS) are given, as are the maximum hourly light levels for each day. Times are in South African Standard Time (SAST). Local Apparent Time is 51, 53, 44 and 30 minutes before SAST for the January, March, April and October experiments respectively.

Experiment	Day	SR	SS	Peak Natural light		Peak Constant Lighting		Daily maximum light level ($uE.m^{-2}.s^{-1}$)
				P_i	P_i^B	P_c	P_c^B	
January	2	0542	2001	0730-1030	0730-1030 1500-1900	0730-1030	0000-0300 0900-1200 1500-1800 (weak)	1980
March	2	0650	1856	0930-1330	0930-1330	0930-1330	0930-1330	1660
	3	"	"	0930-1330	0930-1330	1530-1830	1530-1830	1630
April	2	0717	1726	1500-1800	1500-1800	1500-1800	1500-1800	1260
	3	"	"	0900-1800	1200-1500	0900-1200	1200-1500	1400
	4	"	"	1200-1500	1200-1500	0900-1200	0900-1200 1500-1800	1220
October	2	0552	1908	1300-1630	1300-1630	1300-1630 (weak)	1330-1630 (weak)	2200
	3	"	"	0730-1030	0730-1030	1030-1330 (fair)	0730-1330 (fair)	2000
	4	"	"	increasing	increasing	0430-0730	0430-0730	increasing

TABLE 6.2 The range of fluctuation of potential net production is represented by the ratio of the maximum rate divided by the minimum rate of P_c and P_c^B.

$P_{max}/P_{min} = (P_{c\ max}/P_{c\ min} + P^B_{c\ min}/P^B_{c\ min})/2$

L:D = light: dark hours; *not used to calculate P_{max}/P_{min}.

Expt	$P_{c\ max}/P_{c\ min}$	$P^B_{c\ max}/P^B_{c\ min}$	P_{max}/P_{min} (mean)	L : D
Jan	2.7	2.9	2.8	14,3 : 9,7
Mar	(24.1)*	12.4	12.4	12 : 12
Apr	7.3	7.5	7.4	11 : 13
Oct	3.2	3.6	3.4	13.2 : 10.8

In the January and March experiments the peak in P_i was in the morning, three and four hours after sunrise respectively. In April the peak was in the afternoon on day 2, whereas it spanned noon broadly on days 3 and 4. On day 2 of the October experiment the peak was in the early afternoon, but on day 3 it was in the morning, about three hours after sunrise.

P_i^B followed similar trends to P_i. In the January experiment P_i^B peaked before and after noon. Noon depressions were also apparent on day 2 in the April and October experiments but were not as prominent as in January.

6.3.6 Production under a constant light regime

Both net production (P_c) and net production per unit chlorophyll *a* (P_c^B) under a constant light regime generally show fluctuations similar to those under natural light. High values occur during daylight hours and low values at night (Fig. 6.6 and Table 6.1). However, in the October experiment this pattern is not clear. The high net production levels measured between days 2 and 3 are probably due to nitrate contamination (see Section 6.3.3) boosting net production and thus masking possible fluctuations.

In the January experiment a midnight peak in P_c^B (between days 1 and 2) was caused by low chlorophyll *a* concentration (Fig 6.4), not by an increase in P_c. Noon depressions in P_i^B (under natural light) were not prominent in P_c^B, although they were sometimes detectable.

6.3.7 Fluctuations in potential production (P_{max}/P_{min})

The extent to which P_c and P_c^B varied over 24 hours (during which time the parent population was exposed to a natural light regime) is expressed by the ratio P_{max}/P_{min} (the maximum production value divided by the minimum value). Mean daily minima and maxima for each experiment were used.

Results are summarized in Table 6.2. $P_{c\ max}/P_{c\ min}$ agrees with $P^B_{c\ max}/P^B_{c\ min}$ except in March when $P_{c\ max}/P_{c\ min}$ (24.1) was twice $P^B_{c\ max}/P^B_{c\ min}$ (12.4). As the greatest range reported in the literature is 1 to 12 (Doty and Oguri 1957), it is likely that the $P^B_{c\ max}/P^B_{c\ min}$ value of 12.4 in March is correct.

6.4 DISCUSSION

6.4.1 Photo-inhibition

Variations in phytoplankton production under a natural light regime in the present study can be partly explained in terms of ambient light levels. Production appears to increase with an increase in light until the phytoplankton is light saturated. In January high light levels at noon ($\sim$ 2000 μE.m^{-2}.s^{-1}) caused inhibition of photosynthesis and a depression in P_i^B. On day 2 in the October experiment slightly cloudy conditions at noon resulted in relatively weak depression of production. On day 3, however, production peaked before noon, and did not recover from the inhibiting noon light levels ($\sim$ 2000 μE.m^{-2}.s^{-1}) sufficiently quickly to generate an afternoon peak, probably because the high light levels were sustained for longer than in January. In April, whilst the P_i^B peaks spanned noon on days 3 and 4, the main peak on day 1 was in the late afternoon, following an early afternoon depression. It is unlikely that the maximum hourly light levels during this period ($\leqslant$ 1400 μE.m^{-2}.s^{-1}) were high enough to inhibit photosynthesis, suggesting that the depression in P_i^B on day 1 was not caused by photo-inhibition. The large range calculated for that particular production measurement indicates that the observed decrease may be an artifact.

In March P_i^B peaked in the late-morning and showed no obvious noon depression. It seems likely that the light levels in both March and April were too low to cause severe photo-inhibition. This is supported by the findings of Steeman Nielsen (1975) that on a bright day, maximum rates of photosynthesis are found at a depth at which about 30-50% of the surface light is found, whereas on a dull day the highest rates are found close to the surface. Brief periods (one to three hours) of cloud cover appear to play a minor role in the present study; a temporary decrease in light intensity due to cloud in January and October caused only minor changes in P_i^B.

6.4.2 Diel rhythms

That diel fluctuations are also apparent under a constant light regime suggests that something other than light

plays a part in regulating production rates. Doty and Oguri (1957) suggested a daily endogenous rhythm in the photosynthetic ability of phytoplankton. Yentsch and Ryther (1957) and Shimada (1958) explained periodicity in terms of chlorophyll *a* variation which was found to be dependent on light and varied diurnally with the intensity of solar radiation. Lorenzen (1963) found that the changes in chlorophyll *a* content were partially responsible for fluctuations in the rate of photosynthesis, but they were not large enough to account for the total fluctuations. He eliminated the effect of chlorophyll *a* by standardizing to unit biomass using the assimilation number (grams carbon assimilated per hour per gram chlorophyll *a* present at saturating light levels) as a measure of potential production. Persistent fluctuations demonstrated that, in addition to the variation caused by fluctuations in chlorophyll *a*, an independent factor (possibly an internal rhythm) was modifying the photosynthetic rate. Other workers have found either no variation in chlorophyll *a* (Eppley *et al*. 1971), or that chlorophyll *a* changes are not responsible for the observed rhythms (Hastings *et al*. 1961, quoted by Sweeney, 1969).

Present findings suggest that under natural and constant light regimes, variation in chlorophyll *a* was not responsible for the observed periodicity in net production. Chlorophyll *a* concentration was not dependent on light, nor did it vary diurnally with the intensity of solar radiation, contrary to the findings of Yentsch and Ryther (1957). Natural phytoplankton populations off the Cape Peninsula are largely dominated by diatoms (unpublished data) which are unlikely to change their chlorophyll *a* content in response to changes in light (Jorgensen 1964, Brown and Richardson 1968).

As found by Lorenzen (1963), variation in dark respiration (Fig. 6.5 and 6.6) is too small to be responsible for photosynthetic fluctuations. Temperature variations (Fig. 6.2) do not explain fluctuations as temperature and net production do not vary in sympathy.

Malone (1971) linked periodicity in production with geographic zone and size composition of the phytoplankton. He found no periodicity in temperate zones whereas in tropical

zones nannoplankton showed diel periodicity but netplankton did not. The present study area is considered a temperate zone and is dominated by diatoms which generally characterize upwelling ecosystems (Parsons 1979). Malone's hypothesis does not appear to apply in the southern Benguela region since definite periodicity has been demonstrated.

The existence of a rhythm regulating potential photosynthesis is no longer disputed (Sournia 1974). Two main hypotheses have been put forward to explain this phenomenon (Stross et al. 1973). The first, which may be called the "phasing" hypothesis, is that the photosynthetic potential oscillates in response to intrinsic organization of the cell with a light-dark cycle. The second or "forcing" hypothesis is that some time dependent deficiency (e.g. nutrients) or destructive action (e.g. photo-destruction) causes the oscillation.

Stross et al. (1973) tested these hypotheses and found that the photosynthetic rhythms could result from both an intrinsic and a forcing oscillation. The findings of the present study appear to support this view. First, that P^B_i and P^B_c show similar fluctuations suggests that the light history of the phytoplankton affects its photosynthetic ability. The phytoplankton "expects" a certain light regime and therefore regulates its photosynthetic mechanism accordingly. Second, nutrient concentrations have been found to influence the time of peak production. Newhouse and Knauer (quoted by Malone 1971) proposed that the time of peak photosynthetic rate in the ocean is a function of the availability of nutrients in the water, i.e. peak photosynthesis will be earlier in the day when nutrient concentrations are low (and presumably limiting), than when they are high.

Nitrate has been shown to be the primary limiting nutrient in the Cape Upwelling area. Primary production may be reduced by nitrate concentrations of less than 4-5 μg-at NO_3-N.ℓ^{-1} (Andrews and Hutchings 1980). In all four experiments the nitrate concentration was below 5 μg-at.ℓ^{-1} except on days 1 and 2 in April. It seems that the high concentrations on day 2 did not limit photosynthesis and were responsible for the afternoon peak in P^B_c. On days 3 and 4 the lower and presumably limiting concentrations appear to be responsible for

the earlier peaks. Even though low nitrates may have reduced production in the other three experiments, the expected morning peaks were not consistently found.

Plankton populations in upwelling areas do not attain the state of dynamic equilibrium found in stable oceanic waters. Phytoplankton growth rates tend to be more variable due to variation in availability of nutrients. In any one mass of upwelled water, luxury nitrate levels are unlikely to be maintained for more than three to five days (unpublished data obtained from a drogue study). After this, varying degrees of nitrate concentrations influence the periodicity of photosynthetic activity, the time of peak production may also vary. Ideally, one should maintain natural phytoplankton populations under a natural light regime at a range of different but constant nutrient levels (possibly using a chemostat) so that varying nutrient levels do not interfere with the investigation of rhythms.

In addition, at low production levels, the accuracy of the oxygen method of measuring production is decreased so that differences in production become increasingly difficult to measure. It might be advisable to use the more sensitive ^{14}C uptake method for such experiments.

