THE DEVELOPMENT AND DECLINE OF PHYTOPLANKTON BLOOMS IN THE SOUTHERN BENGUELA UPWELLING REGION

by

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To Guy

DECLARATION

The co-authored papers (Part I) were written by myself. Some of the data on which these chapters are based were obtained from the co-authors, viz. that in Figures 5, 7 and 9 in Chapter 1 from Dr. L. Hutchings, and the primary productivity data from Sites C, D and E in Chapter 2 from Mr. J.L. Henry. Comments and criticisms by the co-authors were included in the text.

The Plankton Dynamics project (Part II) was instigated and supervised by Dr. L. Hutchings and routine measurements of chlorophyll a, oxygen, nutrients and salinity were made by SFRI technical staff. Data presented in this thesis and interpretations put thereon are my original work unless otherwise acknowledged in the text.

estimate primary productivity. These "Redfield productivity estimates" were similar to ^{14}C-uptake productivity but lower than estimates obtained from changes in particle volume. If the period of maximum nutrient decrease was used for the calculations, the "Redfield productivity estimates" lie between the ^{14}C-uptake and particle volume estimates. Daily rates of ^{14}C-uptake water column productivity ranged between 0.94 and 14.01 g C.m^{-2}.d^{-1} (mean 3.80 g C.m^{-2}.d^{-1}) and were similar to or higher than productivity estimates reported for other upwelling areas. Phytoplankton biomass in the upper 50 metres ranged between 8 and 506 mg chll a. m^{-2} (mean 208 mg chll a.m^{-2}); on average, about half the biomass occurred below the 1% light level indicating that self-shading is an important factor limiting primary production in the Benguela upwelling system. The temporal scale of phytoplankton bloom development was investigated in terms of changes in chlorophyll a concentrations in the euphotic zone. The build up and decline of the primary phytoplankton (diatom) bloom in newly upwelled water occurred within 6-8 days. The initiation of blooming appears to be controlled by the stability of the water body (vertical and horizontal), and the decline of the bloom was usually associated with reduced nutrient levels and is considered to result mainly from phytoplankton cells sinking out of the surface layers. Dispersive processes may also contribute to bloom decline. Zooplankton grazing made little impact on the phytoplankton community. The wide coastal band of chlorophyll-rich water seen in satellite images to well beyond the outer limit of the drogue tracks, suggests that both regenerated nutrients and new nutrients (entrained into surface waters after the primary bloom), maintain primary production in shelf waters at moderate levels for longer than the 6-8 days suggested by this study.

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GENERAL INTRODUCTION

Upwelling areas, including the southern Benguela region, are distinguished by their high primary productivity and fish yields. However, the pulsing nature of the upwelling system off the Cape Peninsula coupled with the paucity of phytoplankton and high concentrations of nutrients in the water which upwells, result in highly variable concentrations of phytoplankton in the coastal ecosystem. Consequently the availability of phytoplankton to other trophic levels (e.g. zooplankton, fish) is not uniform and may limit the occurrence and productivity of these organisms. It follows that information both on the feeding ecology of consumers and on the development of phytoplankton communities is necessary to evaluate trophic interactions in the ecosystems. This thesis is concerned with the latter aspect.

Part I (Chapters 1 and 2) serves as a review of the research done on phytoplankton ecology in the southern Benguela, and helps put Part II into perspective in terms of the broader upwelling region. In Chapter 2 the rationale and methods for using productivity/chlorophyll relationships to estimate productivity rates from chlorophyll measurements are presented with a view to applying such calculations to extensive sets of chlorophyll measurements for obtaining areal phytoplankton productivity estimates for the Benguela ecosystem. Chapter 1 was prepared for the "International Symposium on the Most Important Upwelling Areas off Western Africa (Cape Blanc and Benguela)" in Barcelona, while Chapter 2 forms one of a suite of papers in the book "South African Ocean Colour and Upwelling Experiment" (Shannon 1985). Consequently their presentation format is different from the rest of the thesis.

Part II (the major part of the thesis) is primarily concerned with the development and decline of phytoplankton blooms in pulses of newly upwelled water off the Cape Peninsula and the time scales associated with such changes in phytoplankton biomass. Because of the highly dynamic nature of upwelling in this area, attention is also directed toward the physical destination of the "patches" of upwelled water and the chemical changes which occur in it. ^{14}C-uptake estimates of primary productivity are compared with independant productivity estimates from increases in particle volume and those infered from in situ nutrient and oxygen changes. Losses from the phytoplankton community in the upper 20 metres are calculated by subtracting in situ biomass at the end of each study from the cumulative productivity (plus initial biomass) over the study period. An attempt is made to account for these losses in terms of grazing, sinking and dispersive processes, and to put the study in perspective in the whole coastal upwelling zone.

PART I : REVIEW

CHAPTER 1: PHYTOPLANKTON DISTRIBUTION AND DYNAMICS IN THE SOUTHERN BENGUELA CURRENT

- Introduction
- Review of phytoplankton studies
  - Early exploratory surveys
  - Phytoplankton distribution in relation to upwelling
  - Phytoplankton biomass distribution in the southwest Cape
  - Phytoplankton production and population growth
    - Rates of production
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- Acknowledgements
- References

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Phytoplankton distribution and dynamics in the Southern Benguela Current

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Palabras clave: Fitoplancton, distribución, dinámica, sur de Benguela.
Key words: Phytoplankton, distribution, dynamics, southern Benguela.

SUMMARY: This paper reviews developments in research into the ecology of phytoplankton in the southern Benguela region. Species identification, cell counts and chlorophyll *a* distribution from shipboard measurement give some indication of the overall spatial and seasonal distribution of phytoplankton. This is followed by some results of more intensive surveys, which include estimates of primary production, both at fixed inshore stations and on six cruises when the ship followed drogues placed in upwelled water. The drogue studies show that a short but intense burst of diatom growth strips most of the nitrate from the newly upwelled water within five to eight days, during which time the water mass stays close to the shore.

RESUMEN: DISTRIBUCIÓN Y DINÁMICA DEL FITOPLANCTON EN LA REGIÓN MERIDIONAL DE LA CORRIENTE DE BENGUELA. — En este trabajo se hace una revisión del desarrollo de la investigación en ecología del fitoplancton en la región sur de Benguela. La identificación de especies, el contaje de células y la distribución de clorofila *a* a partir de medidas tomadas a bordo, dan una indicación de la distribución espacial y estacional del fitoplancton. A ello siguen algunos resultados de investigaciones más intensivas que incluyen estimaciones de la producción primaria, tanto en estaciones fijas en la costa como en seis campañas siguiendo boyas situadas en agua aflorada. Los estudios realizados con boyas muestran que una corta pero intensa explosión en el crecimiento de las diatomeas consume gran parte del nitrato del agua recién aflorada en el término de 5 a 8 días, durante los cuales la masa de agua se mantiene próxima a la costa.

INTRODUCTION

Phytoplankton research in the Benguela Current was instigated by pelagic fishing activity off the west coast of southern Africa, centred in St. Helena Bay off the South African coast, and further north in Walvis Bay off the Namibian coast. (Fig. 1). The purpose of this paper is to review the state of phytoplankton research in the southern Benguela region along the west and south coasts of South Africa from Lamberts Bay (32° S, 18° E) to San Sebastian Bay (34° S, 21° E) (Fig. 1). We start with the early exploratory surveys which provided the basis for more recent developments in local research,

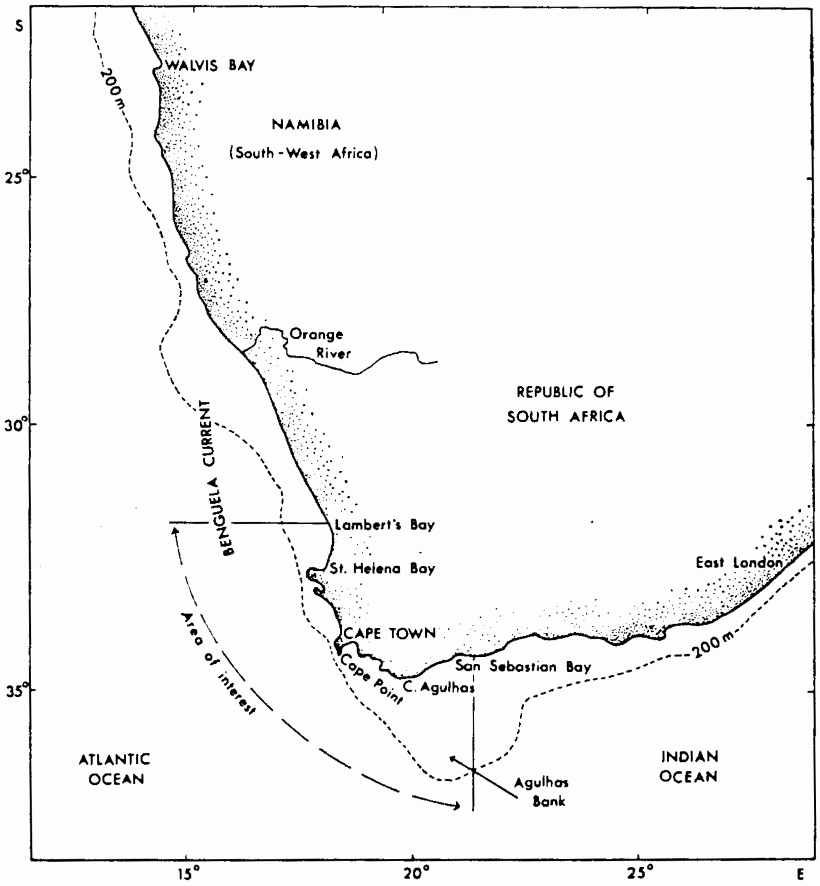

FIG. 1. — The south and west coast of southern Africa showing the area between Lamberts Bay and San Sebastian Bay where most phytoplankton research in the southern Benguela Current region has been done.

and attempt to link results of the various surveys and projects to provide an overview of phytoplankton ecology in the oceans off the South-West Cape of South Africa.

REVIEW OF PHYTOPLANKTON STUDIES

EARLY EXPLORATORY SURVEYS

Systematic phytoplankton research in the southern Benguela began in the early 1950's, soon after the arrival of the research vessel "Africana II". Occasional sampling was also done locally (e.g. COPENHAGEN and COPENHAGEN, 1949), and by passing expeditions such as the Danish Galathea Expedition of 1950-52 (STEEMANN NIELSEN and JENSEN, 1957) and the Discovery Expedition (HART and CURRIE, 1960). In the early 1950's the South African Division of Fisheries launched an extensive programme to investigate the general biology of the two major commercially-exploited pelagic fish species, the pilchard, *Sardinops ocellata* (Pappe), and the maasbanker, *Trachurus trachurus* (Linne). As these fishes are planktivorous (DAVIES, 1957; KING and MCLEOD, 1976), monthly investigations into the abundance and seasonal variation of the plankton in the fishing grounds in St. Helena Bay (Fig. 1) during 1950-51 and 1954 constituted an important part of the programme. DE JAGER*(1954, 1957) investigated seasonal and spatial distribution of different phytoplankton species in terms of cell abundance, using both 80 μm mesh tow-nets and discrete bottle samples down to 50 metres. He found that the densest blooms (up to 3.7×10^6 cells.l^{-1}) occurred in the upper 20 metres; that the phytoplankton was usually dominated by diatoms (the most common genus being *Chaetoceros*), but that dinoflagellates occasionally appeared in large numbers for short periods. Phytoplankton was found to be most abundant in spring and summer, coincident with increased light and southerly winds, and was reduced in winter and least abundant in autumn.

The next significant series of hydrographic surveys (1961-67) was conducted along similar lines. These Routine Surveys were far more extensive than previous ones and covered a grid 330 km wide from Lambert's Bay to San Sebastian Bay (Fig. 2 a) — the major extent of the pelagic fishery. E. A. COGLAN-NEL identified phytoplankton species and counted cells in bottle samples from 10 metres, and measured the settled volumes of N50V net samples (50-0 metres) for these surveys. The results, other than a few selected examples by co-workers, SHANNON (1969), HOY (1970) and DE DECKER (1973), have yet to be published in full (HORSTMAN, in prep.). DE DECKER (1973) presents a synopsis of the results when he compares the phytoplankton on the Agulhas Bank (Fig. 1) with that on the west coast. Average cell counts on the Bank (maximum of 13×10^6 per litre) were about one tenth of those on the west coast (maximum of 24×10^6 per litre). However, high counts (exceeding 10^6 cells per litre) were recorded on a number of occasions on the Bank (53 times as opposed to 125 times off the west coast), and occurred inshore to the west of Cape Agulhas, usually in summer. Settled volumes from 50-0 metre net-hauls were also generally higher on the west coast.

While dinoflagellate species became more common inshore to the east of Cape Agulhas and offshore all over the Bank, there were no clear floral boundaries betwen west and south coasts. In fact, most of the 25 diatom species contributing to blooms on the Bank are temperate or cold-water forms commonly found in the cold upwelling waters off the west coast (DE DECKER, 1973). DE DECKER points out that there is a strong similarity between inshore flora on either side of Cape Point, and that diatom communities off

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*De Jager did not estimate flagellates (counting magnification 125x), thus these statements refer strictly only to diatoms and dinoflagellates.

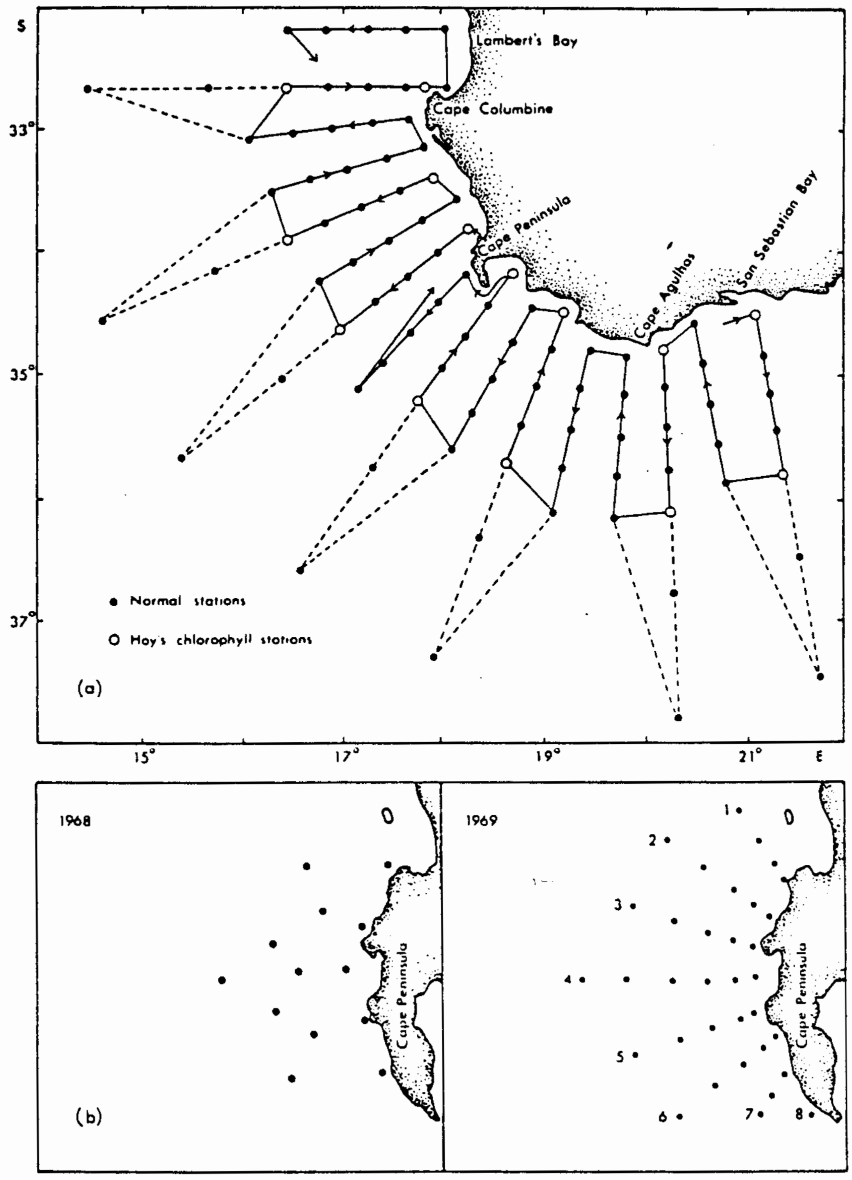

FIG. 2. — Station positions for: (a) the Routine Grid between July 1963 and December 1967 (station positions for the period from 1961 to July 1963 were slightly different), and (b) the Upwelling Cruises in November 1968 and December 1969, showing the station line numbers for the 1969 cruise.

the south coast show predominantly Atlantic characteristics at least as far as Cape Agulhas, beyond which changes take place only gradually.

In a palaeo-environmental study on the continental-shelf between the Cape Peninsula and Cape Agulhas, DAVEY (1971) reports highest concentrations of fossil dinoflagellate cysts in the sediments inshore of the shelf break. This may be partly the result of periodic blooms of dinoflagellates, but more important the relatively stable water column facilitates sedimentation in this area whereas in the more turbulent conditions on the shelf break sedimentation would be greatly reduced.

During 1965-66 chlorophyll measurements using the spectrophotometric method of the SCOR/UNESCO Working Group 17 (1966) were made for the first time at 7 inshore (0 and 10 metres) and 7 offshore (0 metres) stations (Fig. 2 a) on the Routine Grid (HOY, 1970). Even though variation in total chlorophyll could not always be related to cell numbers or species, HOY (1970) found chlorophyll concentrations were highest (up to 45 $\text{mg}\cdot\text{m}^{-3}$) and most variable at the inshore stations on the west coast (Table 1) in late summer and autumn, whereas on the south coast there was no clear seasonal pattern but concentrations were generally lower than on the west coast. In contrast to DE JAGER'S (1957) phytoplankton estimates (settled volumes and cell counts) which demonstrate very low biomass in St. Helena Bay in the autumn of 1954, HOY'S (1970) chlorophyll measurements for the same area (Routine Station 24-1.5) exhibit a definite maximum in autumn. This difference may be attributed to natural variation between years, or perhaps to the decline in pilchard biomass which occurred in 1963-64 (SHELTON, 1982). These early sporadic attempts to assess phytoplankton distribution and abundance were later replaced by more intensive sampling programmes using semi-automated and improved techniques — mainly chlorophyll determinations. As the rapidity of changes in upwelling zones became more apparent, more frequent sampling was initiated.

TABLE 1

Mean total chlorophyll concentrations ($\text{mg}\cdot\text{m}^{-3}$) for onshore and offshore stations on the south and west coasts calculated from HOY'S (1970) data.

	ONSHORE		*OFFSHORE*	
	West coast	*South coast*	*South coast*	*West coast*
Mean	5.8	3.0	1.8	1.4
(std. dev.)	(5.8)	(2.8)	(3.4)	(2.3)
No. of samples	46	60	60	46

PHYTOPLANKTON DISTRIBUTION IN RELATION TO UPWELLING

Because of the obvious enhancement of primary productivity on the west coast due to upwelling (DE JAGER, 1957; HART and CURRIE, 1960), attention was next focussed on the physical mechanisms of upwelling and its biological consequences (ANDREWS and CRAM, 1969; ANDREWS, CRAM and VISSER, 1970; CALVERT and PRICE, 1971; BANG, 1973; BANG and ANDREWS, 1974; ANDREWS and HUTCHINGS, 1980, and others). In November 1968, (ANDREWS and CRAM, 1969) and December 1969 (ANDREWS, CRAM and VISSER, 1970; ANDREWS and HUTCHINGS, 1980) two intensive surveys (Upwelling Cruises) were conducted in the near-shore region off the Cape Peninsula (Fig. 2 b) to determine rates of upwelling, subsequent nutrient enrichment and potential primary production. This is an area where intense upwelling frequently occurs, particularly in spring and summer (SHANNON, 1966) when south-east winds predominate. Newly upwelled water is poor in chlorophyll a (Fig. 3 a), but rich in nutrients, so,

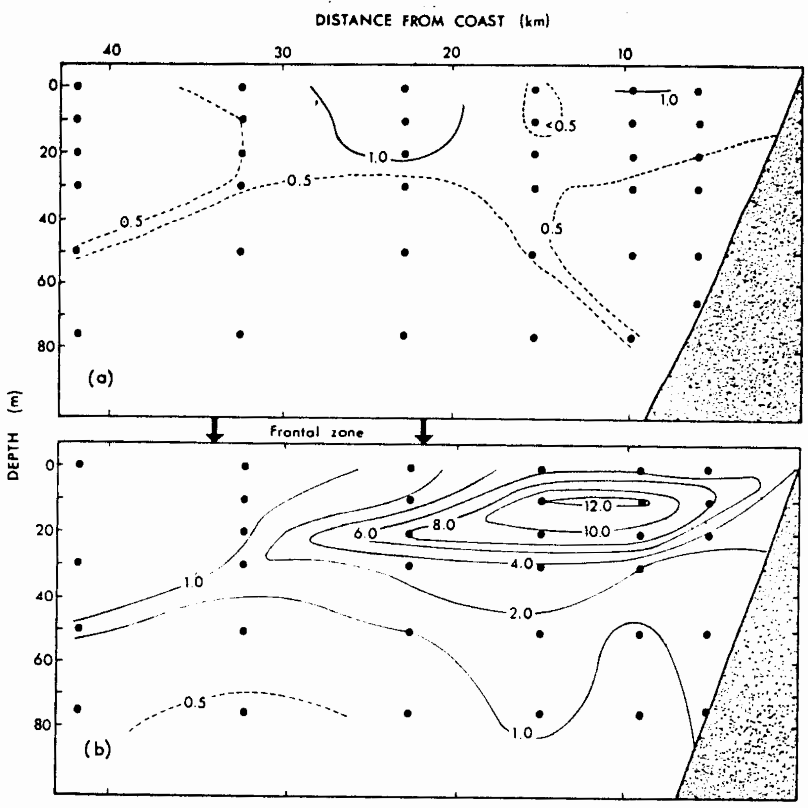

FIG. 3. — Vertical distribution of phytoplankton (mg chll. $a \cdot m^{-3}$) along Line 4 of the 1969 Upwelling Cruise: (a) during upwelling on 16 December, and (b) during downwelling on 13 December. (From ANDREWS and HUTCHINGS, 1980.)

although phytoplankton levels are low, the potential for growth is high. Consequently, when offshore, upwelling-inducing winds subside, the older, more mature upwelled water, which floods back towards the coast during downwelling, is rich in chlorophyll *a* (Fig. 3 b).

The oceanic front, which is defined by strong horizontal temperature and salinity gradients at the sea surface, separates the warm offshore water from the cold upwelled water inshore. In Figure 3 b the vertical distribution of chlorophyll *a* from inshore to offshore, indicates that the denser upwelled water sinks at the front moving under the oceanic water as is illustrated by the subsurface chlorophyll *a* maxima in the thermocline zone (Fig. 11 in ANDREWS and HUTCHINGS, 1980). This surface front responds rapidly to changes in wind direction, moving offshore during southeast winds, and onshore during westerly winds or quiescent conditions. However, a more permanent subsurface front exists at the shelf break during the upwelling season (BANG and ANDREWS, 1974). This front is the effective boundary between the low phytoplankton stocks typical of oceanic water, and the high biomass in coastal upwelled water.

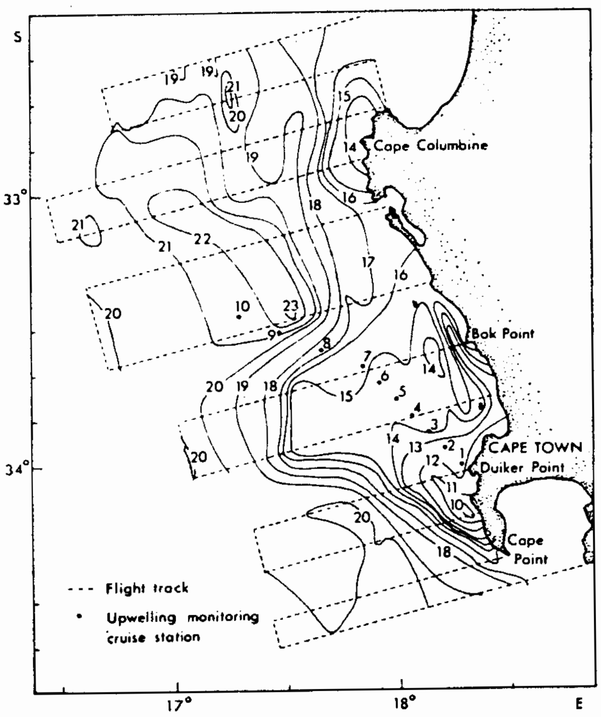

FIG. 4. — Surface temperature (°C) distribution (from Airbone Radiation Thermometer data) of the southern Benguela Current during upwelling on 14 January 1973, with station positions for the Upwelling Monitoring cruises. (From ANDREWS and HUTCHINGS, 1980.)

The existence of one or more "plumes" of cold water moving in a northwesterly direction during upwelling, as demonstrated by airbone radiation thermometry (ART) (ANDREWS and CRAM, 1969; ANDREWS *et al.*, 1970), prompted ANDREWS and HUTCHINGS (1980) to choose a line of stations running northwest from Duiker Point on the Cape Peninsula (Fig. 4), and monitor this line on a monthly basis for two and a half years from October 1970 to March 1973 (Upwelling Monitoring Cruises), then again from January-June 1977 (unpubl.) and March 1983 (HUTCHINGS *et al.*, 1984) following apparent weather anomalies. By assuming that this line of stations was orientated along the upwelling plume, they equated the spatial changes offshore with temporal changes in terms of the development of phytoplankton populations in upwelled water.

The essence of this work was to establish the seasonality of upwelling in terms of physical, chemical and biological parameters. The results, with regard to phytoplankton, show that the standing stock (mg·chll $a \cdot m^{-2}$ integrated from 0-50 m) is on average much higher, more variable, and extends further offshore during the summer upwelling season (September-March) than between April and August (Fig. 5). The considerable variation found during spring, summer and part of autumn is due to phytoplankton being sampled during different phases of the upwelling cycle, as well as to variations in the orientation of the upwelling plume. The relatively uniform distribution in winter, however, is due to turbulence, reduced light and reduced upwelling.

In 1975, the South Coast Upwelling Monitoring (SCUM) programme produced a set of data similar to, but more extensive than, that of the west coast Upwelling Monitoring Cruises of ANDREWS and HUTCHINGS (1980). Once a month a grid of 40 stations (Fig. 6 a) was sampled in the pilchard and anchovy spawning-grounds on the south coast (CRAWFORD, SHELTON and HUTCHINGS, 1980) between Cape Point and Danger Point (TROMP and HORSTMAN, in prep.). Preliminary results show that monthly changes in chlorophyll *a* concentrations in the nearshore area were closely related to the occurrence of easterly winds which induce upwelling. Species composition and dominance changed from a mixed community in a warm stable water mass to a less diverse community after upwelling. Diatoms generally dominated, although sometimes dinoflagellates were more abundant offshore, as was found by COGLAN-NEL in the 1961-67 Routine survey (DE DECKER, 1973).

PHYTOPLANKTON BIOMASS DISTRIBUTION IN THE SOUTHWEST CAPE

Even though by this stage a fair amount was known about the distribution of dominant phytoplankton species and about the effects of upwelling on phytoplankton stocks in localised areas, there was little quantitative information on overall phytoplankton biomass or production in the southwest Cape coastal zone, which supports substantial pelagic fisheries. However, two more recent surveys have provided data suitable to address the question of biomass distribution.

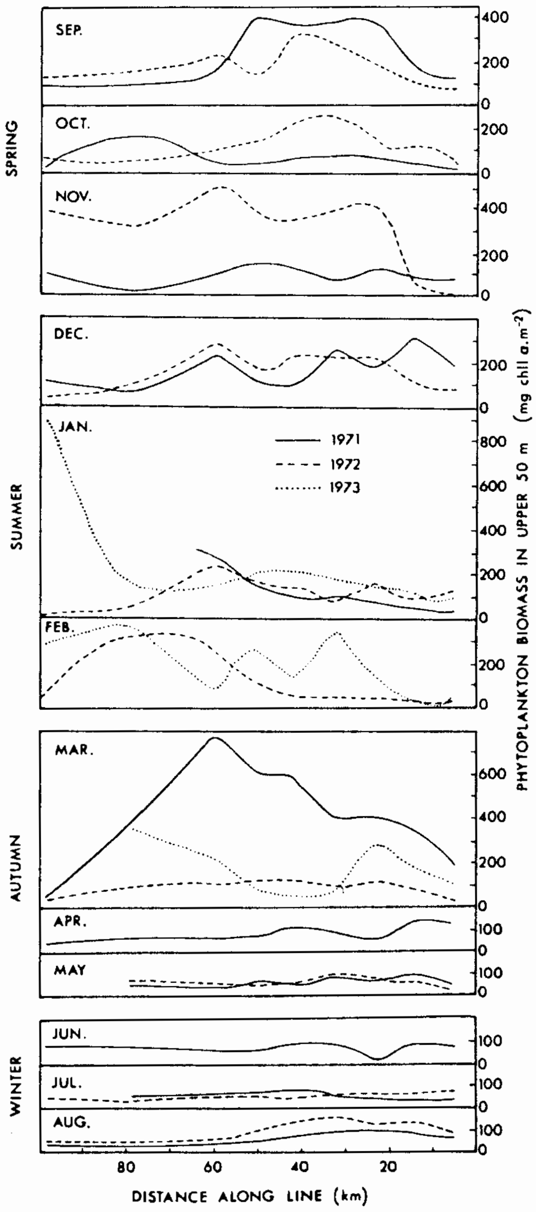

FIG. 5. — Distribution of phytoplankton biomass (mg chll $a \cdot m^{-2}$) in the upper 50 metres along the Upwelling Monitoring line of stations from January 1971 to March 1973.

First, in association with a program for sampling pelagic fish eggs and larvae (Cape Egg and Larval Programme or C.E.L.P.) (Shelton, 1982), chlorophyll *a* measurements were made monthly from August 1977 to August 1978 at eight depths in the upper 100 metres at 120 stations in a 110-kilometre-wide coastal strip from Lamberts Bay on the west coast to San Sebastian Bay on the south coast (Fig. 6 b). Second, during 1978-83 chlorophyll concentrations were de-

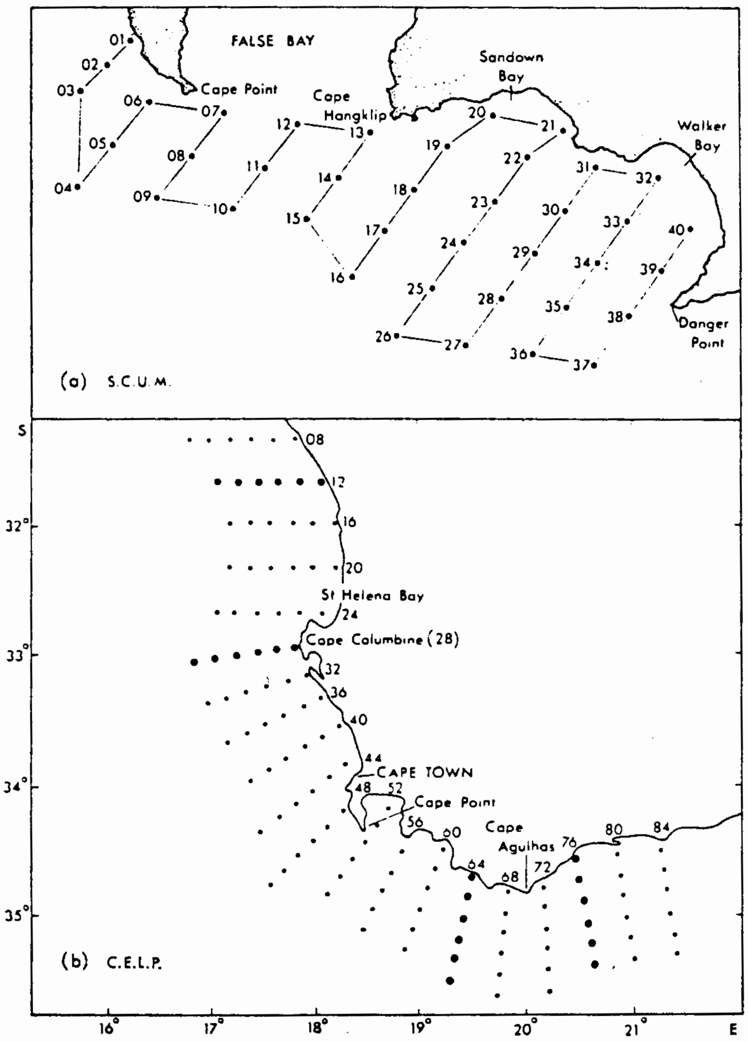

Fig. 6. — Station positions for: (a) the South Coast Upwelling Monitoring (SCUM) cruises from January to December 1975, and (b) for the Cape Egg and Larval Program (CELP) from August 1977 to August 1978. Heavy dots indicate the lines (12, 28, 64 and 76) used for vertical sections.

termined over a somewhat larger area from the northern Namibian border (18° S, 14° E) round to East London (34° S, 28° E) on the east coast of South Africa on a number of occasions by the *Nimbus-7* satellite coastal zone scanner (SHANNON *et al.*, 1983). Combined results of these two approaches are presented by SHANNON *et al.* (1984 b). In this paper, we present a brief synopsis of the shipborne results. Data show that the vertical distribution of phytoplankton (Fig. 7) is largely dependent on physical mechanisms domi-

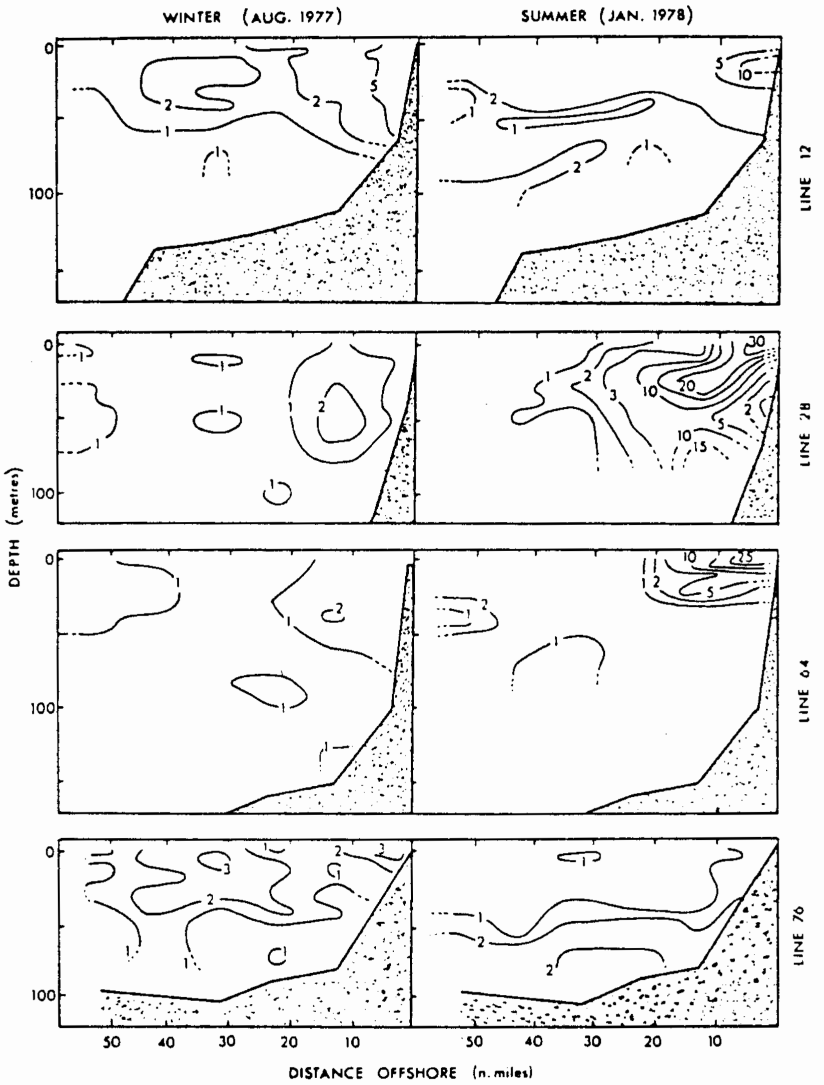

FIG. 7. — Vertical distribution of phytoplankton (mg chll $a \cdot m^{-3}$) during winter and summer along four lines of stations (12, 28, 64, 76) on the CELP grid.

nating in particular areas or seasons. In winter, phytoplankton is generally more evenly distributed in the water column on both west and south coast — probably due to storm-mixing and reduced light preventing rapid build-up of high concentrations of phytoplankton. In summer, the shallower upper mixed layer, increased nutrients due to upwelling and increased light, result in the build-up of high concentrations of phytoplankton inshore in the upper 20-40 m along the coast from Cape Agulhas westwards. East of Cape Agulhas and further offshore along the whole coast, where the effects of nutrient enrichment due to upwelling are not marked, stabilization results in only moderate chlorophyll levels in spring, followed by reduced levels in summer due to nutrient limitation in strongly stratified waters. Very close, inshore in the vicinity of the Cape Peninsula upwelling centre, Brown (1980) demonstrates that mean phytoplankton biomass is similar in winter and summer even though vertical distribution patterns may be very different for these seasons.

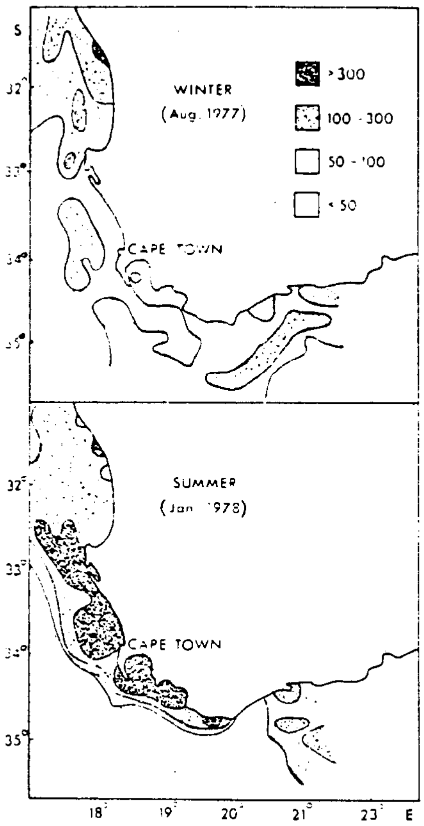

Fig. 8. — Distribution of phytoplankton biomass (mg chll $a \cdot m^{-2}$ from 0-50 metres) in the southern Benguela area during winter and summer.

This change in vertical distribution with season is also evident in terms of horizontal distribution (Fig. 8). In winter, biomass (mg chl $a \cdot \mathrm{m}^{-2}$ integrated from 0-50 m) tends to be fairly uniformly distributed in the coastal area, except in the extreme north. Here higher levels may be attributed to upwelling persisting throughout the year (SHANNON, 1966), and on occasions when stormy weather mixes the water column to the bottom thereby releasing accumulated nutrients into the upper layers as happened on the Agulhas Bank during August 1977. In summer, the area from Cape Agulhas to Cape Columbine shows strong horizontal gradients offshore, with the chlorophyll-enriched band (>50 mg$\cdot \mathrm{m}^{-2}$) relatively narrow off Cape Agulhas and widening northwards. However, north of Cape Columbine horizontal gradients weaken and widespread but moderate biomass levels were observed throughout the summer. Spring and Autumn data show distributions intermediate to those in winter and summer, with turbulence and irradiance playing roles similar to those in temperate seasonal cycles.

PHYTOPLANKTON PRODUCTION AND POPULATION GROWTH

Rates of production

Neither standing stocks nor mean concentrations of phytoplankton, on their own, are necessarily ecologically relevant in terms of food suply to other trophic levels. Both the «threshold» feeding concentrations required by consumers (STEELE, 1974; LASKER, 1975) and the match or mismatch of primary producers and consumers in time and space (LASKER, 1975) may be relevent in terms of trophic interactions, and, of course, the *rate* of production of phytoplankton can greatly influence the yield of phytoplankton and so affect the productive capacity of the coastal zone.

Attempts to assess phytoplankton production in the southern Benguela area, whether it be actual or potential production, are summarized in Table II. Potential production (marked with an asterix) represents an upper limit to primary production under saturating-light conditions, but it is unlikely that they can be used as realistic estimates of phytoplankton production in natural waters.

Actual production estimates obtained from a reasonable number of measurements (i.e. HENRY, 1979; BROWN, 1980, 1983a, 1984; CARTER, 1982) show fairly similar mean daily-rates of about 3 g C$\cdot \mathrm{m}^{-2} \cdot \mathrm{day}^{-1}$ close inshore on the west coast. Variation within each data set, however, is considerable and is thought to depend mainly on phytoplankton biomass and daylength, because nutrients seldom limit production close to the shore (BROWN, 1980). These estimates are slightly higher than, but still comparable with, estimates in upwelling areas off Northwest Africa (1.96 g C$\cdot \mathrm{m}^{-2} \cdot \mathrm{day}^{-1}$) and Peru (1.89 g C$\cdot \mathrm{m}^{-2} \cdot \mathrm{day}^{-1}$) (BARBER and SMITH, 1981).

TABLE II

Estimates of primary production in the southern Benguela region from St. Helena Bay on the west coast to the Agulhas Bank on the south coast of South Africa (n = number of measurements, *1 = unless otherwise specified, *2 = rate of potential production, *3 = unpublished revision, *4 = revised estimate (BROWN, 1984).

			Phytoplankton production		
Author	*Location*	*Time of year*	*Estimated from*	*n*	*Rate (g C·m^{-2}·day^{-1})*^{*1}
HENRY (1979)	St. Helena Bay	Nov.-Feb.	^{14}C uptake		
	— mean		(simulated *in situ*)	8	3.1^{*3}
	— inshore	»		5	4.3^{*3}
	— offshore	»		3	1.0^{*3}
HENRY *et al.* (1977)	Langebaan Lagoon	Through year	Oxygen production (*in situ*)	20	0.38 (gC·m^{-3}·day^{-1})
	Saldanha Bay	»	Surface chll *a* and water transparency measurements	324	1.7
STEEMANN	Cape Columbine	Dec.	^{14}C uptake	1	1.8
NIELSEN and	Cape Peninsula	Jan.		1	1.4
JENSEN (1957)	False Bay	Jan.		2	1.5
BROWN (1983a)	Cape Columbine	March	^{14}C uptake	5	3.1
	Cape Peninsula to Cape Columbine	Dec.	(corrected for night respiration)	12	3.6
	Cape Peninsula	Feb.		11	3.0
	Cape Peninsula	March		14	3.0
		Oct.		12	4.0
		Nov.		2	3.9
		Dec.		9	3.4
ANDREWS *et al.* (1970)	Cape Peninsula	Nov.-Dec.	*In situ* dissolved oxygen levels	1	8.5
			Mass of upwelled nitrogen and phosphorus	4	31.0 (per upwelling day)^{*2} 10.4 (per average day)^{*2}

Andrews and Hutchings (1980)	Cape Peninsula	Through year	Oxygen production (in constant saturating light)	48	10.0*[2]
Brown (1980, 1984)	Cape Peninsula	Through year	Oxygen production (*in situ*)	58	3.1 (3.8)*[1]
	Oudekraal (active upwelling site)	Winter		10	1.9 (2.2)*[1]
	»	Summer		35	2.4 (2.5)*[1]
	Robben Island (stable site)	Summer		13	5.0 (5.6)*[1]
Carter (1982)	Cape Peninsula (Oudekraal kelp bed)	Through year	Oxygen production (*in situ*)	29	3.1
		Summer		7	4.56
		Autumn		8	0.72
		Winter		6	2.84
		Spring		8	4.28
Borchers and Field (1981)	»	April	^{14}C uptake (*in situ*)	2	1.1
Cliff (1979)	False Bay (off Dalebrook)	Summer	Oxygen production (*in situ*)	6	0.01 g $C \cdot m^{-3} \cdot day^{-1}$
Brown *et al.* (1979)	False Bay (red tide at Gordons Bay)	Sept.	Oxygen production (*in situ*)	1	3.7 g $C \cdot m^{-3} \cdot day^{-1}$
Brown (1983 b)	Agulhas Bank	Nov.	^{14}C uptake (*in situ*)		
	— mean			5	1.1
	— upwelling area			1	2.62
	— non upwelling area			4	0.73
Shannon and Henry (1983)	Cape Columbine to Cape Agulhas	Nov.-Feb.	Chl data from satellite colour scanner and productivity indices	—	∼ 4
	Cape Agulhas	March		—	∼ 2

Annual production at a site of active upwelling off the Cape Peninsula has been estimated independently by Brown (1984) and Carter (1982) to be 0.89 and 1.13 $\text{kg C}\cdot\text{m}^{2-}\cdot\text{y}^{-1}$ respectively, whereas at a more stable site nearby it was estimated to be 1.62 $\text{kg C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Brown, 1984). Although these values are higher than Ryther's (1969) and Whittle's (1977) annual estimates for upwelling areas (0.3 and 0.23 $\text{kg C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ respectively), they are unlikely to overestimate production in the coastal zone off the Cape Peninsula because the measurements were made close to the coast where biomass levels are relatively lower than further offshore, as can be seen in the biomass distribution along the Upwelling Monitoring line (Fig. 5). If anything, these measurements should underestimate mean production for the coastal zone.

Production estimates have, over the years, come under severe criticism for a number of reasons (e.g. Strickland, 1960; Vollenweider, 1969; Williams *et al.*, 1979; Peterson, 1980). A certain amount of methodological work has been done locally in an attempt to reduce possible errors (Brown, 1982 a, b and c, 1983 c; Brown and Field, in prep.). A short-coming in the implementation of production results is the extrapolation of relatively few measurements to large areas of ocean. A novel approach has been adopted by Shannon and Henry (1983) to minimize this limitation. They use *Nimbus-7* satellite images of chlorophyll distribution together with shipboard ^{14}C uptake chlorophyll measurements collected in representative areas of ocean, to calculate primary production over extensive areas in the coastal zone. Although there are numerous shortcomings in using such remote-sensing methods for estimating phytoplankton biomass and, more particularly, production rates, this approach holds interesting potential for calculating phytoplankton input for large areas with variable boundaries such has southern Benguela ecosystem.

Population dynamics

While estimates of phytoplankton biomass and production at fixed points give an idea of overall distribution and potential yield of phytoplankton, an understanding of the time scales associated with, and the factors affecting the development of phytoplankton populations in upwelled water requires intensive study of individual patches of upwelled water. The first attempt to mark a patch of water using a drogue and to monitor the development of the phytoplankton populations, was by Andrews and Cram (1969; Andrews *et al.*, 1970). This preliminary study was followed by the work of Hutchings *et al.* (1983). A series of six Plankton Dynamics cruises were conducted off the Cape Peninsula during the upwelling season between December 1979 and March 1983. Sampling took place three times a day alongside a tetrahedral drogue which was suspended at 10 metres and assumed to be moving with a patch of water. Water samples were routinely taken three times per day from ten depths between the sea surface and a depth $\leq$ 100 metres to measure oxygen, nutrients, chlorophyll, particle numbers and volume, and species composition. At selected depths ^{14}C uptake (BROWN, 1983 a) and the relative assimilation of ^{14}C into different biochemical fractions (BARLOW, 1982, 1983 a-b, in prep.) were measured as were particulate protein, carbohydrates and CHN. Zooplankton WP-2 net samples were taken above and below the thermocline, and the rate of copepod grazing in the euphotic zone was measured (OLIVIERI and HUTCHINGS, 1983). In March 1983 emphasis was placed on phytoplankton losses due to sedimentation and on heterotrophic activity in the water column. As the analyses of these data are in various stages of completion we shall highlight only some of the more general findings.

Phytoplankton species analyses by OLIVIERI (1983 a, b) for the December 1979 drogue cruise (as well as for Upwelling Monitoring transect cruises between September 1972 and February 1973), show no evidence of a species succession (MARGALEF, 1958, 1968) which was suggested might occur when upwelled water matures and stratification with attendant physical, chemical and biological changes takes place so as to alter the environs of the colonizing species. In the case of the drogue cruise, the "seed" diatom species in the upwelling water remained dominant throughout the cruise. However, it is possible that changes in species composition may have occurred *after* the bloom, as the monitoring period lasted only 5 days, thus only just covering the sharp decrease in biomass which indicated the end of the bloom. It may also be worth noting that, although the 1972/73 transect data showed no species succession along the Upwelling Monitoring line or with time, the samples were poorly preserved (OLIVIERI, 1983 b) and consequently the presence of fragile flagellates may be gone unrecorded.

The March 1983 Upwelling Monitoring species analyses by MITCHELL-INNES (HUTCHINGS *et al.*, 1984) and corresponding Coulter Counter particle spectra showed a rather different picture. Cell counts showed that although diatoms occurred at all stations, microflagellates were more numerous. Particle spectra, however, showed that in terms of particle volume, while the diatom-chain-sized particles (equivalent sphere diameter of >20 µm) were dominant, the nannoplankton fraction comprised about one third of the total particle volume — a considerably larger fraction than occurred in other Plankton Dynamics cruises analysed. However, in terms of actual volume, the microflagellate fractions were only slightly more abundant during the March 1983 Upwelling Monitoring cruise than during other cruises. It appears that microflagellates may occur in relatively constant "background" numbers, and that only when the bloom-causing diatoms decrease does the *relative* importance of microflagellates increase. The March 1983 results should not necessarily be construed to be the norm, however, as the survey was conducted at the end of a so-called anomalous summer where the frequency of upwelling decreased noticeably compared with previous years (SHANNON *et al.*, 1984 a). It would seem that careful ship-board species analyses are necessary to resolve this question.

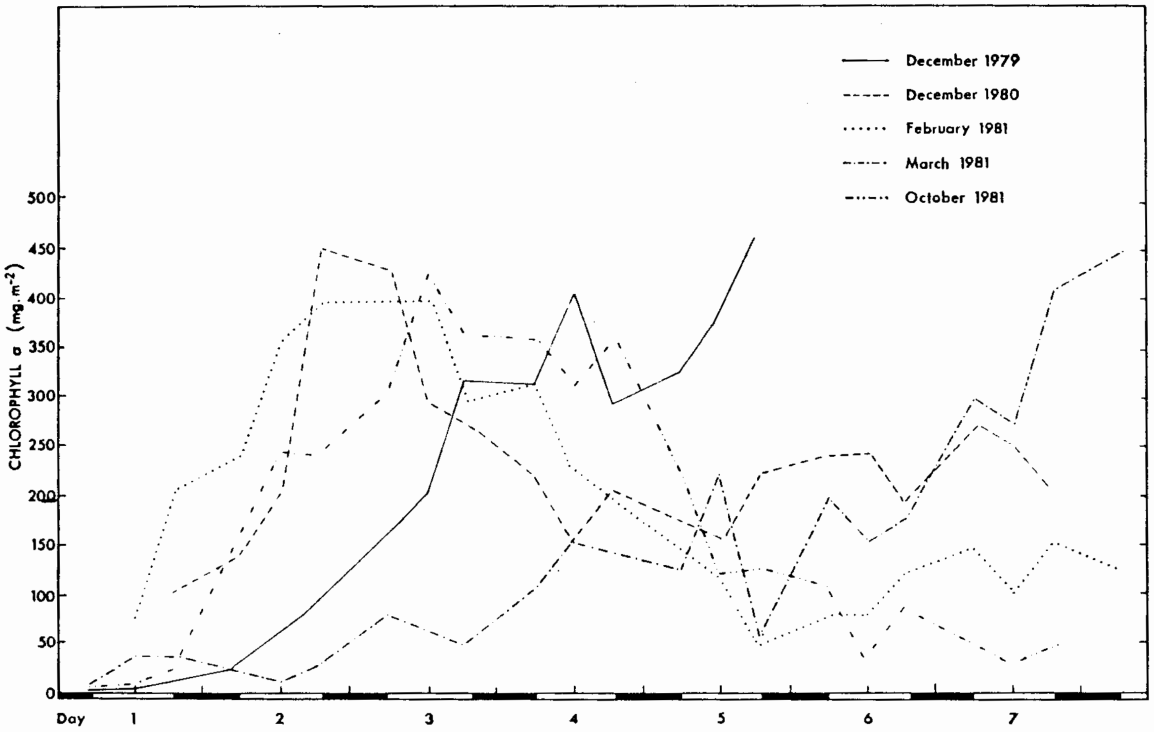

FIG. 9. — Phytoplankton biomass (mg chll $a \cdot m^{-2}$ from 0-40 metres) during five drogue-tracking Plankton Dynamics cruises.

Changes in biomass (in terms of chlorophyll *a* per m^{-2}) over the Plankton Dynamics monitoring periods (Fig. 9), suggest that a short, but intense burst of (diatom) growth strips most of the nitrate from the newly upwelled water within 5 to 8 days (HUTCHINGS *et al.*, 1983). Daily production, as calculated from ^{14}C uptake experiments (BROWN, 1983a), does not account for observed changes in biomass (Fig. 10). This suggests that other processes, such as dispersion, sedimentation, zooplankton grazing, etc., play an important role in regulating phytoplankton biomass.

The biochemical composition and pattern of ^{14}C assimilation into photosynthetic products was monitored by BARLOW (1982, 1984a-b, in prep.) for different environmental conditions during the drogue cruises. When nitrates were depleted to < 1 mg at$\cdot NO_3 - N \cdot m^{-3}$, carbon uptake into protein was

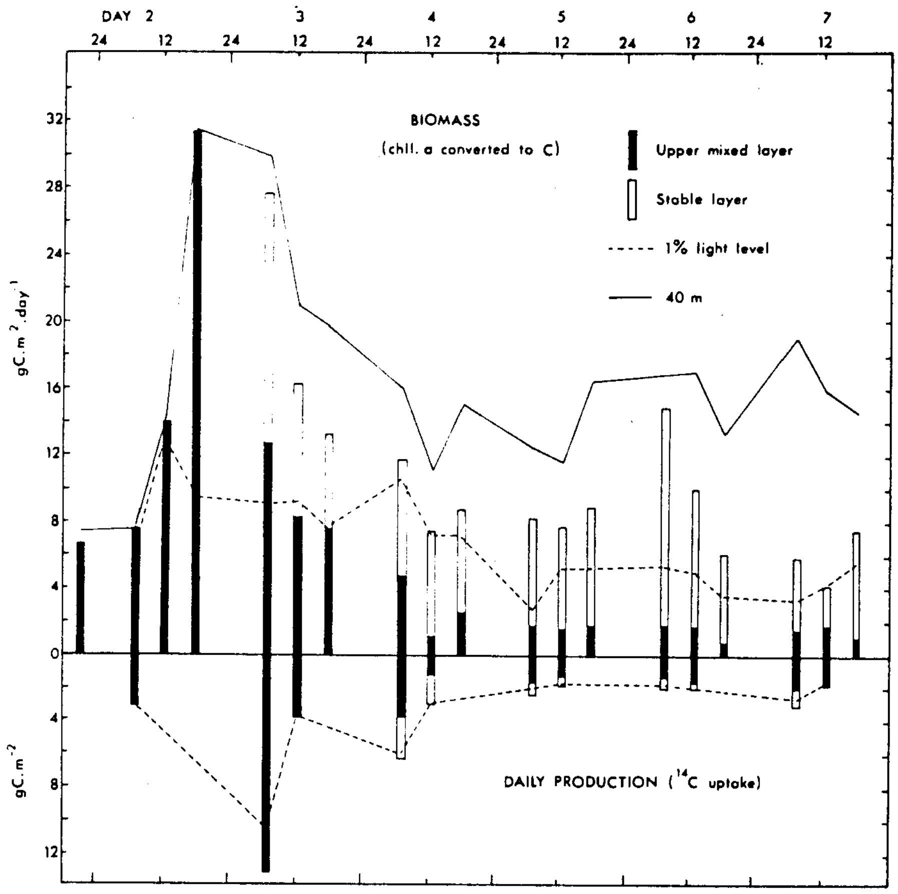

FIG. 10. — Phytoplankton biomass and production during the December 1980 Plankton Dynamics cruise.

reduced and protein and chlorophyll *a* concentrations increased deeper down in the water column as cells sank out of the upper mixed layer (Barlow, 1984a). The phytoplankton community adapted to decreasing light by maintaining the synthesis of protein at the expense of carbohydrate. Barlow (*ibid*) postulates that this may be a mechanism whereby the community remains viable until mixing transports the cells back to the surface layers. Although production per mg chlorophyll *a* was found to be higher in a turbulent water column than in a stable one, a large proportion of the assimilated carbon was in the form of low molecular-weight metabolites. Because relatively more protein was found under stable conditions, Barlow (1984b) suggests that actual phytoplankton growth in a stable environment is faster than under turbulent conditions. However in a deeply mixing environment where nutrients are plentiful, the assimilation of carbon (at low light levels) into protein and amino acids is higher than the assimilation into carbohydrates. These results indicate that "C_3-photosynthesis" dominates in the upper euphotic zone while "C_4-metabolism" is more prevalent further down in the euphotic zone (Barlow, in prep.).

The pattern of nitrate depletion during the development of phytoplankton populations (Fig. 11), suggests that phytoplankton biomass distribution along the Upwelling Monitoring line (which is assumed to follow the upwelling plume) increases to a maximum, then decreases further offshore as nutrients become increasingly limiting. However, this is usually not the case (Fig. 5). In a number of instances, a peak in biomass occurs about 20-40 kilometers from the shore, with a second peak occurring considerably further offshore. The first peak is probably attributable to the initial burst of diatom growth immediately after upwelling with the resultant decay from a combination of grazing, sedimentation and nutrient limitation. The second peak, however, may be due to one or a combination of the following reasons:

(i) replenishment of nutrients in the water column due to degradation by micro-heterotrophs or to excretion by micro- or net zooplankton;

(ii) entrainment of deep nutrients into the euphotic zone by turbulence due to wind which tends to be stronger offshore, although this would be offset by increased water column stability;

(iii) differential rates of water movement away from the Cape Peninsula. Inspection of drogue tracks from the Plankton Dynamics cruises (Fig. 12) suggests that the path taken by upwelled water varies somewhat from that of the line of Upwelling Monitoring stations. After station 7 the drogues tended to move in a northerly direction (relative to the line of stations), and remained within 50 km of the coast. Upwelling off the southern part of the Cape Peninsula (Andrews and Cram, 1969) could place nutrient-rich water close to the frontal zone where acceleration due to the associated jet currents (Bang and Andrews, 1974; Shannon *et al.*, 1981) may result in this water

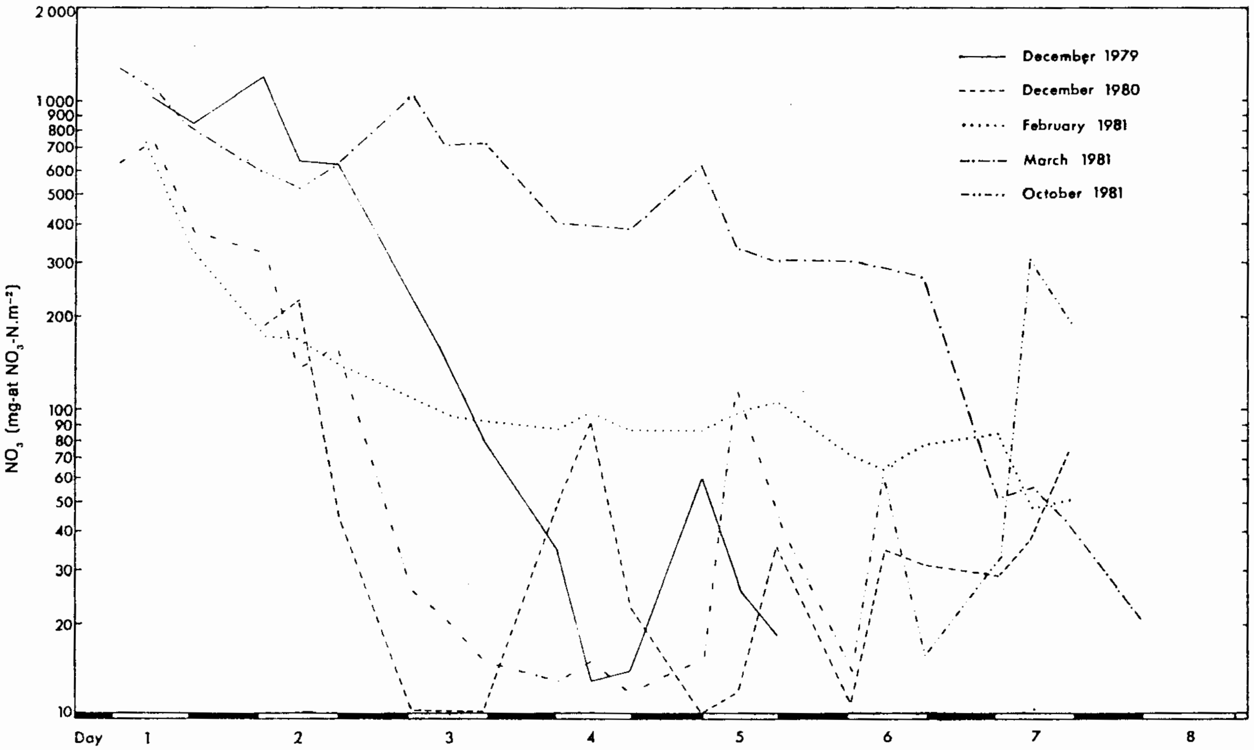

FIG. 11. — Distribution of nitrates (mg-at NO—N·m^{-2}) in the euphotic zone during five drogue-tracking Plankton Dynamics cruises.

effectively overtaking that which upwelled at station 1, so the second peak may be equivalent to the first one, but for a different body of upwelled water. If follows that the outer peak could be an artifact in terms of the assumption that the spatial separation of stations is comparable to temporal separation in the development of phytoplankton in a body of upwelled water.

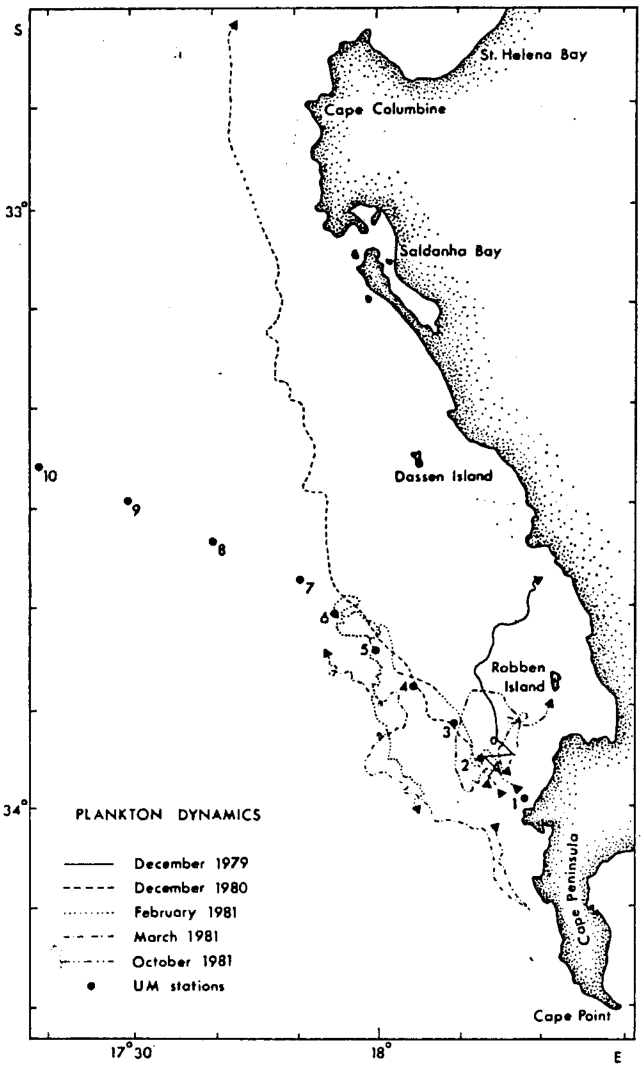

FIG. 12. — The paths taken by five drogues during the Plankton Dynamics cruises, with the station positions for the Upwelling Monitoring (UM) cruises.

Daily thermal colour images obtained by remote sensors (using satellite or aircraft depending on the dimensions of the area of interest) combined with simultaneous shipboard monitoring, could help explain the origin of such phytoplankton distribution patterns.

Most of the extensive surveys to date have been conducted, at best, on a monthly basis. As the generation time of phytoplankton may be of the order of a day, and, as has been demonstrated off the west coast (ANDREWS *et al.*, 1970; BROWN, 1980; BARLOW, 1982; HUTCHINGS *et al.*, 1983; OLIVIERI, 1983 a), large changes in phytoplankton distribution can occur over a matter of a few days, monitoring once a month is not frequent enough to ensure a representative picture for a particular month or season, especially during the upwelling season (September-April) when wind reversals can occur 4 or 5 times in a month (HUTCHINGS, 1981). A combination of approaches, including extensive and intensive surveys, laboratory-based studies and the use of easily measured indices to facilitate monitoring the environment, is required to understand and quantify the functioning of this eco-system, particularly if an environmental input is to be used in management strategies of local fisheries.

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REFERENCES

Andrews, W. R. H. and D. L. Cram. — 1969. Combined aerial and shipboard upwelling study in the Benguela Current. *Nature, London,* 24: 902-904.

Andrews, W. R. H., D. L. Cram and G. A. Visser. — 1970. An estimate of the potential production due to upwelling off the Cape Peninsula. *Proc. Ist Natl. Oceanog. Symp. Durban, South Africa.* Paper B3, 16 pp.

Andrews, W. R. H. and L. Hutchings. — 1980. Upwelling in the southern Benguela Current. *Prog. Oceanog.,* 9, 81 pp.

Bang, N. D. — 1973. *The southern Benguela system: finer oceanic structure and atmospheric determinants.* Ph.D. thesis, University of Cape Town, 181 pp.

Bang, N. D. and W. R. H. Andrews. — 1974. Direct current measurements of an oceanic frontal jet in the upwelling regime west of Cape Town. *J. mar. Res.* 32: 405-417.

Barber, R. T. and R. L. Smith. — 1981. Coastal upwelling ecosystems, in *Analysis of Marine Ecosystems.* (ed.) A. R. Longhurst. Academic Press. London, pp. 31-68.

Barlow, R. G. — 1982. Phytoplankton ecology in the southern Benguela Current. III. Dynamics of a bloom. *J. Exp. Mar. Biol. Ecol.,* 63: 239-248.

— 1983. Physiological changes during the growth and decline of phytoplankton blooms. *Proc. 5th Nat. Oceanog. Symp.,* Grahamstown, South Africa. B20.

— 1984. a. Physiological Dynamics of the decline of a phytoplankton bloom after an upwelling event. *Mar. Ecol. Progr. Ser.,* 16: 121-126.

— 1984. b. Physiological responses of phytoplankton to turbulent and stable environments in an upwelling region. *J. Plank. Res.,* 6 (3): 385-397.

— In prep. Carbon assimilation patterns in deeply mixed phytoplankton communities from the southern Benguela region.

Borchers, P. and J. G. Field. — 1981. The effect of kelp shading on phytoplankton production. *Bot. Mar.,* 24: 89-91.

Brown, P. C. — 1980. *Phytoplankton production studies in the coastal waters off the Cape Peninsula, South Africa.* M.Sc. thesis, University of Cape Town, 1-98.

— 1982a. A note on the effect of bottle size on phytoplankton production measurements. *Fish. Bull. S. Afr.,* 16: 21-24.

— 1982b. Phytoplankton production measured *in situ* and under simulated *in situ* conditions in the the southern Benguela upwelling region. *Fish. Bull. S. Afr.,* 16: 31-31.

— 1982c. The effect of temporary exposure of phytoplankton to midday irradiances on *in situ* productions estimates in the southern Benguela upwelling region. *Fish. Bull. S. Afr.,* 16: 39-44.

— 1983a. Phytoplankton development in newly upwelled water. *S. Afr. J. Sci.,* 79 (4): 144.

— 1983b. Phytoplankton production on the Agulhas Bank - a first look. *Proc. Ist Ann. Cong. Phycol. Soc. S. Afr.,* Johannesburg, South Africa: p. 7.

— 1983c. Evaluation of the 'time factor' and 'light factor' methods for estimating daily phytoplankton production at the sea surface. *S. Afr. J. mar. Sci.,* 1: 139-143.

— 1984. Primary production at two contrasting nearshore sites in the southern Benguela upwelling region. 1977-1979. *S. Afr. J. Mar. Sci.,* 2 (in press).

Brown, P. C. and J. G. Field. — In prep. Diel variation in production rates of natural phytoplankton populations in the southern Benguela upwelling region.

Brown, P. C., L. Hutchings and D. Horstman. — 1979. A red-water outbreak and associated fish mortality at Gordon's Bay near Cape Town. *Fish. Bull. S. Afr.,* 11: 46-52.

Calvert, S. E. and N. B. Price. — 1971. Upwelling and nutrient regeneration in the Benguela Current, October 1968. *Deep-Sea Res.,* 18: 505-523.

Carter, R. A. — 1982. Phytoplankton biomass and production in a southern Benguela kelp bed system. *Mar. Ecol. Prog. Ser.,* 8: 9-14.

Cliff, G. — 1979. *The contribution by phytoplankton, bacteria and detritus to a rocky shore ecosystem.* M.Sc. thesis, University of Cape Town, 145 pp.

Copenhagen, W. J. and L. D. — 1949. Variation in the phytoplankon of Table Bay, October, 1934 to October, 1935. *Trans. Roy. Soc of S. Afr.,* 32: 113-123.

SHANNON, L. V. and J. L. HENRY. — 1983. Phytoplankton primary production in the Benguela Current from ship and satellite measurements. *S. Afr. J. Sci.*, 79 (4): 144.

SHANNON, L. V., S. A. MOSTERT, N. M. WALTERS and F. P. ANDERSON. — 1983. Chlorophyll concentrations in the southern Benguela current region as determined by satellite (*Nimbus*-7 coastal zone colour scanner). *J. Plank. Res.*, 5 (4): 565-583.

SHANNON, L. V., R. J. M. CRAWFORD and D. C. DUFFY. — 1984a. Pelagic fisheries and warm events - a comparative study. *S. Afr. J. Sci.*, 80 (2): 51-60.

SHANNON, L. V., L. HUTCHINGS and P. A. SHELTON. — 1984b. The spatial and temporal distribution of chlorophyll in southern African waters as deduced from ship and satellite measurements. *S. Afr. J. Mar. Sci.*, 2 (in press).

SHELTON, P. A. — 1982. The South African pelagic fishery in ICSEAF Division 1.6 in 1981. *ICSEAF 1982 (Part II) Colln Scient. Pap. Int. Comm. SE Atl. Fish.*, pp. 327-336.

STEELE, J. H. — 1974. *The structure of marine ecosystems.* Havard University Press, Cambridge, Mass.

STEEMANN NIELSEN, E. and E. A. JENSEN. — 1957. Primary oceanic production. The autotrophic production of organic matter in the oceans. *Galathea Rep.*, 1: 49-136.

STRICKLAND, J. D. H. — 1960. Measuring the production of marine phytoplankton. *Bull. Fish. Res. Bd. Can.*, 122: 1-172.

TROMP, B. B. S. and D. HORSTMAN. — In prep. Gross features of the SW Cape coastal waters.

VOLLENWEIDER, R. A. (ed.) — 1969. *A manual on methods for measuring primary production in aquatic environments.* Blackwell Scientific Publications, Oxford and Edinburgh, 1-213.

WHITTLE, K. J. — 1977. Marine organisms and their contribution to organic matter in the oceans. *Mar. Chem.*, 5: 381-411.

WILLIAMS, P. J. le B., R. C. T. RAINE and J. R. BRYAN. — 1979. Agreement between the ^{14}C and oxygen methods of measuring phytoplankton production: reassessment of the photosysthetic quotient. *Oceanologic Acta*, 2 (4): 411-416.

CHAPTER 2: PHYTOPLANKTON PRODUCTION, CHLOROPHYLL *a* AND LIGHT PENETRATION IN THE SOUTHERN BENGUELA REGION DURING THE PERIOD BETWEEN 1977 AND 1980

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South African Ocean Colour and Upwelling Experiment.
Shannon, L. V. (Ed.). Cape Town: Sea-Fisheries Research Institute: 211–218.
1985

Chapter 14

PHYTOPLANKTON PRODUCTION, CHLOROPHYLL *a* AND LIGHT PENETRATION IN THE SOUTHERN BENGUELA REGION DURING THE PERIOD BETWEEN 1977 AND 1980

P.C. BROWN AND J.L. HENRY

Phytoplankton production data, together with chlorophyll *a* and light penetration measurements, collected in the southern Benguela upwelling region over roughly the same period as the *Nimbus-7* satellite ocean colour experiment, are summarized. During the upwelling seasons (spring–autumn) mean chlorophyll *a* concentrations in the euphotic zone are high and variable (mean = 8,7, range = 0,4–24,9 $mg \cdot m^{-3}$) and phytoplankton production is reasonably well correlated with chlorophyll *a* measurements. During winter, however, the correlation between production and chlorophyll *a* is low, probably because of the small number and spread of production data available. Because of the much better coverage attained for chlorophyll *a* measurements (from satellite images or extensive ship surveys), as compared with production measurements, it is considered that production/chlorophyll *a* regressions would be useful for estimating primary production for large areas such as the Benguela upwelling ecosystem.

Gegewens oor die produksie van fitoplankton, tesame met metings van chlorofil *a* en ligindringing, wat in die suidelike Benguela-opwellingsgebied versamel is ongeveer dieselfde tyd as die oseaankleurproef met die *Nimbus-7*-satelliet, word opgesom. Gedurende die opwellingseisoene (lente–herfs) is gemiddelde konsentrasies van chlorofil *a* in die eufotiese sone hoog en veranderlik (gemiddelde = 8,7, bestek = 0,4–24,9 $mg \cdot m^{-3}$) en is die produksie van fitoplankton redelik goed met chlorofil *a*-metings gekorreleer. In die winter is die korrelasie tussen produksie en chlorofil *a* egter laag, waarskynlik weens die geringe getal en verspreiding van beskikbare gegewens oor produksie. As gevolg van die veel beter dekking wat verkry is vir chlorofil *a*-metings (uit satellietbeelde of omvattende skeepsopnames), vergeleke met produksiemetings, word gemeen dat produksie/chlorofil *a*-regressies nuttig sou wees vir die skatting van primêre produksie vir groot gebiede soos die Benguela-opwelling-ekostelsel.

The main aim of the *Nimbus-7* ground truth experiment in the Benguela upwelling region (Shannon *et al.* 1983) was to relate satellite radiance measurements to chlorophyll *a* distribution, so as to provide a synoptic method of measuring this parameter, a widely used index of phytoplankton biomass, over an area which approximately corresponds to the geographic range of the major South African pelagic fish stocks. In terms of ecosystem energetics, however, estimates of phytoplankton biomass should be used in combination with estimates of production, in order to establish the overall primary productivity of the system. Although the measurement of phytoplankton production was not a prime objective of the *Nimbus-7* experiment, its relevance was noted, and some measurements were made in the southern Benguela upwelling region during this period (Henry 1979, Brown 1984, Brown and Hutchings 1985).

The phytoplankton production data, which were collected in the southern Benguela region during the period of the *Nimbus-7* experiment, are summarized in this paper. Production / chlorophyll *a* relationships have been investigated with a view to predicting primary production from extensive chlorophyll *a* measurements in the Benguela region in a manner similar to that employed by Fiala and Jacques (1974) and Smith *et al.* (1977) off North-West Africa, by Smith *et al.* (1982) off California and by Smith (1984) off Somalia and Peru.

METHODS

Data collection

Sites where measurements of primary production were made are shown in Fig. 1. Data, on which this paper is based, were obtained from three sources, viz:

(a) Most data were collected at Sites A and B off the Cape Peninsula (Brown 1984). The only winter data on primary production available for the whole area was collected at Site A between June and August 1978.

(b) During the first summer of the *Nimbus-7* experiment (November 1978–February 1979), some production measurements were made in St Helena Bay and west of Cape Columbine at Sites C, D and E (Henry 1979).