6.4.3 Extent of diel fluctuations (P_{max}/P_{min})

Lorenzen (1963) found that day length and total radiation influenced the extent of variation in potential production, the largest variation ($P_{max}/P_{min} = 9$) occurring when day length approaches 12 hours. Previously Doty (1959) had correlated latitude with variation in P_{max}/P_{min} suggesting that the nearer the equator, the more regular the "pulsing effect" of the light-dark cycle. Lorenzen (1963) interpreted the variation as being due to differences in day length, irrespective of latitude. Indirectly, latitude effects P_{max}/P_{min} because of its effect on daylength.

In the present study P_{max}/P_{min} appears to be linked to the daily ratio of light: dark hours. The minimum P_{max}/P_{min} value (2.9) was in January (summer) when the difference in number of light and dark hours was greatest (14.3 light: 9.7 dark). The maximum P_{max}/P_{min} value (12.4) was in March

(autumn) when the number of light and dark hours were equal (12 light: 12 dark). P_{max}/P_{min} for the other two experiments were midway between the two extremes, i.e. 3.4 in October (13.2 light: 10.8 dark hours) and 7.4 in April (11 light: 13 dark hours). These findings confirm Lorenzen's (1963) theory that the highest P_{max}/P_{min} value occurs when day and night are of equal length and the lowest when day and night periods are most different.

6.4.4 Estimation of daily net production

Estimation of daily net production has proved to be difficult (Vollenweider 1969). Daily net production ($P_{i\ 24\ calc}$) can be calculated from any one short term *in situ* experiment in the following way:

$$P_{i\ 24\ calc} = (P_i . DT) - (R_i . NT)$$

where P_i = *in situ* net production (mg $C.m^{-3}.h^{-1}$)

R_i = *in situ* respiration (mg $C.m^{-3}.h^{-1}$)

DT = number of daylight hours

NT = number of darkness hours

This estimate varies with the time of incubation since the calculation assumes that the measurements are representative of all daylight hours. A more accurate, but impractical, way of measuring daily net production ($P_{i\ 24\ meas}$) is by using the mean hourly net production obtained from a series of short term incubations spanning a 24 hour period:

$$P_{i\ 24\ meas} = \frac{(\Sigma P_i).24}{n}$$

where n = the number of incubations in the 24 hour period. This value approaches the actual daily net production, thereby providing a comparison for calculated daily production. In the four experiments $P_{i\ 24\ meas}$ was obtained from sets of eight incubations spanning 24 hours. It was found to vary between 111 mg $C.m^{-3}.day^{-1}$ on day 3 in the March experiment and 1247

TABLE 6.3 Estimation of daily net production from individual short term measurements ($P_{i\ 24\ calc}$) and actualy daily net production ($P_{i\ 24\ meas}$) (see text). F and F^1 are factors for correcting $P_{i\ 24\ calc}$ and $P^B_{i\ 24\ calc}$ for diel variation in net production. $F = P_{i\ 24\ meas}/P_{i\ 24\ calc}$ and $F^1 = P^B_{i\ 24\ meas}/P^B_{i\ 24\ calc}$. 1/F and $1/F^1$ indicate by how much $P_{i\ 24\ meas}/P_{i\ 24\ calc}$ and $P^B_{i\ 24\ calc}$ over- or underestimate $P_{i\ 24\ meas}$ and $P^B_{i\ 24\ meas}$ respectively. High respiration rates resulted in very low or negative $P_{i\ 24\ calc}$ - these values (*) were not used in the calculation of mean correlation factors.

Expt	Time (SAST)	P_i				P^B_i			
		$P_{i\ 24\ meas}$	$P_{i\ 24\ calc}$	F	1/F	$P^B_{i\ 24\ meas}$	$P_{i\ 24\ calc}$	F^1	$1/F^1$
Jan	0600-0900	819	1141	0.72	1.39	74	83	0.89	1.12
(Day 2)	0900-1200	"	1140	0.72	1.39	"	92	0.81	1.23
	1200-1500	"	708	1.20	0.83	"	58	1.28	0.78
	1500-1800	"	579	1.41	0.71	"	86	0.86	1.16
March	0630-1030	226	358	0.63	1.59	24	54	0.45	2.22
(Day 2)	0930-1330	"	262	0.83	1.20	"	43	0.56	1.78
	1230-1630*	"	81	2.80	0.36	"	16	1.56	0.64
	1530-1930*	"	-83	-	-	"	-14	-	-
March	0630-1030*	111	19	5.85	0.17	17	4	4.67	0.21
(Day 3)	0930-1330*	"	27	4.12	0.24	"	5	3.50	0.28
	1230-1630*	"	-101	-	-	"	-14	-	
	1530-1930*	"	-214	-	-	"	-17	-	
April	0600-1000*	235	-17	-	-	41	-4	-	-
(Day 1)	0900-1300	"	153	1.54	.65	"	33	1.27	0.79
	1200-1600	"	87	2.69	.37	"	13	3.18	0.31
	1500-1900	"	292	0.81	1.24	"	52	0.79	1.26
April	0600-1000*	276	-145	-	-	113	-52	-	-
(Day 3)	0900-1300	"	178	1.55	0.64	"	69	1.64	0.61
	1200-1600	"	282	0.98	1.02	"	157	0.72	1.39
	1500-1900	"	223	1.24	0.81	"	51	2.22	0.45
April	0600-1000	192	122	1.58	0.63	33	15	2.17	0.46
(Day 4)	0900-1300	"	137	1.41	0.71	"	19	1.74	0.57
	1200-1600	"	75	2.56	0.39	"	12	2.67	0.37
	1500-1900*	"	-5	-	-	"	2	(15.14)	0.07
Oct	0430-0730*	662	188	3.52	0.28	59	15	4.01	0.25
(Day 2)	0730-1030	"	245	2.70	0.37	"	27	2.22	0.45
	1030-1330	"	400	1.66	0.60	"	34	1.73	0.58
	1330-1630	"	1109	0.60	1.68	"	99	0.60	1.68
	1630-1930	"	505	1.31	0.76	"	48	1.24	0.81
Oct	0430-0730*	1247	270	4.62	0.21	162	41	3.93	0.25
(Day 3)	0730-1030	"	1612	0.77	1.29	"	242	0.67	1.49
	1030-1330	"	1148	1.09	0.92	"	147	1.10	0.91
	1330-1630	"	953	1.31	0.76	"	108	1.50	0.66
	1630-1930	"	1117	1.12	0.90	"	122	1.33	0.75

mg $C.m^{-3}.day^{-1}$ on day 3 in the October experiment (Table 6.3).

A factor, $F(P_{i\ 24\ meas}/P_{i\ 24\ calc})$, was calculated to correct each short term estimate of daily production for diel variation. The reciprocal, 1/F, indicates by how much $P_{i\ 24\ calc}$ over- or underestimates the actual daily net production, $P_{i\ 24\ meas}$. Similarly, a second factor F^1, was calculated to correct $P^B_{i\ 24\ calc}$ (Table 6.3). Occasional high respiration rates produce large variation in F and F^1. These have been excluded from calculation of mean day time correction factors. Variation in F and F^1 when respiration rates are normal reflects differences in the time of peak in production and in P_{max}/P_{min}, and demonstrates the problem of obtaining reliable correction factors which can be generally applied. Mean correction factors for incubations before noon, spanning noon, and after noon were 1.2 (S.E. = 0.20, n = 10), 1.3 (S.E. = 0.16, n = 12) and 1.3 (S.E. = 0.18, n = 10) respectively. It appears that measurements before noon approximate daily production most closely. However the standard error (S.E.) of F is the smallest for the period spanning noon. Measurements over this period approximate daily production most consistently. These results emphasize the approximations of daily net production from short term experiments at the sea surface may be in error by as much as 200-300%.

Hammer *et al.* (1973), Anderson (1974) and Gargas *et al.* (1979) found that extrapolations from short term (two to four hour) incubations to full day productivity estimates result in large errors. It seems that longer incubation periods better approximate mean rates of production for predicting daily rates, because they smooth out the effects of temporary changes in weather conditions as well as diel changes in incident light and in the actual and potential production of the phytoplankton.

As pointed out in Chapter 2, rates of production vary with duration of incubation when using the ^{14}C uptake method, but not when using the oxygen method. An incubation period of longer than four hours would seem inadvisable for the ^{14}C method. For the oxygen method, however, the time of incubation is limited by the extent of oxygen saturation of the incubating samples or merely by the time available. Many workers use either the period from dawn to noon or noon to dusk. When

measuring the penetration of light into the sea one should wait until the sun is at least 30° above the horizon (Strickland 1958). This would not be possible if the incubation was started at dawn. By choosing either morning or afternoon for incubation, one could miss the peak in production, whereas the period spanning noon should cover at least part of it. Thus a convenient period would be the six hours spanning noon. This usually allows enough time to establish sampling depths based on percentage light levels and take the necessary water samples.

This study on diel variation is based on experiments at the sea surface only. MacCaull and Platt (1977) found that the rhythm in the assimilation number (P_m^B) is still pronounced at the 22% light depth (5 metres) above which at least three-fourths of the production in the euphotic zone occurs. However, Saijo and Ichimuro (1962), Harris (1973) and Fee (1975) found that diel fluctuation in productivity is generally confined to the surface layer.

On correcting for diel variation down the water column, Goldman (1961), Allen (1973) and Fee (1975) found that estimates of annual integrated production are reduced by between 4% and 20%. Fee (1975) suggested that errors associated with sampling and data analysis frequently exceed the correction for integrated diel variations.

Because variation in ambient light decreases with depth, the "pulsing effect" of the day-night cycle is reduced. This should cause P_{max}/P_{min} to decrease with depth. Thus the effects of diel variation in production are likely to be less significant in the whole euphotic zone than at the surface alone. However, the existence of such a rhythm should not be ignored, and the times of incubation should be chosen to minimize the effects of the rhythm on estimates of daily production.

Gargas *et al.* (1979) formulated a model to reduce the error in estimating daily production arising from differences in time collection, and to enable production to be calculated for any hour of the day. However, the model is based on the assumptions that variation in production is sinusoidal, that production at noon is twice that at these times. The authors point out that the equation is an empirical one based

on conditions in the Baltic Sea in September, and that it should be verified for other times of the year and for other bodies of water. Present data suggest that a more complex model might be necessary to predict either daily production or production at specific times of the day in the Cape upwelling region since incident light, the light history of the phytoplankton and nutrient levels all appear to influence variation in production rates during the day.

6.5 SUMMARY

Production under natural and constant light regimes shows diel fluctuations at different times of the year. The extent of fluctuation (P_{max}/P_{min}) is greatest when day and night are of equal length, and smallest when day and night periods are most different.

The time of peak production appears to be related to previous and ambient light conditions in addition to nutrient concentrations.