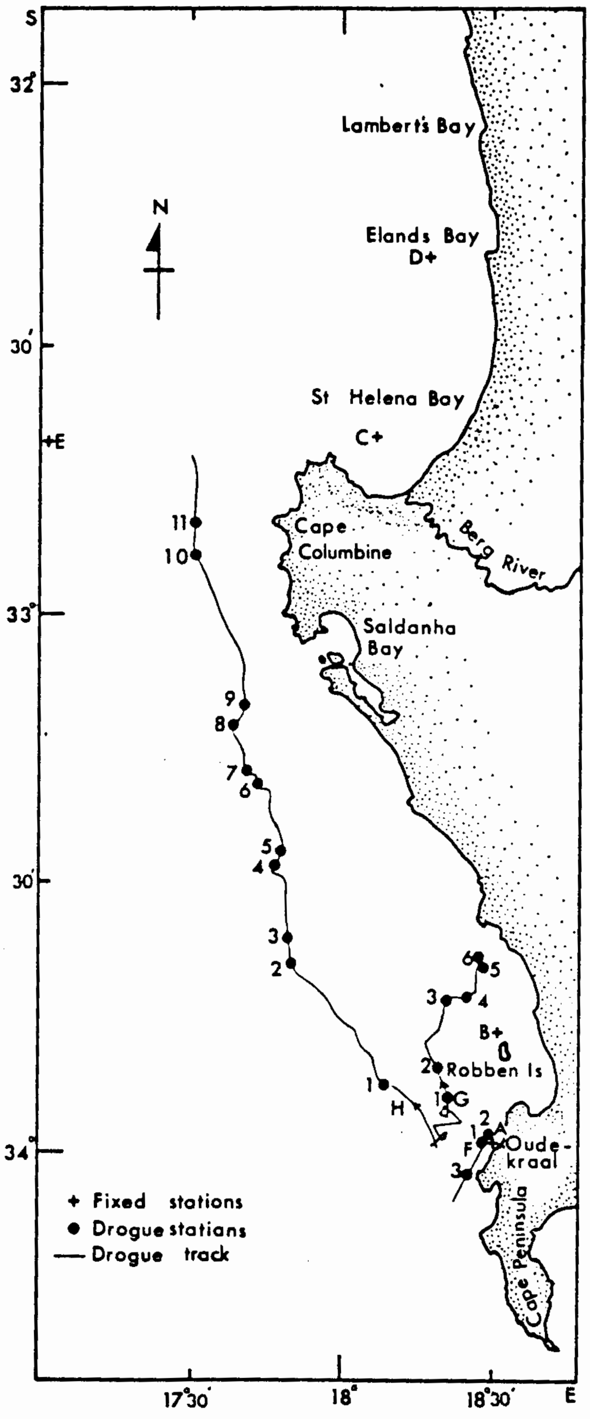

Fig. 1: The study area, showing fixed sampling sites off the Cape Peninsula (A and B) and off Cape Columbine (C, D and E), as well as stations along three drogue tracks (F and G — December 1979, H — December 1980) where production measurements were made

(c) Investigations into the development of phytoplankton populations in upwelled water (Brown 1983, Hutchings *et al.* 1983) provided production data during December 1979 and December 1980. On these cruises, drifting buoys with drogues set at 10 m were used to follow patches of upwelled water and monitor the dynamics of the phytoplankton populations.

Sampling

At each station, water samples were collected at the sea surface and from depths to which 50 per cent, 25 per cent, 10 per cent and 1 per cent of the surface light penetrated, by means of 5 dm^3 and 7 dm^3 NIO plastic samplers. Light penetration was established with an underwater quantum sensor (Lambda LI-192S) as recommended by the Scientific Committee on Oceanic Research (1974) or, in some cases, from Secchi disc depths (Poole and Atkins 1929). Temperature profiles were made with a bathythermograph to 140 m, or to 5 m above the sea bed for shallow stations. Subsamples were taken for analyses of salinity, nutrient, chlorophyll *a* and primary production. Chlorophyll *a* was measured according to the spectrophotometric method of the SCOR/UNESCO Working Group 17 (1966): one or two dm^3 of water were filtered through glass-fibre filters, coated with magnesium carbonate, at a vacuum of 30 kPa.

Measurements of primary production

Primary production was measured by either the carbon-14 uptake method (Strickland and Parsons 1972) or the light-and-dark-bottle oxygen method (Strickland 1960). Water samples were drawn, in the shade, into 125 cm^3 glass reagent bottles and incubated for a period of four hours between 09h30 and 15h30, either *in situ* or in a deck incubator in which *in situ* conditions were simulated (Brown 1982). During the drogue studies, two incubations were conducted daily, one in the morning and another in the afternoon, and here the mean of the two measurements has been used.

Estimates of production from the oxygen and carbon-14 methods were combined, because the results of 10 sets of replicate experiments (Sea Fisheries Research Institute, unpublished data) were not statistically different ($p > 0,2$) when subjected to the Wilcoxon signed-ranks test (Dixon 1977).

Daily production, P_{24}, was calculated as follows:

$$P_{24} = P_{int}(d - 0,1n)$$

where P_{int} = hourly depth-integrated production, d = number of hours of daylight (sunrise to sunset),

Table I: The number of depth-integrated primary production and chlorophyll *a* measurements made in the euphotic zone at each site during spring, summer, autumn and winter

Site	Date	Number of measurements made				
		Spring (Sept.–Nov.)	Summer (Dec.–Feb.)	Autumn (March–May)	Winter (July–Aug.)	Total
A	Nov. 77 — Dec. 78	13	13	1	8	35
B	April 77 — March 79	0	5	8	0	13
C	Nov. 78 — Feb. 79	1	4	0	0	5
D	Feb. 79	0	2	0	0	2
E	Feb. 79	0	1	0	0	1
F	Dec. 79	0	1	0	0	1
G	Dec. 79	0	2	0	0	2
H	Dec. 80	0	6	0	0	6
All sites	Nov. 77 — Dec. 80	14	34	9	8	65

and n = night hours (sunset to sunrise).

RESULTS AND DISCUSSION

The number of depth-integrated measurements of primary production and chlorophyll *a* which were made at each site (Fig. 1) during the period 1977–1980 is given in Table I. The paucity of data and their uneven distribution, together with the inherently large spatial and temporal variations in phytoplankton production (Brown 1984, Brown and Field in press) and biomass (Andrews and Hutchings 1980, Shannon, Hutchings, Bailey and Shelton 1984) in the dynamic southern Benguela upwelling system, prevent meaningful comparison of average production measurements between sites or areas within the system. Consequently data have been grouped together and summarized in Table II on a seasonal basis. A commentary on these data follows.

Chlorophyll *a* at the sea surface and in the euphotic zone

Chlorophyll *a* concentrations, both at the sea surface (C_o) and the mean value in the euphotic zone (C_e), were higher and more variable during the upwelling seasons (spring to autumn) than in winter (Table II). The reason for this is that during the "summer" months dense blooms of phytoplankton develop in the cool nutrient-rich water. The latter is poorly seeded with phytoplankton (i.e. has very low concentrations of chlorophyll *a*) when newly upwelled into the euphotic zone (Andrews and Hutchings 1980, Barlow 1982, Hutchings *et al.* 1983, Brown and Field in press). In contrast to the summer situation, reduced upwelling, increased turbulence and a reduction in irradiance combine to prevent the build-up of dense concentrations of phytoplankton during winter (Brown 1984).

Although there was a good linear correlation between C_o and C_e during the upwelling seasons (Fig. 2a) and also in winter (Fig. 2b), the slopes of the curves were different. During winter, C_o (at concentrations greater than 2 $mg \cdot m^{-3}$) was consistently

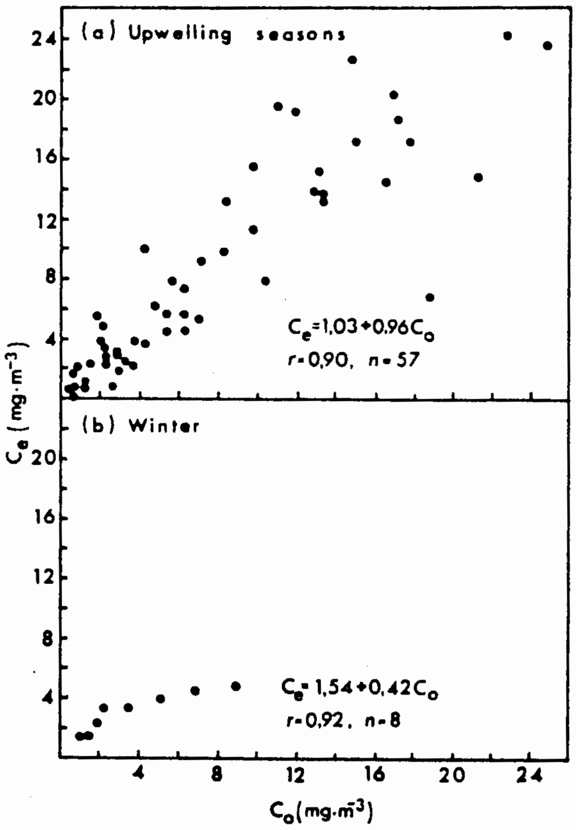

Fig. 2: Plots of C_e versus C_o during (a) the upwelling seasons and (b) winter

Table II: Measurements of chlorophyll *a* concentration at the sea surface (C_o) and in the euphotic zone (C_e), depth-integrated chlorophyll *a* (C_{int}) and hourly depth-integrated production (P_{int}) in the euphotic zone, the 1-per-cent light depth ($D_{1\%}$), the number of data points (n), mean number of hours of daylight for each season, and daily production (P_{24})

Season	C_o (mg·m⁻³)			C_e (mg·m⁻³)			C_{int} (mg·m⁻²)			P_{int} (mg C·m⁻²·h⁻¹)			$D_{1\%}$ (m)			n	Daylight (h)	P_{24} (mg C·m⁻²·d⁻¹)
	mean	sd	range	mean	sd	range	mean	sd	range	mean	sd	range	mean	sd	range			
Spring	8,5	7,7	(0,4–24,9)	9,9	8,5	(0,6–23,6)	117	77,2	(20–236)	367	240	(22–832)	18	9	(9–35)	14	12,9	4 332
Summer	6,5	5,6	(0,6–21,2)	6,9	5,6	(0,2–19,5)	95	56,9	(6–253)	307	214	(2,8–839)	19	9	(7–40)	34	12,9	3 962
Autumn	8,3	7,8	(1,2–22,7)	9,3	8,9	(1,1–24,4)	108	65,5	(41–203)	316	230	(65–754)	18	9	(8–37)	9	11,3	3 169
Winter	3,8	2,8	(1,0–8,9)	3,1	1,3	(1,5– 4,9)	83	32,0	(43–131)	276	121	(145–437)	27	4	(18–29)	8	10,3	2 465

higher than C_e, whereas during the upwelling seasons these estimates were almost the same. In concurrence with our findings during the upwelling seasons, Shannon, Schlittenhardt and Mostert (1984) and Sturm *et al.* (1984) reported that C_o and C_e (measured in the southern Benguela region during February 1980) were, for practical purposes, identical. That the correlation between C_o and C_e during the upwelling seasons was not as strong as it was in winter, is presumably because the depth of the chlorophyll *a* maximum is more variable during the upwelling seasons: As blooms develop in response to pulses of upwelling, a chlorophyll *a* maximum initially develops near the sea surface, then progressively deepens as the cells sink and nutrient limitation of production takes effect in surface waters (Hutchings *et al.* 1983). In winter, however, even when the water column does stabilize (a rarer occurrence than in summer), thereby allowing differential distribution of chlorophyll *a*, the relatively weak chlorophyll *a* maximum tends to be at or near the sea surface. This is partly because the lower levels of ambient light in winter are less likely to result in photo-inhibition near the sea surface, and partly because lower winter production reduces the intense stripping of nutrients and consequent depletion of chlorophyll *a* in surface waters. Moreover, the increased frequency of turbulent conditions in winter is likely to replenish surface nutrients and mix phytoplankton.

Depth of the euphotic zone

The fairly good logarithmic correlations (Table III) between C_o and C_e and the depth of the 1-per-cent light level ($D_{1\%}$), particularly during the upwelling seasons ($r^2 = 0,84$ for $D_{1\%}$ vs C_e and $r^2 = 0,65$ for $D_{1\%}$ vs C_o), are illustrated in Fig. 3. The regressions enable the depth of the euphotic zone, i.e. $D_{1\%}$, to be calculated from chlorophyll *a* estimates (C_o or C_e) obtained either directly from spectrophotometric

Table III: The logarithmic forms of the regression equation ($y = a + b \ln x$), the coefficients of determination (r^2) and the number of data points (n) for the correlations between $D_{1\%}$ versus C_o and C_e during the various seasons

Correlation	Season	a	b	r^2	n
$D_{1\%}$ vs C_o	Upwelling Winter Both	28 30 29	- 6,53 - 2,80 - 6,53	0,65 0,34 0,62	57 8 65
$D_{1\%}$ vs C_e	Upwelling Winter Both	30 31 31	- 7,16 - 3,86 - 7,32	0,84 0,23 0,82	57 8 65

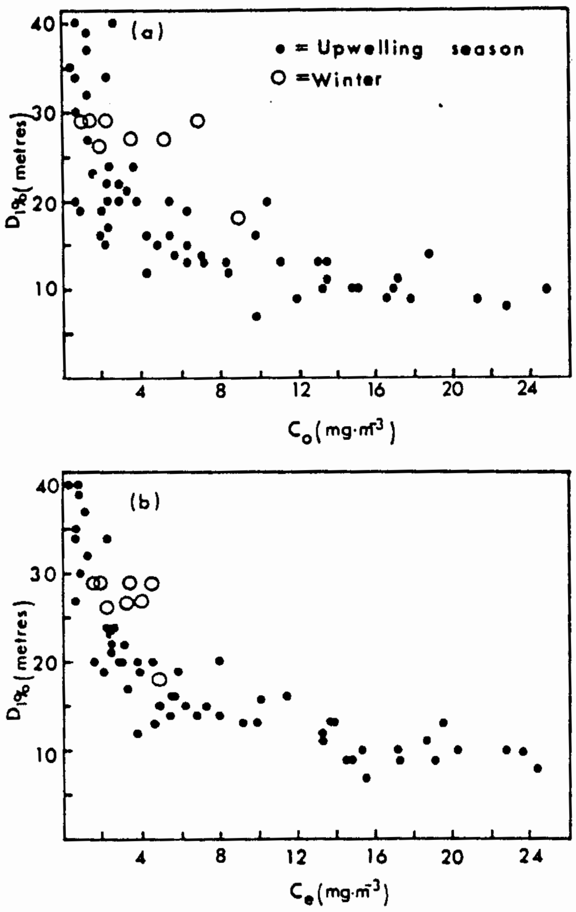

Fig. 3: Plots of (a) $D_{1\%}$ versus C_0 and (b) $D_{1\%}$ versus C_e during the upwelling seasons and winter. The logarithmic forms of the regression equations and coefficients of determination are summarized in Table III.

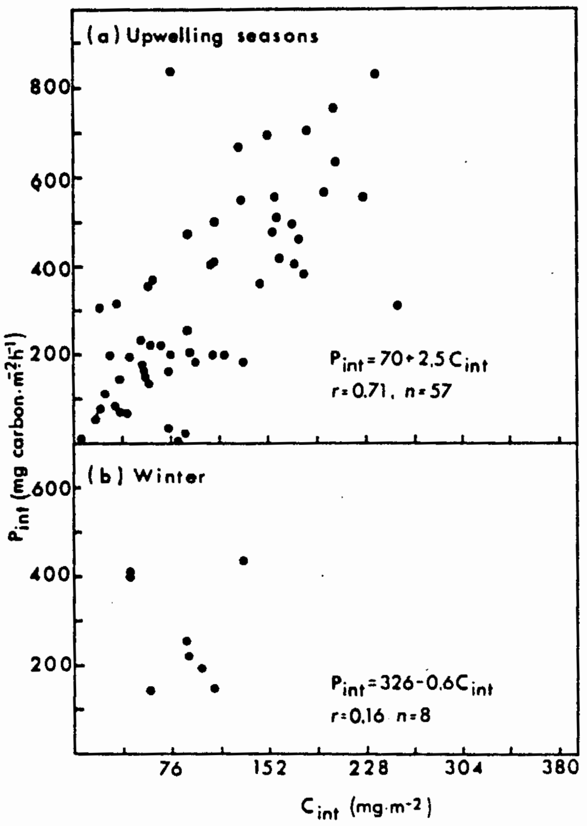

Fig. 4: Plots of P_{int} versus C_{int} during (a) the upwelling seasons and (b) winter

measurements, or indirectly from satellite images. Moreover, when only surface chlorophyll *a* measurements (C_o) are available, mean chlorophyll *a* concentrations in the euphotic zone (C_e) can be calculated (see Fig. 2). It follows that depth-integrated chlorophyll *a* in the euphotic zone (C_{int}) can be estimated indirectly by multiplying C_e by $D_{1\%}$. This approach should prove useful, not only when $D_{1\%}$ is unknown, but also when limited subsurface chlorophyll data are available.

Chlorophyll *a* and production

The lower chlorophyll *a* concentrations in winter allow light to penetrate deeper than during the upwelling season (Table II), newly upwelled water excepted (Brown and Field in press). Consequently C_{int} and P_{int} were only slightly higher during the upwelling season than in winter. During summer, daily production was nearly double the winter value, although hourly production was only slightly greater than in winter (Table II), because the daylight period is longer in summer (Brown 1984).

Although there was little correlation ($r \leqslant 0{,}24$) between the winter values of P_{int} and either C_{int}, C_e or C_o (Figs 4, 5 and 6), the correlations during the upwelling seasons were considerably better ($r = 0{,}65 - 0{,}71$) and lay within the range of values reported for other upwelling areas, viz. 0,60 for North-West Africa (Fiala and Jacques 1974, Smith *et al.* 1977), 0,92 for Peru, 0,69 for Somalia (Smith 1984) and 0,73 for upwelling areas in the Atlantic and Pacific Oceans (Lorenzen 1970). Brown and Field (in press) found strong linear correlations between production at the

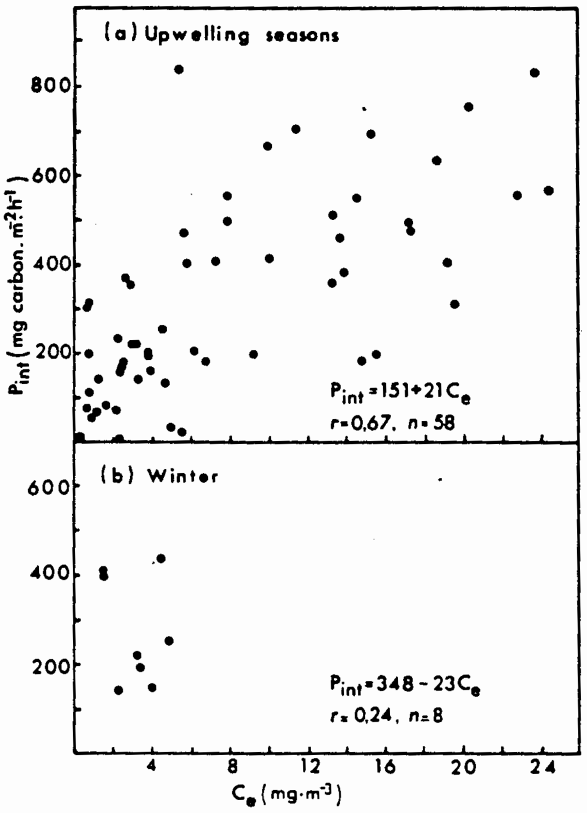

Fig. 5: Plots of P_{int} versus C_e during (a) the upwelling seasons and (b) winter

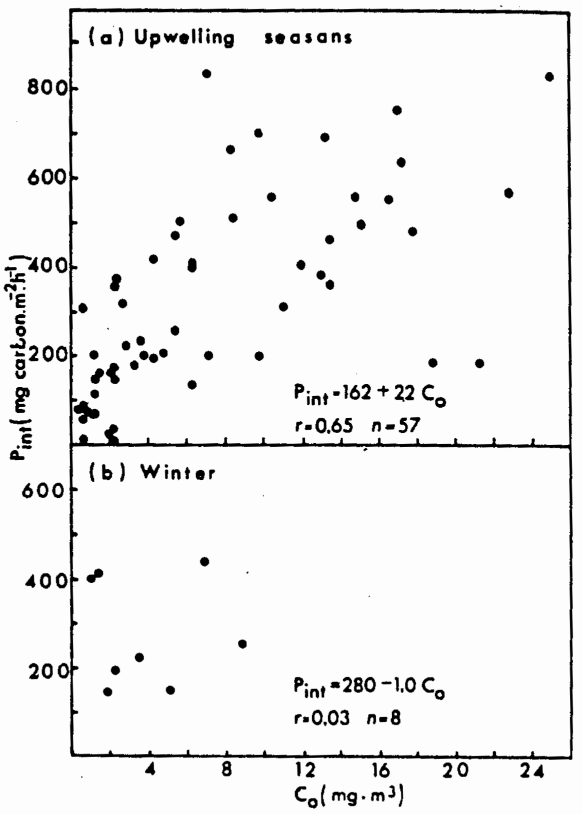

Fig. 6: Plots of P_{int} versus C_o during (a) the upwelling seasons and (b) winter

sea surface and chlorophyll *a* concentrations at Sites A and B during the upwelling seasons, particularly when chlorophyll *a* concentrations were less than 12 mg·m⁻³ ($r = 0{,}90$, $n = 29$). The correlation weakened when chlorophyll *a* concentrations of higher than 12 mg·m⁻³ were included in the analysis ($r = 0{,}78$, $n = 40$) and weakened further when depth-integrated estimates of production and chlorophyll *a* were used ($r = 0{,}47$, $n = 24$). However, for the larger data set employed herein (Fig. 4a), the correlation between P_{int} and C_{int} was better ($r = 0{,}71$, $n = 57$). The above findings suggest that phytoplankton production in upwelled water is limited at first primarily by biomass (i.e. chlorophyll *a*) and then, as the population matures, by light (self-shading effect) and nutrients, both of which play increasingly important roles in determining production. It follows that a decreasing percentage of variation in P_{int} may be explained in terms of C_{int} (or C_e and C_o), and that supplementary information is required to improve predictions of production, particularly if specific point estimates of chlorophyll *a* are to be used.

Suggested uses of regressions

If gross estimates of phytoplankton production are required for large areas, regressions such as have been developed here may prove useful for calculating production from the extensive sets of chlorophyll *a* measurements available from satellite colour images and from extensive ship surveys (e.g. Shannon, Hutchings, Bailey and Shelton 1984). The inaccuracy in predicting production at a single point should be weighed against the vastly increased area for which data are available.

It should be noted that low concentrations of chlorophyll *a* are typically found in both newly upwelled, nutrient-rich water, and in nutrient-poor, aged upwelled or oceanic water. Because of the difference in the availability of nutrients in these water types, one would expect different relationships between production and chlorophyll *a*. It is therefore desirable that different regressions should be developed for different water masses and oceanographic conditions. (These can be distinguished on the basis of available supplementary data such as water temperature, nutrient concentrations, geographical position and season.) Sea surface temperatures from satellite infra-red imagery could perhaps even be used in conjunction with the temperature-nitrate relationship of Andrews and Hutchings (1980) for estimating the nutrient-status of the environment. Such information could, in turn, suggest which production-chlorophyll regression equation would be the most appropriate for predicting phytoplankton production in different parts of the Benguela ecosystem. This procedure would of necessity require the collection of primary-production and accessory data from a much wider geographic area. Estimates of primary production for the Benguela system will be refined by work directed along these lines.

CONCLUSIONS

(1) Chlorophyll *a* concentrations at the sea surface (C_o) and mean concentrations in the euphotic zone (C_e) were well correlated ($r = 0{,}90$ and $0{,}92$ for summer and winter data sets respectively). The relationship in winter was different from that during the upwelling seasons. The chlorophyll *a* concentrations were both more variable and, on average, two or three times higher during the upwelling seasons than in winter.

(2) The depth of the euphotic zone ($D_{1\%}$) can be predicted with reasonable accuracy from C_o, or preferably, from C_e.

(3) Depth-integrated phytoplankton production (P_{int}) during the upwelling seasons correlated fairly well with C_o and C_e and particularly with depth-integrated chlorophyll *a* (C_{int}). In winter the correlation was much weaker, this being partly due to the small number and range of production data.

(4) Individual estimates of phytoplankton production, calculated from satellite measurements of chlorophyll *a* at specific sites, are inherently unreliable because of the variable influence of environmental factors on production/chlorophyll *a* relationships. Moreover, when large-scale estimates of production are required, as in ecosystem models of the Benguela region, the extrapolation of a few production measurements over large areas of ocean negates the value of even the most precise individual measurements. However, large-scale estimates of primary production based on satellite observation of ocean colour can be justified by the much larger area for which data on biomass distribution are available. This improved data coverage more than compensates for the variance associated with the biomass-production regressions. More experimental data will permit the development of a suite of regression equations for different seasons, areas and conditions.

LITERATURE CITED

ANDREWS, W.R.H. and L. HUTCHINGS 1980 — Upwelling in the southern Benguela Current. *Prog. Oceanogr.* **9**(1): 81 pp. + 2 Figures.

BARLOW, R.G. 1982 — Phytoplankton ecology in the southern Benguela Current. 1. Biochemical composition. *J. expl mar. Biol. Ecol.* **63**(3): 209-227.

BROWN, P.C. 1982 — Phytoplankton production measured *in situ* and under simulated *in situ* conditions in the southern Benguela upwelling region. *Fish. Bull. S. Afr.* **16**: 31-37.

BROWN, P.C. 1983 — Phytoplankton development in newly upwelled water. *S. Afr. J. Sci.* **79**(4): p. 144.

BROWN, P.C. 1984 — Primary production at two contrasting nearshore sites in the southern Benguela upwelling region, 1977–1979. *S. Afr. J. mar. Sci.* **2**: 205-215.

BROWN, P.C. and J.G. FIELD in press — Factors limiting phytoplankton production in a nearshore upwelling area. *J. Plankt. Res.*

BROWN, P.C. and L. HUTCHINGS 1985 — Phytoplankton distribution and dynamics in the southern Benguela Current. In *International Symposium on the Most Important Upwelling Areas off Western Africa (Cape Blanco and Benguela). Barcelona, November 1983.* **1**. Bas, C., Margalef, R. and P. Rubiés (Eds). Barcelona: Instituto de Investigaciones Pesqueras: 319–344.

DIXON, W.J. (Ed.) 1977 — Nonparametric analysis. *Biomedical Computer Programs P-series.* Los Angeles; University of California Press: 605-619.

FIALA, M and G. JACQUES 1974 — Relations entre ATP, chlorophylle et production dans la couche euphotique d'une zone d'up-welling. *Téthys* **6** (1-2): 261-268.

HENRY, J.L. 1979 — Radiocarbon productivity measurements off the Cape west coast. Poster paper presented at 4th National Oceanographic Symposium, Cape Town, South Africa: S 189.

HUTCHINGS, L., BARLOW, R.[G.], BROWN, P.C. and E.T. OLIVIERI 1983 — Drogue drift and phytoplankton blooms in newly upwelled waters in the southern Benguela Current. Abstracts of the CSIR/SANCOR 5th National Oceanographic Symposium, Grahamstown, January 1983. **S288**: B 16.

LORENZEN, C.J. 1970 — Surface chlorophyll as an index of the depth, chlorophyll content and primary productivity of the euphotic layer. *Limnol. Oceanogr.* **15**(3): 479-480.

MOSTERT, S.A. 1983 — Procedures used in South Africa for the automatic photometric determination of micronutrients in seawater. *S. Afr. J. mar. Sci.* 1: 189-198.

POOLE, H.H. and W.R.G. ATKINS 1929 — Photo-electric measurements of submarine illumination throughout the year. *J. mar. biol. Ass. U.K.* 16: 297-324.

SCIENTIFIC COMMITTEE ON OCEANIC RESEARCH 1974 — SCOR Working Group 15 (With UNESCO and IAPSO). Photosynthetic radiant energy recommendations. *SCOR Proc.* **10**(1): 37-42.

SCOR/UNESCO WORKING GROUP 17 1966 — Determination of photosynthetic pigments. In *Determination of Photosynthetic Pigments in Seawater.* UNESCO Monographs on Oceanographic Methodology 1: 9-18.

SHANNON, L.V., HUTCHINGS, L., BAILEY, G.W. and P.A. SHELTON 1984 — Spatial and temporal distribution of chlorophyll in southern African waters as deduced from ship and satellite measurements and their implications for pelagic fisheries. *S. Afr. J. mar. Sci.* 2: 109-130.

SHANNON, L.V., MOSTERT, S.A., WALTERS, N.M. and F.P. ANDERSON 1983 — Chlorophyll concentrations in the southern Benguela current region as determined by satellite (*Nimbus-7* coastal zone colour scanner) *J. Plankt. Res.* 5(4): 565-583.

SHANNON, L.V., SCHLITTENHARDT, P. and S.A. MOSTERT 1984 — The *Nimbus-7* CZCS experiment in the Benguela Current region off southern Africa, February 1980. 2. Interpretation of imagery and oceanographic implications. *J. geophys. Res.* **89**: 4968-4976.

SMITH, S.L. 1984 — Biological indications of active upwelling in the northwestern Indian Ocean in 1964 and 1979, and a comparison with Peru and Northwest Africa. *Deep-Sea Res.* 31 (6-8A): 951-967.

SMITH, W.O., BARBER, R.T. and S.A. HUNTSMAN 1977 — Primary production off the coast of northwest Africa: excretion of dissolved organic matter and its heterotrophic uptake. *Deep-Sea Res.* **24**: 35-47.

SMITH, R.C., EPPLEY, R.W. and K.S. BAKER 1982 — Correlation of primary production as measured aboard ship in southern Californian coastal waters and as estimated from satellite chlorophyll images. *Mar. Biol.* **66**: 281-288.

STRICKLAND, J.D.H. 1980 — Measuring the production of marine phytoplankton. *Bull. Fish. Res. Bd Can.* **122**: vii + 172 pp.

STRICKLAND, J.D.H. and T.R. PARSONS 1972 — A practical handbook of seawater analysis, 2nd Ed. *Bull. Fish. Res. Bd Can.* 167: 310 pp.

STURM, B., WALTERS, N.M., MARACCI, G. and P. SCHLITTENHARDT 1984 — The *Nimbus-7* CZCS experiment in the Benguela Current region off southern Africa, February 1980. 1. Surface truth measurements and algorithm description (unpublished manuscript).

PART II : PHYTOPLANKTON BLOOM DYNAMICS IN UPWELLED WATER OFF THE CAPE PENINSULA

CHAPTER 3: INTRODUCTION

Upwelling areas are renowned for high organic production (Ryther 1969, Cushing 1971). In the southern Benguela upwelling region, high plankton and fish biomass and production have been documented (see reviews by Brown and Hutchings 1985, Shannon and Pillar 1986, Shelton, Boyd and Armstrong 1985), and attributed directly or indirectly to rich inorganic nutrient concentrations in the upwelling water. The main upwelling season is from September until April. However, the pulsing tongue-like nature of upwelling in the southern part of the region (i.e. from Cape Columbine to the Cape Peninsula) (Nelson and Hutchings 1983) coupled with the paucity of phytoplankton and rich nutrient concentrations in the water which upwells, results in highly variable concentrations of phytoplankton in the coastal zone (Andrews and Hutchings 1980, Brown 1984). Consequently the availability of phytoplankton to consumers is not uniform in time or space, and may limit the occurrence and productivity of organisms at higher levels in the food web in this area. It follows that insight into both the feeding ecology of consumers and the development of phytoplankton populations, together with the dynamics of water after upwelling, is necessary to evaluate trophic interactions in the ecosystem.

Numerous airborne radiation thermometry (ART) maps (e.g. Andrews and Cram 1969, Jury 1980 and 1985, Nelson and Hutchings 1983, Taunton-Clark 1982 and 1985) and satellite thermal images (Shannon et al 1985) of the southern Benguela region illustrate the existence of one or more tongues of cold water orientated roughly to the northwest during upwelling off the Cape Peninsula. The existence of these tongues prompted Andrews and Hutchings

(1980) to monitor a line of stations, the Upwelling Monitoring (UM) line, running northwest from Duiker Point on the Cape Peninsula (see Fig.4, Chapter 1) on a monthly basis for two and a half years from October 1970. Repeated hydrographic transects demonstrated the semi-permanent nature of the plume as well as high variability in nutrient concentrations and phytoplankton biomass (see Fig.5, Chapter 1) off the Cape Peninsula during the upwelling season. Satellite colour images (Shannon et al 1983, 1985) show chlorophyll distribution to be consistent with concurrent thermal images, preceeding wind patterns, and the results of direct investigations of the effects of upwelling on the spatial and temporal distribution of phytoplankton (e.g. Andrews and Hutchings 1980, Brown 1984, Brown and Field 1986). In other words, chlorophyll concentrations are low during upwelling in the vicinity of an active upwelling site, whereas they are high adjacent to or downstream of the upwelling source, and high close inshore along the whole coastline during quiescent periods. To date the interpretation of satellite images has not been detailed enough either to reflect possible small to meso-scale patchiness, or to give an idea of the variation in chlorophyll concentration within a large patch, since concentrations are expressed in fairly wide ranges (i.e. 0.1-0.3, 0.3-1, 1-3, 3-10, 10-30 mg chll.m^{-3}) and uncertainity exists as to the absolute concentrations of chlorophyll as inferred from the satellite images (J.J.Agenbag, SFRI, pers.comm.). However, the sporadic supply of phytoplankton may limit zooplankton (Borchers and Hutchings 1986) and pelagic fish distribution in the Cape Peninsula - Cape Columbine area.

The major aim of Part II of this thesis is to examine the manner in which phytoplankton populations develop in upwelled water with emphasis on the time scale of such events, so as to complement the transect study of Andrews and Hutchings (1980) which emphasised spatial variations across the shelf zone. Because their Upwelling Monitoring (UM) line of stations was assumed to lie along the upwelling tongue, spatial changes offshore were equated with temporal changes in terms of the development of phytoplankton populations in upwelled waters. As can be seen in Fig.5 of Chapter 1, phytoplankton biomass generally increased offshore during the upwelling season, and peaked about 20-40 km along the UM line with secondary peaks further offshore. However, the equivalent time scale along such a line can be quantified only by monitoring phytoplankton development in a single water body.

Various approaches have been used in other studies to investigate such processes in a body of sea water. These fall into three broad categories, viz.

(1) the mesocosm approach, in which a large body of water is enclosed and maintained in as natural a state as possible during the monitoring period,

(2) drogue studies, where a drogue is deployed in the sea to "mark" a patch of water, and the water close to the drogue is monitored, and

(3) repetitive grid sampling, where the area of interest is surveyed repetitively so as to monitor changes in patches of plankton which occur in or develop in the area.

Approach (3) has been used off Peru (Beers et al 1971), off Northwest Africa (Jones and Halpern 1981) and off the Cape

Peninsula, South Africa (Andrews and Hutchings 1980). Shortcomings of this approach include the inability to control the physical dispersion of the original water mass with time. More importantly, the logistics of such an approach usually do not allow the frequency of sampling suitable for detailed examination of the dynamics of a phytoplankton population (during peak growth periods phytoplankton generation times may be only a few hours (Sournia 1974) and so sampling should be more frequent than daily). Such frequent sampling is more feasible using approaches (1) and (2).

The mesocosm approach (1), which has been reviewed by Grice and Reeve (1982), involves the use of either a large floating plastic bag which encloses a column of natural sea water and its contained plankton assemblages <u>in situ</u>, (e.g. Strickland and Terhune 1961, Harrison <u>et al</u> 1977, Parsons 1978, Eppley <u>et al</u> 1978), or a large land-based plankton tower (Peterson 1939, von Bodungen <u>et al</u> 1976, Blach <u>et al</u> 1978) into which large volumes of natural sea water are transfered (eg. Mullin and Evans 1974, Pilson <u>et al</u> 1979). Both apparatuses were designed to overcome the problem of water column shear, a factor which cannot be controlled in approaches (2) or (3). Shortcomings of the mesocosm approach, however, include the possibility of inadequate representation of the meso-zooplankton which would influence normal grazing pressures, and also the "wall effect" of the enclosure converting the system from one dominated by pelagic organisms to one dominated by organisms which settle on the sides of the container. Probably more important, however, is the reduction in vertical advection and consequent increased sinking rates of phytoplankton. Practical constraints include the expense of such apparatus and the fact that floating plastic bags are limited to calm seas, a condition which seldom lasts for more than a day or two in the southern Benguela region. Consequently, the second approach (i.e. the use of a drogue to follow a water mass while it is monitored) was used in the present investigation. Such an approach has been employed in a number of biological studies, particularly in upwelling areas where rough conditions usually preclude the use of large enclosures, eg. Andrews and Cram (1969), Ryther _et al_ (1971), Herbland _et al_ (1973), Herbland and Voituriez (1974), Nelson and Goering (1978), MacIsaac _et al_ (1985). The main short-coming of this approach is the doubtful ability of a "patch" of water to maintain its physical integrity with time (Beers _et al_ 1971). Dispersion of the original water mass may be caused by physical processes such as horizontal shear, diffusion, turbulence, intrusion of other water bodies etc. In particular, the scales of motion important to microscopic phytoplankton particles are different from those which influence drogue-sized particles.

Moreover, drogues are positively buoyant and so do not detect sinking motions in the water column. Slippage of water past the drogue may also complicate such an approach. However, in the present study it is assumed that the patches, into which the drogues were deployed, were large and uniform enough so that these effects would be minimal. In the interpretation of results, attention is directed towards possible artefacts resulting from such an assumption. While, at its worst, such an investigation may not allow one to calculate absolute rates of nutrient uptake and phytoplankton growth from state changes in the water column, it does reflect the _in situ_ conditions after the net action of the physical and biological processes which occur after upwelling.

The general strategy employed in the present study was as follows: a large patch of the most recently upwelled water off the Cape Peninsula was identified. A drogue was deployed in the middle of the coldest patch, and changes in the biomass of the phytoplankton population and associated environmental parameters were monitored by sampling three times daily alongside the drogue for up to seven days while various incubations (including measurements of primary production and zooplankton grazing) were performed *in situ* and on deck. The exercise was repeated five times (the Plankton Dynamics Cruises A-E) during the upwelling season (September - April) between 1979 and 1981, so as to obtain some idea of variation in the destination of upwelled water and in the pattern of development of phytoplankton populations in this region.

Physical aspects of the study are presented in Chapter 5, gross chemical and biological features in Chapter 6, nutrient ratios and limitation in Chapter 7 and primary production in Chapter 8. Detail on biochemical measurements is described by Barlow (1982, 1984 a and b), while Coulter counter particle spectra and production, phytoplankton species analyses and zooplankton biomass and grazing pressures are described by Olivieri (1983), Olivieri, Hutchings, Brown and Barlow (1985) and Olivieri and Hutchings (1985 a and b).