Comparisons of daily net production estimates ($P_{i\ 24\ meas}$) obtained from a series of short term experiments over 24 hours with estimates calculated from single experiments ($P_{i\ 24\ calc}$), show that the latter may result in errors of up to 200-300%. Differences in the time of peak production make it impossible to give reliable correction factors which can be generally applied. However it is likely that diel variation in net production decreases with depth, so that its effect on integrated daily production is greatly reduced. Nonetheless, it is suggested that the time of incubation should span noon to minimize the effect of the diel rhythm on production.

CHAPTER 7

PHYTOPLANKTON PRODUCTION AND BIOMASS IN THE COASTAL WATERS OF THE CAPE PENINSULA

7.1 INTRODUCTION

The intense, wind-induced upwelling of cold, nutrient-rich, Atlantic Central water causes dense phytoplankton blooms to form off the Cape Peninsula, particularly from spring to autumn.

Primary production in upwelled water is influenced by several factors such as source water, seeded material, previous and current light levels and nutrient concentrations, and the stability of the water column (Barber and Smith 1980). At present few of these factors are well described for the southern Benguela Current. Andrews and Hutchings (1980) found high rates of potential gross production off the Cape Peninsula at stations 22 and 50 kilometres northwest of Duiker' Point with nitrate as the limiting nutrient. Although their measurements did not allow in situ production to be estimated, they showed a rise in potential production in summer, and that phytoplankton below the 1% light level is often potentially active.

In this chapter, changes in primary production associated with changes in the upwelling system are investigated. A comparison is drawn between an extremely active upwelling site (Oudekraal) and a site which is only indirectly affected by upwelling (Robben Island). An attempt is made to determine the factors responsible for variation in phytoplankton biomass expressed as chlorophyll a, net production (P), and net production per unit of chlorophyll a (P^B).

7.2 METHODS

Wind

Andrews and Hutchings (1980) found that, in the vicinity of the Cape Peninsula, wind is closely related to upwelling. Winds blowing between south and east are favour-

able for upwelling, northerly and westerly winds cause downwelling while those from SSW and WSW, and NNE and ENE have negligible effect. They found good correlation between wind directions measured at the Cape Point lighthouse and on ships off the Peninsula, but wind speed recorded on the ships was 40% lower.

When primary production measurements were made in the present study, wind speed and direction were recorded daily at 10h00, but from August 1978 they were also recorded hourly from 10h00 to 15h00. Continuous measurements were not possible because the vessel returned to port each afternoon and there were no wind recorders on shore. Consequently wind data recorded at the Cape Point and Robben Island light houses are used in conjunction with Oudekraal and Robben Island oceanographic data respectively. Mean 12-hourly wind stress factors were calculated in a similar manner to that of Andrews and Hutchings (1980), except that S-SW winds were included in the "upwelling" or offshore winds at Oudekraal but not at Robben Island. The orientation of the coast at Oudekraal ($\sim 230^{\circ}$) is such that south-westerlies are long shore and thus capable of causing upwelling (Jury 1980) (See Fig. 1.1). The correction factor used by Andrews and Hutchings was not applied to the wind data from Cape Point because, according to Jury (1980), winds at Oudekraal are stronger due to the funnelling effect of the mountain ridge on the Peninsula. Wind data collected simultaneously at the Cape Point light house and from the ship stationed at Oudekraal generally agreed, except on certain occasions when a strong south-east blew at Cape Point but not at Oudekraal. On some of these occasions temperature profiles and the clarity of the water showed active upwelling at Oudekraal and on other occasions, downwelling. The upwelling may either have been induced by entrainment into the wind-driven upwelling plume south of Duiker Point, or may have been due to the lag in the effect of the wind on upwelling at Oudekraal, as Jury (1980) found marked diel variation in wind stress. Strong south-east winds would sometimes blow at night and drop in the morning (diel variation in wind was not observed at Cape Point). Downwelling would normally be expected when the wind stops. Even if strong wind persisted

in the south, clockwise rotation of the south-east caused by an increase in wind towards the south-west (positive wind curl) could also aid downwelling at Oudekraal. It is clear that the close agreement between wind and upwelling observed by Andrews and Hutchings (1980) does not always apply to locations close inshore.

The proximity of the light house and its position close to sea level ensured that wind data from Robben Island were more representative of that study area than the Cape Point data were of the Oudekraal site.

Temperature

Conventionally changes in density with time are used to define upwelling but because of the close relationship between temperature and density in this region (Bang 1973), the uplift of isotherms was considered to be indicative of upwelling (Andrews and Hutchings 1980).

Light

Daily measurements of global and diffuse radiation ($maW.m^{-2}.day^{-1}$) and of sunshine hours at D F Malan airport, about 24 kilometres from both sampling sites, were supplied by the SA Weather Bureau. Incident light ($\mu E.m^{-2}.s^{-1}$) during production experiments was measured on the vessel.

Integration of measurements down the water column

Discrete measurements of net production, chlorophyll *a* and nitrate concentrations were linearly integrated either to the depth of the 1% light level ($D_{1\%}$) (which often coincided with the compensation depth (D_c) or to the bottom of the mixed layer (D_{ML}) when $D_{1\%}$ was deeper than D_{ML}. D_{ML} was selected at the midpoint of the thermocline if the inflection was sharp, or just above the bottom of the thermocline if it was indistinct.

Data Analysis

A stepwise multiple regression analysis was used to investigate factors related to variation in chlorophyll *a*, net production and net production per unit chlorophyll *a*.

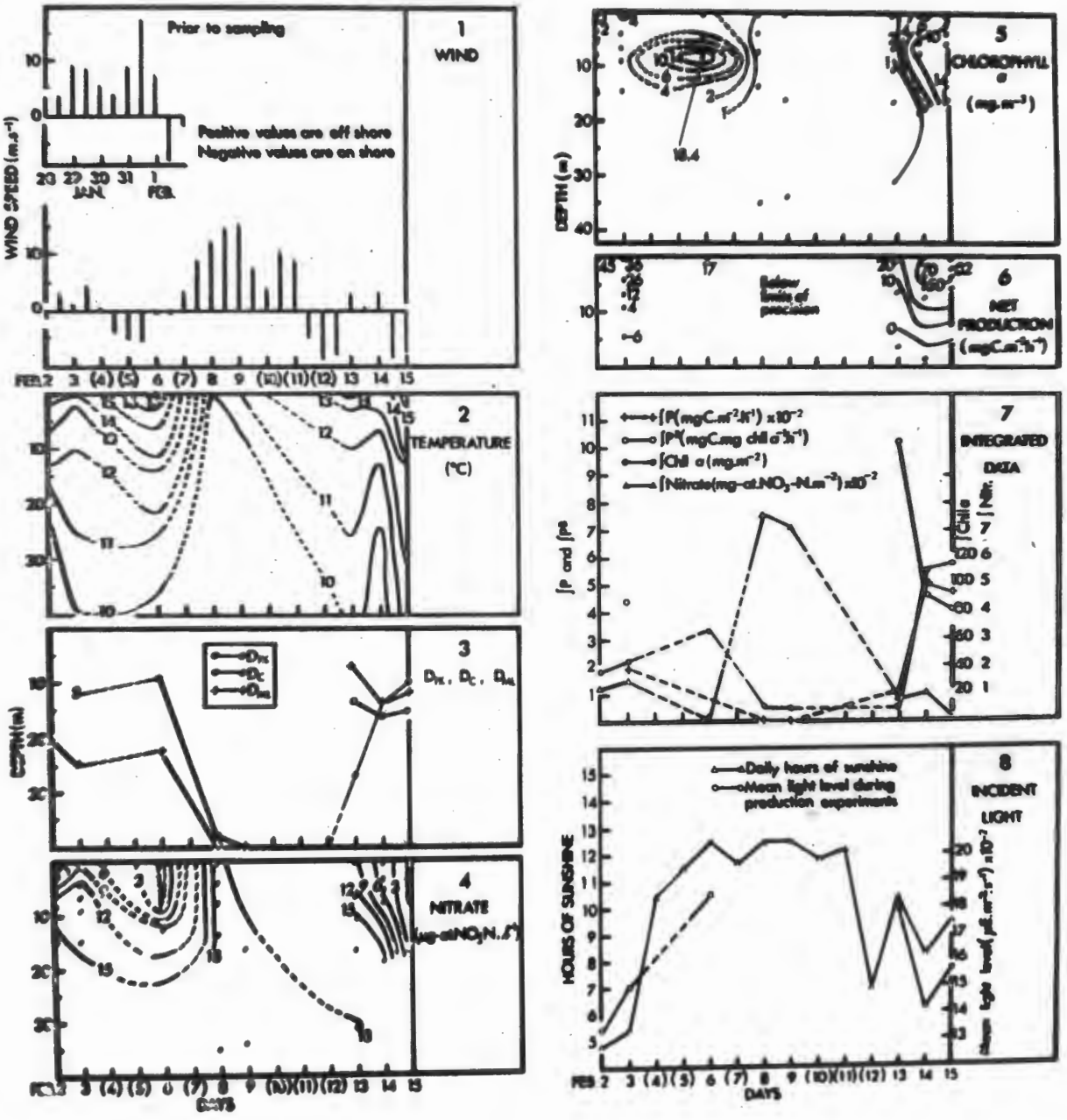

Fig. 7.1

Oudekraal (upwelling season) 2 - 15 Feb 1978. Dates on which there was no sampling are in brackets. Broken lines indicate lack of data. $D_{1\%}$ = depth of 1% light level. D_{ML} = depth of mixed layer, D_c = compensation depth, $\int P$ = integrated net production, $\int P^B$ = integrated net production per unit chlorophyll *a*, $\int$Chll *a* = integrated chlorophyll *a*, $\int$Nitr = integrated nitrates.

7.3 RESULTS AND DISCUSSION

7.3.1 Time series

Data have been selected to illustrate changes in the physical, chemical and biological states of the water column during the upwelling season at Oudekraal (Fig. 7.1) and Robben Island (Fig. 7.2) and in winter at Oudekraal (Fig. 7.3).

Oudekraal (upwelling season) 2-15 February 1978

At Oudekraal the wind was variable (Fig. 7.1.1). Wind reversals can occur four or five times per month and the wind direction is seldom consistent for more than four to six days (Andrews and Hutchings 1980). On the first day of the sampling period (2 February) the wind direction changed from a mild onshore to an offshore wind. As can be seen from the temperature data in Fig. 7.1.2 this caused slight upwelling. Between 4-6 February a strong offshore blow lasting four days commenced and caused intense upwelling. This disrupted the thermocline and brought 10°C water to the surface. On 12 February the wind reversal to onshore depressed the isotherms and a thermocline developed. Subsurface isotherms (~8 metres) rose in response to a weak offshore wind on 13-14 February but dipped again on 15 February with north-westerly winds.

An effect of the intense upwelling between 6-8 February was a sharp drop in the depths of the 1% light level and of the mixed layer (Fig. 7.1.3). When production was measured at this time the compensation depth lay close to the 1% light depth.

Nitrate concentrations (Fig. 7.1.4) are closely linked to up- and downwelling and vary inversely with temperature. High concentrations (~20 $\mu g\text{-at } NO_3\text{-N} . \ell^{-1}$) were recorded during upwelling on 8 February.

During pronounced upwelling chlorophyll *a* concentrations were low (< 1 mg.m^{-3}) (Fig. 7.1.5). They increased with increasing temperature and high subsurface maxima developed in aged upwelled water on 6 February and 14-15 February.

Net production (Fig. 7.1.6) appeared to be inversely related to nitrates and temperature, and was positively related

to chlorophyll a. It was lowest in upwelling water (8-9 February), when levels were too low to measure accurately and highest in aged upwelled water (15 February). On stabilization of the water column (13 February) net production was highest at the surface. On 14 February a subsurface maximum developed at about 3.5 metres and on the next day productivity was highest at 2 metres. Subsurface production maxima on 14-15 February were shallower than chlorophyll a maxima, suggesting that self shading limited phytoplankton production.

Fig. 7.1.7 shows that integrated net production ($\int P$) and biomass ($\int$ chll a) in the euphotic zone were low during upwelling but increased as downwelling proceeded (13-15 February). Because of the inaccuracy of production measurements at low levels, net production per unit biomass ($\int P^B$) could not be estimated during upwelling. When production attained measurable levels on 13 February P^B was high but decreased on 14-15 February, possibly because of nitrate limitation (Fig. 7.1.4). Despite the decrease in average photosynthetic activity ($\int P^B$), population growth (shown by an increase in chlorophyll a) caused an increase in net production.

Thus net production appears to be linked to wind, temperature, the depths of the mixed layer and 1% light level and nitrate and chlorophyll a concentrations. The number of sunshine hours per day and the mean light level during production experiments (Fig. 7.1.8) appears not to influence production or biomass. This suggests that incident light does not limit the rate of production in the water column significantly during the upwelling season.

Robben Island (upwelling season) January - March 1979

Strong offshore (south-east) winds blew before sampling commenced at Robben Island in January and before and during the Jan/Feb sampling period (Fig. 7.2.1). There was comparatively little wind in February and March. Isotherms showed little response to wind and a thermocline persisted throughout the sampling period despite strong offshore winds between 27-31 Jan (Fig. 7.2.2). Surface temperature varied between 12.6 and 15.0°C. Fig 7.2.3 shows that the 1% light depth

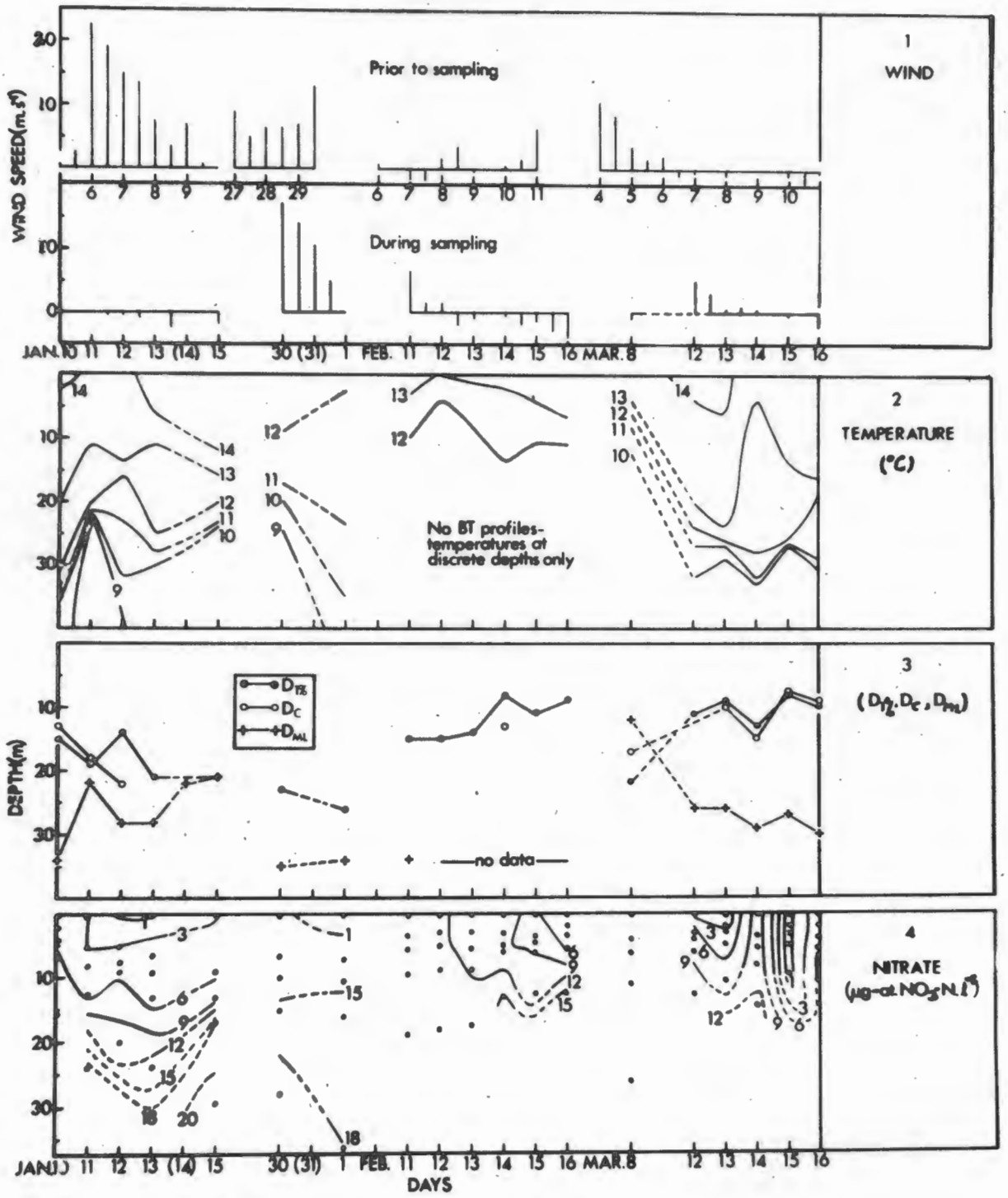

Fig. 7.2
Robben Island (upwelling season) Jan - March 1979.
As in Fig. 7.1

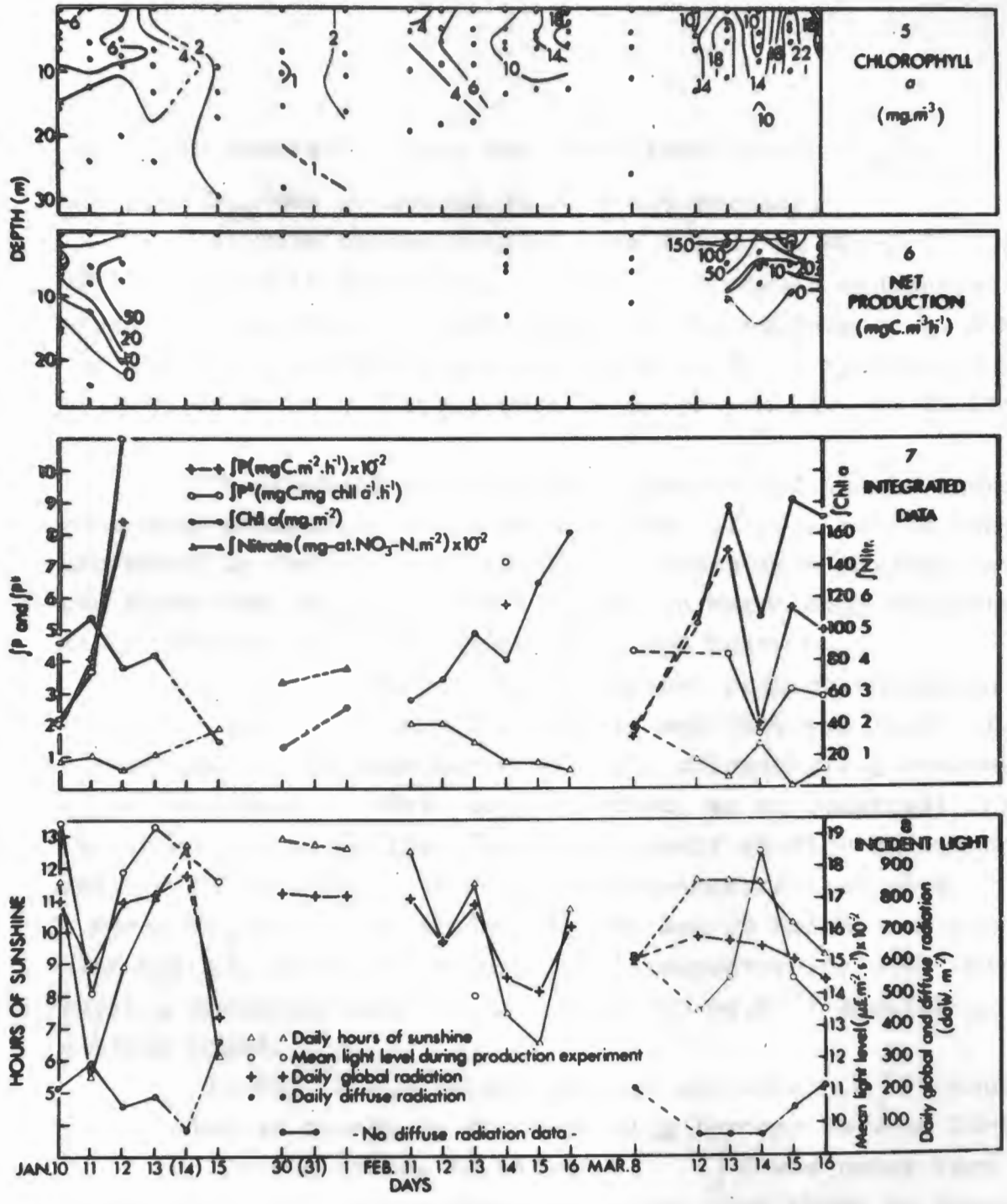
5
CHLOROPHYLL
a
(mg.m³)
DEPTH (m)
6
NET
PRODUCTION
(mgC.m⁻³h⁻¹)
7
INTEGRATED
DATA
∫P(mgC.m⁻².h⁻¹)x10⁻²
∫Pᴮ(mgC.mg chl a⁻¹.h⁻¹)
∫Chl a(mg.m⁻²)
∫Nitrate(mg-at.NO₃-N.m⁻²)x10⁻²
∫P and ∫Pᴮ
∫Chl a
∫Nitr.
8
INCIDENT LIGHT
HOURS OF SUNSHINE
Mean light level(μE.m⁻².s⁻¹)x10⁻²
Daily global and diffuse radiation
(daW. m⁻²)
△ Daily hours of sunshine
○ Mean light level during production experiment
+ Daily global radiation
• Daily diffuse radiation
- No diffuse radiation data -
JAN.10 11 12 13 (14) 15 30 (31) 1 FEB. 11 12 13 14 15 16 MAR.8 12 13 14 15 16
DAYS

Fig. 7.2 cont.