CHAPTER 4: METHODS

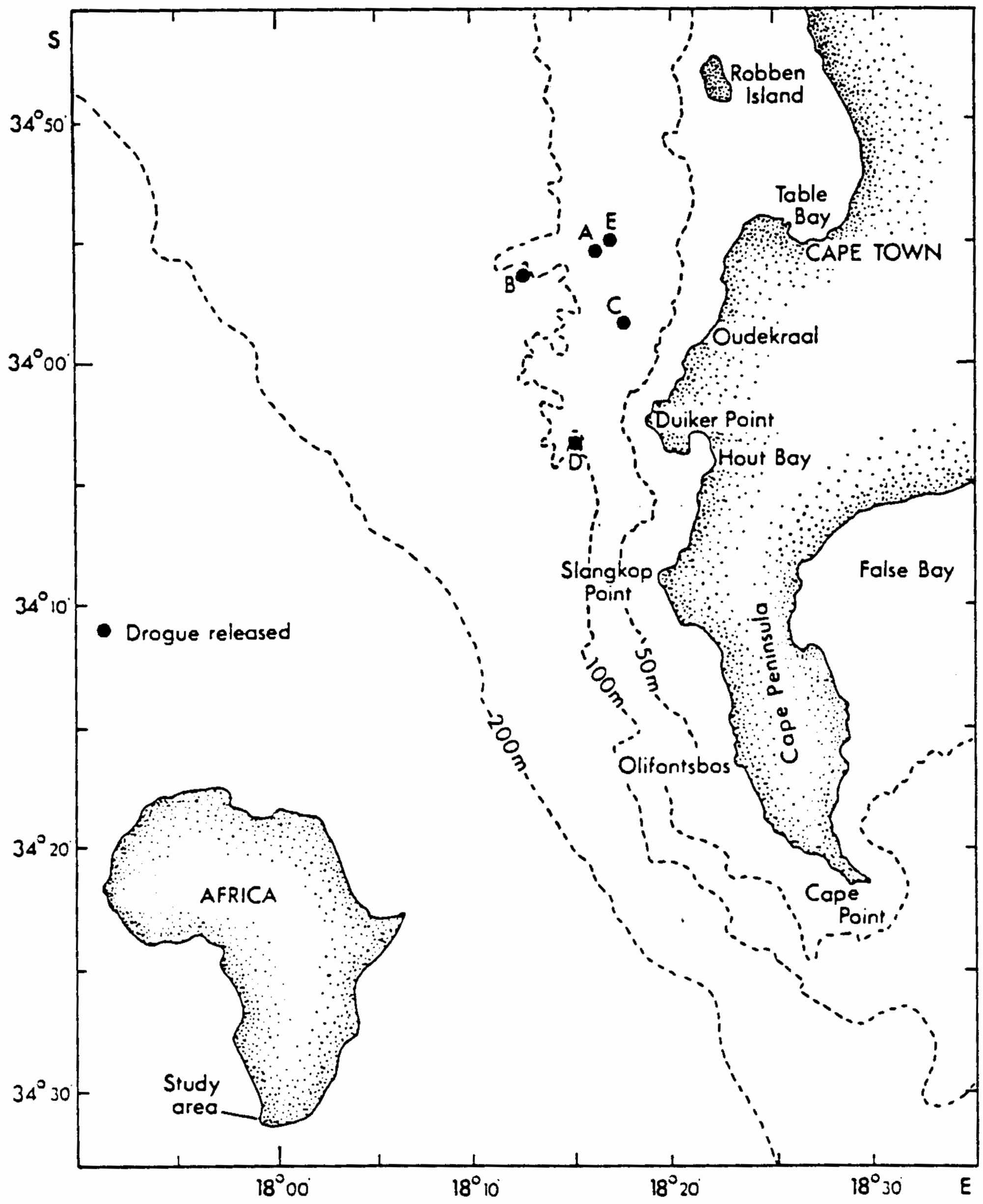

Fig.4.1: The Cape Peninsula showing the deployment positions of the drogue during Cruises A, B, C, D and E.

The Plankton Dynamics drogue studies were conducted off the Cape Peninsula (Fig.4.1) during 7-11 December 1979 (Cruise A), 3-9 December 1980 (Cruise B), 4-11 February 1981 (Cruise C), 6-13 March 1981 (Cruise D) and 20-26 October 1981 (Cruise E) from the R.V. Africana II.

Underway mapping of sea surface temperature and salinity, together with periodic bathythermograph (BT) profiles (e.g. Olivieri 1983, for Cruise A) and observations of sea colour and clarity, enabled demarcation of the largest patch of clear, cool, relatively newly upwelled water apparent off the Cape Peninsula at the time. Some flexibility in the starting time of each cruise allowed the research vessel to sail after a few days of strong southeast winds. Once a suitable patch was detected, a 3 m biplanar tetrahedral canvas drogue set with the mid point at 10 m, was deployed in the patch and tracked for between 4 and 8 days. The drogue design, shown in Fig.4.2, was based on that of Boyd (1983), but it was larger as a radio transmitter and flashing light were attached to the superstructure to facilitate tracking. During Cruises A and B a similar but smaller (approximately 2 m by 3 m) drogue was used without the radio transmitter unit. The superstructure was as light as possible to minimize windage and drag. Drogue position, along with wind speed and direction, was recorded each hour on board ship. Navigation fixes were made using Decca or Radar; wind speed was measured from the ship with a cup anemometer at a height of 10 m above the sea, with direction estimated by the ship's officer. Hourly wind data prior to and during each study were also obtained from the Cape Point and Cape

Columbine lighthouses (see Figs 5.1-5.5).

Incident photosynthetically active radiation (PAR) was monitored using a Lambda LI-190S atmospheric sensor coupled to a LI-500 integrator. Because of instrument failure during December 1980 (Cruise B) and March 1981 (Cruise D, Days 5 - 6), total hourly radiation measurements (daW-h.m^{-2}) made by the South African Weather Bureau at the DF Malan Airport near Cape Town were used. Total radiation was converted to PAR (µE.m^{-2}.s^{-1}) using predictive regression equations obtained for concurrent data sets from Cruise A in December 1979 (PAR = 20.6 daW + 19.4, r = 0.96, n = 94) and from Cruise D (Days 1-4) in March 1981 (PAR = 18.8 daW + 58.0, r = 0,93, n = 77), for the missing PAR measurements in Cruises B and D respectively.

Sampling was conducted at approximately 08h30, 12h30 and 18h00 local time each day. During Cruise A a fourth station was conducted at 22h00 to obtain a night-time sample of zooplankton and a temperature profile only. Submarine light penetration was established during daylight stations with an underwater quantum sensor (Lambda LI-192S), and a bathythermograph (BT) temperature profile was made. Ten water samples were then drawn with 18 l or 5 l NIO bottles from the upper 100 m or shallower. Sampling depths were chosen to cover the euphotic zone (100%, 50%, 25%, 10% and 1% light depths), the thermocline zone and the deeper layer. Subsamples were then drawn for analyses of oxygen, nutrients, chlorophyll a, biochemical composition, particle spectra and phytoplankton species, and for primary productivity and zooplankton grazing experiments. Discrete temperature measurements and water samples for salinity measurements were

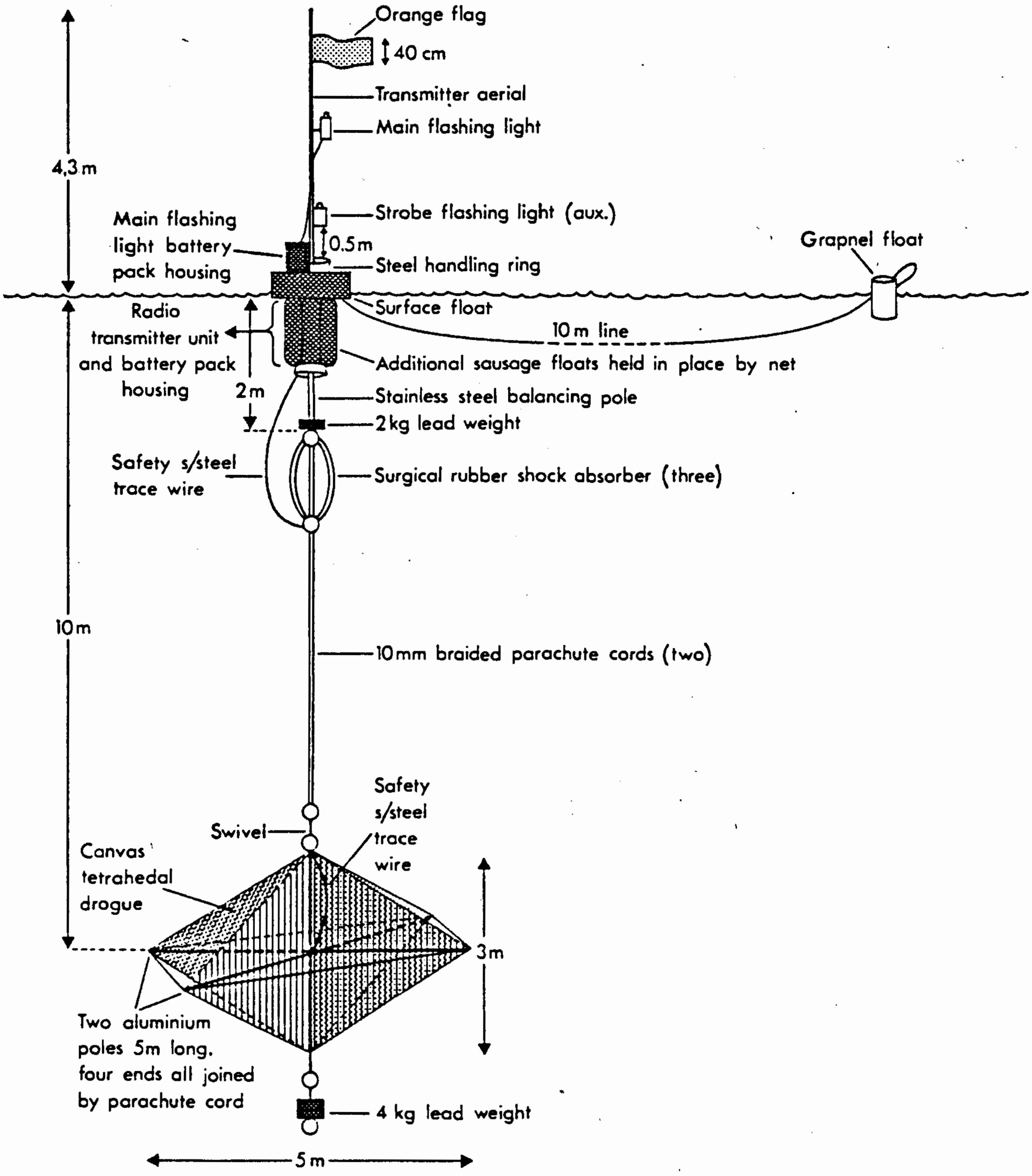

Fig.4.2: The drogue

obtained at the same depths using Nansen-Pettersen bottles for sigma-t density analyses, as no CTD was available on the R.V. Africana II.

Salinity was measured on an inductively coupled salinometer and oxygen concentrations were determined using Winkler titrations. Water samples for nutrient analysis were stored at -20°C until analysed for phosphate, nitrate (including nitrite) and silicate on a Technicon Auto analyser according to the methods of Mostert (1983). For chlorophyll a analysis, one litre of water from each depth was filtered through a 47 mm Toyo GC-50 glass fibre filter at a vacuum of 30 kPa, stored frozen, and analysed spectrophotometrically in 90% acetone (Swart and Barlow 1981).

Water samples for ^{14}C-uptake primary productivity experiments were drawn at the morning and noon stations from the 100%, 50%, 25%, 10% and 1% light depths, and incubated either in situ or in a deck incubator (at stations 4, 12, 15, 18 and 20 of Cruise C) where in situ light levels were simulated in bottles coated with a spectrally neutral mixture of clear varnish and black polyurethane paint (Brown 1982b). Morning and afternoon incubations usually commenced between 09h30 and 10h00 and between 13h30 and 14h45 respectively, and lasted for 3-$3^1/_2$ hours (Cruise A) or 4-$4^1/_2$ hours (Cruises B-E). During Cruise E productivity measurements at the 25% light depth were omitted and additional samples were taken between the 10% and 1% light depths (when the depth interval was large) and/or below the 1% light depth (to investigate the possible underestimation of column productivity).

A modification of the Strickland and Parsons (1972) ^{14}C-uptake method was used. Five (or ten for Cruise E) microcuries of radioactive carbon in the form of NaH_2CO_3 were added to each 125ml water sample (1 dark and 3 light per depth). The time before and after incubation was kept at a minimum and samples were collected in the shade, and stored cool and in the dark to prevent the phytoplankton being light shocked (Brown 1982c). Photosynthesis was arrested by filtering the samples onto 47 mm Toyo GC-50 glass fibre filters (0.7 µm mean pore size), which were rinsed carefully with filtered sea water, dried, and then fumed with concentrated HCl for one hour to remove any residual inorganic ^{14}C. The filters were stored in mini scintillation vials in 6.5 ml of Pico-Fluor scintillation cocktail (Insta-Gel for Cruise A).
A Packard Prias Liquid Scintillation Counter was used to measure the activity of the samples ashore. The uptake of organic carbon (in mg $C.m^{-3}.h^{-1}$) was calculated for each bottle sample according to the method of Strickland and Parsons (1972); dark uptake was subtracted from the mean light uptake to give an estimate of productivity at each depth. Depth-integrated or column productivity was obtained by linear integration of discrete estimates. Daily productivity may be calculated by several methods; these methods will be described in Chapter 8.

CHAPTER 5: THE PHYSICAL ENVIRONMENT

- 5.1 Introduction
- 5.2 Drogue movement, wind and currents
- 5.3 Physical features of the water column
  - 5.3.1 Temperature, salinity and density
  - 5.3.2 Bathythermography, wind and irradiance
- 5.4 Discussion
  - 5.4.1 Slippage and dispersion
  - 5.4.2 Drogue movements

5.1 Introduction

Physical aspects of the Benguela upwelling area have been throughly reviewed by Nelson and Hutchings (1983) and by Shannon (1985a) and co-workers (Shannon 1985b). A summary of features relevant to the present study is presented here.

In the southern Benguela region, upwelling is induced primarily by longshore equatorward winds (mostly southeast) which drive surface water away from the coast (for general discussion of the theoretical aspects of upwelling refer to Brink 1983). SE winds are most intense between spring and autumn when the South Atlantic atmospheric high pressure system periodically elongates and ridges round the continent. Cold subsurface water wells to the surface from depths not greater than about 200 m (Nelson 1985), and, depending on the submarine and terrestrial topography, is expressed either three dimensionally (3-D) as a tongue of cold water with surface isotherms forming closure with the coast (as off the various capes and headlands), or, in a more two dimensional (2-D) manner, as a narrow strip of cold water adjacent to the coast. This quasi 2-D upwelling occurs along the relatively featureless coast north of St Helena Bay as shown by Taunton-Clark (1985, Fig.7b and c) and Jury (1985, Figs 8d and 17). The Cape Peninsula and Cape Columbine areas, however, are considered to be two of the major centres (Taunton-Clark 1985) of distinctly 3-D upwelling in the southern Benguela region. Because Africa ends at 35°S, easterly moving cyclones are allowed free passage past the continent. This results in a <u>modulated</u> upwelling cycle with days in the area south of 31-32°S. The consequent formation, growth and decay of tongues of cool water in response to these cyclical wind patterns has stimulated considerable oceanographic interest not only in the physical mechanisms responsible for such phenomena, but also in the increased biological productivity resulting from the rapid uplift of nutrient-rich waters into the euphotic zone.

Aerial radiation thermometry (ART) data obtained during various stages of upwelling events (Andrews and Cram 1969, Jury 1980, 1985 and Taunton-Clark 1982 and 1985) show several distinct upwelling sites along the Cape Peninsula, the tongues of which merge to form the Cape Peninsula tongue (Nelson and Hutchings 1983). In his attempt to quantify tongue development, Taunton-Clark (1985) shows that the Duiker Point to Oudekraal area (see Fig.4.1) is the Cape Peninsula tongue base and the primary upwelling site in the southern Benguela itself.

Nelson (1985) points out that satellite colour images show convoluted filaments of water (containing relatively high concentrations of chlorophyll) stretching to the northwest far beyond the boundaries of the thermal tongue, and attributes their existence to surface currents advecting the products of biological activity initiated at the upwelling centre.

Until the advent of current metering and drogue tracking programs by the Sea Fisheries Research Institute (Nelson and Hutchings 1983, Nelson 1985, Holden 1981 and 1985, Shannon <u>et al</u> 1981), knowledge of circulation patterns in the southern Benguela area was limited and inferred indirectly. Currents in the Cape Peninsula-Cape

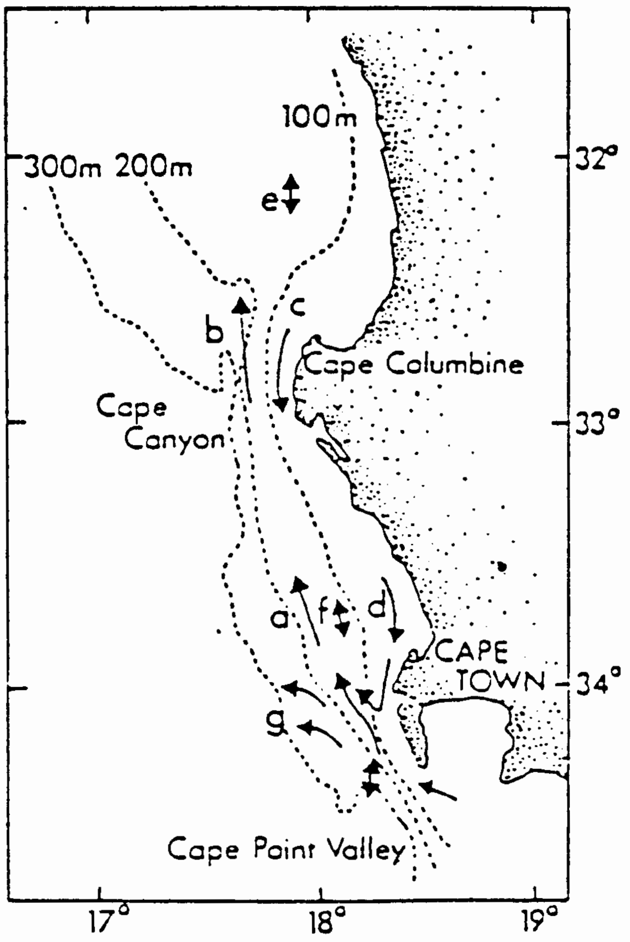

Fig.5.1: Currents in the Cape Peninsula and Cape Columbine areas (from Nelson and Hutchings 1983): permanent shelf edge baroclinic jets (a and b); near-shore net southward currents (c and d), with a distinct retroflection at Slangkop; weak variable currents (e and f); intermittent westward flow (g).

Columbine area are summarized by Nelson and Hutchings (1983) (Fig.5.1). Briefly, permanent shelf-edge baroclinic jet-currents exist off both capes, with net southward counter-currents closer to the coast. Further north off Table Bay and St. Helena Bay, currents between the jet- and counter-currents tend to be weak and variable. A distinct counter-current retroflection zone occurs off Slangkop Point on the Cape Peninsula. Intermittent westward flow occurs over the continental slope and beyond when the Cape Peninsula jet accelerates in response to upwelling-inducing atmospheric events. Intrusion of warm Agulhas Current water around Cape Point (particularly during summer), tends to accentuate the shelf-edge front and its associated jet current.

The present study was formulated with the aim of identifying a patch of newly upwelled water and monitoring it, to establish the sequence of events which occur after upwelling. The pulsed nature of upwelling off the Cape Peninsula should facilitate dissection of discrete events in the upwelling process and the biological consequences.

This chapter deals primarily with physical aspects of the study; firstly, with the drogue movement and factors affecting it, and, secondly, with physical features of the water column along each drogue track.

TABLE 5.1: A summary of drogue and wind dynamics during the five drogue studies (A-E)

CRUISE	TRACKING PERIOD		DROGUE MOVEMENTS						WIND (AS MEASURED ON BOARD SHIP)			
			DISPLACEMENT		DISTANCE COVERED	SPEED			MEAN DIRECTION	RUN	SPEED	
			DISTANCE	DIRECTION		HOURLY		DAILY				
	(hours)	(days)	(km)	(degrees)	(km)	$(cm.s^{-1})$		$(km.d^{-1})$	(degrees)	(km)	$(m.s^{-1})$	
						mean	range	range			mean	range
A (Dec 79)	102	4.25	32	023(NNE)	67	18	0-64	12.0-20.1	196	3252	7.5	1-16
B (Dec 80)	144	6	151	341(NNW)	200	39	0-155	23.6-51.6	190	4902	9.5	2-16
C (Feb 81)	168	7	43	263(WSW)	155	26	0-128	13.8-31.8	186	5334	8.8	0-20
D (Mar 81)	167	7	45	318(NW)	123	20	0-52	13.5-21.6	166	6359	10.5	0-20
E (Oct 81)	160	6.7	13	036(NNE)	115	20	0-73	13.1-22.5	225	4062	7.0	0-18

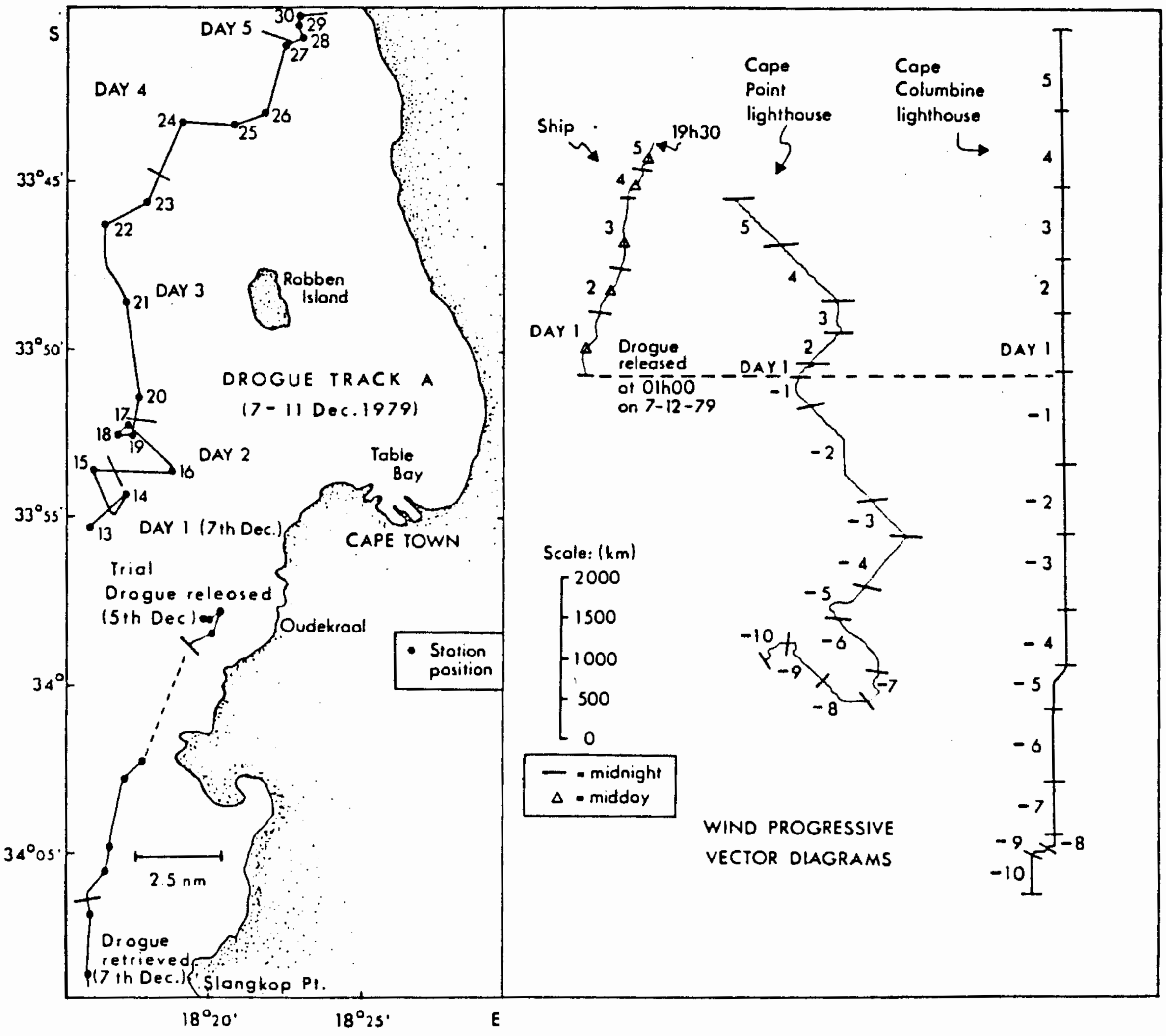

Fig.5.2: Drogue track A (7-11 December 1979) showing station positions, and progressive vector diagrams for hourly wind measurements on board ship and at the Cape Point and Cape Columbine lighthouses. The track of the trial drogue (5-7 December) is also illustrated.

5.2 Drogue movement, wind and currents

On five occasions during the 1979/80, 1980/81 and 1981/82 upwelling seasons a drogue was deployed in recently upwelled water off the Cape Peninsula within the 50 and 100 metre depth-contours between Table Bay and Hout Bay (see Fig.4.1) in the vicinity of the Oudekraal-Duiker Point upwelling centre.

Basic drogue movement and wind statistics are presented in Table 5.1. During each cruise (A-E), the drogue was tracked for between 6 and 7 days, except in December 1979 (Cruise A) when it was retrieved after $4^1/_4$ days. Overall northward displacement varied between 13 km NNE in October 1981 (Cruise E) and 151 km NNW in December 1980 (Cruise B), while in Febrary 1981 (Cruise C) the drogue ended up 43 km west of its position of release. Although wind speed and directions varied widely during each cruise, mean speeds and direction are of interest. During the first 3 cruises (A, B and C) the wind blew from the south (186°-196°) at mean speeds of between 7.5 and 9.5 $m.s^{-1}$. During Cruise D (March 1981) the mean direction was from the southeast (166°) and the highest mean speed (10.5 $m.s^{-1}$) was observed, whereas during Cruise E (October 1981), winds were variable but, on average blew from the WSW (225°) at a mean speed of 7 $m.s^{-1}$.

Individual drogue tracks and progressive vector diagrams (PVD) for hourly wind measurements on board ship and at the Cape Point and Cape Columbine lighthouses are illustrated in Figs 5.2-5.6. Southerly to southeasterly winds predominated strongly prior to each study and, except for in October 1981, during the first few days after deploying the drogue. Currents, as depicted by drogue

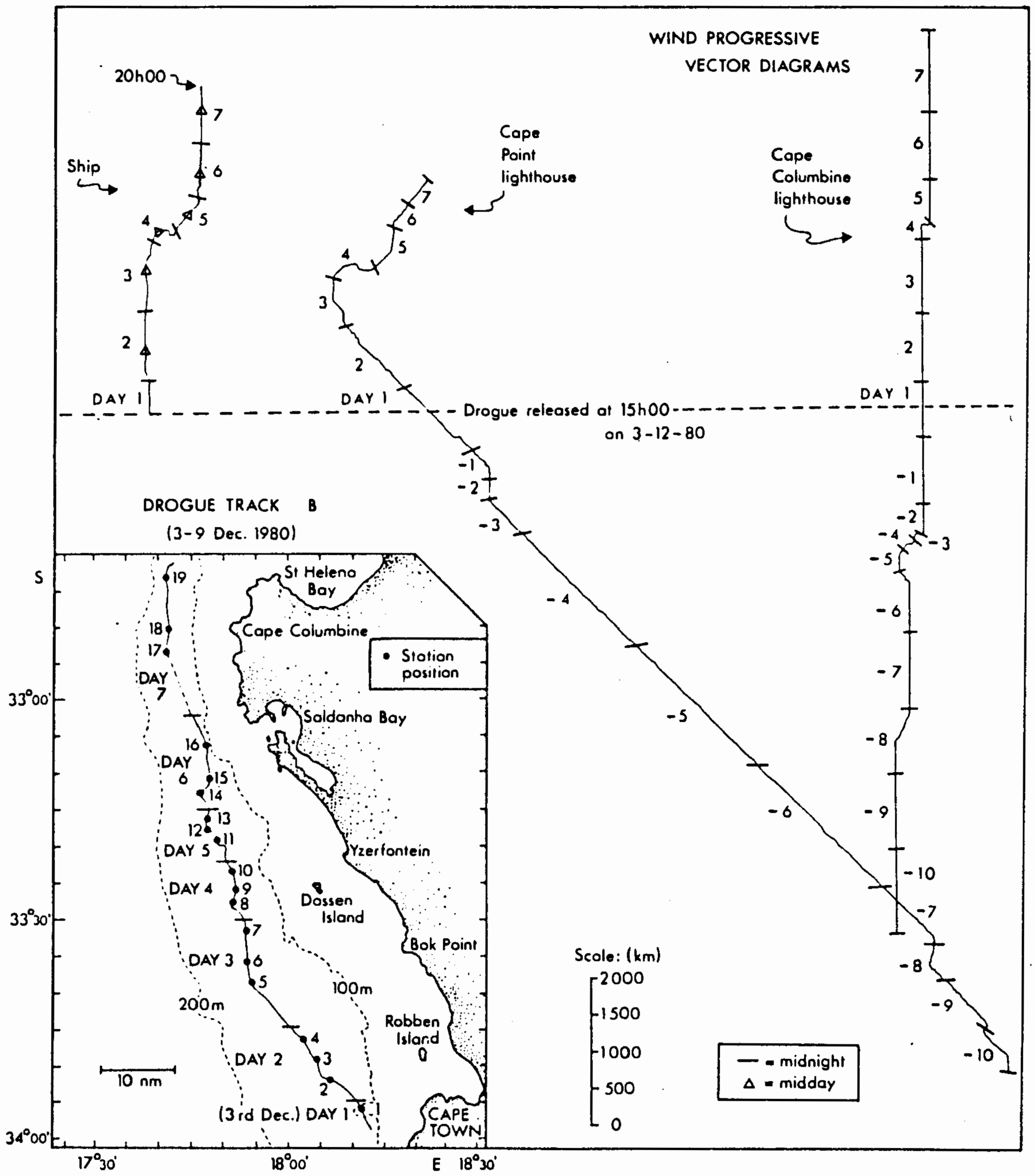

Fig.5.3: Drogue track B (December 1980) showing stations positions, and progressive vector diagrams for hourly wind measurements on board ship and at the Cape Point and Cape Columbine lighthouses.

movement, were generally in a direction similar to the wind. In a number of instances, however, current and wind directions were not the same (see below). This supports the assumption that windage due to the drogue superstructure was minimal. A description of drogue movements, in relation to wind, local current patterns, etc., is presented below for each cruise.

Cruise A (Fig.5.2): Opposed drogue and wind direction was particularly apparent during December 1979. Prior to the release of the main drogue, a trial drogue (Fig.5.2) moved steadily southwards close to the coast, opposing southerly winds of 5-10 $m.s^{-1}$. It appeared to be entrained in a coastal counter-current similar to that described by Nelson (1985). However, after the main drogue was released further offshore and northwards, continuous southerly winds blew from Day 1 to Day 3 and the drogue meandered northwards, briefly reversing on each of Days 1 and 2 (between stations 14 and 15 and between stations 17 and 19 respectively) (for detail on wind variation refer to Fig.5.11). Thereafter (Days 4 and 5) the drogue moved northwards then towards the northeast. The shape of the drogue track was roughly similar to that of the PVD of wind measured from the ship.

Cruise B (Fig.5.3): Persistent southerly winds accompanied the fastest mean drogue speed and greatest northward displacement measured during the five cruises, with the drogue travelling from the Cape Peninsula to Cape Columbine between the 100 and 200 m isobaths in six days. The wind reversal between 10h00 and 24h00 on Day 4 did not markedly alter the course of the drogue, which appeared to be in a jet current moving at speeds of up to 155 $cm.s^{-1}$ (Table 5.1). Nelson and Hutchings (1983) and Nelson (1985)

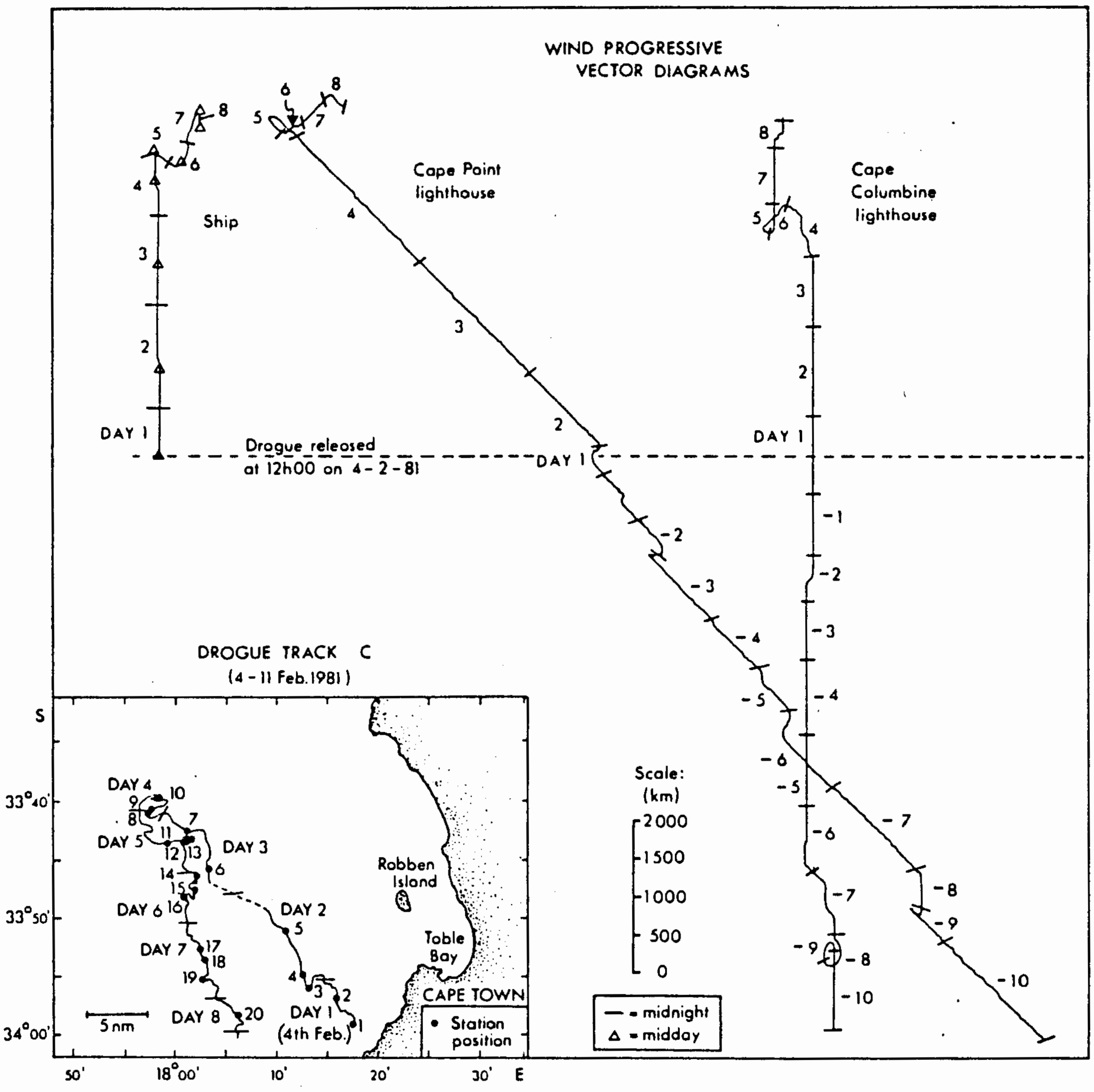

Fig.5.4: Drogue track C (February 1981) showing station positions, and progressive vector diagrams for hourly wind measurements on board ship and at the Cape Point and Cape Columbine lighthouses.

have discussed the jet-like formation of topographically steered currents in this zone.

Cruise C (Fig.5.4): In February 1981 strong southerly winds (mean = 12.0 $m.s^{-1}$) blew for four days. The drogue moved offshore with the wind but changed direction on Day 4, just prior to the wind reversal on Day 5. However, when the wind swung back to the south on Day 6, the drogue continued moving southwards against the wind. This water movement appeared to be a barotropic adjustment to a change in sea level after the strong winds subsided (G. Nelson, pers. comm.).

Cruise D (Fig.5.5): In March 1981 the drogue was deployed in moderate to light southerly winds and moved southwards against the wind in a manner similar to that of the December 1979 trial drogue described above (see Fig.5.2). At noon on Day 2, the drogue reversed direction off Slangkop and moved offshore towards the northwest, accompanied by strong (> 13 $m.s^{-1}$) southerly winds. The drogue reversal occurred in an area where Nelson (1985) has described a retroflection of the inshore counter-current. He postulated that entrainment of the counter-current into a northward-flowing current further offshore is compensation for the acceleration of the shelf-edge jet off the Cape Peninsula. Moderate southerly winds from Day 6 onwards accompanied the drogue as it meandered northwestwards until it was retrieved on Day 8.

Cruise E (Fig.5.6): The wind at Cape Columbine, prior to the deployment of the drogue in October 1981, was lighter and more variable than before the other cruises (Figs 5.2-5.6). At Cape

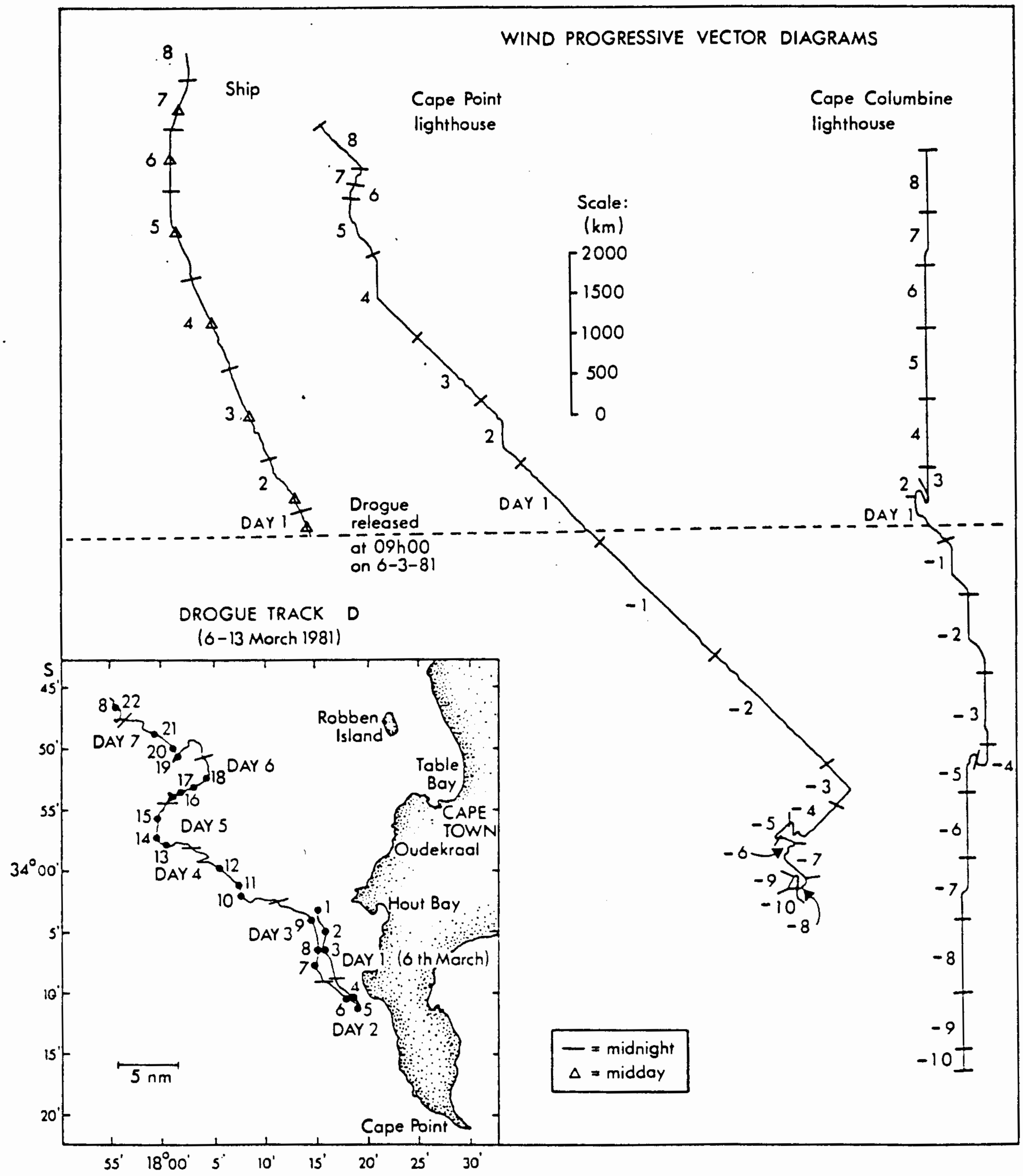

Fig.5.5: Drogue track D (March 1981) showing station positions, and progressive vector diagrams for hourly wind measurements on board ship and at the Cape Point and Cape Columbine lighthouses.