($D_{1\%}$) was generally above the mixed layer depth (D_{ML}); the mean $D_{1\%}$ was 15 metres (S.D. = 5.6 metres).

Nitrate concentrations were < 1 µg-at NO_3-N.ℓ^{-1} on 12-13 Jan and 15 March (Fig. 7.2.4). Although concentrations of up to 15 µg-at.ℓ^{-1} were found at the surface (e.g. 8 March) the very high concentrations (~20 µg-at.ℓ^{-1}) typical of upwelling water at Oudekraal were found only below the 1% light depth.

Chlorophyll a was evenly distributed in the euphotic zone when concentrations were low (Fig. 7.2.5), but as they increased in January and February, a subsurface maximum developed above the 1% light level whereas in March high concentrations (8-25 mg.m^{-3}) were both above and below $D_{1\%}$.

Fig. 7.2.6 shows subsurface net production maxima shallower than chlorophyll a maxima, and that the depth of the net production maximum decreased when chlorophyll a concentrations increased. This suggests that, as at Oudekraal, production appeared to be light limited by self shading during downwelling conditions. When nitrate concentrations were 1 µg-at NO_3-N.ℓ^{-1} on 12 Jan, 13 Jan and 15 March, net production was 19, 2 and 181 mg C.m^{-3}.h^{-1} respectively, with chlorophyll a concentrations (7.0, 1.4 and 25 mg.m^{-3}) showing a similar trend.

In Fig. 7.2.7 integrated net production ($\int P$) usually showed similar trends to chlorophyll a (except between 10-12 Jan) and inverse trends to nitrates. $\int P$ was never very low and attained values considerably higher than those at Oudekraal.

Incident light presented in Fig. 7.2.8 showed little influence on rates of production or chlorophyll a suggesting that, as at Oudekraal, it was not a limiting factor during the upwelling season.

Oudekraal (winter) 4-12 July and 22-23 Aug 1978

In winter onshore (north-west) winds dominate in the vicinity of the Cape Peninsula (Andrews and Hutchings 1980). However, there were strong south-east winds before and during July and August sampling periods at Oudekraal (Fig. 7.3.1) but these had little effect on the isotherms (Fig. 7.3.2). The temperature varied from between 10-11°C to 13.6°C so that

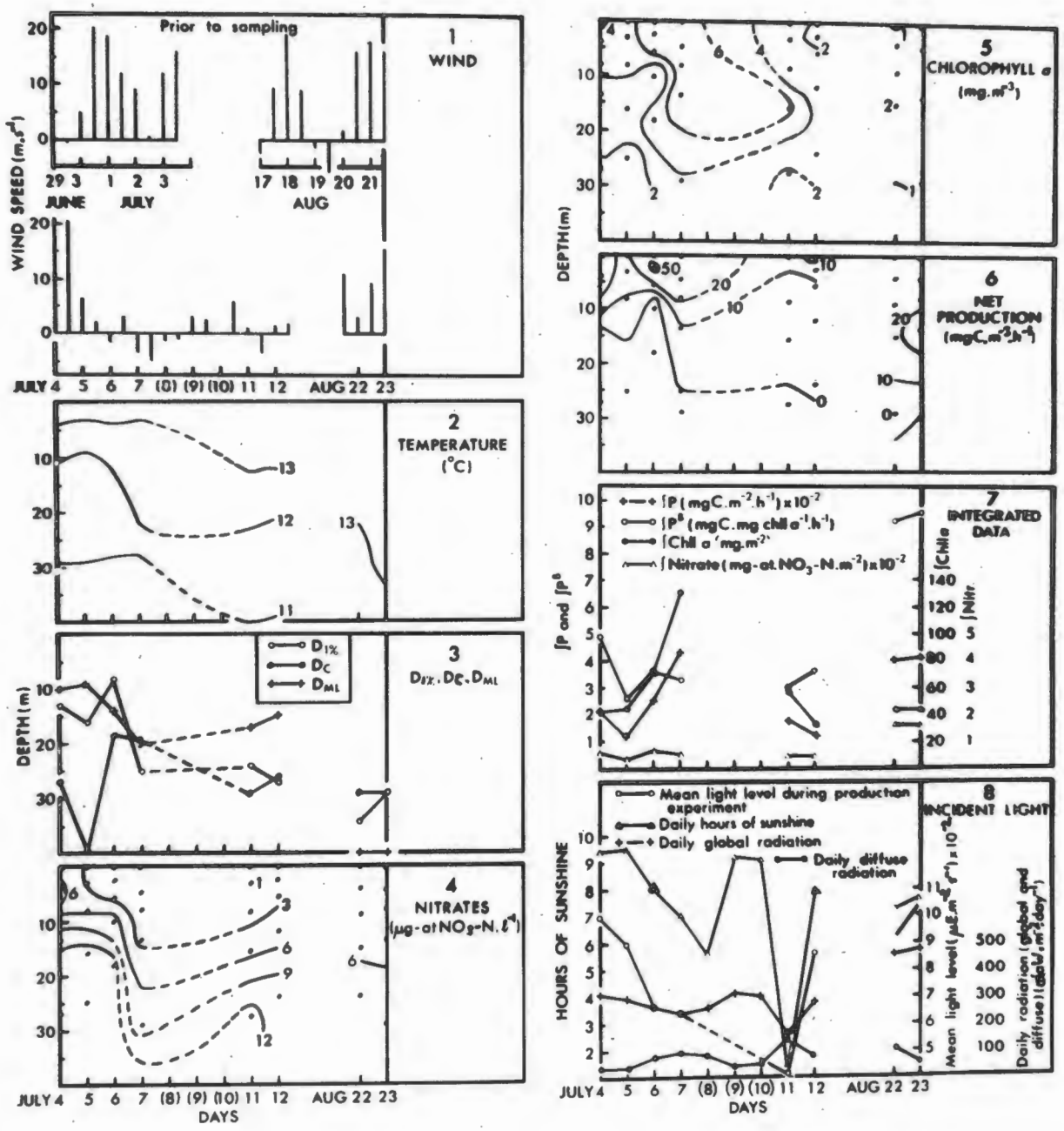

Fig. 7.3
Oudekraal (winter) July - Aug 1978.
As in Fig. 7.1

water of 10°C and less was absent even close to the bottom. There was a thermocline in July at 14 metres but not in August. The 1% light level and compensation depths were generally below the bottom of the mixed layer.

Figs 7.3.4 and 7.3.5 show intermediate nitrate and chlorophyll a concentrations. Neither the very low nor high concentrations common during the upwelling season were found. Net production estimates at discrete depths (Fig. 7.3.6) did not reach levels as high as those during the upwelling season; but integrated net production (Fig. 7.3.7) was more consistent and attained maximum levels similar to those measured during downwelling in summer. Above the compensation depth discrete net production estimates showed no consistent trends with temperature, nitrate concentration or depth (including relative light levels).

Incident light presented in Fig. 7.3.8 shows little influence on chlorophyll a or the rate of production. However levels were generally lower than during the upwelling season.

7.3.2 Wind

At Oudekraal offshore winds can cause intense upwelling with a response time of as little as four hours (Jury 1980). The less pronounced response of isotherms to offshore winds at Robben Island may be partially explained by the overall wind pattern in the area. The south-east wind blowing over False Bay splits into two branches on either side of Table Mountain (Jury 1980). The seaward branch (the Bakoven Downslope Jet) rises over the ridge of mountains on the Cape Peninsula and descends near Oudekraal. The landward branch (the Cape Flats Jet) flows east of Table Mountain towards Milnerton on the mainland opposite Robben Island (see Fig. 1.1). It appears that Robben Island sometimes lies in the "wind shadow" of Table Mountain and at other times on the west edge of the Cape Flats Jet, depending on the exact direction of the wind. In either case the core of the jet lies east of Robben Island and the resultant upwelling plume is directed off the mainland coast further north. Even when the south-east wind at Robben Island is strong, it does not cause active upwelling, probably because the wind further east is even stronger. The difference in wind

velocities (negative wind curl) may result in less intense upwelling and may even cause downwelling due to the formation of eddies on the edge of the plume. The complexity of water circulation patterns in the Table Bay area (van Ipperen 1971) may explain the high variability observed in nitrate and chlorophyll *a* concentrations at Robben Island. Nutrient rich water which upwelled further north or south may be introduced horizontally by eddies into the euphotic zone at Robben Island.

Sea conditions are more uniform along the coast in winter. Periodic storms with north-westerly winds mix the water column down to the bottom and prevent water of less than 10°C from intruding close inshore so when strong south-east winds do blow the biological consequences of upwelling are not the same as in summer.

7.3.3 Nutrient limitation of phytoplankton

Andrews and Hutchings (1980) showed that nutrient limitation starts manifesting itself on phytoplankton production per unit biomass (P^B) at nitrate concentrations of 4-5 µg-at NO_3-N.ℓ^{-1}; in fact, the highest chlorophyll *a* and net production levels were attained under these conditions. Only on one out of the nine occasions during this period when nitrate concentrations were <1µg-at.ℓ^{-1} was production reduced to levels below the limits of measurement (25 Jan 1978) (not shown).

At Robben Island nitrate concentrations of <1µg-at.ℓ^{-1} encountered between Jan-March 1979 show different stages of the effects of nitrate depletion (Fig 7.2.4). On 15 March chlorophyll *a* (25 mg.m^{-3}) and net production (181 mg C.m^{-3}.h^{-1}) attained maximum levels despite low nitrates (Figs. 7.2.5 and 7.2.6). On 12 Jan net production (19 mg C.m^{-3}.h^{-1}) appeared to be suppressed and the chlorophyll *a* concentration (7 mg.m^{-3}) was moderately low. A decrease in P^B in the three examples (7, 2.8, 1.4 mg C.mg chll a^{-1}.h^{-1}) shows that the photosynthetic activity of the phytoplankton was also reduced. Although the measurements were not made sequentially on the same water body, they suggest that during initial periods of depletion phytoplankton cells may use their nitrate reserves (Parsons *et al.* 1977) so that there is a lag on the effect of nitrate depletion. The frequency of upwelling off the Cape Peninsula probably prevents

the brief periods of nitrate depletion from noticeably suppressing production in the nearshore region. Consequently the duration of nitrate depletion is important when considering its effect on the rate of production and biomass of phytoplankton.

The difference in production and biomass between 12-13 Jan and 15 March may also be attributed to the dominating phytoplankton species. In January the diatom, Thalassiosira aestivalis, was dominant whereas in March an unidentified, naked microflagellate was dominant (Barlow, pers. comm.). Flagellates can attain high biomass production levels at low nutrient concentrations because of their favourable surface : volume ratio and their ability to migrate to below the nutrient depleted zone, absorb nutrients and then swim to the surface to photosynthesize. Some flagellates also have a lower half-saturation constant (k_s) for the uptake of nitrate than do diatoms (Eppley et al. 1969). These attributes may partially account for the higher biomass and net production in March.

In winter, nitrate concentrations at Oudekraal (Fig. 7.3.4) were more uniform than during the upwelling season, ranging between 1-8 µg-at $NO_3N.\ell^{-1}$ in the mixed layer. Although there appeared to be no definite upwelling in winter, nutrients would have been frequently introduced into the upper layers during storms. It seems likely that mixing and reduced insolation in winter together prevent the build up of phytoplankton stocks and the subsequent depletion of nitrates both at Oudekraal and Robben Island.

7.3.4 Phytoplankton in upwelling water

A lag of variable duration between upwelling and the apparent onset of phytoplankton growth has been observed both locally and in other upwelling areas (Barber and Smith 1980). The instability of the water column during upwelling is unlikely to limit production at Oudekraal because the clarity of the water ensures sufficient light for photosynthesis throughout the water column. However, stabilization of the water column generally precedes the observable onset of phytoplankton growth. Conditions governing the duration of the lag are not known but

may be attributed to low concentrations of phytoplankton in the source water, the presence or absence of growth stimuli or inhibitors, the light history of the phytoplankton in the source water, or the species composition.

The water that upwells at Oudekraal once the surface water has been moved offshore, is typically between 8 and 10°C, has a chlorophyll a concentration of <1 mg.m^{-3}, a high nitrate concentration and a very low rate of production. As upwelling persists, the temperature and chlorophyll a concentration of the water decrease while the nitrate concentration and clarity of the water increase.

On three occasions chlorophyll a concentrations of >1 mg.m^{-3} (up to 18 mg.m^{-3}) were found in upwelling water of <10°C (not shown in Figures). In Nov 1977 no production measurements were made but on 20 Jan and 7 Dec 1978 there was active growth in the upwelling water. Abnormally high chlorophyll a levels were unlikely to be due to a high chlorophyll a content of the source water because the chlorophyll a concentration near the bottom was <1 mg.m^{-3}.

In Nov 1977 high chlorophyll a concentrations (10-15 mg.m^{-3}) in relatively cool (10-11°C) water above a shallow thermocline suggested a short lag between upwelling and growth. Closely spaced successive bouts of up- and downwelling caused by short south-east blows alternating with calm spells would allow intense growth close to the shore. The high chlorophyll a concentration in the upwelling water (<10°C) may be attributed to mixing of upwelling and "growing" water, or to unusually active growth of phytoplankton. The upwelling water may have moved in and out of the euphotic zone several times with the phytoplankton becoming conditioned to high light levels and growing actively before the water was warmed at the surface. In most cases, however, both chlorophyll a concentration and net production were very low in upwelling water at Oudekraal.

7.3.5 Phytoplankton in stabilized water

On stabilization of the water column the evenly distributed phytoplankton stocks increase and rates of production reach measurable levels. At the onset of growth, even though

net production may not be very high, net production per unit biomass (P^B) should be at its highest (e.g. 13 Feb 1978, Fig. 7.1.7. Once nitrate concentrations are reduced to limiting levels ($\sim$4-5 µg-at $NO_3N.\ell^{-1}$), P^B decreases, but overall net production continues to increase due to an increase in population (e.g. 14 Feb 1978, Figs. 7.1.5 and 7.1.7. To begin with, production is highest near the surface and decreases down the water column. Consequently the effects of nutrient depletion are manifest first near the surface so that subsurface production and chlorophyll a maxima usually develop. As chlorophyll a concentrations increase the depth of the production maximum decreases, probably because of self shading (e.g. 14-15 Feb 1978, Figs. 7.1.5 and 7.1.6). This indicates that light limitation induced by self shading becomes an important factor limiting phytoplankton in aged upwelled water.

Once nitrates have been depleted and the nitrate reserves in the cell used up, net production is limited and consequently phytoplankton stocks are reduced (e.g. 13 Jan 1979, Figs. 7.2.4 - 7.2.6). This condition is likely to be more common further offshore as nitrates are more frequently replenished by upwelling in the nearshore area.

High chlorophyll a concentrations are sometimes found below the 1% light level (e.g. March 1979, Fig. 7.2.5). This may be caused by photoplankton sinking in the calm conditions that generally prevail at Robben Island in autumn. That high concentrations were also maintained near the surface may have been due to the influx of nutrients by horizontal mixing, or by regeneration of nutrients by zooplankton which tend to be more abundant in autumn (Hutchings 1979).

Integrated net production in the euphotic zone at Robben Island was seldom very low and attained levels considerably higher than those at Oudekraal. This was probably because of the stabler water column at Robben Island. Incident light levels were high and nitrate concentrations seldom limiting at both sites. Conditions at Robben Island were probably similar to those prevailing further offshore in the upwelling plume emanating from Oudekraal.

7.3.6 Factors affecting phytoplankton biomass and production

An attempt was made to relate factors that might be responsible for variation in biomass (chlorophyll *a*), net production (P) and net production per unit biomass (P^B) using a stepwise inclusion of ecological parameters into a multiple regression equation (Allen and Learn 1973).

The ecological parameter (free variable) explaining the largest proportion of variance in the independent variable in question (chlorophyll *a*, P or P^B) entered into the model first and the other parameters entered subsequently in order of their importance. Likely ecological parameters were selected for examination if they could be expressed quantitatively. Each parameter was plotted against the dependent variables and those which showed a definite relationship were used in the models. Care was taken not to use free variables which were highly correlated with one another as this would weaken the analysis.

Parameters selected for examination were: temperature, salinity, light and nitrates for chlorophyll *a* and P^B, as well as chlorophyll a and the extinction coefficient (k) for P. Light data were available in two forms; as a percentage of the light intensity immediately below the sea surface (percentage light) and as the mean ambient light level (ambient light) during the period that production samples were incubated (usually between 12h00 and 16h00). Because these two were highly correlated they were used separately in different models. The effect of temperature on biomass and production did not appear to be linear and, therefore, an additional temperature term (temperature squared) was included in the analyses. Chlorophyll *a* and the extinction coefficient which were highly inter-correlated were used separately in different models for P.

Tables 7.1 - 7.2 and 7.3 - 7.4 list the parameters in order of their entry into the analyses and show the percentage of the total variance in biomass and production, that was accounted for by each parameter (explained variance). Only parameters significant at the 95% confidence level were included in equations.

TABLE 7.1: Explained variance of phytoplankton biomass (chlorophyll a) at Robben Island and Oudekraal with stepwise inclusion of ecological parameters in the regression equation. Parameters selected for examination were nitrates ($\mu g.at.NO_3\text{-}N.\ell^{-1}$) salinity (‰), temperature(°C), temperature squared $(°C)^2$ and percentage light. The final regression coefficients and constants are displayed. The number of observations (n) used in the analysis is indicated (* = equation significant at the 1% level) Equations are of the form: $Y=b_1V_1+b_2V_2+b_3V_3+Constant$ where b_1, b_2, b_3 are the coefficients of "free" variables V_1, V_2, V_3.

	Robben Island (upwelling season)	Oudekraal (upwelling season)	Oudekraal (winter)	All data
1st variable selected	Nitrate*	Nitrate *	Salinity *	Nitrate*
Explained variance (%)	21.4	36.1	23.6	27.9
Coefficient (b_1)	-0.559	-0.429	8.548	-0.436
2nd variable selected	$(Temp)^2$ *	% light *		% light*
Explained variance (%)	7.0	2.9		3.2
Coefficient (b_2)	-0.001	-0.022		-0.025
3rd variable selected	Temp			
Explained variance (%)	3.2			
Coefficient (b_3)	1.105			
Constant	-0.644	9.700	-297.335	10.013
n	133	379	56	568

TABLE 7.2: As in Table 7.1 except the percentage light parameter was replaced by ambient light ($\mu E.m^{-2}.s^{-1}$).

	Robben Island (upwelling season)	Oudekraal (upwelling season)	Oudekraal (winter)	All data
1st variable selected	Salinity *	Nitrate *	Salinity *	Nitrate *
Explained variance (%)	16.5	37.5	42.2	24.9
Coefficient (b_1)	-48.428	-0.441	13.490	-0.521
2nd variable selected	Nitrate *	Amb. light *		Salinity *
Explained variance (%)	19.8	3.9		8.1
Coefficient (b_2)	-0.674	-0.0017		-12.356
3rd variable selected	Amb. light			Amb. light *
Explained variance (%)	6.5			4.3
Coefficient (b_3)	-0.0030			-0.002
Constant	1699.249	11.003	-471.420	442
n	88	198	47	333

Data were grouped for analysis in four ways:

(i) data collected during the upwelling season at Robben Island;

(ii) data collected during the upwelling season at Oudekraal;

(iii) data collected in winter at Oudekraal, and

(iv) all data collected at Robben Island and Oudekraal.

Biomass (chlorophyll a)

From Tables 7.1 and 7.2 it is clear that nitrates explained the most variance in chlorophyll a during the upwelling season at Oudekraal (~36%) and Robben Island (~20%). The coefficient was negative, indicating a depletion of nitrates with an increase in the phytoplankton population.

A further 3% of the variance at Oudekraal (upwelling season) was explained by percentage light (4% by ambient light). At Robben Island different parameters emerged when percentage or ambient light was used in the model, suggesting that nitrates, temperature, salinity and light all influence phytoplankton biomass in that area. In winter at Oudekraal, however, the only significant parameter was salinity (24-42%).

Net production (P)

Table 7.3 shows that chlorophyll a explained most of the variance in net production at Robben Island (35%) and at Oudekraal in winter (38%); but at Oudekraal in the upwelling season, nitrates explained more variance (32%), followed by chlorophyll a (14%) and ambient light (8%). Temperature explained 22% of the variance at Oudekraal in winter, whereas at Robben Island ambient light explained 4%.