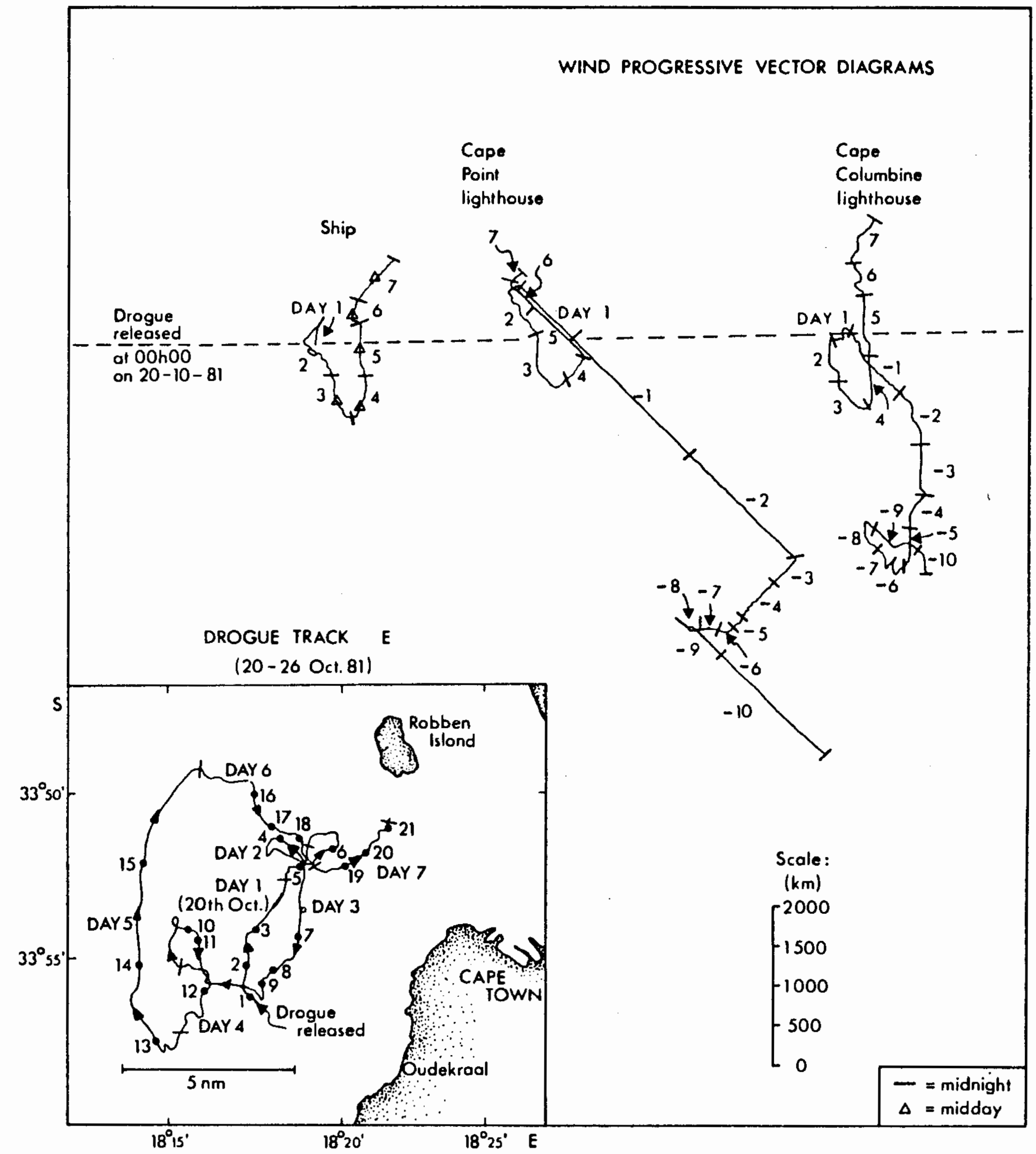

Fig.5.6: Drogue track E (October 1981) showing station positions, and progressive vector diagrams for hourly wind measurements on board ship and at the Cape Point and Cape Columbine lighthouses.

Point the wind pattern was similar to that in March 1981 (Cruise D) when light, variable winds followed by two days of strong southeasterlies preceeded the hydrobiological study. However, when the drogue was released, the southeast wind dropped and generally weaker and more variable winds persisted for the duration of the study (Fig.5.6). Light S-SE winds to calm conditions prevailed on Day 1 (20 October) and the drogue moved northwards. On Day 2 the wind reversed and blew from the north (NE to NW) for two days at speeds of up to 13 $m.s^{-1}$. The drogue meandered in the area southwest of Robben Island on Day 2, tracing two loops before moving southwards on Day 3, then westwards against prevailing winds. On the night of Day 3-4, the wind subsided, reversed, and moderate south to southwesterly winds blew for the remainder of cruise, except for a calmer period on Day 6 when lighter (mean speed 4.3 $m.s^{-1}$) and more variable (E to SW) winds prevailed. As can be seen in Fig.5.6, the drogue moved northwards with the wind on Day 5, then back towards the coast against the prevailing wind on Day 6. Fresh southwesterlies (mean speed 8.2 $m.s^{-1}$) on Day 7 accompanied the drogue towards the northeast.

Drogue movement during Cruise E may be interpreted in the light of the supportive physical measurements by Holden (1981). The RV Sardinops made daily transects across the path of the drogue and recorded wind speed and direction (these data were similar to those measured on RV Africana II), water column temperature and current profiles to about 10 metres off the bottom using a Neil Brown acoustic current meter. The north-south and east-west components of the currents measured daily at six stations (three on either side of the drogue) are graphically summarized in

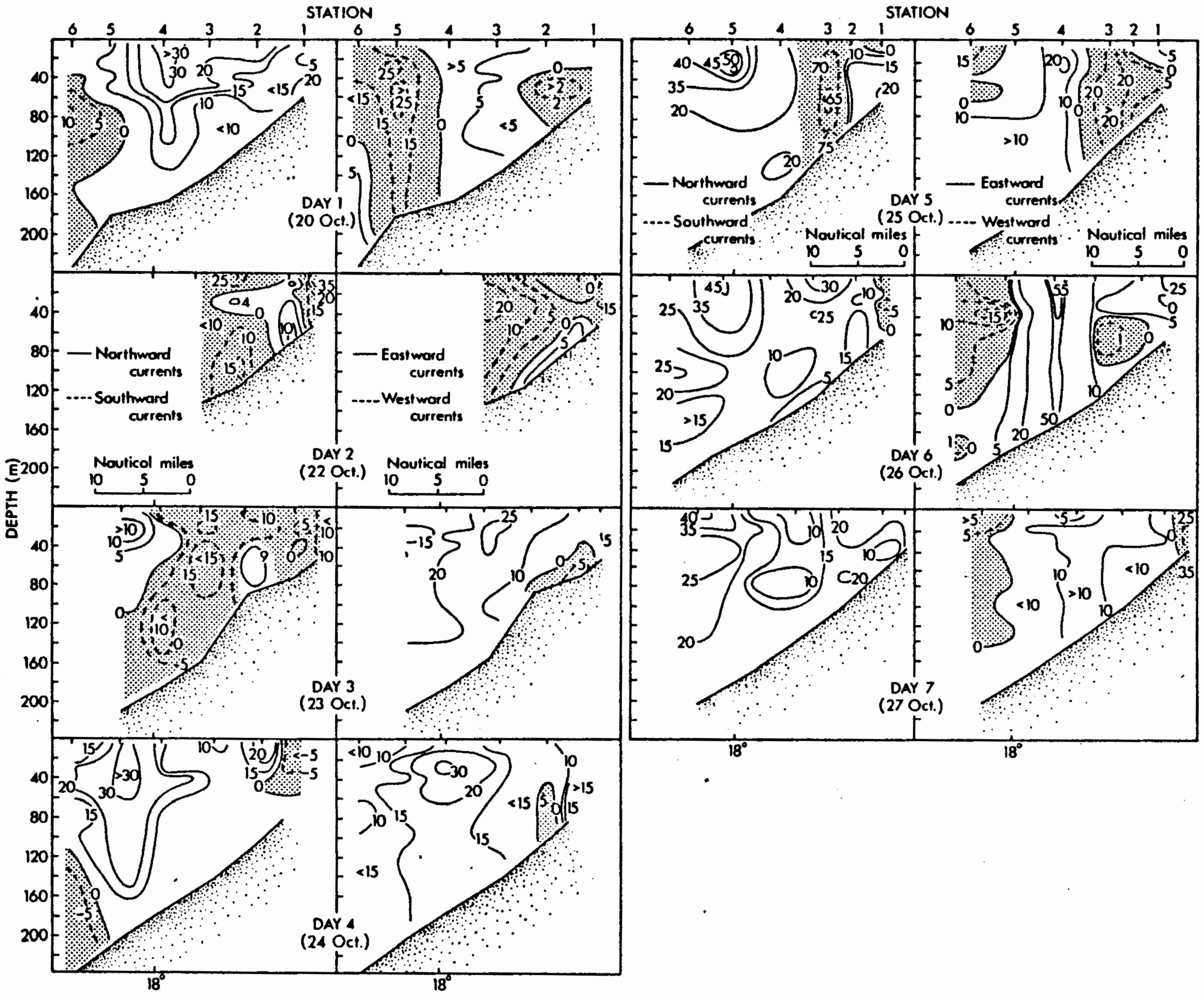

Fig.5.7: Daily transects of current measurements across the path of Drogue E showing north-south and east-west components of the current (after Holden 1981). Shading represents southward and westward flow. The drogue position was between stations 3 and 4.

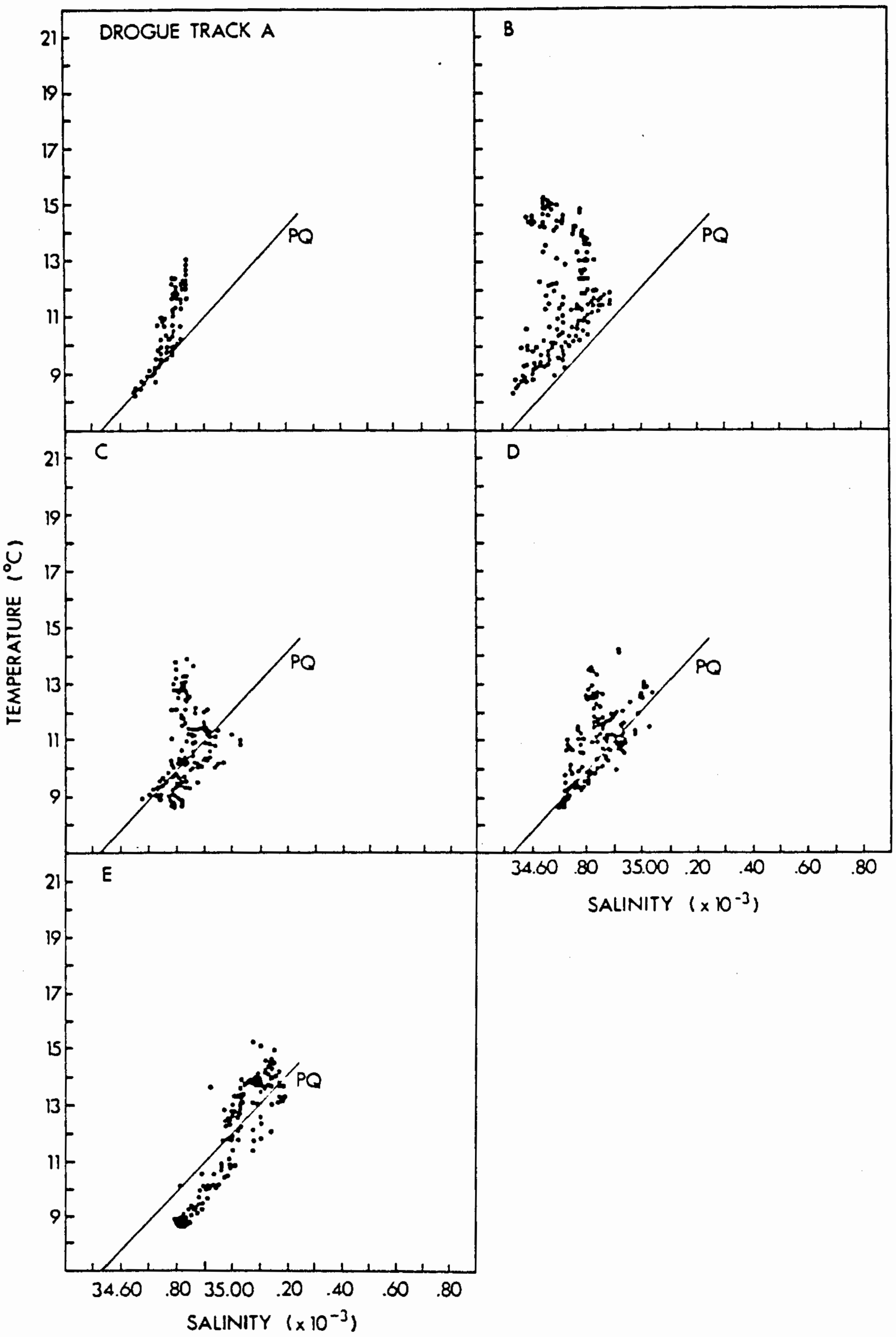

Fig.5.9: Temperature-salinity scatter diagrams for data collected along Drogue tracks A-E, with the line PQ which according to Nelson (1985) is characteristic of the water off the Cape Peninsula.

Fig.5.7. These data reveal a complex current structure with permanent northward flow above the 70 m and 180 m isobaths (Holden 1981). Southward currents and reduced northward flow on Days 2 and 3 were associated with the wind reversal during this period as the resumption of southerly winds on Day 4 resulted in the re-establishment of strong northerly flow. However, the presence of a strong narrow southerly current on Day 5 is not understood, and may have been an artefact of measurement (Holden, pers. comm.). Nonetheless, the erratic drogue movements during Cruise E may be explained by the drogue's location in a shear zone between northerly and southerly currents depicted in Fig.5.7. Entrainment into either current could result in opposed drogue and wind movement.

5.3 Physical features of the water column

5.3.1 Temperature, salinity and density

Vertical sections of temperature, salinity and density (sigma t) along the track of each drogue are presented in Fig.5.8. Mean temperatures in the upper 10 metres increased along the drogue tracks, ranging between 10.4-12.7°C, 11.4-14.9°C, 9.9-13.3°C, 10.2-13.7°C and between 11.8-14.7°C for Drogue tracks A-E respectively. Deep water temperatures were less variable, with 8-9°C water occuring below 40-50 metres when the sounding was less than 100 metres (Drogue tracks A and E). At soundings greater than 100 m (Drogue tracks B, C and D), this uniformly cool water was deeper, usually below 80 m.

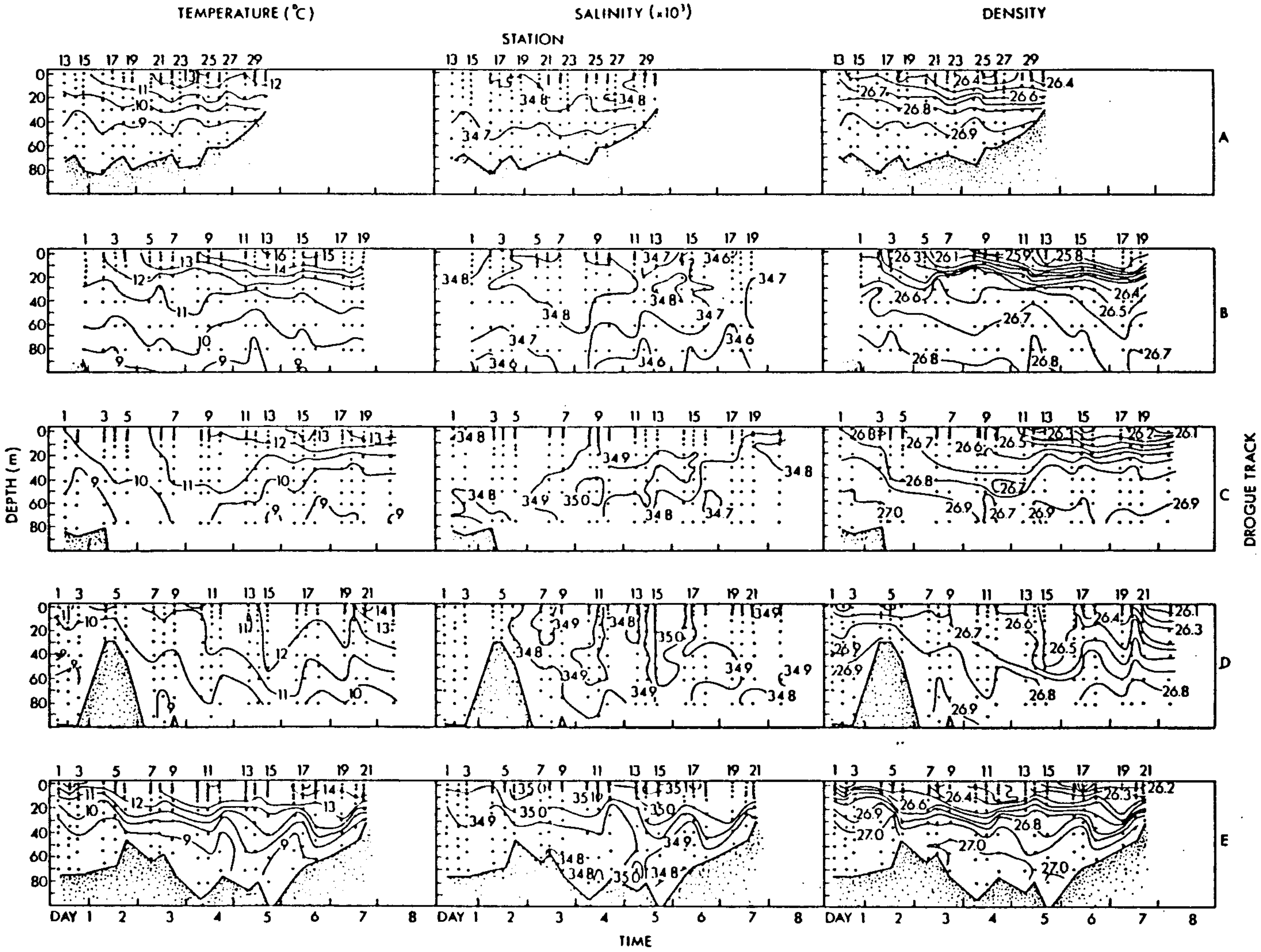

Fig.5.8: Vertical sections of temperature, salinity and density (sigma t) along Drogue tracks A-E.

Temperature and density sections show similar structure, with isolines generally horizontal but dipping from the sea surface as sun-warming and mixing increased surface temperatures (thereby decreasing densities). Salinity did not appear to contribute much to changes in density as it usually decreased slightly with depth. However, a weak subsurface salinity maximum occurred at some stations along Drogue tracks B, C and D (between about 20 and 50 metres) suggesting that low salinity water had upwelled and moved over more saline water.

Temperature-salinity (t/s) scatter diagrams are presented for each cruise in Fig.5.9, and contrasted with the line PQ which is characteristic of the t/s relationship for most of the water (shelf and oceanic) occurring off the Cape Peninsula (Nelson 1985). Although t/s analyses in shallow coastal waters do not allow precise identification of water types, the scatter diagrams illustrate some interesting points. For Cruises A, C and D, the lower temperature and salinity values coincide with the PQ line, whereas equivalent data for Cruises B and E lie roughly parallel to PQ but above and below it respectively, suggesting that the salinity of the upwelled water was lower than normal for Cruise B, whereas for Cruise E it was higher. This suggests that the water which upwells is not necessarily uniform and perhaps not of the same origin. The more saline water encountered along Drogue track E (October 1981) may reflect the seasonal transition from winter to spring, as salinities throughout the water column in winter are higher than during the upwelling season (see Fig.27 in Andrews and Hutchings, 1980). At higher temperatures, deviation above the original t/s slope of each cruise was clearly due to sun-warming of surface water. The point of inflection (which

TABLE 5.2: Variation in the mean salinity of the surface to 10 m layer along each drogue track

CRUISE	MEAN	SD	RANGE	DIFFERENCE	% DIFFERENCE
A	34.80	.03	34.75-34.84	.09	.26
B	34.74	.07	34.60-34.80	.23	.66
C	34.84	.03	34.80-34.90	.10	.28
D	34.84	.08	34.73-35.01	.28	.80
E	35.06	.06	34.97-35.16	.10	.54

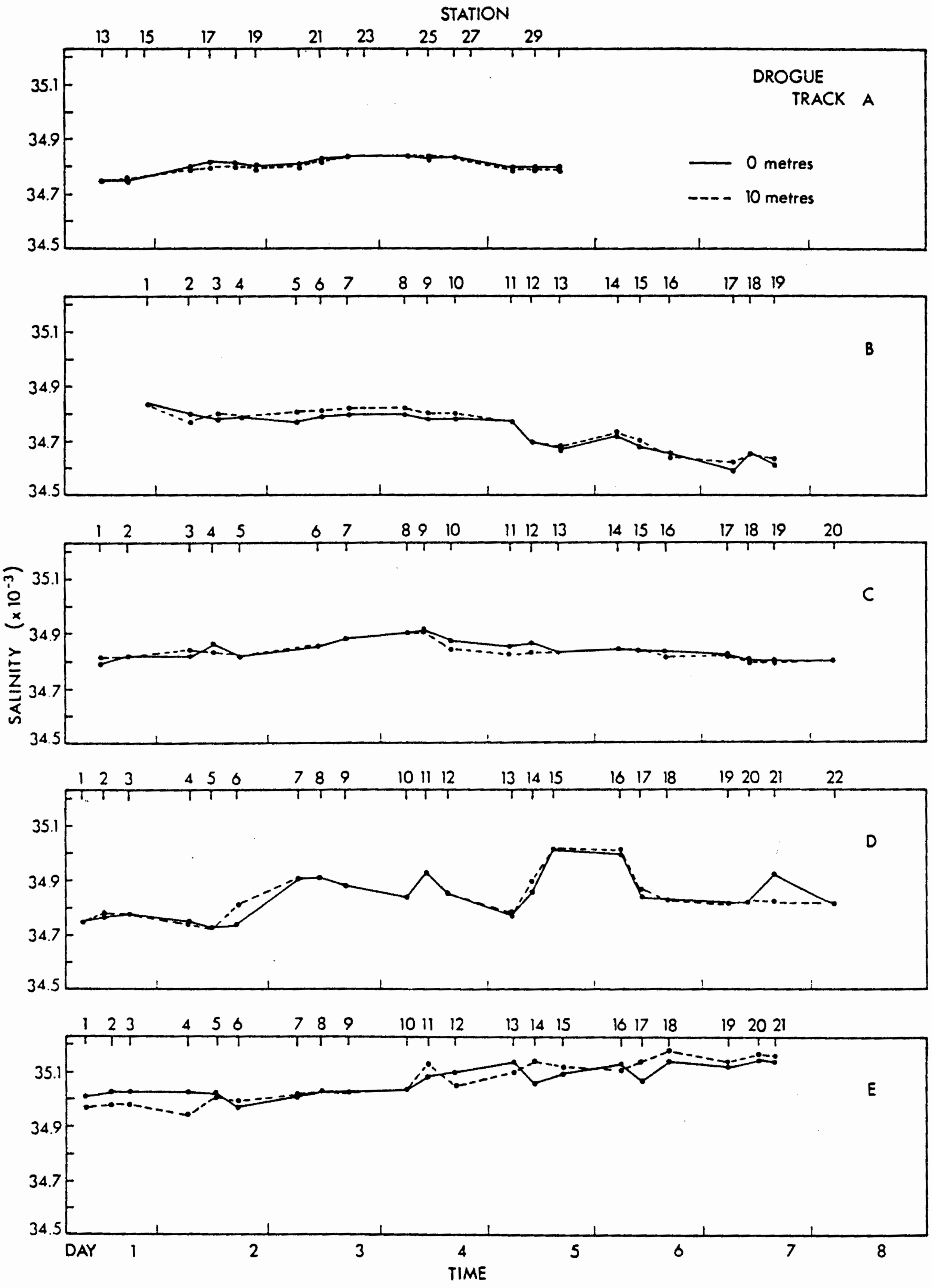

Fig.5.10: Salinity at 0 m and 10 m along Drogure tracks A-E.

initiates deviation from the line characteristic of the cooler, deeper water in each study), is at about 9.5°C for Cruise A, 10°C for Cruise B, 11°C for Cruise C, 9°C for Cruise D and 11.5°C for Cruise E. These differences suggest that the temperature of the source water is not constant but may vary at least between 9°C and 11.5°C. It follows that the use of a specific temperature limit to define active upwelling (e.g. Andrews and Hutchings 1980 used temperatures of less than 10°C) may be misleading.

As salinity is a conservative parameter, it may be used to investigate the physical consistency of the water along each drogue track (Waldron 1985). Table 5.2 shows little variation (less than 1%) in the mean salinity of the upper 10 m layer along each drogue track, and individual salinity values at 0 m and 10 m (Fig.5.10) also suggest that the water masses along Drogue tracks A, B (until station 11) and C were fairly consistent. The decrease in salinity after station 11 along Drogue track B may be due to the entrainment of low salinity water from upwelling sites off Yzerfontein and Cape Columbine (see Fig.5.3). During Cruise D salinity was particularly variable after the drogue turned off Slangkop and meandered towards the northwest (see Fig.5.7). These abrupt changes in salinity (Fig.5.10) suggest that different water bodies mixed into the original water mass; therefore attempts to trace biological sequences along Drogue track D should be treated with care. The gradual increases in salinity along Drogue track E, however, may be due to gradual mixing with more saline water and insolation-induced surface evaporation, as the relatively strong thermocline would have prevented deep, low salinity water from being entrained into the upper layers. Wind reversals (see Fig.5.6) and opposing currents (see Fig.5.7),

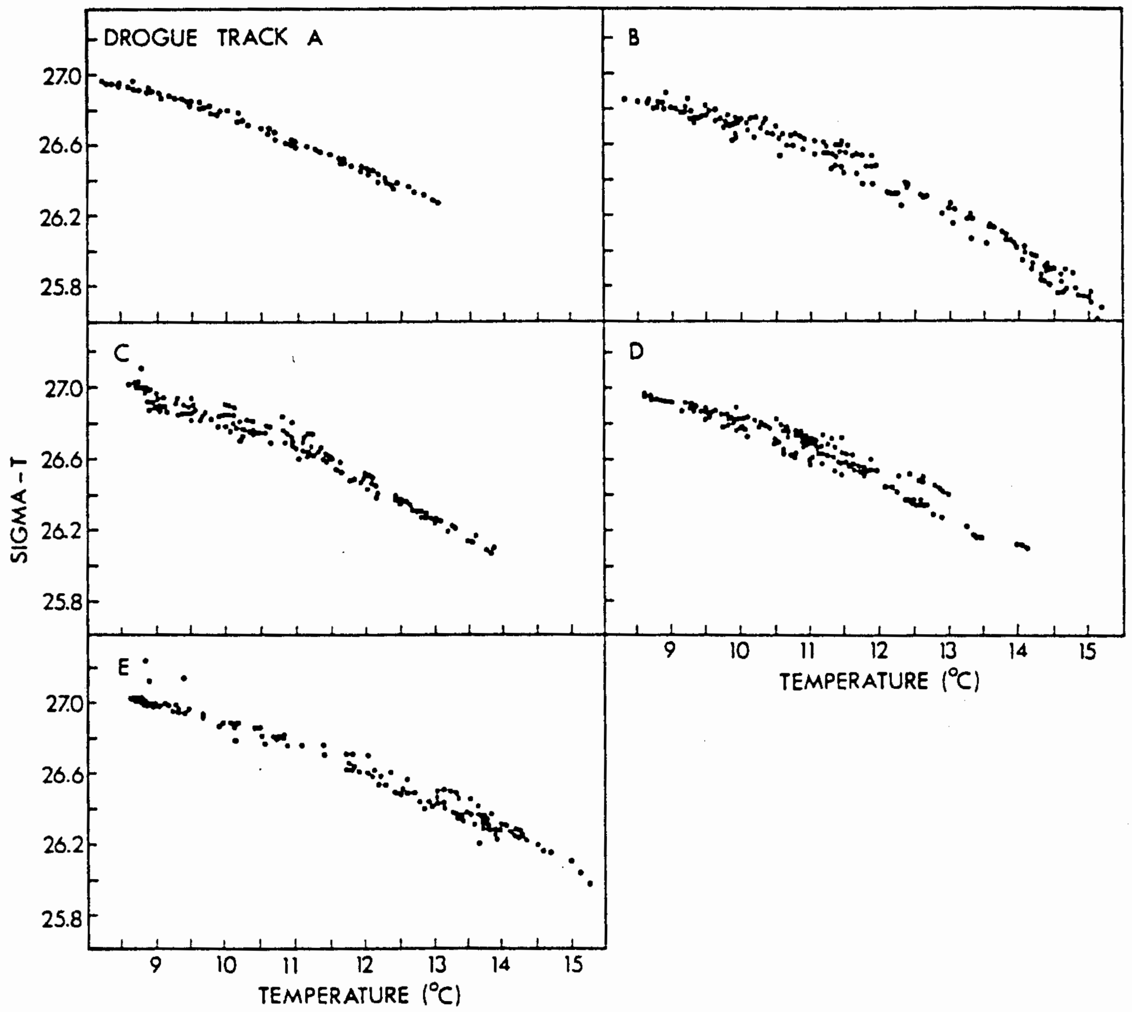

Fig.5.11: Relationships between density and temperature for data collected along Drogue tracks A-E.

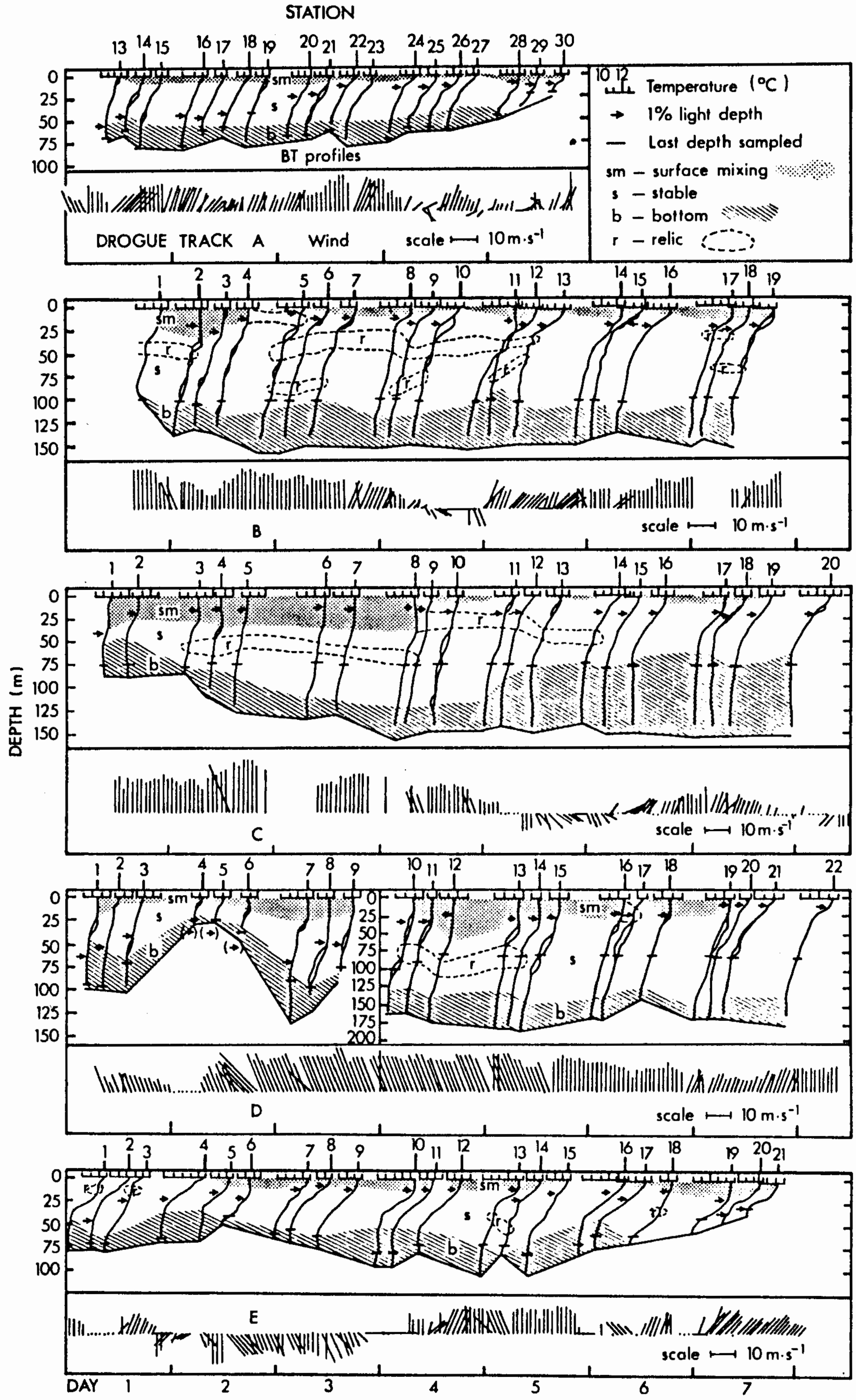

Fig.5.12: Hourly wind stick-vector diagrams and bathythermograph profiles along Drogues tracks A-E. The water column is partitioned into surface mixing (sm), relic (r) and bottom (b) mixed layers, with a stable (s) layer between the sm and b layers. The 1% light depth and the last depth at which water samples were drawn, are also indicated. Wind vectors show the direction in which the wind is blowing.

maintained the drogue in a small area in which the salinity changed gradually.

5.3.2 Bathythermography, wind and irradiance

Temperature and salinity characteristics of South Atlantic water (Sverdrup et al 1942) show that density is largely dependent on temperature in this area. Moreover, strong temperature/density correlations have been drawn for local waters (Fig.5.11 and Bang 1973). Therefore, temperature is considered to be a good indicator of density and bathythermograph (BT) profiles are used to estimate water column stability. It should be noted, however, that this correlation may not extend into the microscale (Bang 1973, Waldron 1985).

Difficulties are often encountered in attempts to establish the depth of mixing in the ocean. For convenience Parsons et al (1977) suggest the use of the bottom of the main thermocline as the lower limit of the surface mixing layer. However, even a slight density gradient is enough to prevent mixing. Therefore, in this study, the water column is considered to be stable if temperature shows a noticeable decrease with depth (see Fig.5.12).

Vertical distribution of nutrient and chlorophyll a concentrations (also partly dependent on water column structure), helped clarify uncertainties regarding the relative stability of isothermal parts of the water column. For example, where obvious nutrient or chlorophyll a gradients exist through an isothermal portion of the water column, it is unlikely that active mixing was occurring, at least not at a rate that would significantly influence phytoplankton distribution or growth.

Series of BT profiles (together with the depth of the 1% light level and wind stick vector diagrams) are presented in Fig.5.12 to illustrate the structure of the water column along each drogue track. During Cruise E a well-developed thermocline was maintained throughout the study. At the commencement of the other cruises, however, only a weak thermocline existed, but in each case its intensity increased along the drogue track.

At each station the water column was partitioned into layers based on its relative stability. Although not always present, the "surface mixing" layer, distinguishable by isothermal water at the sea surface (and also uniform depth profiles of nitrate and chlorophyll a), varied in thickness to a maximum of 63 metres (Cruise D, station 12).

The depth of the 1% light level (normally taken to be the lower limit of the euphotic zone) varied between about 60 m and 9 m (Fig.5.12), and was usually deeper than the surface mixing layer. A noteable exception, however, occurred along the first half of Drogue track C where the depth of the surface mixing layer was sometimes more than twice that of the 1% light depth.

In most instances an isothermal lens of water was also present close to the sea bed. This "bottom mixed" layer, was usually 20-50 metres thick but varied up to a maximum of 90 m (Cruise C, stations 17-20).

The layer between the surface mixing and bottom mixed layers, the "stable" layer, generally comprised the bulk of the water column and was characterized by the existence of temperature (decreasing), nutrient (increasing) or chlorophyll a (variable) gradients; the strongest gradients usually occurred close to the surface mixing layer (and to the 1% light depth) in the main thermocline. However, sometimes cells of isothermal water were contained within the stable layer (see Fig.5.12) and were probably relics attributable to previous upwelling and mixing events (Bang 1973). BT profiles along Drogue track C provide an example of possible formation of such a "relic" mixed layer in that the subsurface isothermal layer at stations 9 to 14 appears to have originated from surface turbulence between stations 1 and 8.

Inspection of the wind stick vector diagrams together with the BT profiles (Fig.5.12) suggests that the depth of the surface mixing layer may be roughly related to wind speed. For example, moderate winds (mean speed = 7.5 $m.s^{-1}$) during Cruise A were associated with a relatively shallow surface mixing layer (mean depth = 6 m, range = 0-15 m), whereas the strong winds during the first three days of Cruise C (mean speed = 13.9 $m.s^{-1}$) accompanied a deeper surface mixing layer (mean depth = 32 m, range = 25-40 m) (Fig.5.12). However, it should be noted that the effect of the wind is modified by the structure of the water column; a weak temperature gradient being more susceptible to wind erosion than a highly stratified one.