In the second set of models (Table 7.4) chlorophyll a was replaced by the extinction coefficient, k, which generally explained more of the variance in P than did chlorophyll a but

TABLE 7.3: Explained variance of net production at Robben Island and Oudekraal. Parameters selected for examination were nitrates ($\mu g\text{-at } NO_3\text{-N}.\ell^{-1}$), salinity (‰), temperature (°C), temperature squared $(°C)^2$, ambient light ($\mu E.m^{-2}.s^{-1}$) and chlorophyll *a* ($mg.m^{-3}$). Otherwise as in Table 7.1).

	Robben Island (upwelling season)	Oudekraal (upwelling season)	Oudekraal (winter)	All data
1st variable selected	Chll *a* *	Nitrate *	Chll *a* *	Chll *a* *
Explained variance (%)	34.8	32.3	38.4	35.0
Coefficient (b_1)	3.738	-1.051	3.637	3.126
2nd variable selected	Amb. light	Chll *a*	Temp *	Amb. light *
Explained variance (%)	4.2	14.0	22.1	8.0
Coefficient (b_2)	0.013	2.071	9.090	0.0131
3rd variance selected		Amb. light		Temp
Explained variance (%)		8.3		1.3
Coefficient (b_3)		0.013		2.617
Constant	-6.99	12.754	-116.593	-34.829
n	76	96	42	214

TABLE 7.4: As in Table 7.3 except chlorophyll *a* was replaced by the extinction coefficient, k (m^{-1}).

	Robben Island (Upwelling season)	Oudekraal (upwelling season)	Oudekraal (winter)	All data
1st variable selected	k *	k *	Temp *	k *
Explained variance (%)	46.2	47.0	34.9	46.4
Coefficient (b_1)	189.200	133.722	9.748	155.172
2nd variable selected		Amb. light	k	Amb. light
Explained variance (%)		4.1	10.9	1.3
Coefficient (b_2)		0.0086	107.666	0.0064
Constant	-28.160	-21.621	-133.474	23.069
n	66	85	28	179

also resulted in the exclusion of some of the other parameters.

Net production per unit biomass (P^B)

The variance in P^B is not readily explained. Only 16% was accounted for in stepwise regression models and that was attributed to ambient light (data not tabulated).

While stepwise regression analyses do give an indication of factors related to phytoplankton production and biomass in this study, the results do not account for sufficient variance to confidently base predictions on the regression models. However, the analyses do show that net production is largely dependent on biomass which, in turn, is strongly negatively correlated with nitrates. In fact, after the source water has upwelled nitrate concentration is dependent on phytoplankton biomass. From this type of analysis there is no indication of nitrates limiting phytoplankton production or biomass. Closer examination of individual data (see Section 7.3.3) explains more about nutrient limitation.

7.3.7 Daily, Seasonal and Annual Production

Mean hourly, daily and seasonal rates of net production in the euphotic zone during both the upwelling season (September to April) and winter (May to August) at Oudekraal and Robben Island are given in Table 7.5. At Robben Island, production during the upwelling season was estimated from results between January and March, whereas production in winter was assumed to be similar to Oudekraal as conditions tend to be uniform along the coast in winter (Andrews and Hutchings 1980).

Daily net production was calculated by multiplying the hourly rate by the number of daylight hours and subtracting the organic carbon used up by respiration during the night (respiration was assumed to be 10% of gross production) using the following equation:

$$\int P_{24} = \int P.DT - \int Resp.NT;$$

where $\int P_{24}$ = daily net production in the euphotic zone;

$\int P$ = hourly net production;

DT = number of daylight hours;

$\int Resp$ = hourly respiration;

NT = number of night hours.

No correction was made for diel variation in production (see Chapter 6).

Seasonal net production was calculated by multiplying the daily rate by the number of days in the season. Annual net production is the sum of that during the upwelling season and in winter.

TABLE 7.5 Hourly, daily and seasonal net production estimates at Oudekraal and Robben Island. (S.D. = standard deviation, n = number of measurements used to calculate mean, * = Jan - March hourly rate used in calculation, ** Oudekraal winter hourly rate used in calculation.

	OUDEKRAAL		ROBBEN ISLAND	
	Upwelling Season	Winter	Upwelling Season	Winter
Months:	Sept-Apr	May-Aug	Sept-Apr	May-Aug
No. of days	242	123	242	123
No. of daylight hours (mean)	13.02	10.34	13.02	10.34
No. of night hours (mean)	10.98	13.66	10.98	13.66
Net Production:				
1) hourly ($mg.C.m^{-2}.h^{-1}$ ± S.D. (n)	207 ± 202 (35)	216 ±155 (10)	398 ±232 (13)	-
2) daily ($mg.C.m^{-2}.day^{-1}$)	2432	1906	(4950)*	(1906)**
3) seasonal ($g.C.m^{-2}.season^{-1}$)	589	234	(1198)*	(234)**
Annual Net Production ($gC.m^{-2}.y^{-1}$)	823		1432	

Annual net production at Robben Island was almost twice as high as at Oudekraal. As Robben Island waters are thought to be similar to offshore or aged upwelled water, it seems that use of inshore measurements of primary production at Oudekraal could seriously underestimate production rates for the Cape Peninsula Upwelling region as a whole. Satisfactory integration with time and space requires many more measurements, particularly offshore. However, a rough estimate of annual net production of 1.13 kg $C.m^{-2}.y^{-1}$ (the mean of Oudekraal and Robben Island estimates) is about four times as high as Ryther's (1969) estimate (0.3 $kgC.m^{-2}.y^{-1}$) for upwelling areas. The mean daily production estimate at Robben Island between Jan-March (4950 $mgC.m^{-2}.day^{-1}$) is about two and a half times the estimates in upwelling areas off Northwest Africa (1964 $mgC.m^{-2}.day^{-1}$) and Peru (1894 $mgC.m^{-2}.day^{-1}$) in March-April (Barber and Smith 1980).

7.4 CONCLUSIONS

In summer phytoplankton production and biomass in the nearshore area of the Cape Peninsula, particularly off Oudekraal, are highly variable due to periodic, wind-induced, intense upwelling of nutrient-rich water containing very low concentrations of phytoplankton, and to downwelling of warmer aged, phytoplankton-rich upwelled water. Once the water column stabilizes after upwelling and conditions optimum for growth are attained, phytoplankton concentrations increase at an exponential rate until nutrient concentrations become limiting. At this stage net production per unit biomass decreases but because of increased biomass, the overall net production continues to rise. Once nutrients in the water column have been depleted and nitrate reserves in the cell used up, net production is limited and eventually phytoplankton stocks are reduced. The latter condition is likely to be more common further offshore than inshore at Oudekraal where nitrates are more frequently replenished by upwelling.

Intense upwelling seldom occurs at Robben Island but nutrients appear to be introduced into the euphotic zone by lateral mixing of high-nutrient water which probably upwelled further north or south. Consequently a far more stable physical

and biological environment is maintained at Robben Island than at Oudekraal. As a result, phytoplankton production and biomass tend to be higher and more consistent at Robben Island.

CHAPTER 8

GENERAL CONCLUSIONS AND RECOMMENDATIONS

The four experiments conducted during this study provide some practical suggestions on how to measure phytoplankton production in the southern Benguela Current.

The size of the incubation bottle used for production measurements appears to be unimportant within the 125-1000 mℓ range. It is suggested that 125 mℓ bottles be used to reduce the chance of including herbivorous zooplankton, which can reduce primary production estimates (anomalous results were obtained from 60 mℓ bottles, and these are not recommended). From zooplankton densities established, using a plankton pump, one would expect some influence on primary production measurements, particularly in the larger bottles. It appears that the bucket and NIO bottle used for drawing primary production samples did not sample zooplankton as efficiently as did the pump. On other occasions large numbers of herbivores have been observed in NIO bottle samples so precautions should be taken to reduce the chance of including them.

Exposure of production samples to high light intensities experienced at noon during manipulations on deck was found to inhibit rates of production of phytoplankton samples taken from near the bottom of the euphotic zone, particularly when below a thermocline. Consequently it is recommended that production samples be shielded from bright light during sampling, especially when the water column is strongly stratified. When samples are lowered into the sea for *in situ* incubation the period of exposure to surface light should be kept as brief as possible. However, integrated production estimates ($mgC.m^{-2}$) are not unduly affected. The increased production in near-surface samples due to increased light levels appears to compensate for the inhibition of samples from deeper down in the water column.

In situ rates of production were simulated in a deck incubator. Spectrally neutral filters were used to simulate

in situ light intensities in the euphotic zone and a quantum meter used to match simulated with *in situ* light levels. Oxygen production estimates on deck were slightly higher than *in situ* estimates. The increase is not attributed to differences in the spectral composition of the light but may be caused by slightly higher light levels and temperatures in the deck incubator. ^{14}C uptake experiments do not show significant differences but more data are required to draw firm conclusions. However, the differences observed between simulated and *in situ* measurements are small relative to other experimental errors. Thus, because of its convenience, it is recommended that the simulated *in situ* technique be employed in local waters, when ship's time is limited.

Diel periodicity in net production at the sea surface has been demonstrated under natural and constant light with peaks during the day. The time of peak appears to be related to previous and ambient light levels and possibly to nutrient concentrations. The extent of fluctuations in potential net production (P_{max}/P_{min}) is greatest (12.4) when day and night are most different, suggesting that the "pulsing effect" of the day-night cycle influences P_{max}/P_{min}.

Daily net production was measured on several occasions by integrating the results of eight incubations spanning 24 hours under natural light conditions. An attempt was made to calculate correction factors for diel variation so that a short term incubation during daylight could be used to estimate daily production. However, differences in the extent of variation and the times of peaks in production make it impossible to give reliable correction factors which can be generally applied. Fortunately it appears that diel variation in production decreases with depth so that its effect on integrated daily production ($mgC.m^{-2}$) is small relative to other errors. However, the time of incubation should be chosen to minimize the effect of periodicity on production estimates. The six hour period spanning noon is recommended for oxygen production measurements because estimates of daily production from incubations over this period are more consistent than those before or after noon. This also allows time for making underwater light

measurements and drawing water samples for production measurements. Because incubation periods of longer than four hours are not recommended for the ^{14}C method of measuring production, the four hours spanning noon are suggested for ^{14}C uptake measurements.

Changes in phytoplankton production and biomass are associated with changes in the upwelling system off the Cape Peninsula. It appears that the nearshore area is affected by upwelling in two ways; directly (as at Oudekraal) when intense upwelling disrupts the thermocline and brings clear, cold nutrient-rich water with very low phytoplankton stocks to the surface, and indirectly (as near Robben Island) when nutrients appear to be replenished by lateral mixing with water which upwelled in the vicinity. Rates of primary production are known to be high in upwelling areas (Ryther 1969). However, this study shows that within the upwelling system, production rates are lower in the immediate vicinity of an intense upwelling site than in the adjacent areas where the water column is stable.