The direction of the wind also seemed to influence the turbulent state of the water column along the drogue tracks. For instance, onshore winds, which generally blow for short periods during the

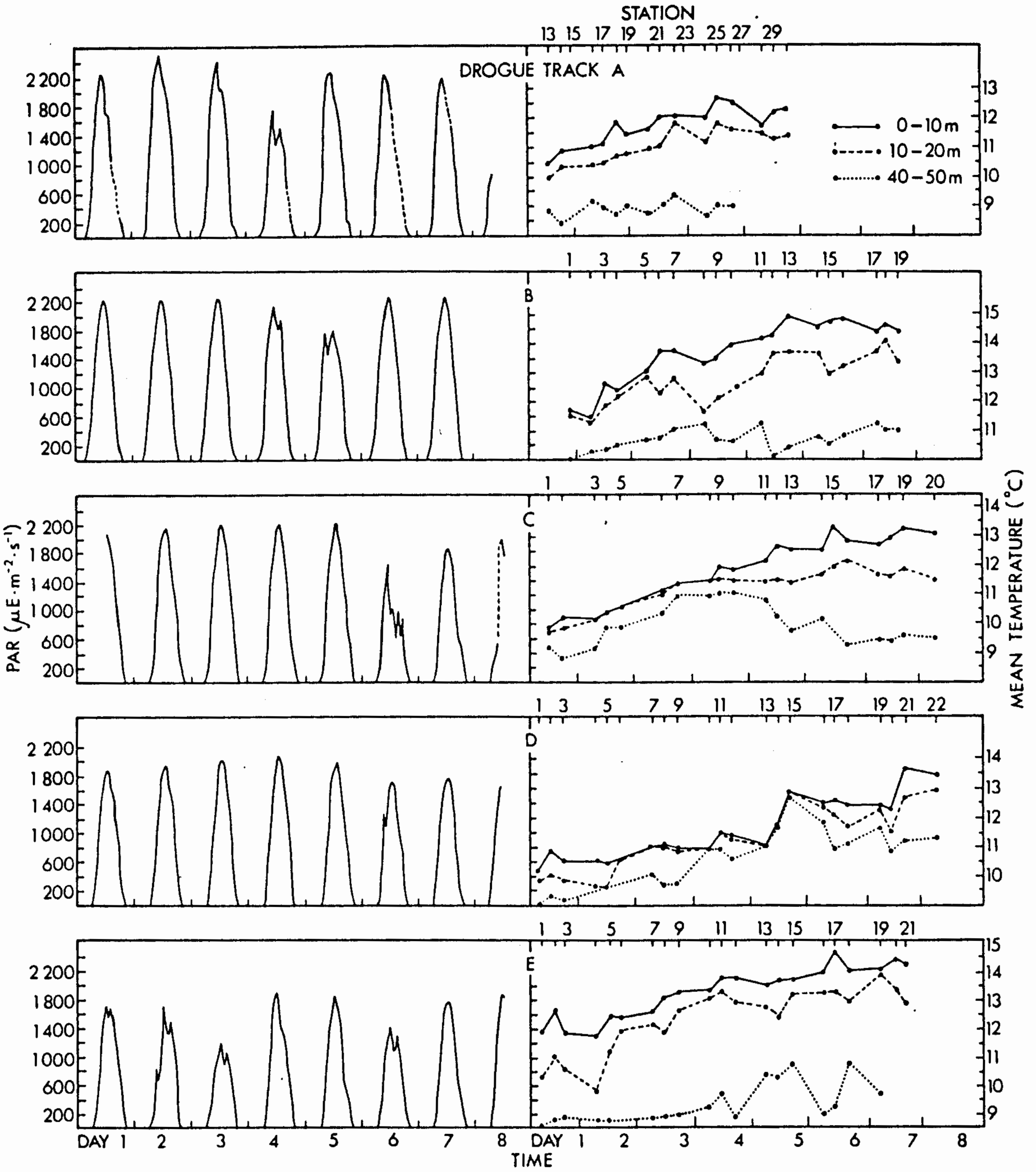

Fig.5.13: Incident hourly photosynthetically active radiation (PAR) and mean temperatures along Drogue tracks A-E. PAR for Cruise B was calculated from total radiation measurements (see Chapter 4).

upwelling season, are less liable to cause turbulence than offshore winds because they tend to bring a shallow film of warm water shorewards (Bang and Andrews 1974) thereby stabilizing the water mass. Examples of this can be seen along Drogue tracks A (stations 25-26), B (stations 9-10), C (stations 11-12) and E (stations 3-4). However, when northwesterly winds persist for more than a day (as occured on Days 4-7 along Drogue track E), significant surface mixing can occur.

Opposing wind and current directions may also aid destabilization of the near-surface layer. This seemed to be the case between stations 16 and 18 along Drogue track C.

Stabilization of the cold turbulent upwelling water is undoubtedly caused by the heating effect of the sun, either directly at the sea surface or indirectly when warmed "older" upwelled water mixes with newly upwelled water. Mean temperatures along the drogue tracks are presented in Fig.5.13 together with incident photosynthetically active radiation (PAR), which may be considered an index of heat input. Temperatures near the sea surface tend to increase along the drogue tracks; the occasional decrease may be due to entrainment of deeper colder water into the surface layer, or perhaps, to slippage of water past the drogue, allowing "younger" upwelled water to overtake the sampling position.

5.4 Discussion

5.4.1 Slippage and dispersion

Two problems (briefly mentioned in Chapter 3) are fundamental to this type of study, viz. slippage and dispersion. Firstly, slippage of the drogue through the water is a technical matter related to the geometry of the drogue (see Fig.4.2). Following Holden (1985), windage and drogue slippage were estimated by calculating the frictional drag on both the float, above (Fw) and below (Fs) the surface, and on the drogue itself (Fd) for which a drag coefficient of 1.4 was used (Vachon 1980). The mean wind speed measured during the five cruises ($9\ m.s^{-1}$) and the corresponding surface current speed ($28\ cm.s^{-1}$) derived from the empirical wind/surface current relationship of Pond and Pickard (1978), were used in the calculations. (The ratio, Fw/Fs, indicated that the contribution of the drogue superstructure to surface drag was about 35%.) Drogue slippage, estimated by balancing the drag force of the drogue, Fd, against the combined forces of the float (Fw and Fs), was found to be about 20% of the mean current speed ($25\ cm.s^{-1}$) during the 5 cruises. As slippage speeds are typically 10-20% of the true water speed (Holden 1985), estimated slippage of the drogue in the present study was considered to be normal.

Secondly, in an attempt to ascertain to what extent the same body of water was being followed by the drogue, and, the typical scales involved in the dispersive processes operative around the drogue, Boyd (1982) deployed six 1-m drogues at 2, 10 and 20 m in the vicinity of the main drogue on a number of occasions during Cruise E. He found that considerable dispersion of the drogues at different depths may be caused by shear and estimated that particles at 9 and 11 m would have, on average, separation speeds of 2.1 cm.s^{-1}. On the other hand, horizontal separation of drogues at the same depth was an order of magnitude less (about 0.19 cm.s^{-1} at 10 m). It should be noted, however, that Boyd's rates of "horizontal separation" supply only a lower limit to the actual diffusion of particles in the water. The drogues, being several orders of magnitude larger than the phytoplankton cells which they were attempting to track, cancelled out the effects of diffusion on the population of particulate matter in the water body, and, therefore, could not simulate the effects of diffusion. Nonetheless, Boyd concluded that the combined effects of pair-separation and shear would rapidly destroy any horizontal patchiness that might otherwise occur on a scale of less than a few hundred metres. The dynamics of larger scale (5-10 km) plankton patches, however, could not be determined in this study.

For the purposes of the hydrobiological study, however, the effects of both dispersion and slippage will be ignored. It is assumed that the patches into which the drogue was released, were sufficiently large and uniform to compensate these effects.

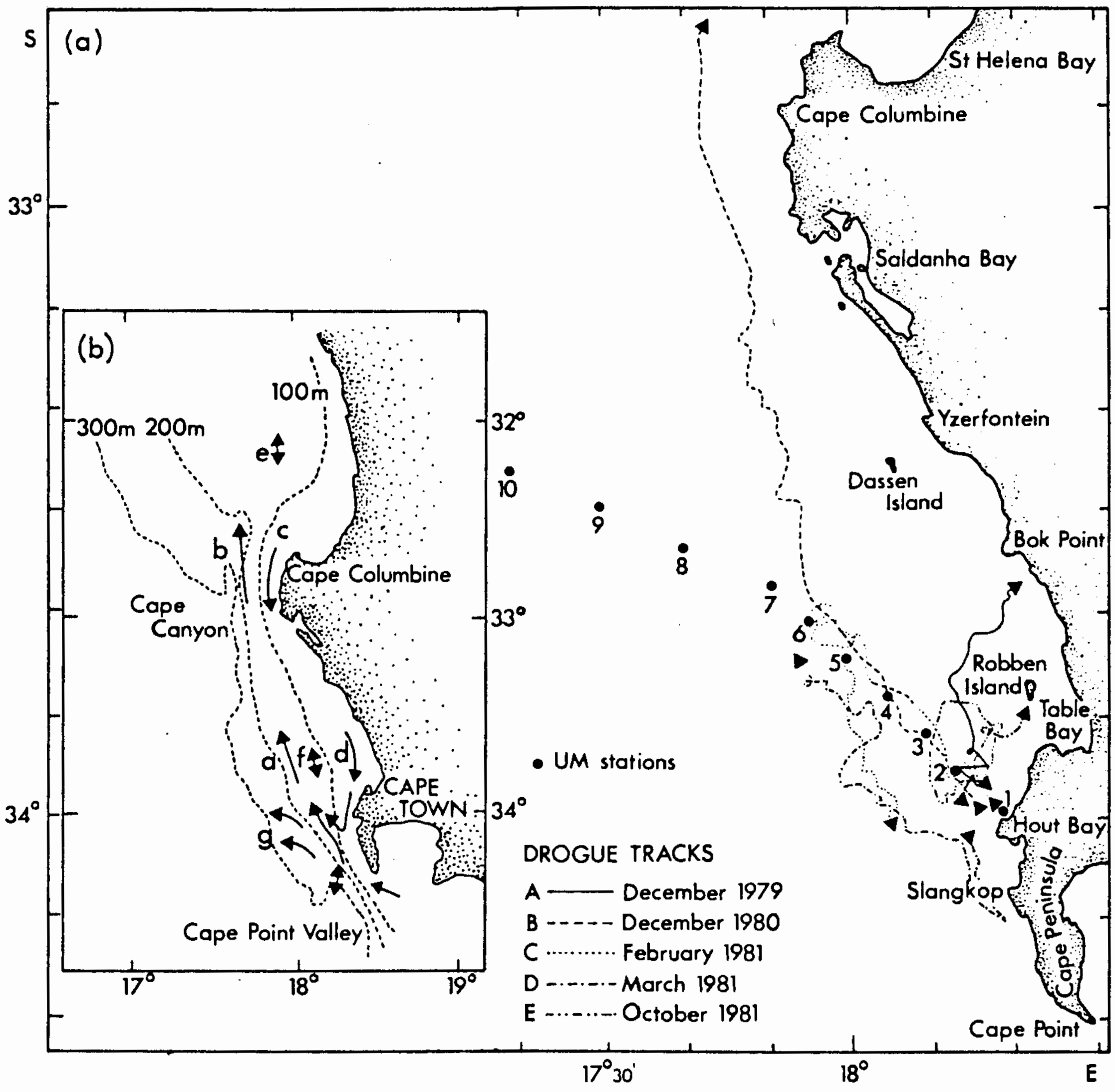

Fig.5.14: (a) The five drogue tracks during the Plankton Dynamics cruises, and the station positions for the Upwelling Monitoring (UM) cruises.
(b) A schematic diagram of currents off the Cape Peninsula and Cape Columbine (from Nelson and Hutchings 1983), showing permanent shelf-edge baroclinic jets (a and b), near-shore net southward currents (c and d) with distinct retroflection at Slangkop, weak variable currents (e and f), and intermittent westward flow which occurs when the shelf-edge jet accelerates (g).

5.4.2 Drogue movements

Rough similarity between the wind PVDs and corresponding drogue tracks suggest that the movement of near surface water (i.e. upper 10 m) tended to be influenced mainly by the prevailing winds (southerly). This is perhaps not surprising as the same larger scale meteorological processes are responsible for both (Nelson 1985). However, detailed inspection of the data showed some obvious deviation of the drogue tracks from the wind as measured from the ship (see progressive and stick vectors). Interpretations based on local current patterns as described by Nelson (1985) and Nelson and Hutchings (1983) and on actual current measurements during Cruise E (October 1981) by Holden (1981), may better explain the drogue movements. For comparative purposes the five drogue tracks are presented together in Fig.5.14, along with the Upwelling Monitoring (UM) line of stations (Andrews and Hutchings 1980) and a schematic diagram of currents in the area (Nelson and Hutchings 1983). The drogue tracks, which were within 50 km from the coast, show that the path taken by upwelled water varies somewhat from the UM line. This implies that to equate spatial changes offshore (along the UM line) with temporal changes (associated with phytoplankton bloom development) may be misleading. However, drogue movements appear to be consistent with the major current patterns associated with the study area.

During Cruise B, for example, the drogue appears to have been entrained into a northward jet-current which is presumably part of the Benguela current proper. On the other hand, in March 1981 (Cruise D) the drogue was deployed in a southerly nearshore counter-current the existence of which has been noted on many occasions between Cape Columbine and Slangkop; the drogue's sudden reversal offshore on the second day coincided with the Slangkop retroflection area. During Cruise C (February 1981) the drogue reversal was reminiscent of the sudden switching of the currents reported by Nelson (1985) to be a common feature of the area; the paths of two of his radio-tracked drogues (Debbie and Jane) showed a similar pattern in November 1978.

The meanderings of the drogue during Cruise E (October 1981) partly result from the weaker and more variable (compared with the other studies) winds blowing at the time. Probably more important, however, was the presence of juxtaposed northward and southward-flowing currents creating a shear zone in the vicinity of the drogue, so that entrainment of the drogue into either current would cause drogue movement to be independent of the wind. Moreover, the study was conducted during the transition from winter to spring when the increased dominance of southerly winds initiates the upwelling season. The quiescent periods and frequent fluctuations in wind during October 1981 reflect the less stable meterological pattern typical of seasonal transition periods.

High frequency changes in the meteorology are more likely to be closely reflected in the winds than by the ocean, which has far more inertia than the atmosphere and which, at a depth of about 200 m, has been found to have a response time of approximately four days (Nelson 1985). However, response times of currents near the sea surface are likely to vary with prevailing conditions such as the slope of the sea surface, direction of wind reversal and the extent to which the ocean has been "primed" for upwelling.

Taunton-Clark (1985), for example, reports that the sea surface (down to about 30 m) may respond to wind events in a matter of hours. Although prevailing winds do influence water movement in this area, other factors also play a part in setting up currents and thus determining drogue movements. For instance, periodic reversals in currents in the Cape Columbine region appear to be caused by coastally trapped waves moving polewards, driven by remote forcing functions such as coastal lows, or movements in the location of the South Atlantic high pressure cell (Holden 1986, Shannon et al 1986). Because of the unstable meteorological and circulation patterns off the Cape Peninsula, simulation models by G. Nelson (pers. comm.) show that small temporal or spatial variation in drogue deployment may result in considerable variation in the path traced by the drogue. Results from the present study support this view.

CHAPTER 6: GROSS CHEMICAL AND BIOLOGICAL VARIATIONS ALONG THE DROGUE TRACKS

6.1 Introduction

6.2 Nutrient, chlorophyll _a_ and oxygen distributions

    6.2.1 "Bottom mixed" water

    6.2.2 Hydrographic conditions at commencement of drogue studies

6.3 Phytoplankton bloom development in the euphotic zone

6.4 Summary

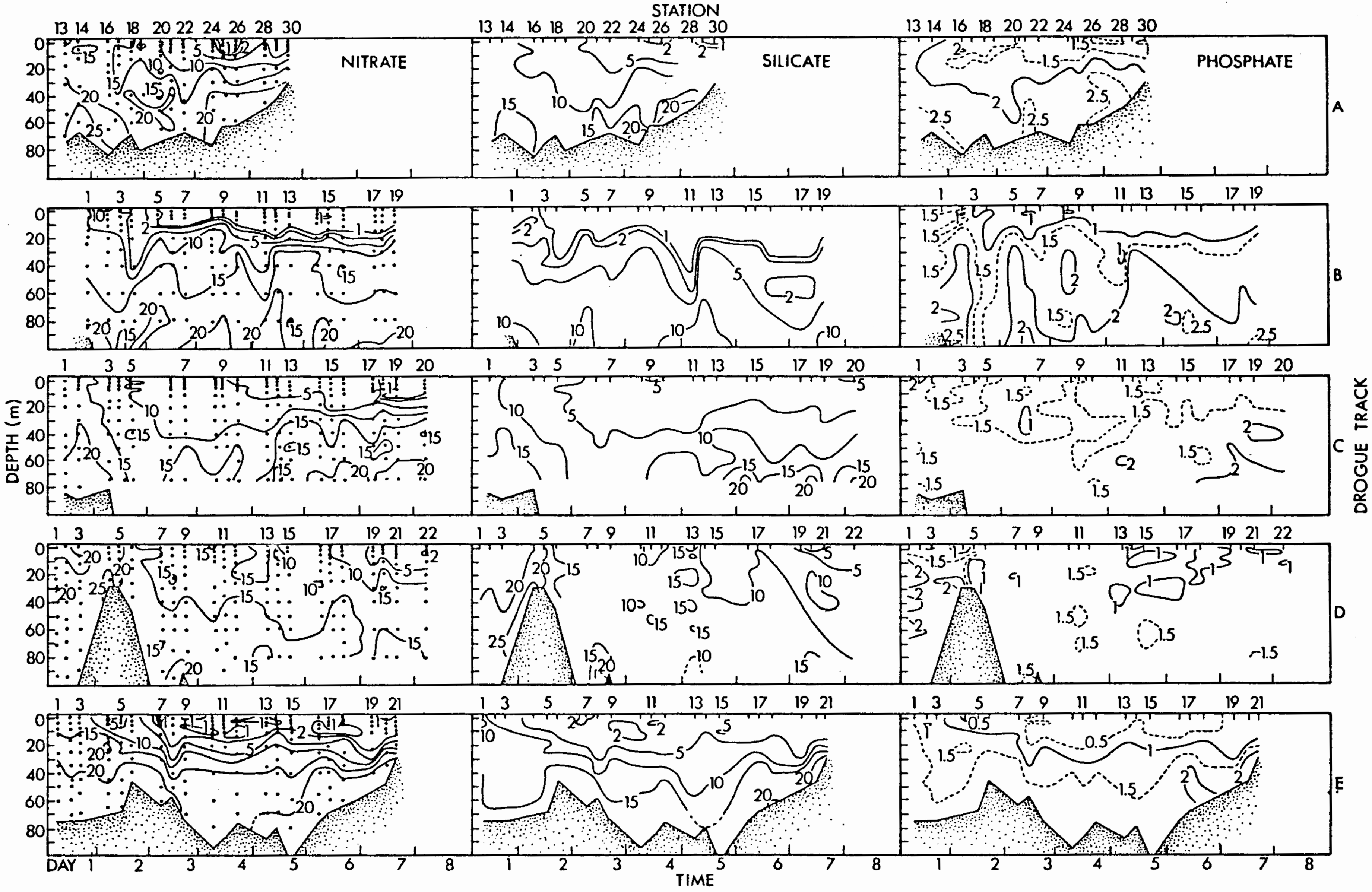

Fig.6.1: Vertical sections of nitrate, silicate and phosphate concentrations ($mmol.m^{-3}$) along Drogue tracks A-E.

6.1 Introduction

In this chapter, nutrient, oxygen and chlorophyll a distributions along the tracks of the drogue are presented and discussed in terms of phytoplankton bloom development. Factors likely to influence phytoplankton growth (such as nutrient concentrations, light penetration, the depth of vertical mixing and zooplankton grazing) are critically assessed in each case, and an attempt is made to quantify the time scales associated with bloom development, in terms of both the build up and decline of the primary bloom after upwelling.

6.2 Nutrient, chlorophyll a and oxygen distributions

Vertical sections of nitrate, silicate and phosphate concentrations along each drogue track are presented in Fig.6.1. Nitrate and silicate concentration varied widely (from less than 1 to 26.8 and 25.1 $mmol.m^{-3}$ respectively) but generally decreased in the surface waters along the drogue tracks while high concentrations occurred at depth. Phosphate concentrations were less variable (c 0.3-2.81 $mmol.m^{-3}$) but showed a similar although weaker tendency to increase with depth and decrease along the drogue track. Thus, the isoline structures, particularly for the nitrate and silicate sections, were similar.

Silicate concentrations along Drogue track B were exceptionally low; virtually all the values above the 1 $mmol.m^{-3}$ isoline (which ranged between about 10 and 30 m after station 3) were

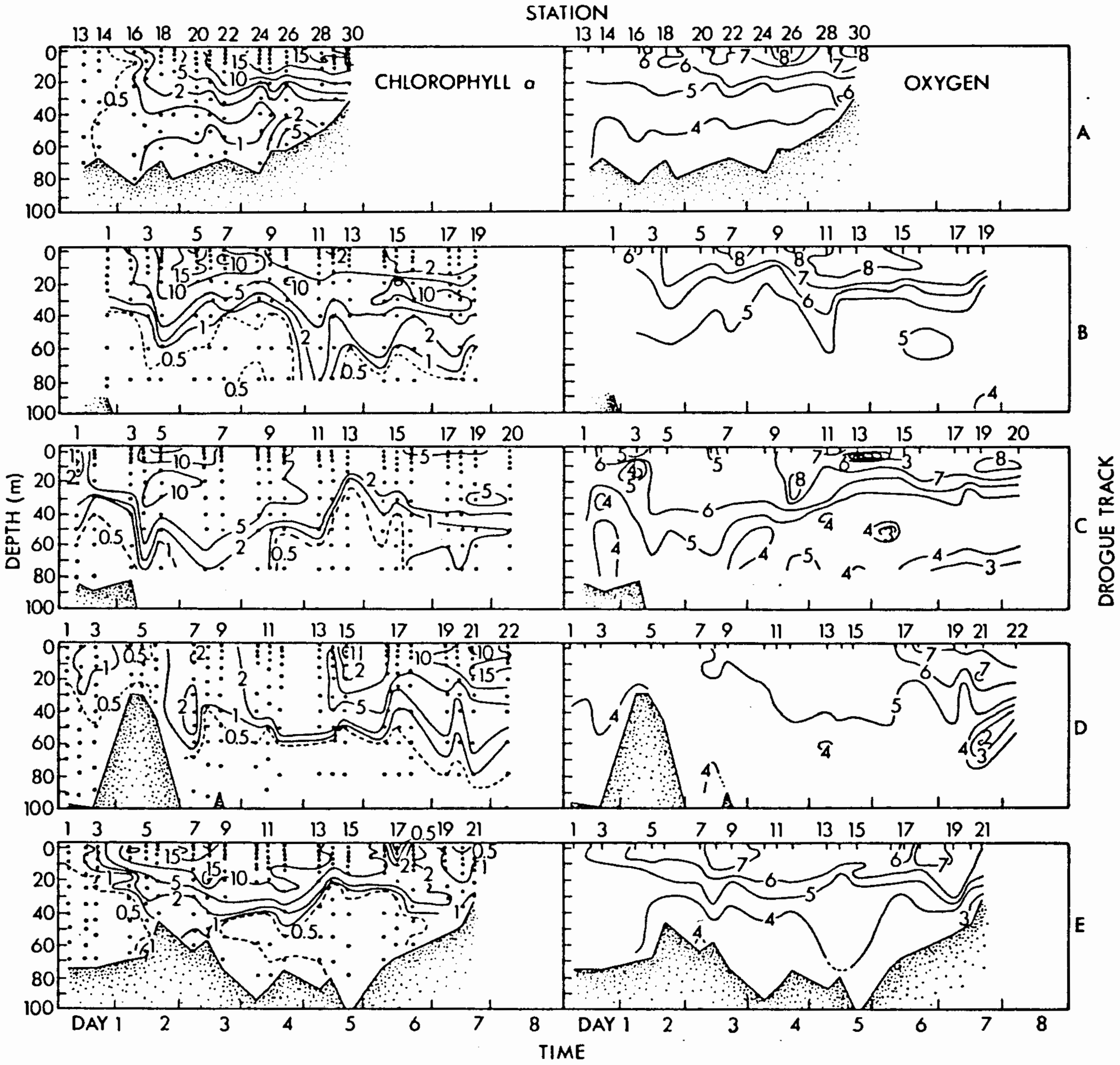

Fig.6.2: Vertical sections of chlorophyll a (mg.m^{-3}) and dissolved oxygen (dm^3.m^{-3}) concentrations along Drogue tracks A-E.

zero. In two and a half years of monthly monitoring off the Cape Peninsula values of zero were not reported by Andrews and Hutchings (1980). Moreover, individual nitrate:silicate ratios below 50 m were consistently higher (1.2-12.1) than for other cruises (0.6-2.1, see Section 7.2). Although one is hesitant to reject these data outright, they are treated with caution and excluded from "typical" mean values.

Fig.6.2 shows that chlorophyll a and dissolved oxygen concentrations vary widely (0-21.2 mg chll a.m^{-3} and 1.94-9.80 dm^3 oxygen .m^{-3}) with trends inverse to those of the nutrient concentrations (i.e. concentrations decreased with depth and increased along the drogue track) except that chlorophyll a concentrations along Drogue tracks B, C and E reached a maximum and then decreased.

6.2.1 "Bottom mixed" water

Because water samples were drawn only from depths down to 100 m or shallower, the "bottom mixed" layer, as defined from BT traces (see Fig.5.12), was often not sampled when the water column was deep. Along Drogue tracks A and E, however, the bottom mixed layer was generally within the sampling range, and variations in the parameters measured along the drogue tracks (temperature, salinity, density, and nutrient, oxygen and chlorophyll a concentrations) are depicted for these two cruises in Fig.6.3. Results for all the cruises are summarized in Table 6.1.

Temperature and salinity were generally low and did not vary greatly. The nutrient content of the bottom mixed layer was always high relative to surface water (mean concentrations

TABLE 6.1: Mean values (and ranges) of parameters measured in the "bottom mixed" layer along the five drogue tracks, and in "upwelling" and "oceanic" water as calculated from Andrews and Hutchings' (1980) Table 1

DATA SET	TEMPERATURE (°C)		SALINITY		DENSITY (sigma t)		NITRATE (mmol.m^{-3})		SILICATE (mmol.m^{-3})		PHOSPHATE (mmol.m^{-3})		OXYGEN (dm^3.m^{-3})		CHLOROPHYLL a (mg.m^{-3})	
	mean	(range)	mean	(range)	mean	(range)	mean	(range)	mean	(range)	mean	(range)	mean	(range)	mean	(range)
Cruise A	8.55	(8.2-8.9)	34.65	(34.65-34.70)	26.93	(26.87-26.97)	20.4	(15.6-26.8)	14.1	(10.3-21.3)	2.24	(1.60-2.74)	3.83	(3.41-4.12)	1.5	(0.1-9.4)
Cruise B	9.15	(8.5-9.9)	34.60	(34.55-34.72)	26.78	(26.63-26.86)	19.8	(10.4-25.3)	suspect data		2.13	(1.23-2.64)	4.40	(3.61-4.75)	0.4	(0-0.7)
Cruise C	8.98	(8.7-9.2)	34.77	(34.71-34.94)	26.95	(26.87-27.11)	21.9	(16.5-25.3)	15.9	(10.0-22.9)	1.82	(1.35-2.20)	4.07	(2.77-4.82)	0.7	(0.3-1.3)
Cruise D	9.09	(8.6-9.9)	34.74	(34.71-34.79)	26.90	(26.81-26.96)	21.0	(15.4-26.0	20.2	(11.8-25.1)	1.47	(0.44-1.12)	3.89	(3.26-4.62)	0.3	(0.1-0.8)
Cruise E	8.80	(8.6-9.1)	34.83	(34.79-34.84)	27.01	(26.98-27.23)	20.9	(16.9-23.6)	16.4	(13.2-19.4)	1.74	(1.23-2.10)	3.82	(3.21-4.29)	0.3	(0-1.5)
Cruises A - E	8.90	(8.2-9.9)	34.72	(34.55-34.94)	26.91	(26.63-27.23)	20.8	(10.4-26.8)	16.6	(5.8-25.1)	1.88	(0.44-2.74)	4.00	(2.77-4.82)	0.6	(0-9.4)
"Upwelling" Water	9.06	-	34.69	-	-	-	20.0	-	16.0	-	1.43	-	4.34	-	0.7	-
"Oceanic" Water	18.8	-	34.40	-	-	-	0.8	-	4.67	-	0.4	-	5.57	-	0.4	-

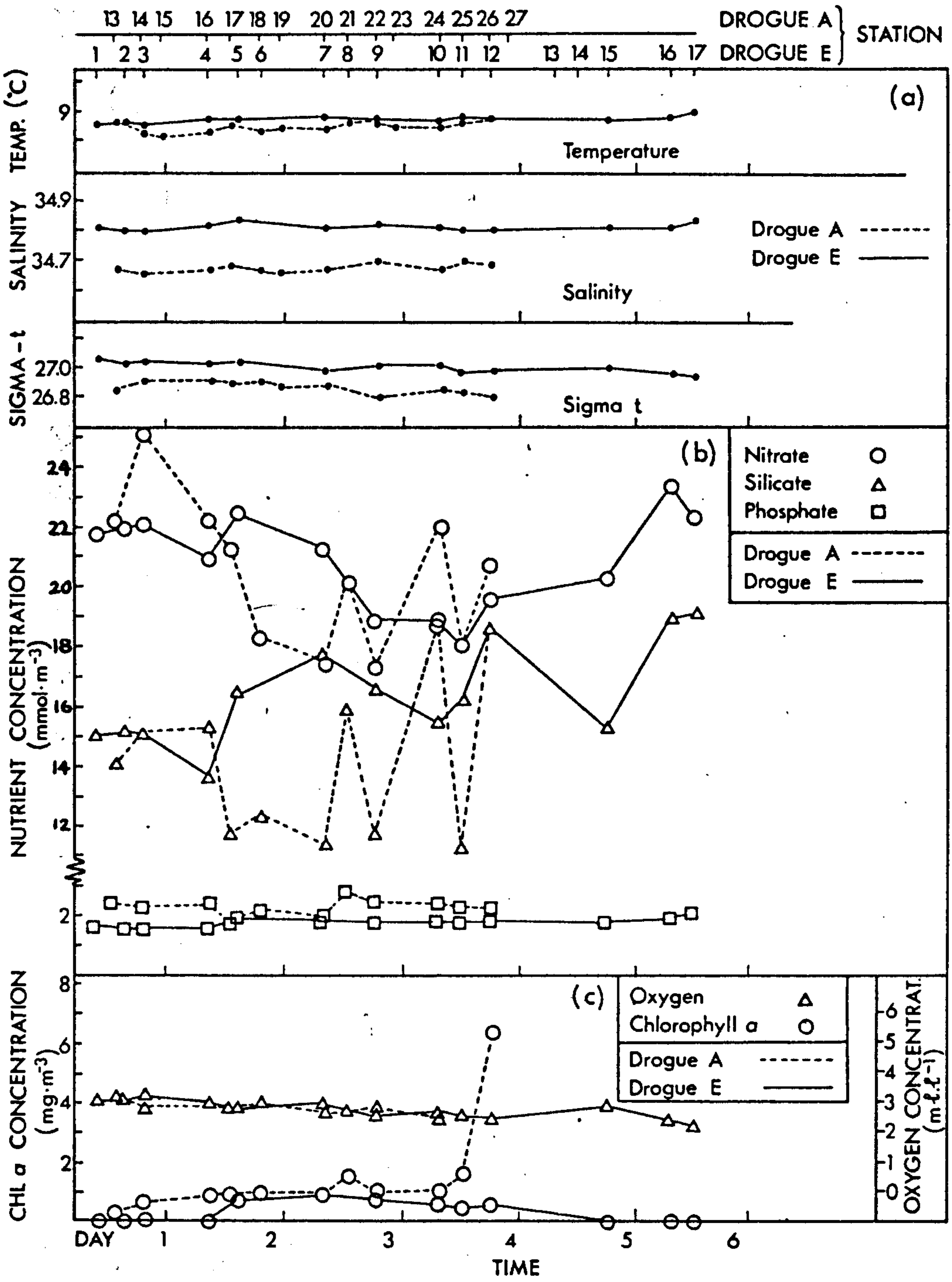

Fig.6.3: (a) Temperature, salinity and density, (b) nutrient concentrations and (c) chlorophyll a and oxygen concentrations in the bottom mixed layer along Drogue tracks A and E.

TABLE 6.3: Sea surface (S) and deep (D) measurements at the first station after release of the drogue

CRUISE	DEPTHS S-D (m)	TEMPERATURE (°C)	SALINITY	DENSITY (sigma t)	NITRATE (mmol.m^{-3})	SILICATE (mmol.m^{-3})	PHOSPHATE (mmol.m^{-3})	CHLL <u>a</u> (mg.m^{-3})	OXYGEN (dm^{3}.m^{-3})
A	0-63	10.84-8.43	34.75-34.66	26.61-26.94	20.7-25.7	11.6-13.4	2.29-2.23	0.1-0.1	5.12-4.11
B	0-85	11.97-8.93	34.84-34.69	26.47-26.89	9.8-21.5	-	1.73-2.43	4.4-0	5.92-4.49*
C	0-80	10.00-8.72	34.79-34.83	26.79-27.03	18.8-21.2	14.8-15.4	2.05-1.35	1.6-0.3	5.42-4.26
D	0-93	10.62-8.62	34.75-34.71	26.65-26.95	17.6-20.8	16.6-22.5	1.13-1.83	0.9-0.1	4.28-3.45
E	0-70	12.74-8.62	35.01-34.81	26.45-27.03	12.7-22.5	10.3-16.0	1.27-1.54	0.7-0	4.83-4.16

* As oxygen was not measured at station 1, data from station 2 are presented

of nitrate and silicate were 20.8 mmol.m^{-3} and 16.6 mmol.m^{-3} respectively) (see Fig.6.1, Table 6.1). Nutrient concentrations varied up to two-fold during any one cruise period, reflecting either differences in the amount of nutrient regeneration that had occurred during the formation of the source water or, more likely, differences in the nutrient-enrichment of source water as it moves across the shelf (Bailey and Chapman 1985).

Variation in the oxygen concentration of bottom mixed water (mean = 4.0 dm^{3}.m^{-3}, range = 2.77-4.82 dm^{3}.m^{-3}) may also reflect differences in the amount of organic decomposition. It should be noted, however, that no oxygen-deficient water (i.e. water with less than 2 dm^{3}.m^{-3} dissolved oxygen) was encountered in the bottom mixed water. In fact, only on one occasion was its presence recorded during the five cruises; and that was an isolated measurement at 60 m at station 21 along Drogue track D (Table 6.2). A further eight low oxygen concentrations (2-3 dm^{3}.m^{-3}) were encountered above the bottom mixed layer or, in one case (C 19), just bordering it (Table 6.2). Of these samples C 13-14 and D 21-22 show that a midwater oxygen minimum sometimes occurred. The low concentrations at C 17-21 were recorded at the deepest depth sampled (75 m), therefore it was not possible to ascertain whether a midwater oxygen minimum existed or not in these cases (at E 21 the low oxygen measurement was close to the sea bed in shallow water). Because sampling was limited to 100 m or less, the midshelf oxygen minimum, reported close to the bottom off the Cape Peninsula by De Decker (1970) and Andrews and Hutchings (1980), may sometimes have gone unrecorded in the present study.

TABLE 6.2: Low oxygen concentrations encountered during cruises A-E

CRUISE	STATION	DEPTH (m)	OXYGEN CONC. ($dm3.m^{-3}$)	COMMENT
C	13	3	2.71	oxygen minimum
	14	50	2.13	" "
	17	75	2.55	Last depth sampled
	18	75	2.57	" " "
	19	75	2.77	" " "
	20	75	2.56	" " "
D	21	60	1.94	Oxygen minimum
	22	40	2.75	" "
E	21	29	2.72	Last depth sampled

The very low chlorophyll *a* concentrations in the bottom mixed layer (see Table 6.1) suggest that the decay processes responsible for the high nutrients had long since occurred. An exceptionally high chlorophyll *a* value (9.4 mg chll *a*.m^{-3}) was recorded near the sea bed along Drogue track A (station 26, 58 m). It is probable that this high chlorophyll *a* measurement was due mainly to detritus (chlorophyll *a* measurements were not corrected for phaeopigments). This assumption is supported by Monteiro's (1986) results based on the more discriminatory HPLC techniques for measuring pigments. He found that such deep secondary chlorophyll *a* maxima in Benguela waters are due to chlorophyll *a* breakdown products such as chlorophyllide *a*, phaeophorbide *a* and phaeophytin *a*.

Comparison of mean temperature, salinity and nutrient, oxygen and chlorophyll *a* concentrations in the bottom mixed layers along the five drogue tracks with mean values for "upwelling" water from Andrews and Hutchings (1980) (see Table 6.1), suggests that bottom mixed water is similar to and may be representative of upwelling source water. However, variation in nutrient concentrations (Fig.6.3) and ratios (see Chapter 7) in deep water suggests that the bottom water sampled at each station was unlikely to be the same body of water along each drogue track. Instead, surface water in which the drogue was suspended probably sheared over a bottom layer of somewhat variable nutrient composition.

6.2.2 Hydrographic conditions at commencement of drogue studies

The existence of at least a weak thermocline (see Fig.5.12) at the commencement of each study, suggests that upwelling was not actively occurring at the site where the drogue was deployed (active upwelling close to the shore can be recognized by cold, isothermal water). Moreover, comparison of surface with deep hydrological measurements (Table 6.3) shows that nutrient concentrations (nitrate and silicate in particular) were clearly lower at the sea surface, while chlorophyll a and oxygen concentrations were higher. This suggests that surface water had been in the euphotic zone for at least long enough for photosynthesis to reduce the nutrients and increase oxygen concentrations.

The differences between surface and deep measurements of temperature, salinity, and nitrate and silicate concentrations (Table 6.3), suggest that the water into which the drogue was deployed during Cruises A, C and D was more recently upwelled and uniform during Cruises B and E. Initial chlorophyll a concentrations were correspondingly low during Cruises A, C and D, whereas at station 1 of Cruise B surface chlorophyll a was high (4.4 $mg.m^{-3}$) in keeping with the reduced nitrate concentration.

The hydrography of the water into which the drogue was deployed in Cruise E is curious. A well defined thermocline (20-35 m) separated surface from deep water; the latter, as in the other studies, reflects the characteristics of Andrews and Hutchings' (1980) "upwelling" water (see Table 6.1). The salinity of the surface water, however, was 35.01, somewhat higher than that for "upwelling" water but within the range for "mixed" water, the characteristics of which lie between those of "upwelling" and "oceanic" water (Andrews and Hutchings 1980). Perhaps the less vigorous offshore winds (see Fig.5.6), which preceded the study, were responsible for "mixed" water being close to the shore.

Moreover, the upwelling season (September-April) had only just begun, and the oceanic front was not yet as firmly established as it is later in the season - see Taunton-Clark's (1982) ART data for that period. This is supported by the t/s data in Fig.5.9 which show that the salinity of the deep water (temperature less than 11.5°C) was higher than expected when compared with Nelson's (1985) PQ t/s relationship. However, Fig.5.9 also shows that salinity values greater than 35 fall either above (owing to sun warming) or near the PQ line thus suggesting that the t/s characteristics of the surface water at least were similar to those recorded by Nelson (1985) for this area.

As in the other studies, nutrient and oxygen concentrations along Drogue track E, suggest that some photosynthesis had already occurred when the drogue was deployed. However, the very low euphotic zone chlorophyll a concentrations (0.7-0 mg.m^{-3}), which are suggestive of more newly upwelled water, may be a reflection either of poor phytoplankton seeding or of zooplankton grazing having prevented the build up of phytoplankton stocks before commencement of the study.

6.3 Phytoplankton bloom development in the euphotic zone

Changes in mean concentrations of nutrient, oxygen and chlorophyll a in the euphotic zone are presented for the five drogue tracks in Fig.6.4. *In situ* oxygen concentrations off the Cape Peninsula are closely correlated with primary production during the upwelling season (Andrews and Hutchings 1980). Consequently, comparison of oxygen concentrations at the sea surface with deep measurements below the euphotic zone at station 1 of each cruise (Table 6.3),

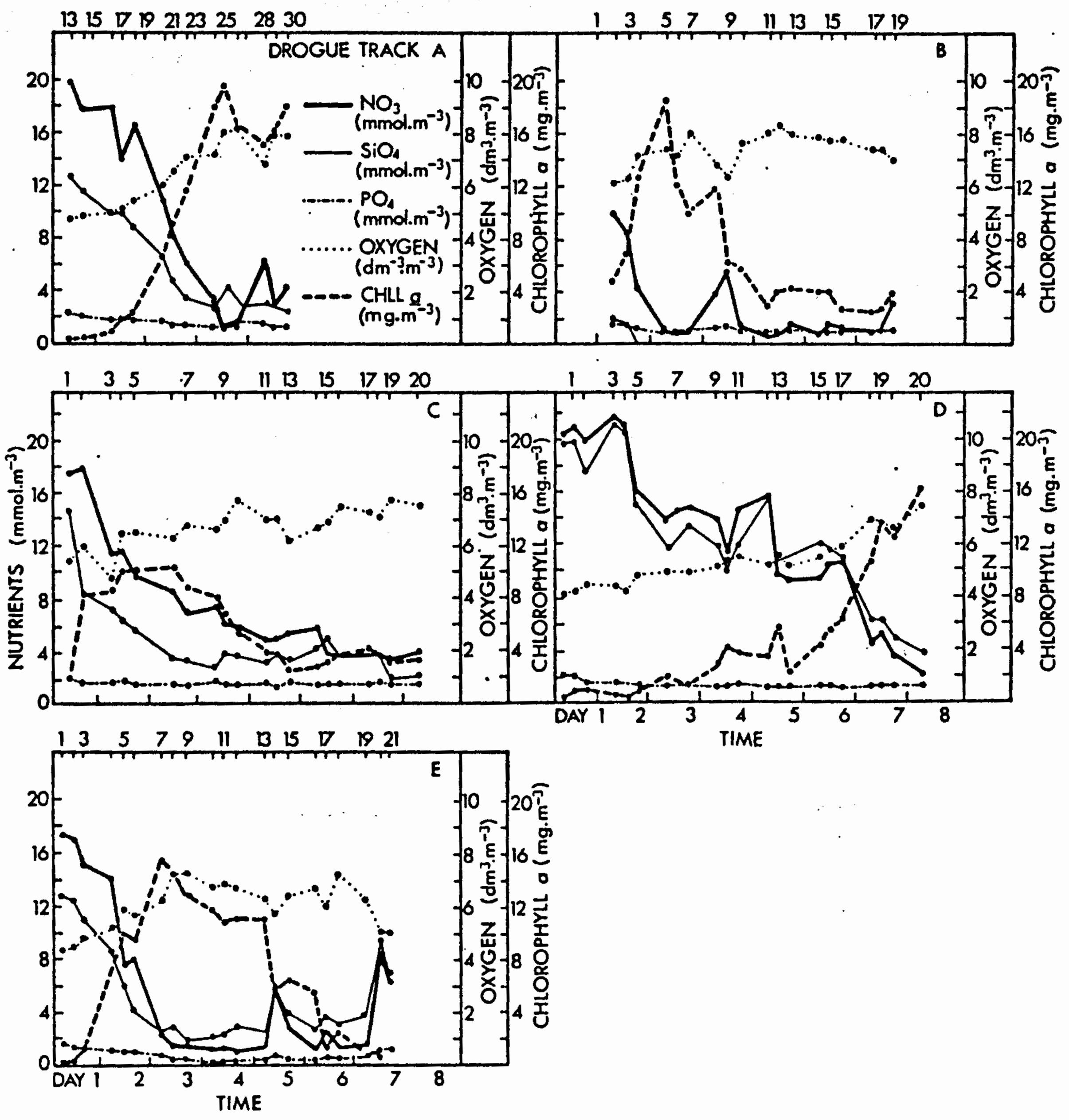

Fig.6.4: Mean concentrations of nutrients (nitrate, silicate and phosphate), dissolved oxygen and chlorophyll a in the euphotic zone along Drogue tracks A-E.

suggests that when monitoring commenced some photosynthesis had already occurred in the upwelled water (very little in the cases of Cruises A, D and E). Increases in oxygen and chlorophyll a along the drogue tracks (Fig.6.4) illustrate increased primary production and the build up of phytoplankton blooms. After reaching a maximum, chlorophyll a concentrations decreased thus indicating the decline of the bloom, whereas oxygen concentrations levelled out close to saturation.

Bloom development during each cruise is assessed below in terms of chlorophyll a concentration. Factors affecting development, such as the depths of surface mixing and the euphotic zone, nutrient concentrations and zooplankton grazing (as assessed from Table 2 of Olivieri and Hutchings 1985b for Cruises B-E) are also discussed.

Cruise A (Dec. 1979): Low wind speeds, resulting in a stable water column with a shallow upper mixing layer (mean depth 6 m, range 0-15 m, see Fig.5.12) allowed rapid phytoplankton growth along Drogue track A. Chlorophyll a concentrations in the euphotic zone increased from 0.18 $mg.m^{-3}$ on Day 1 to 19.4 $mg.m^{-3}$ on Day 4 with sharp decreases in nitrate and silicate concentrations (Fig.6.4). The euphotic zone (surface to 1% light depth) was deep (54 m) in the cold, clear newly upwelled water, but decreased to 11 m at the chlorophyll a peak on Day 4 (station 25). Low nutrients at stations 25-26 were accompanied by a decrease in chlorophyll a. However, an increase in the depth of mixing (to 15 m) at station 28 increased nutrient concentrations in the euphotic zone, delaying the decline of the bloom, as is evident from the renewed increase in chlorophyll a.

The low concentrations of chlorophyll a and oxygen at station 13 (Day 1) suggest that little phytoplankton growth had occurred at the time of drogue deployment. Consequently the 3-day period between stations 13 and 25 may be considered a reasonable estimate of bloom development time after upwelling, when turbulence does not limit primary production.

Cruise B (Dec. 1980): The upper mixing layer along the drogue track was moderately deep on Day 2 (37-20 m) but shallowed from Day 3 (station 5) to average 9.5 m (range 0-17 m) for the remainder of the cruise (see Fig.5.12). The relatively high concentrations of chlorophyll a (4.6 $mg.m^{-3}$) and oxygen (6.08 $dm^{3}.m^{-3}$) and low nitrate (9.7 $mmol.m^{-3}$) concentrations at the beginning of the study, indicated that significant phytoplankton growth had already occurred in the patch of upwelled water selected for monitoring. Consequently, the build up period of the bloom cannot be estimated. Nonetheless, rapid growth, indicated by the sharp increase in chlorophyll a and decrease in nitrate, culminated in a peak in chlorophyll a on Day 3 (station 5) followed by very low nitrate concentrations (0.7 $mmol.m^{-3}$). The euphotic zone decreased rapidly to a minimum at the peak of the bloom (7 m) then increased as the bloom declined to approximately 20 m after station 9.

As the depth of mixing after the peak in the bloom was either the same as or significantly shallower than the 1% light depth (see Fig.5.12), bloom decline is considered to have occurred during stable conditions and was associated with low nutrient concentrations. As zooplankton grazing had a minimal effect on the phytoplankton community (less than 2% of the phytoplankton daily productivity and biomass being consumed each day), it would seem that bloom decline was caused by phytoplankton sinking out of the euphotic zone. Inspection of discrete data (see Fig.6.2) shows that chlorophyll a levelled out after station 14 to concentrations of between 1 and 1.9 mg.m^{-3}, thus indicating a bloom decline period of about 3 days.

Cruise C (Feb. 1981): During the first half of Cruise C, the upper mixing layer (see Fig.5.12) was relatively deep (mean 32 m, range 25-40 m); between 1.3 and 3.2 times as deep as the 1% light depth (mean 14.6 m, range 19.0-12.5 m). The mean chlorophyll a concentration at station 1 (1.84 mg.m^{-3}) indicated that some phytoplankton growth had already occurred before monitoring commenced. However, the large increase in chlorophyll a between stations 1 and 2 seems unrealistic as it represents 13.5 doublings per day. The drogue may have moved into another patch, indistinguishable in terms of temperature, salinity (see Figs 5.8 and 5.10) and nitrate concentration but with lower silicate and higher chlorophyll a concentrations (Fig.6.4). Nonetheless deep mixing appears to have prevented phytoplankton stocks in the euphotic zone from building up to the high concentrations found in the other four cruises, despite substantial drops in nutrients. During this cruise, bloom development appears to have been light limited, as deep mixing would reduce the mean light levels to which phytoplankton cells were exposed. Consequently, although gross productivity may have been similar to that in the other cruises, high respiration (resulting from cells spending relatively longer periods below the compensation depth) was probably responsible for the less intense bloom.

The time of bloom development (build up) is difficult to estimate as some growth had already occurred when monitoring commenced, and also because the drogue may have moved from one patch into another (station 1 to 2). However, the build up period was at least $1^{1}/_{2}$ days and probably longer.

The water column stabilized on Day 4 (station 9) when the drogue reversed direction and moved south. The bloom was already declining presumably due to light limitation resulting from the combined effect of deep mixing (to 35-40 m) and shallow euphotic zone (14-12.5 m) at stations 6-8. Despite water column stabilization and moderate nitrate and silicate concentrations, chlorophyll *a* concentrations continued to decrease steadily until Day 5. During the period of bloom decline (Days 4-5) zooplankton consumption of phytoplankton was estimated at less than 2% of the phytoplankton daily productivity and biomass in the euphotic zone, and thus its effect on bloom development was hardly significant.

A shallow upper mixing layer (mean depth 3.5 m, range 0-10m) persisted during the second half of the cruise, with silicates maintaining consistent concentrations (mean 3.6 $mmol.m^{-3}$), whereas nitrates decreased from 5.9 $mmol.m^{-3}$ to less than 2 $mmol.m^{-3}$ (Fig.6.4). Although there was no clear chlorophyll *a* peak, the decline of the bloom occurred within about 2-3 days. The factors limiting production in the latter stages of bloom decline are not clear, although changes in species composition (Olivieri *et al* 1985) may partially account for a change in productivity.

Cruise D (March 1981): Very low chlorophyll a (0.36 mg.m^{-3}), low oxygen (4.1 $dm^3.m^{-3}$) concentrations and high nutrient concentrations (20.4 mmol.m^{-3} nitrate, and 19.6 mmol.m^{-3} silicate) in the euphotic zone at the commencement of monitoring, suggest that little phytoplankton production had occurred since the water body had upwelled, despite the upper mixing layer (30 m) at station 1 being shallower than the depth of the euphotic zone (63 m). The initiation of surface stabilization at stations 2 and 3 (see Fig.5.12) was reflected by the small but definite increase in chlorophyll a between stations 1 and 3. The subsequent decrease in chlorophyll a and increase in nutrients at stations 4-5 (Day 2) were probably due to the entrainment of more recently upwelled water as the drogue moved away from the coast off Slangkop (see Fig.5.5), and not due to deep mixing as a very definite thermocline (see Fig.5.12) was present. The sudden drop in nutrient concentrations from station 5 to 6 (Day 2-3) with virtually no increase in chlorophyll a, however, is difficult to explain, other than that the drogue moved into a different patch of water, which had previously been subjected to grazing or deep mixing (this would have prevented a build up of phytoplankton but not a decrease in nutrients).

The delay in chlorophyll a build up on Day 3 is strange particularly as the euphotic zone depth was considerably greater than the depth of mixing and grazing rates were low throughout the study period. However, the increase in chlorophyll a on Day 4 appears to have been temporarily retarded by deep mixing down to 63 m on Day 5 (1% light depth was 26 m). A change in the chlorophyll a depth profiles at station 15 (Day 6) suggests that stations 15 and 16 were in yet another patch of water. However, chlorophyll a and nutrient depth-profiles from stations 17 to 22 (Days 6-8) indicate that, during these two days at least, the drogue seemed to maintain itself in a consistent patch of water in which a rapid increase in chlorophyll a from 5.4 $mg.m^{-3}$ to 16.2 $mg.m^{-3}$ was accompanied by a sharp drop in nutrients and a decrease in the depth of the euphotic zone from 25 m (stations 17-18) to about 11 m (stations 19-22). The depth of mixing was variable but unlikely to limit primary productivity significantly. Monitoring of the water body was unfortunately stopped before a definite chlorophyll a peak was attained. The build up period of the final bloom was at least 2 days, probably more.

Prior to station 17 (Day 6), the water mass appeared rather patchy. With the vigorous winds, strong upwelling and moderately deep mixing that occurred, it is likely that the chemical changes were caused by physical mixing and advection rather than by biological activity. The sharp changes in salinity (Fig.5.10) support this view.

Cruise E (Oct. 1981): The water column along Drogue track E was stable with a shallow upper mixed layer (mean depth 6.3 m, range 0-15 m), and a well established thermocline was present throughout the cruise (see Fig.5.12). At the commencement of the study chlorophyll a concentrations were very low (0.7-0 $mg.m^{-3}$) and the euphotic zone was moderately deep (35-45 m) stretching well below the thermocline. The overnight increase in chlorophyll a from Day 1 to 2 seemed too large to be due to phytoplankton growth alone, and thus probably gives an underestimate of bloom build up time (2 days).

The peak in chlorophyll a at station 7 was accompanied by a sharp drop in nutrients and a decrease in the euphotic zone depth to 12 m. For the two days following the peak, the euphotic zone (10-13 m) maintained a depth similar to the depth of mixing (0-15 m), while nutrient concentrations remained low. Irregular peaks in nutrient concentrations between stations 14 and 21 (Days 5-7) are somewhat artificial and are attributed to the variable euphotic zone depth (13-35 m), as the nutricline was generally between 10 and 20 m. The bloom decline spanned 3-4 days and was associated with low nutrients (nitrates were consistently less than 2 $mmol.m^{-3}$), and marginally higher grazing rates (mean 5%, range 3-11% of phytoplankton daily productivity and biomass) than in the other cruises.

6.4 Summary

Relative to the physical characteristics (temperature and salinity) of the deep water, the nutrient concentrations were more variable along each drogue track. This suggests that the "patch" of water which the drogue was following, was shearing over a deeper layer of variable nutrient content, as the changes were too irregular to attribute to normal biological activity in a single water column.

While nutrient concentrations in these upwelling source waters were high, phytoplankton biomass was low. High light levels at the sea surface allowed nutrients in newly upwelled water to be rapidly taken up by phytoplankton so that concentrations in surface waters were reduced to low levels after a few days once the bloom started.

TABLE 6.4: Growth and decline cycles of phytoplankton blooms in upwelled water and a summary of conditions influencing bloom development.

CRUISE	BLOOM DEVELOPMENT CYCLE (days)			CONDITIONS INFLUENCING DEVELOPMENT
	growth	decay	total	
A	3	> 1	> 4	Stable water column allowed rapid bloom build up; nutrient induced bloom decline delayed by entrainment of nutrients into euphotic zone.
B	> 1.5	3	> 4.5	Bloom peaked rapidly after deeply mixing water stabilized at station 2. Low nutrients associated with bloom decline.
C	> 1.5	2-3	3.5-4.5	Low light levels resulting from deep mixing did not prevent bloom initiation, but limited its extent in that chlorophyll concentrations did not increase to high levels of other cruises. Limiting factors in latter stages of bloom are not clear.
D	> 2	-	> 2	Slow build-up of phytoplankton stocks artefactual; due to water around drogue being replaced by more recently upwelled (chlorophyll-poor) water. After station 17 bloom development was similar to that in other stable water masses. Monitoring ceased before bloom declined.
E	> 2	3-4	> 6	Stable water column enabled rapid bloom development. Drogue appeared to move into patch of chlorophyll *a*-rich water; thus apparent 2-day build up period is probably an underestimate. Low nutrients associated with bloom decline.
A-E	3	3-4	6-7	Estimated periods of bloom build up and decline are combined to obtain a complete bloom development of cycle about 6-7 days.

Although a complete cycle of bloom development was not attained during any one cruise, some idea of the variation in build-up and decline periods was obtained by superimposing the peaks of the five chlorophyll a curves presented in Fig.6.4. The growth and decline cycles are summarized in Table 6.4 together with brief comments on prevailing conditions and limiting factors. The complete cycle of bloom development in upwelled water appeared to be completed within 6-7 days. Chlorophyll a increased from concentrations of usually less than 1 $mg.m^{-3}$ in upwelling water to 10-20 $mg.m^{-3}$ at the peak of the bloom, then decreased to concentrations of 1-3 $mg.m^{-3}$ after the bloom, when recycling of nutrients probably maintained phytoplankton stocks at moderately low levels. Turbulence may, of course, entrain nutrients up into the euphotic zone and so prolong the bloom.

It is interesting, however, that firstly, the rate of phytoplankton consumption by zooplankton was low in these studies, and did not account for bloom decline, and secondly that in only one of the five cruises did light limitation due to deep mixing influence bloom development. In this case (Cruise C) the initiation of the bloom was not impeded, but its development was limited so that only moderately high chlorophyll a concentrations were attained. It follows that high nutrient levels and a relatively stable water column after upwelling are responsible for the intense blooms of phytoplankton encountered in the Cape Peninsula upwelling region. Conversely, however, the association of low nutrients with decreasing chlorophyll a concentrations is not sufficient evidence to attribute bloom decline to nutrient limitation of phytoplankton productivity alone. Other processes such as sinking or dispersion may be important factors controlling the decline in blooms in this area.

CHAPTER 7: NUTRIENT RATIOS AND LIMITATION

7.1 Introduction

7.2 Nutrient atomic ratios of occurrence

7.3 Atomic ratios of nutrient utilization and oxygen and carbon production

7.4 Nutrient limitation

7.1 Introduction

Spatial and temporal variability in nutrient concentrations is large in surface waters of upwelling regions (see Fig.6.1). Upwelling introduces nutrient-rich water into the euphotic zone where phytoplankton are able to photosynthesize and thereby remove the nitrate, silicate and phosphate salts from solution and organically bind them. Subsequently the synthesis-regeneration cycle is completed when these nutrients are returned to solution through both the metabolic activities (feeding, excretion, decomposition etc.) of the marine community and by physicochemical dissolution processes.

According to Redfield et al (1963), the atomic ratios of the principal elements present in phytoplankton provide a stoichiometric basis for evaluating the general proportions in which these elements may be expected to change in sea water as a result of biological activity (i.e. photosynthesis or decomposition). Redfield et al (1963) point out, however, that substantial departures from these average ratios (O:C:N:P = -276:106:16:1) may occur. Although Tett et al (1985) express "little doubt that this variation is associated in some manner with changes in the growth rate of the algae", they maintain that phytoplankton chemical composition close to the Redfield ratios does not imply near maximal growth rates as suggested by Goldman et al (1979), and they give examples of slow-growing phytoplankton populations with chemical ratios similar to Redfield's.

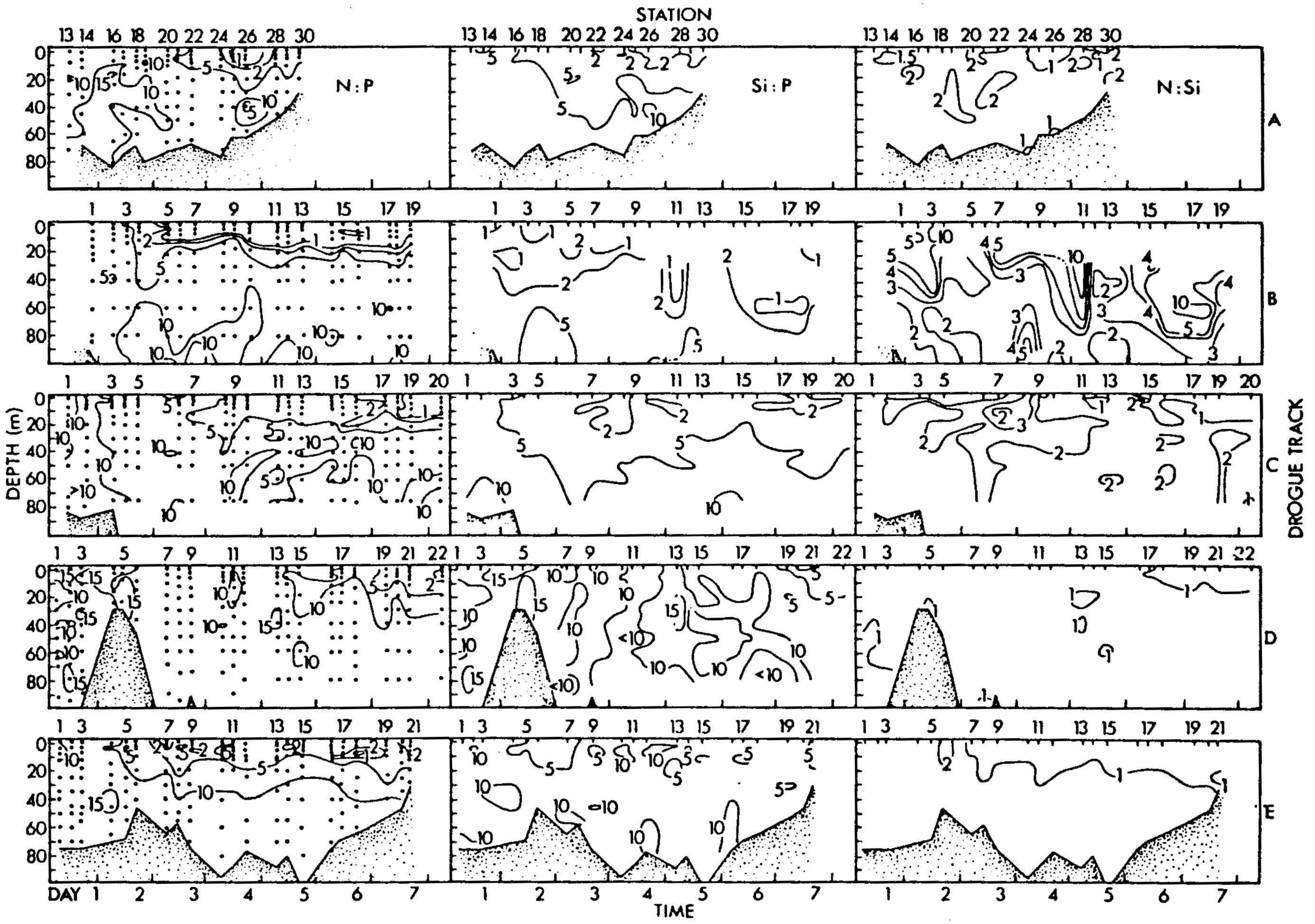

Fig.7.1: Vertical sections of the atomic ratios of occurrence of the major nutrients, nitrate:phosphate (N:P), silicate: phosphate (Si:P) and nitrate:silicate (N:Si) along Drogue tracks A-E. The chlorophyll a peak occurred at stations 25, 5, 5-6, 22 and 7 along Drogue tracks A, B, C, D and E respectively.

The present study provides an opportunity to investigate (somewhat indirectly) the applicability of the "Redfield ratios" to coastal upwelling surface waters as changes in nutrients and oxygen along the drogue tracks are largely attributed to photosynthesis. Nutrient, oxygen and carbon ratios of occurrence and utilization are presented in this chapter, and nutrient limitation is investigated.

7.2 Nutrient atomic ratios of occurrence

Vertical sections of the atomic ratios of the major nutrients occurring in upwelled water, i.e. NO_3-N:PO_4-P (N:P), SiO_4-Si:PO_4-P (Si:P) and NO_3-N:SiO_4-Si (N:Si), are presented for Drogue tracks A-E in Fig.7.1.

At the start of each study N:P ratios ranged between about 9 and 15, except for Cruise B when they were less than 10. As the phytoplankton blooms developed along Drogue tracks A, B, D and E, ratios in surface layers decreased to between 2 and less than 1 at the peak in chlorophyll a (see Fig.6.4). During Cruise C, N:P ratios were greater than 5 at the chlorophyll a peak (stations 5-6). However, when the water stabilized (station 9), ratios decreased steadily to levels of less than 1 by the end of the study.

Si:P ratios showed similar (but not as clear) distribution patterns as the N:P ratios along the drogue tracks, decreasing from about 5-10 for Cruises A, C and E (7-15 for Cruise D) to about 1-4 at the end of the studies. Si:N ratios, however, were about 1-2 at the start of Drogue tracks A, C and E and decreased to less than 1, whereas during most of Cruise D they were close to 1 decreasing to about 0.5 towards the end of the study.

During Cruise B exceptionally low silicate concentrations (see section 6.2 and Fig.6.1) resulted in low Si:P (up to about 5) and high N:Si (up to 12.1) ratios. Ratios could not be calculated for the upper 10-30 m after station 3, because silicate concentrations were zero. The abnormal ratios and unusual occurrence of silicate concentrations of zero, suggest that the silicate data are spurious. Thus they are excluded from further analyses.

While the N:P and Si:P ratios remained relatively constant at depth, they changed quite considerably near the sea surface, presumably because of differences in the uptake and regeneration rates of these nutrients by phytoplankton. N:Si ratios were less variable than N:P and Si:P ratios. This reflects the similar distribution patterns and uptake rates of nitrate and silicate as compared to phosphate (Fig.6.1). Near the sea surface, however, the decrease in N:Si from values greater than 1 to values less than 1 further along the drogue track, suggest that, although nitrate was present in higher or similar concentrations to silicate at the commencement of monitoring, it was depleted more rapidly during phytoplankton growth.

The vertical distribution of nutrients, oxygen and chlorophyll a (see Figs 6.1 and 6.2) suggests little phytoplankton activity below about 50 m. Consequently, in Fig.7.2 mean nutrient ratios are presented separately for the euphotic zone (surface to the 1% light depth) and below 50 m, to illustrate the effects of photo-

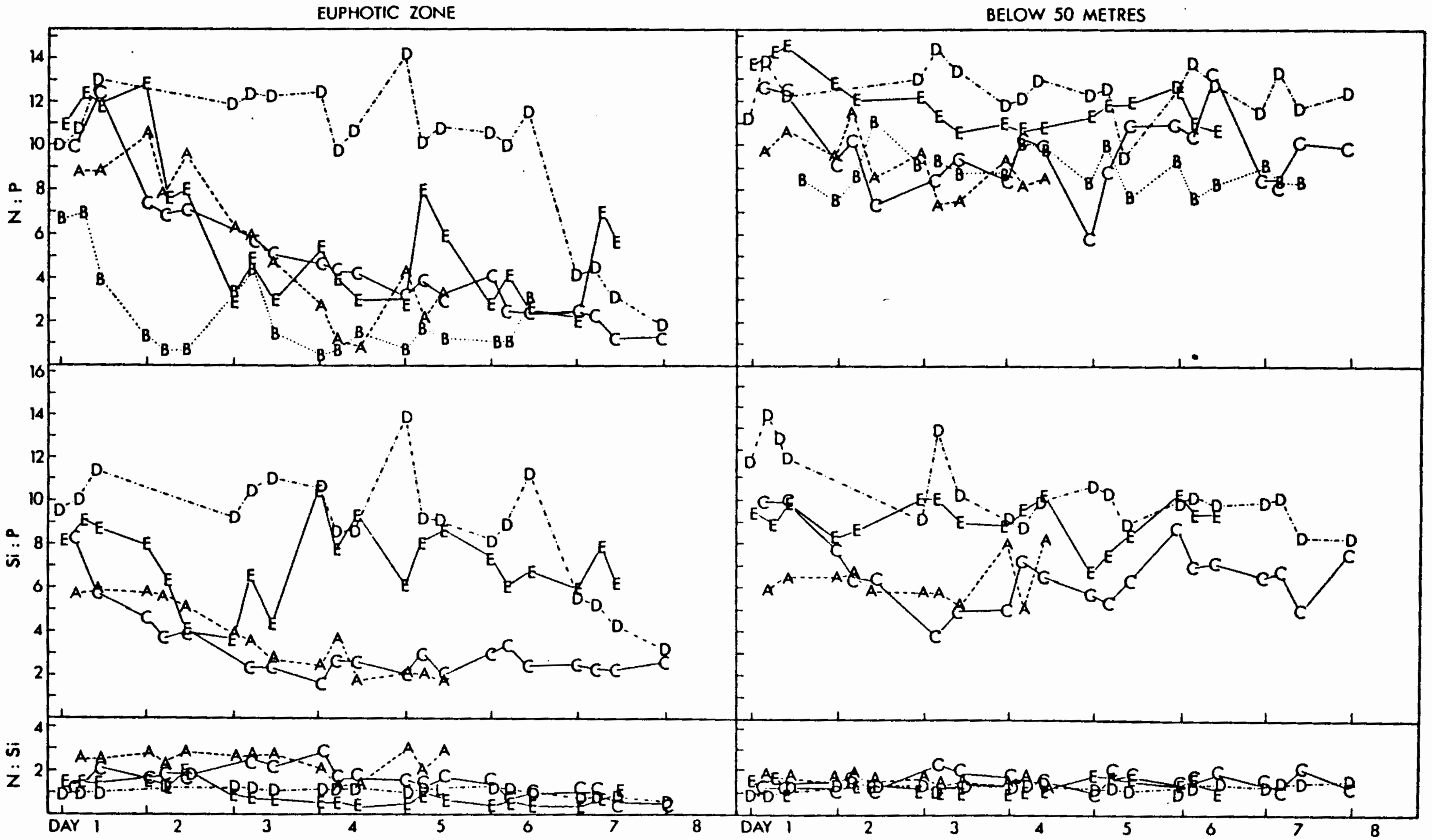

Fig.7.2: Mean atomic ratios (of occurrence) of the major nutrients (N:P, Si:P and N:Si) in the euphotic zone and below 50 m along Drogue tracks A-E.

synthesis on relative nutrient concentrations. Ratios at the beginning of each study (before much phytoplankton growth had occurred) were similar to those in deep water, where N:P ranged between 5.8 and 14.4, Si:P between 3.8 and 14.0, and N:Si between 1.0 and 2.2. These ratios reflect the wide range of proportions in which nutrients may occur in upwelling source water. Euphotic zone ratios generally decreased along the drogue tracks. However, it should be borne in mind that ratios of occurrence are not expected to reflect the Redfield ratios. Rather, Redfield _et al_ (1963) suggest that the ratios of _change_ in nutrient concentration, caused by photosynthetic activity and growth of the phytoplankton, should be similar to the ratio of these elements present in phytoplankton. Such changes will be addressed in the next section (7.3).

Mean nutrient ratios of occurrence (and ranges) for each cruise are summarized along with oxygen and chlorophyll _a_ concentrations in Table 7.1. Furthermore, euphotic zone ratios have been separated into "newly upwelled" water (type 1), "mature" (type 2) and "aged" (type 3) upwelled water categories as defined by Barlow (1982a) in terms of temperature and nitrate concentration (type 1 : <10°C, 15-30 mmol.m^{-3}; type 2: 10-15°C, 2-15 mmol.m^{-3}; type 3: 12-18°C, 0-2 mmol.m^{-3}). Nutrient ratios in "newly upwelled" water were similar to those in deep water, and decreased progressively in types 2 and 3 water, while oxygen concentrations (a rough index of primary productivity) usually increased (Table 7.1). However, chlorophyll _a_ concentrations in Cruises B, D and E decreased from type 2 to type 3 water, thus reflecting the decline of the phytoplankton bloom in the "aged" upwelled water. The relative decreases in N:P and N:Si ratios from type 1 to type

TABLE 7.1: Nutrient ratios (by atoms) and concentrations of oxygen and chlorophyll a below 50 metres and in the euphotic zone

PARAMETER	CRUISE	BELOW 50 METRES[*1]				EUPHOTIC ZONE												
						NEWLY UPWELLED WATER (water type 1)				MATURE UPWELLED WATER (water type 2)				AGED UPWELLED WATER (water type 3)				ALL DATA*[1]
		mean	range	sd	n	mean	range	sd	n	mean	range	sd	n	mean	range	sd	n	mean
N:P	A	9.1	7.3-11.5	1.26	11	9.97	7.5-13.1	1.86	9	2.64	1.6- 4.2	0.77	18	0.57	0.4- 0.7	0.08	8	5.5
	B	8.9	7.5-11.1	0.93	19	9.47	-	0	1	3.51	2.7- 4.6	0.70	10	0.69	0.3- 1.9	0.33	61	2.2
	C	9.7	5.8-13.1	1.75	20	10.10	9.1-11.9	1.18	5	2.58	1.6- 4.1	0.63	31	0.69	0.4- 1.3	0.32	12	4.7
	D	12.4	9.4-14.3	1.10	19	12.01*[3]	8.4-15.3	2.15	12	3.29	1.7- 4.7	0.92	17	1.76	1.7- 1.8	0.05	2	9.6
	E	11.9	10.5-14.4	1.25	17	12.45	9.6-13.9	1.51	6	5.45	3.5- 8.9	1.62	8	2.94	0.7- 8.0	1.31	65	6.1
	(A-E)	10.5			86	11.17			33	3.12			84	1.69			148	5.7
S:P	A	6.3	5.0- 8.2	1.00	11	5.93	5.1- 7.1	0.58	9	2.04	0 - 3.8	0.94	18	2.46	1.2- 4.4	1.09	8	3.7
	B[*2]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	C	6.7	3.8- 9.9	1.58	20	7.77	5.8-8.6	1.15	5	2.53	1.6- 5.5	0.80	31	2.14	1.6- 2.9	0.46	12	3.2
	D	10.3	8.2-14.0	1.50	19	10.92[*3]	7.6-14.7	2.10	12	5.59	2.9-11.1	2.45	20	7.61	3.2-11.1	4.00	5	8.9
	E	9.1	6.7-10.3	1.10	17	8.98	7.5-10.0	1.01	6	5.75	3.4- 8.7	1.38	9	6.67	2.6-14.7	2.37	66	7.1
	(A-E)	8.26			67	8.66			32	3.57			78	5.75			91	5.9
N:S	A	1.5	1.0- 1.7	0.22	11	1.68	1.3-2.1	0.27	9	1.34	0.7- 2.5	0.57	17	0.27	0.1- 0.5	0.12	8	1.4
	B[*2]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	C	1.5	1.0- 2.2	0.34	20	1.35	1.1-2.1	0.41	5	1.10	0.3- 2.1	0.38	31	0.36	0.1- 0.8	0.22	12	1.5
	D	1.2	1.0- 1.5	0.15	19	1.09	0.9-1.2	0.08	15	0.70	0.5- 0.9	0.12	17	0.54	0.5- 0.6	0.03	2	1.0
	E	1.3	1.0- 1.7	0.20	17	1.40	1.0-1.6	0.23	6	1.00	0.5- 1.6	0.34	8	0.45	0.1- 1.0	0.14	66	0.87
	(A-E)	1.4			67	1.33			35	1.05			73	0.42			88	1.2
OXY	A	3.8	3.5- 4.1	0.18	8	4.42	3.9-5.1	0.37	9	7.52	6.7- 8.1	0.51	18	8.41	8.1- 8.8	0.22	8	6.7
	B	4.6	4.4- 4.9	0.16	18	-	-	-	0	6.97	6.6- 7.2	0.23	10	7.80	6.2- 8.9	0.42	60	7.4
	C	4.4	3.7- 5.2	0.43	20	5.43	5.1-5.7	0.23	5	7.03	2.7- 7.5	0.87	31	7.87	7.6- 8.2	0.21	12	6.7
	D	4.2	3.0- 4.7	0.46	19	4.17	3.3-4.6	0.29	15	6.68	5.0- 7.6	0.79	20	6.02	5.0- 7.4	1.30	5	5.4
	E	3.8	3.3- 4.3	0.32	16	3.96	2.9-4.3	0.52	6	6.61	6.2- 7.2	0.30	9	6.70	5.7- 7.7	0.47	64	5.9
	(A-E)	4.2			81	4.38			35	7.00			88	7.31			149	6.3
CHLL	A	1.6	0.3- 7.7	1.97	11	0.46	0.1-0.8	0.26	9	16.77	11.3-20.8	2.91	18	17.91	15.6-21.2	1.79	8	9.7
	B	0.7	0 - 3.2	0.76	18	0	-	0	1	9.59	6.1-13.0	2.88	10	4.90	1.0-21.0	4.80	60	6.5
	C	1.3	0 - 5.4	1.39	20	1.7[*4]	0.9-2.4	0.62	4	3.74	1.9- 7.1	1.20	31	3.64	2.5- 5.8	0.96	11	5.5
	D	0.7	0.2- 2.2	0.48	19	0.56	0.1-1.1	0.29	15	11.30	1.1-17.9	4.87	20	7.74	1.1-17.3	7.31	5	5.1
	E	0.4	0 - 1.0	0.35	17	0.45	0 -1.4	0.57	6	12.14	6.0-15.4	3.38	9	7.93	0 -20.7	5.64	67	6.7
	(A-E)	0.7			85	0.63			35	9.65			88	6.93			151	6.5

[*1] Calculated from mean concentrations at each station.