An attempt was made to follow the development and growth of phytoplankton populations in upwelled water. However, by sampling at a fixed point over a time series, one obtains a set of data which does not represent a sequence of events occurring in a coherent parcel of water. Instead a series of pictures of different stages in different sequences is obtained. However, a hypothetical picture of phytoplankton growth in upwelled water has been assembled by estimating the stage of development from consideration of temperatures, nutrients and chlorophyll *a* concentrations. Although the growth of phytoplankton populations in upwelled water is a continuous process, it can be roughly divided into three phases:

(i) the lag phase,
(ii) the exponential phase, and
(iii) the stationary phases.

The lag phase is that period between the upwelling of cold water into the euphotic zone and the apparent onset of growth.

The duration of the lag varies and conditions governing it are unknown but may be attributed to the very low concentration of phytoplankton in the source water, the presence or absence of growth stimuli or inhibitors, the light history of the phytoplankton in the source water or the species composition.

During the exponential phase production per unit biomass (P^B) is high. When nitrate concentrations drop to limiting levels, P^B is reduced but because of the increased population, net production continues to increase but at a slower rate than previously. This may be considered the beginning of the stationary phase. When nutrients in the water are depleted and reserves in the cell used up, the effect of nutrient limitation manifests itself more strongly as net production is reduced and, eventually, phytoplankton stocks decrease until levels are either low enough to be maintained by the low nutrient concentrations or until upwelling replenishes the nutrients.

By using a drogue to follow a newly upwelled body of water and monitoring changes in it, one can obtain a more coherent picture of events after upwelling (Beers *et al.* 1971, Ryther *et al.* 1971, Herbland *et al.* 1973) than repeatedly sampling at a single location (this study) or at a series of set stations (Andrews and Hutchings 1980). The Cape Peninsula is one of the few regions in the world where the chlorophyll *a* concentration of upwelling water is consistently low. This provides a highly suitable reference point to study the seeding and colonization of upwelled water. Assessment of losses due to sinking, zooplankton grazing, dispersion, nutrient and light limitation would allow estimations of phytoplankton stocks available to pelagic fish in the area.

ACKNOWLEDGEMENTS

I would like to thank Dr. Larry Hutchings of the Sea Fisheries Institute and Prof. John Field and Dr. Cameron Hay of the University of Cape Town for their constructive criticism and valuable help during this project. Both Dr. Vere Shannon and Dr. Garth Newman of S.F.I. gave encouragement and moral support. My thanks also go to the many people in the S.F.I. Plankton and Physical-Chemical Sections for their excellent technical help. The ships' officers and crew, in particular Captain Marshall and his merry men, were always cheerful and co-operative. Ray Barlow deserves thanks for his co-operation while sampling and for useful discussions between bouts of sea-sickness! The mechanical and electronics workshops spent time and thought manufacturing (and often repairing) my equipment. John Henry set up the ^{14}C method of measuring primary production and analysed the samples. Pieter van der Byl and Robert Cooper identified and counted the zooplankton samples. Gerald Wingate wrote computer programmes to help with the analysis of data. Tony van Dalsen, Megan Herbert and Annette Nel did a sterling job of converting scruffy graphs into very presentable diagrams, which were photographically reduced by Jock Campbell. Mariana van Niekerk and Marianne Louw are thanked for typing the draft and Janet Longman for the final copy of this thesis. Partial financial support from the Fisheries Development Corporation of South Africa is greatly appreciated.

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APPENDIX 1: Gross production measurements using different sizes of incubation bottles. Range in brackets. (* one zooplankter in light bottle reduced GP by 80%)

Bottle size	1000 ml	500 ml	250 ml	125 ml	60 ml
Expt No.					
3	19.7 (15.6 - 23.8)	21.6 (20.1 - 23.1)	22.3 (10.4 - 34.2)	17.1 (11.2 - 23.1)	10.7 (7.4 - 14.1)
4	50.9 (45.8 - 55.9)	57.1 (53.6 - 60.6)	59.0 (48.9 - 69.1)	52.8 (48.9 - 56.7)	41.1 (36.5 - 45.8)
5	212.7 (206.2 -219.2)	217.6 (186.5 -248.7)	225.8 (219.2 -232.3)	195.1 (196.3 -209.5)	106.4 (81.8 -130.9)
8	49.9 (43.2 - 56.6)	46.9 (43.2 - 50.6)	43.2 (41.7 - 44.7)	48.4 (46.2 - 50.6)	36.5 (34.2 - 38.7)
9	25.7 (23.4 - 27.9)	26.2 (22.3 - 30.2)	24.6 (23.4 - 25.7)	23.4 (22.3 - 24.6)	24.0 (21.2 - 26.8)
10	122.1 (114.3 -129.8)	125.1 (122.7 -127.4)	126.2 (123.9 -128.6)	134.0 (132.2 -135.8)	113.8 (109.6 -117.9)
11	65.4 (62.3 - 68.6)	53.0 (16.6* - 89.3)	61.8 (49.9 - 73.7)	63.4 (56.1 - 70.6)	101.8 (86.2 -117.4)
12	20.3 (16.5 - 24.0)	17.2 (17.2 - 17.2)	16.1 (13.7 - 18.6)	13.7 (9.6- 17.9)	19.2 (18.6 - 19.8)
13	24.3 (20.8 - 27.8)	33.2 (29.8 - 36.7)	30.3 (23.8 - 36.7)	26.3 (25.8 - 26.8)	18.8 (14.9 - 22.8)
19	88.8 (86.0 - 91.6)	82.6 (73.7 - 91.6)	97.2 (83.7 -110.6)	87.1 (81.0 - 88.2)	82.1 (74.8 - 89.3)

APPENDIX 2: Oxygen production estimates. P_i = *in situ* production, P_d = simulated *in situ* production in a deck incubator, P_s = simulated *in situ* production at the sea surface, P = production integrated in the euphotic zone.

Expt	Date	Depth (m)	% light	Net Production (mg $C.m^{-3}.h^{-1}$)			Integrated Production (mg $C.m^{-2}.h^{-1}$)		
				P_i	P_d	P_s	P_i	P_d	P_s
1	24/1/78	0	100	15.1	-	20.6	348	-	257
		2.5	50	-	-	-			
		5	25	15.8	-	14.5			
		8	10	39.4	-	25.5			
		20	1	-9.2	-	-11.2			
2	26/4/78	0	100	8.9	15.6	-	94	116	-
		2.5	50	15.2	19.0	-			
		4	25	17.8	19.5	-			
		9	10	-3.1	-1.1	-			
		19.5	1	-1.2	-1.7	-			
3	27/4/78	0	100	8.4	10.6	-	162	105	-
		2.5	50	10.5	15.6	-			
		5	25	16.9	15.6	-			
		9	10	10.1	0.6	-			
		21	1	1.6	-5.6	-			
4	6/7/78	0	100	45.2	50.8	40.2	245	351	264
		2.5	50	51.0	58.6	49.7			
		5.5	25	15.4	36.8	23.4			
		10	10	-19.4	7.2	-5.0			
		18	1	-18.4	-5.0	-11.2			
5	17/10/78	0	100	86.8	74.0	-	509	678	-
		1	50	85.8	152.5	-			
		2	25	84.9	132.7	-			
		4	10	64.8	74.0	-			
		10	1	-6.0	1.3	-			
6	18/10/78	0	100	49.9	90.0	-	486	648	-
		1.5	50	106.2	144.3	-			
		3	25	74.1	100.9	-			
		5	10	48.8	58.1	-			
		9	1	4.1	7.4	-			
7	24/10/78	0	100	-	66.4	-	451	511	-
		2	50	53.0	34.6	-			
		4	25	39.6	85.4	-			
		7	10	9.1	10.0	-			
		17	1	-0.7	14.0	-			
8	14/12/78	0	100	19.5	-	23.4	568	-	562
		2	50	-	-	38.5			
		5	25	23.4	-	16.2			
		9.5	10	17.8	-	20.1			
		30	1	8.9	-	6.6			
9	18/12/78	0	100	22.3	31.3	-	332	379	-
		2.5	50	20.7	35.2	-			
		5.5	25	17.2	25.1	-			
		10.5	10	7.4	18.4	-			
		17.5	1	5.3	13.4	-			
10	12/1/79	0	100	23.0	-	18.5	-	-	-
11	13/3/79	0	100	129.5	129.5	119.5	795	865	699
		1	50	138.4	209.9	179.2			
		2	25	147.4	148.0	120.6			
		4	10	83.8	83.2	57.5			
		9.5	1	10.6	7.2	31.3			
12	16/3/79	0	100	57.0	89.9	41.9	503	724	671
		1.5	50	101.2	131.2	111.7			
		3	25	97.9	131.8	98.8			
		5	10	42.2	68.7	88.8			
		10	1	-12.0	-0.6	-1.7			

APPENDIX 3: ^{14}C uptake production estimates. P_i = *in situ* production, P_d = simulated *in situ* production in a deck incubator, P_s = simulated *in situ* production at the sea surface, P = production integrated in the euphotic zone.

Expt	Date	Depth	% light	Net Production (mg $C.m^{-3}.h^{-1}$)			Integrated Production (mg $C.m^{-2}.h^{-1}$)		
				P_i	P_d	P_s	P_i	P_d	P_s
13	7/12/77	0	100	62.02	23.81	-	272	152	-
		1.5	50	52.54	31.02	-			
		8.5	1	1.01	0.28	-			
14	16/5/78	0	100	4.38	4.27	-	64	44	-
		6	50	3.96	3.51	-			
		11.5	25	2.50	1.31	-			
		19.5	10	0.97	0.26	-			
		40	1	-0.70	0.11	-			
15	27/6/78	0	100	4.78	5.88	5.67	108	128	117
		6.5	50	7.11	7.43	6.87			
		13	25	4.32	6.43	5.46			
		22	10	1.13	2.33	-			
16	4/7/78	0	100	13.03	13.72	10.22	216	245	284
		4	50	16.57	19.69	17.00			
		8	25	14.84	17.48	10.35			
		13.5	10	5.25	5.56	15.12			
		27	1	0.76	0.27	0.26			
17	22/8/78	0	100	1.32	1.23	1.23	26	48	25
		4	50	1.30	1.90	1.92			
		9	25	2.16	2.69	0.85			
		15	10	0.68	2.46	1.16			
		29	1	0.13	-0.87	-0.40			
18	26/4/78	0	100	6.30	4.96	-	86	71	-
		3	50	9.21	5.81	-			
		4.5	25	4.57	7.65	-			
		9.5	10	5.01	3.04	-			
		20	1	0.42	0.22	-			
19	27/4/78	0	100	2.77	3.77	-	75	44	-
		3.5	50	4.61	4.52	-			
		6	25	6.14	3.25	-			
		10	10	4.21	1.56	-			
		22	1	0.39	0.06	-			