[*2] Silicate data were unreliable.

[*3] Two data points with very low phosphate concentrations (Stat.5 10-25m) and therefore unreasonably high N:P and S:P ratios have been omitted.

[*4] High chlorophyll a concentrations in cold water.

3 water are in agreement with the findings of Andrews and Hutchings (1980) in that they suggest that nitrate is used up fastest and is thus the most likely of the three nutrients to limit phytoplankton growth in the euphotic zone.

Andrews and Hutchings (1980) used the N:Si ratio to determine the origin of low oxygen water off the Cape Peninsula. Because N is regenerated more rapidly than Si, it was proposed that low-oxygen water with a high N:Si ratio was formed locally whereas that with a low ratio originated from some distant location. Examination of the oxygen and N:Si data in the present study showed no clear picture in this regard; even in the "low-oxygen" water along Drogue track C (see Table 6.2), the N:Si ratio was not consistent, ranging between 0.98 and 2.08.

7.3 Atomic ratios of nutrient utilization and oxygen and carbon production

Changes of N, Si, O and C (as calculated from chlorophyll a measurements) relative to P are obtained for each cruise, firstly, from the slopes of regression analyses presented in Figs 7.3-7.6 for all the data collected for each cruise; and, secondly, from *in situ* changes in the nutrient, oxygen and chlorophyll a content of the upper 20 m (Table 7.2) during the period prior to the peak in integrated chlorophyll a (see Fig.6.4). The depth of 20 m was chosen because the drogue was set at 10 m so that its movements might, on average, represent that of the water column 10 m above and 10 m below the drogue. Moreover, 20 m usually encompassed most of the euphotic zone and the surface mixing layer.

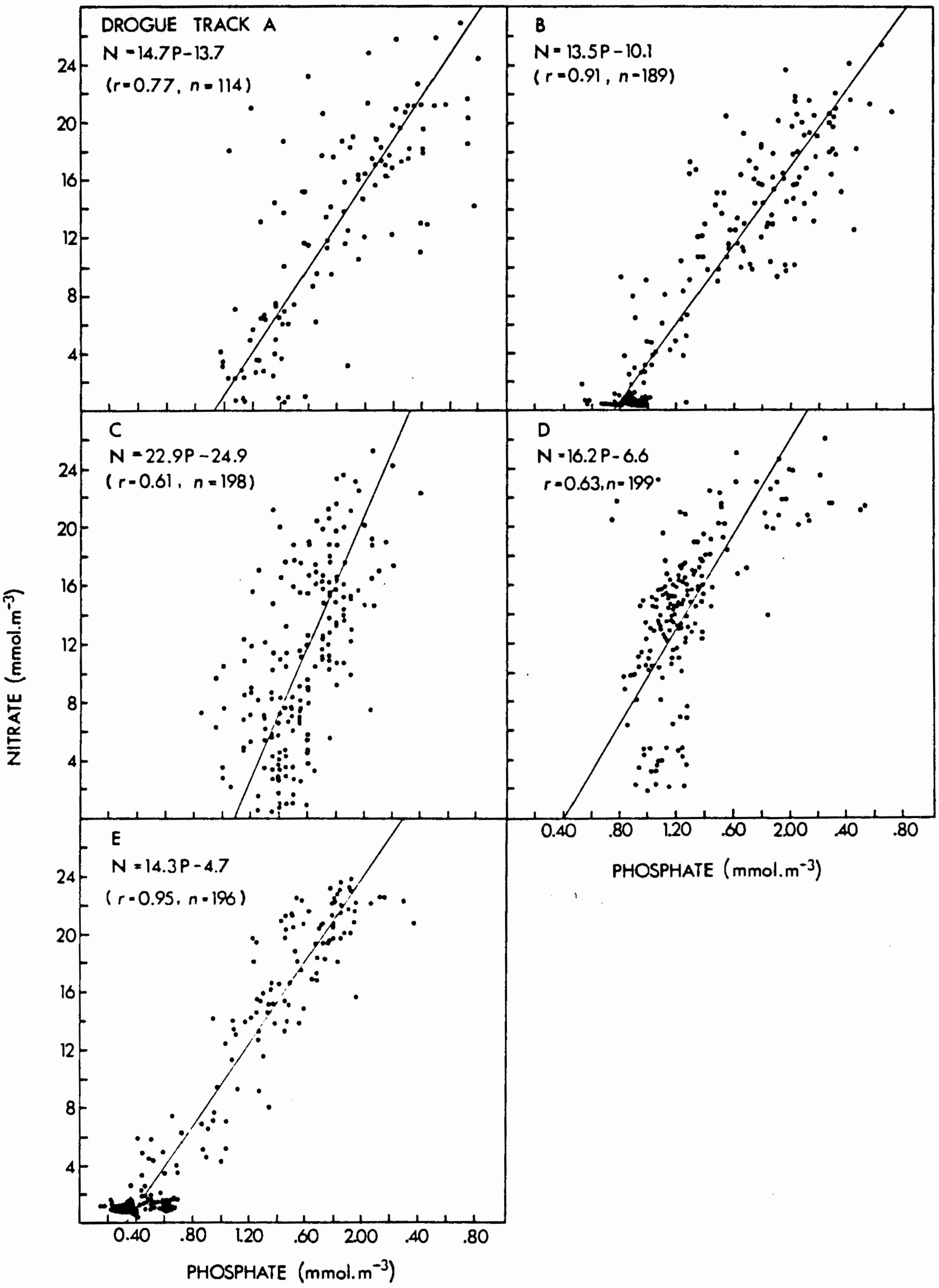

Fig.7.3: Relationships between nitrate and phosphate concentrations along Drogue tracks A-E. The geometric regression equation for the combined data sets (A-E) is $N = 13.9\ P - 8.0$, $r = 0.73$, $n = 896$.

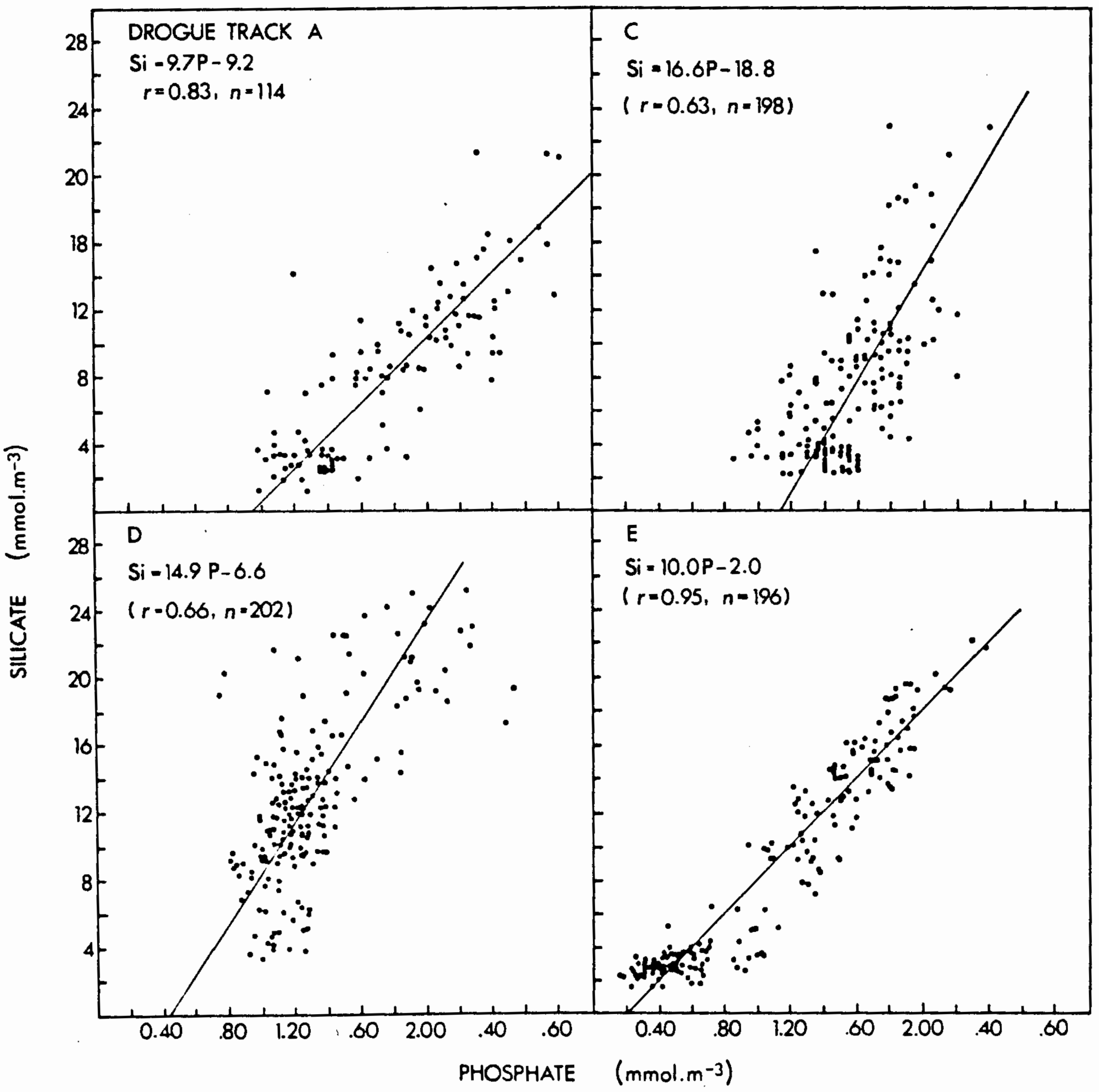

Fig.7.4: Relationships between silicate and phosphate concentrations along Drogue tracks A-E. The geometric regression equation for the combined data sets (A-E) is Si = 10.9 P - 5.8, r = 0.57, n = 710.

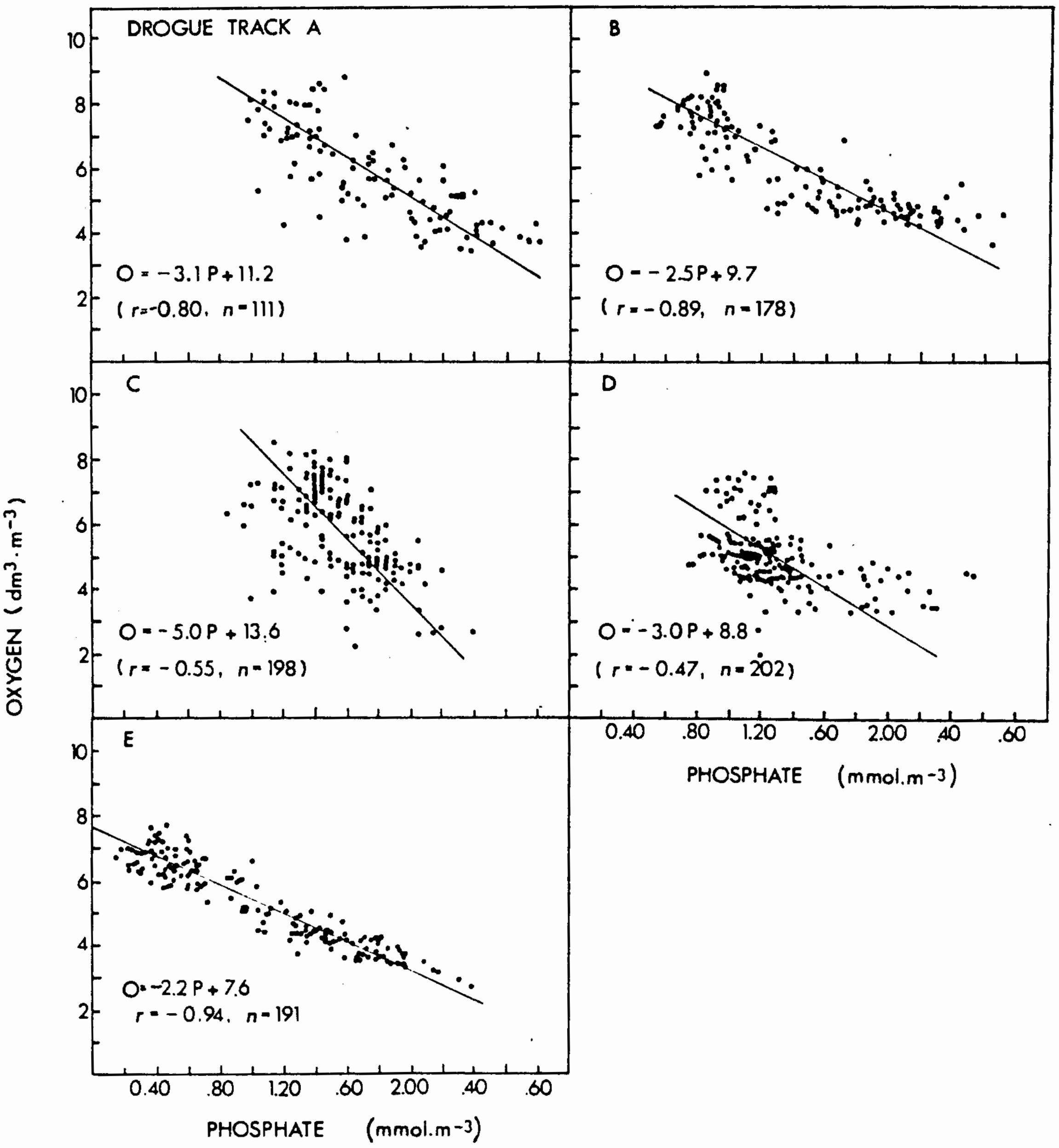

Fig.7.5: Relationships between dissolved oxygen and phosphate concentrations along Drogue tracks A-E. The geometric regression equation for the combined date sets (A-E) is O = -2.6 P + 9.2, r = -0.56, n = 880.

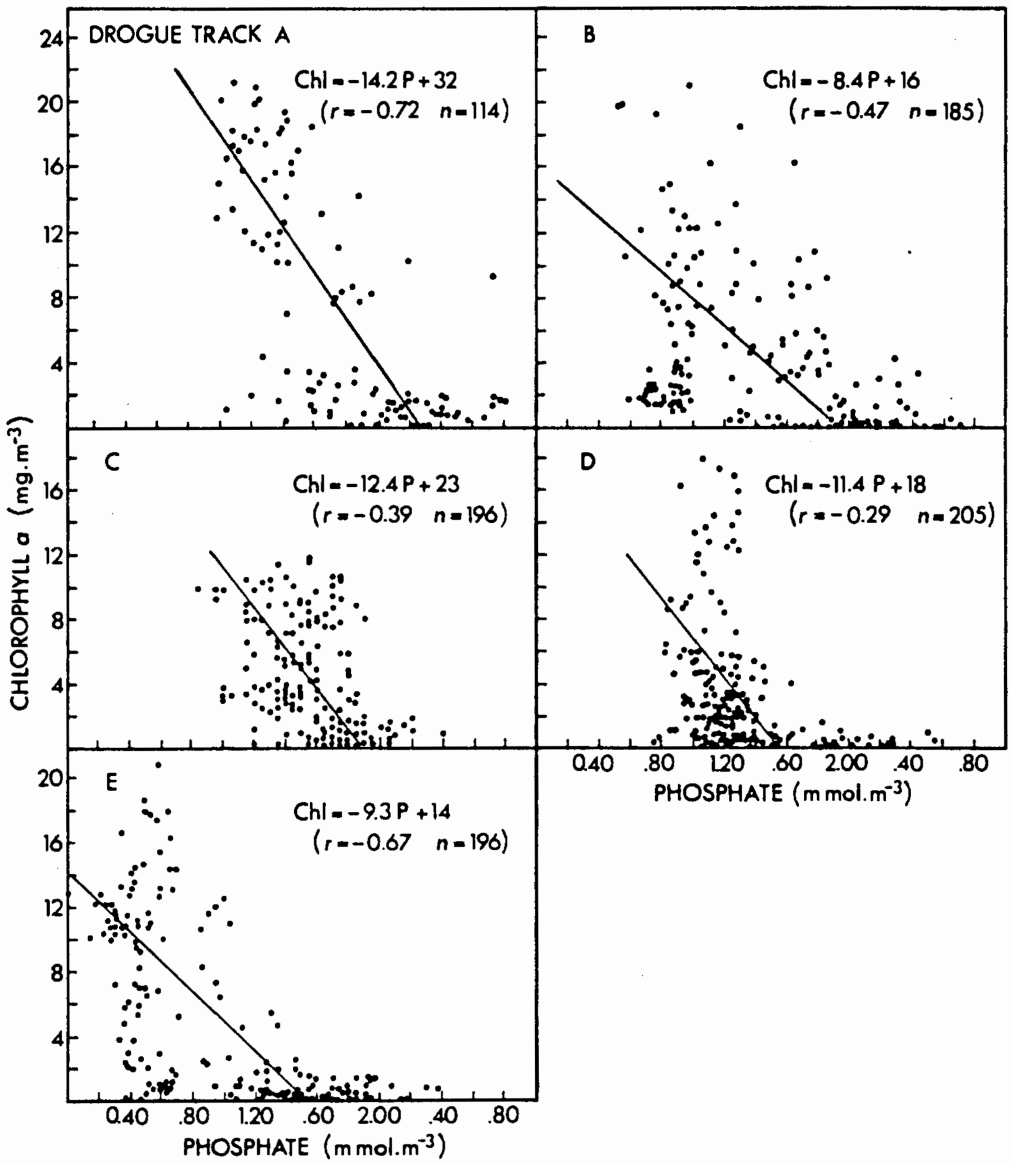

Fig.7.6: Relationships between chlorophyll a and phosphate concentrations along Drogue tracks A-E. The geometric regression equation for the combined date sets (A-E) is Chl = -9.5 P + 17.7, r = -0.42, n = 893.

TABLE 7.2: Changes in the nutrient, oxygen and chlorophyll a content of the upper 20 m layer prior to the peak in chlorophyll a

CRUISE (station range)	PHOSPHATE ($mmol.m^{-2}$)	NITRATE ($mmol.m^{-2}$)	SILICATE ($mmol.m^{-2}$)	OXYGEN ($dm^3.m^{-2}$)	CHLL a ($mg.m^{-2}$)
A (13-22)	15.0	233.0	155.2	-36.0	-224.5
B (2-5)	9.1	133.6	-	-16.8	-231.2
C (1-5)	9.5	154.3	187.8	-19.0	-173.4
D (1-22)	17.0	327.2	283.3	-53.5	-291.0
E (1-8)	22.2	284.0	182.1	-47.2	-296.3

TABLE 7.3: Atomic ratios of change for nutrients, oxygen*[1] and carbon*[2] (equivalent Redfield ratios are 1:16:15:-276:-106)

DATA SET	METHOD	ATOMIC RATIOS OF CHANGE					MEAN RATIOS				
		P	N	Si	O	C	P	N	S	O	C
Cruise A	Regression analyses (See Figs 7.3-7.6)	1	14.7	9.7	-276	-59	1	16.3	12.8	-283	-47
" B		1	13.5	-	-226	-35					
" C		1	22.9	16.6	-447	-52					
" D		1	16.2	14.9	-266	-51					
" E		1	14.3	10.0	-198	-39					
Cruise A	*In situ* changes in the upper 20 m layer along drogue track (Table 7.2)	1	15.5	10.3	-215	-62	1	15.7	13.8	-206	-74
" B		1	14.7	-	-165	-106					
" C		1	16.2	19.8	-179	-76					
" D		1	19.2	16.7	-281	-71					
" E		1	12.8	8.2	-190	-56					
Cape Peninsula: (Andrews and Hutchings 1980)											
1969-70	Regression analyses	1	19.1	17.5	-243	-43.2	1	20.7	18.4	254	-
1971-72		1	19.7	20.0	-227	-					
1972-73		1	23.3	17.7	-293	-					
1969 (0-50m)	*In situ* changes in the total amount present in the coastal area from upwelling to downwelling conditions	1	9.3	11.3	-	-	1	10.5	11.0	-	-
1969 (50-100m)		1	11.7	10.8	-	-					
St. Helena Bay:											
(Bailey and Chapman 1985)	Regression analyses	1	13-27	-	-276to -635	-					
(Waldron 1985)	Regression analyses	1	9.9	8.7	-	-					
(Bailey and Chapman 1985)	*In situ* changes	1	12.2	9.2	-118	-					
Cape Columbine:											
(Waldron 1985)	Regression analyses	1	12	5	-	-					

[*1] Oxygen units in Table 7.2 and Fig.7.5 ($dm^3.m^{-2}$) were converted to $mmol.m^{-2}$ as follows: $dm^3.m^{-2}$ x 1.43 - 32 - 1000 = $mmol.m^{-2}$

[*2] Carbon was calculated from chlorophyll *a* measurements in Table 7.2 and Fig.7.5 using a C:chll *a* ratio of 50:1. Carbon units were converted from $mg.m^{-2}$ to $mmol.m^{-2}$ by dividing by 12, the atomic weight of carbon.

This approach is based on the assumption that chemical changes in the water mass, into which the drogue was placed, were due to phytoplankton metabolism and not due to physical factors.

The resulting atomic ratios of nutrient utilization and oxygen and carbon production are summarized in Table 7.3 together with similar ratios calculated from other Benguela data sets (Andrews and Hutchings 1980, Bailey and Chapman 1985 and Waldron 1985). ΔN:ΔP ratios, obtained from regression analyses in the present study, were lower than equivalent ratios listed for the Cape Peninsula, but higher than (or similar to) those for St Helena Bay and Cape Columbine (Table 7.3). On the other hand, ratios calculated from *in situ* changes were higher in the drogue studies than in the Cape Peninsula or St Helena Bay studies. However, mean ΔN:ΔP ratios for the drogue studies (from both regression analyses and *in situ* changes) are almost identical to the equivalent Redfield ratio (16:1). This suggests that, on average, nitrogen and phosphate are taken up in similar proportions to those in which they occur in phytoplankton.

According to Redfield *et al* (1963), silicon enters the biochemical cycle in about the same proportion as nitrogen, the atomic ratio of change of ΔSi:ΔP being approximately 15:1 (Richards 1958). Ratios calculated from the drogue studies ranged between 8.2:1 and 19.8:1, the mean ratios for *in situ* changes (13.8:1) and regression analyses (12.8:1) being similar to but slightly lower than the Redfield ratio of 15:1. ΔSi:ΔP ratios for the Cape Peninsula (including this study) were generally higher than for the St Helena Bay/Cape Columbine area (Table 7.3), thus suggesting that the rate of silicate utilization relative to phosphate was higher off the Cape Peninsula than further north. This may have some implications regarding the taxonomic composition of the phytoplankton in these areas as only certain taxa (mostly diatoms) require silicate. It follows that variation in ΔSi:ΔN amongst the five drogue studies could also reflect differences in the phytoplankton composition. Thus diatoms might be expected to be more prominent in the phytoplankton populations along Drogue tracks A and E than during the other cruises. Phytoplankton samples concentrated on 37μm mesh appeared to be completely dominated by diatom species for all the cruises. Unfortunately, however, poor preservation of phytoplankton bottle samples (Olivieri et al 1985) precluded an investigation of many of the smaller taxa which are independent of silicon. Particle spectra suggest that significant biomass of smaller cells occurred only during Cruise D (March 1981). However, the fact that ΔSi:ΔP ratios for this cruise were second highest (Table 7.3), suggests that these small cells were probably also diatoms.

Oxygen and organic carbon are produced during photosynthesis (the atomic ratios of change of ΔO:ΔP and ΔC:ΔP are thus negative). In the drogue studies the mean atomic ratio of change of oxygen to phosphate (ΔO:ΔP) obtained from regression analyses (-283:1), is very similar to the Redfield ratio (-276:1). Individual ratios, however, vary more widely than do Andrews and Hutchings' (1980) values for the Cape Peninsula and are lower than those for St Helena Bay (Table 7.3). Ratios calculated from in situ changes along the drogue tracks were generally lower (mean ΔO:ΔP=-206:1) than regression ratios, but not as low as the values for St Helena Bay. It should be noted, however, that the latter were regeneration ratios based on phytoplankton decomposition and were calculated using values of apparent oxygen utilization rather than dissolved oxygen concentrations (see Bailey and Chapman 1985).

Carbon to phosphate ratios of change ($\Delta C:\Delta P$) were calculated from changes in chlorophyll a using a carbon:chlorophyll a ratio of 50:1 as was found to be appropriate in a similar study off Peru (Ryther et al 1971) and similar to the ratio (56:1) reported by Bailey and Chapman (1985) for St Helena Bay. $\Delta C:\Delta P$ obtained from regression analyses are consistently lower (-35:1 to -59:1) than those calculated from in situ changes (-55:1 to -106:1), while both are lower than the Redfield ratio (-106:1).

In summary, the mean atomic ratios of change measured here (Table 7.3) were similar to the Redfield ratios, except for $\Delta C:\Delta P$ which was considerably lower. This may be related to the choice of carbon:chlorophyll a ratio used to convert chlorophyll a values to carbon (refer to Banse 1977 for a review of the problems associated with the determination of C:chlorophyll a ratios of natural phytoplankton). That Andrews and Hutchings (1980) found considerable variation in the carbon:chlorophyll a ratio (30:1 to 211:1) off the Cape Peninsula, suggests that the general application of a single ratio is probably not realistic. Anyway, it is more likely that losses to the phytoplankton population (resulting from processes such as zooplankton grazing, cells sinking out of the upper 20 m, dispersion, etc.), would have been more influential in biasing the $\Delta C:\Delta P$ ratio in the present study.

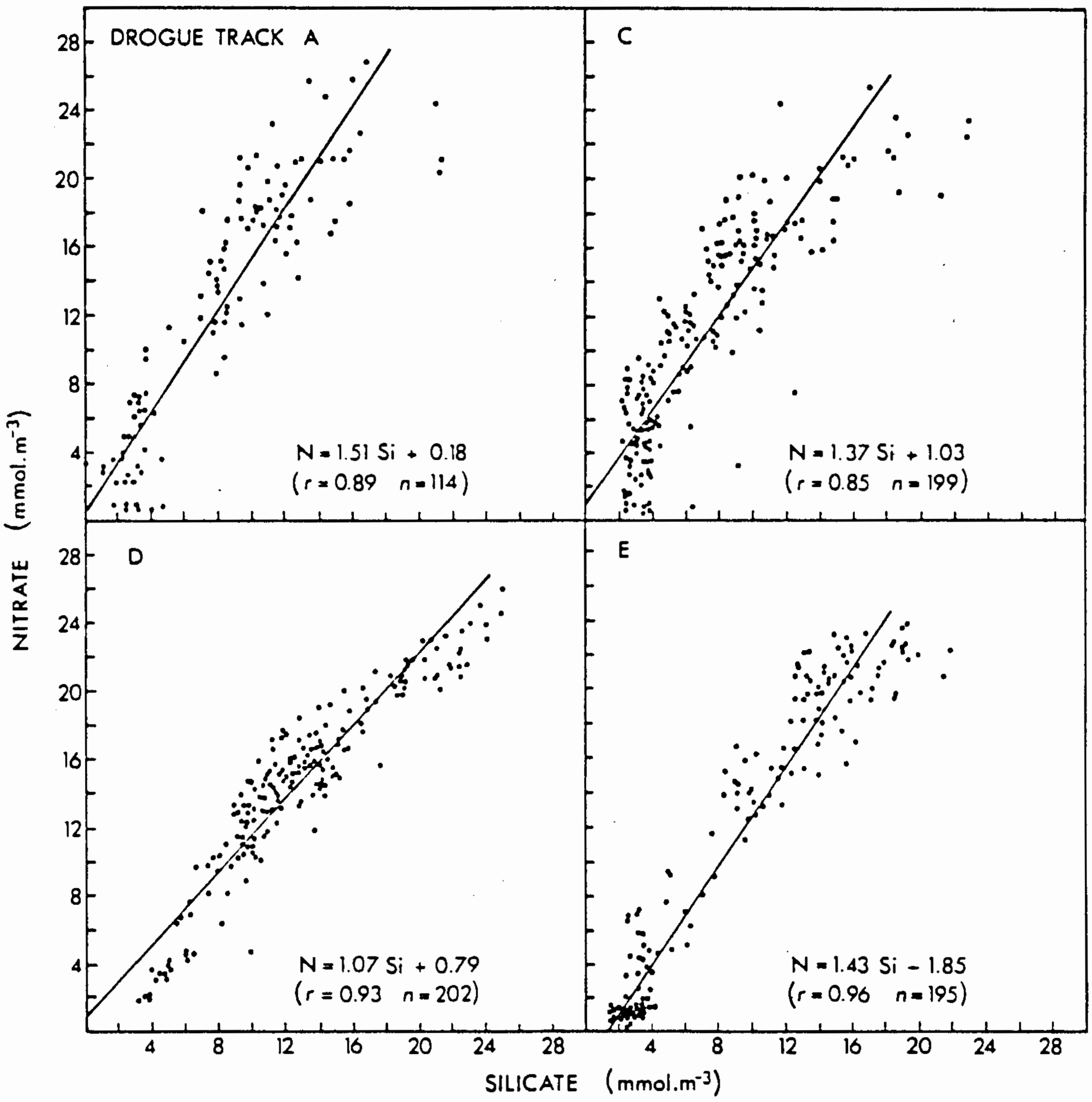

Fig.7.7: Relationships between nitrate and silicate concentrations along Drogue tracks A-E. The geometric regression equation for the combined data sets (A-E) is N = 1.27 Si - 0.2, r = 0.90, n = 710.

7.4 Nutrient limitation

Potential nutrient limitation of primary production may be assessed in various ways; quasi-directly by examining temporal changes in nutrients along the drogue tracks (e.g. Fig.6.4), or indirectly by plotting one nutrient against another (Figs 7.3, 7.4 and 7.7) and estimating from their relative changes which is likely to be depleted first. The slopes and axis intercepts of the regression lines in Figs 7.3 and 7.4 strongly suggest that both nitrate and silicate are not only taken up more rapidly than phosphate, but are also exhausted first, and thus are more likely to limit phytoplankton growth than phosphate is.

The relative depletion of nitrate and silicate, however, is not so clear. The ratios of utilization of nitrate relative to silicate, reflected in the slopes of the regression lines (Fig.7.7) and <u>in situ</u> changes (see Table 7.2) are summarized in Table 7.4. Except for Cruise C (<u>in situ</u> changes), ΔN:ΔSi ratio was greater than 1. This suggests that nitrate was generally used at a faster rate than silicate. Although close to zero, the Y-intercepts of the N/Si regression lines (Fig.7.7 and Table 7.4) for Cruises A, C and D were positive, whereas for Cruise E the intercept was negative. This suggests that nitrate was limiting only during Cruise E, while for the other cruises silicate was. Closer inspection of the scatter diagrams themselves (Fig.7.7), however, showed that at low concentrations the linear regression lines (for Cruises C and D in particular) did not reflect data distribution; silicate concentrations did not drop as low as nitrate concentrations. This was also reflected in Fig.6.4 where mean nitrate concentrations in the euphotic zone dropped to lower

TABLE 7.4: Atomic ratios of utilization of nitrate relative to silicate (ΔN:ΔSi) as estimated from in situ changes along the drogue tracks (Table 7.3) and from regression analyses (Fig.7.7). The Y-intercept for each regression is also listed with the corresponding potentially limiting nutrient

CRUISE	ΔN:S		Y-INTERCEPT	POTENTIALLY LIMITING NUTRIENT
	From in situ changes	From regression analyses		
A	1.50	1.51	+0.18	Silicate*
C	0.82	1.38	+1.03	Silicate*
D	1.15	1.09	+0.79	Silicate*
E	1.56	1.43	-1.89	Nitrate

* Non-linearity at low concentrations suggests that silicate seldom runs out first

TABLE 7.5: Nutrient concentrations and daily rates of utilization in the upper 20 metres, and the time in which nutrient depletion would occur when calculated using the mean rate of utilization on Days 1 and 2

CRUISE	DAY NUMBER	STATION RANGE	NUTRIENT CONCENTRATION AT BEGINNING OF STATION RANGE ($mmol.m^{-3}$)			RATE OF NUTRIENT UTILIZATION ($mmol.m^{-3}.day^{-1}$)			TIME CALCULATED FOR NUTRIENT DEPLETION (days)		
			nitrate	silicate	phosphate	nitrate	silicate	phosphate	nitrate	silicate	phosphate
A	1	13-17	18.4	11.4	2.12	4.9	3.0	0.52	3.75	3.80	4.08
	2	17-21	13.5	8.4	1.61	5.2	3.4	0.20	2.60	2.47	8.00
	3	21-25	8.3	5.0	1.37	3.8	-0.8	0.10	2.18	-	14.00
	4	25	4.5	5.8	1.31	-	-	-	-	-	-
B	2	2-5	9.7	-	1.47	6.7	-	0.45	1.45	-	3.20
	3	5	3.0	-	1.02	-	-	-	-	-	-
C	1	1-4	17.6	14.8	1.85	6.0	8.7	0.18	2.94	1.70	10.20
	2	4-7	11.6	6.1	1.67	4.7	3.2	0.32	2.47	1.92	5.20
	3	7	6.9	2.9	1.35	-	-	-	-	-	-
D	1-2	1-7	19.8	18.4	1.95	3.1	3.5	0.40	6.41	5.23	4.87
	3	7	13.6	11.4	1.16	-	-	-	-	-	-
E	1	1-4	15.5	12.1	1.56	2.4	4.0	0.53	6.58	3.06	2.94
	2	4-7	13.2	8.1	1.03	9.0	4.9	0.21	1.47	1.66	4.90
	3	7-10	4.2	3.2	0.82	2.7	1.2	0.57	1.59	2.74	1.44
	4	10	1.6	2.0	0.25	-	-	-	-	-	-

levels than silicate (except for Cruise C).

Using a more direct approach of assessing possible nutrient limitation, in situ changes in nutrient concentrations were examined. In Table 7.5 mean concentrations and rates of utilization of nitrate, silicate and phosphate in the upper 20 m layer along each drogue track, are presented on a daily basis until the peak in chlorophyll *a*. While the rate of phosphate utilization was much lower than that of nitrate or silicate, nitrate utilization was usually faster (6 times out of 9) than that of silicate. These data were used to calculate the number of days required for each nutrient to be exhausted (assuming new nutrients are not entrained into the water body and that the rates of nutrient utilization remained constant), thereby effectively normalizing the initial concentrations of nutrients. It is interesting that, using this method to assess potential nutrient limitation (Table 7.5), silicate would have been exhausted before nitrate on 6 out of 8 occasions (on one occasion exhaustion times were equal). Thus, although the rate of nitrate uptake was usually faster than that of silicate, the calculated exhaustion of silicate was sooner because of relatively low initial silicate concentrations (Table 7.5).

Of interest on Day 3 of Cruise E, was the fact that the period calculated for the exhaustion of phosphate was marginally shorter than that for nitrate. However, because phosphate is known to be rapidly regenerated (Grill and Richards 1974), it is unlikely that phosphate limitation would occur in nature.

Because monitoring of the upwelled water started at different stages of bloom development on each cruise, nutrient depletion times were also calculated for upwelling source water, for which nutrient concentrations in the bottom mixed layer (see Table 6.1) are assumed to be representative. Mean nutrient depletion times after upwelling were calculated to be 3.8 days (range = 2.3-5.7 days) for silicate, 4.1 days (range = 2-5.2 days) for nitrate and 5.5 days (range = 1.3-8.0 days) for phosphates. It follows that 3.8 days represents the average period available for phytoplankton bloom development, assuming there is no lag in the onset of growth (Barber et al 1971). This is consistent with the actual growth (3 days) and decline (3-4 days) periods of phytoplankton blooms, estimated from changes in chlorophyll a during the five drogue studies (see Table 6.4). The mean nutrient depletion times also suggest that silicate is potentially likely to limit diatom production more often than nitrate.

Comparison of the predicted times of nutrient depletion (Table 7.5) with actual measurements in the euphotic zone (Figs 6.1 and 6.4), shows, firstly, that nutrients were not completely depleted in the short periods predicted, and, secondly, that nitrate concentrations, contrary to the above predictions, were reduced to lower concentrations than were silicates. During Cruise B, however, Barlow (1984b) demonstrated increased uptake of carbon into protein when the nutrient supply was low. Such preferential protein synthesis may cause a change in the relative uptake rates of nitrate and silicate under nutrient stress, and thus could be responsible for nitrates usually reaching undetectable levels before silicates. Moreover, it should be borne in mind that the approach taken in this study is based on the assumption that nutrient-uptake kinetics (reviewed by Parsons et al 1984) for different nutrients and phytoplankton species are similar, and that nutrient-limitation sets in at threshold concentrations of zero. Variation in such factors, together with the possibility of nutrient requirements being met by internal reserves within phytoplankton cells, may complicate the issue (see Brown and Field 1986). However, the calculations made in this study are considered to be useful as an indication of where to direct more detailed studies on the limiting effects of low nutrients.

Nutrient regeneration and input of new nutrients by mixing may also occur and prolong growth. Phosphate regeneration is known to be rapid, e.g. Harrison (1983) reports mean turnover times of 2.8 days in coastal waters. Thus it is not surprising that large fluctuations in phosphate concentration were not apparent along the drogue tracks (Fig.6.4) particularly after the peak in chlorophyll a when phosphate concentrations appeared to be in a state of dynamic equilibrium. Nitrates were rapidly depleted, but, as regenerated nitrogen (ammonia and urea) was not measured, nitrogen depletion per se was probably overestimated (see Probyn 1985, Brown and Field 1986). Silicon regeneration, however, is slower than that of nitrogen (Dugdale 1972) and may not occur in the short time scale of a drogue study. Thus the possibility of silicon limitation in the southern Benguela, particularly in the present studies which appeared to be dominated by diatoms (Olivieri et al 1985), should not be disregarded purely on the grounds that nitrate concentrations were reduced more than those of silicate.

CHAPTER 8: PRIMARY PRODUCTION IN RELATION TO THE ENVIRONMENT

8.1 Introduction

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8.1 Introduction

Quantitative ecosystem studies require estimates of the standing stocks (biomass) and yield (production) of the primary producers which form the supporting base of most food webs. However, problems associated with such estimates in the marine pelagic environment are numerous, and range from practical considerations involving technique details to more theoretical aspects of the methodology such as the interpretation of measurements and their relevance to plant production and ecosystem models (Hobson et al 1976, Holm-Hansen 1974, Kremer and Nixon 1978, Harris 1978, 1980 and 1984, Morris 1980, Peterson 1980, Tilzer 1984 and others).

Current methods of estimating phytoplankton biomass (Strickland 1960, Strathman 1967, Gillbricht 1969, Vollenweider 1969, Hallegraeff 1977, Sournia 1978, Harris 1984 and others) include the examination of particulate matter (directly with the aid of microscopes, or indirectly using particle counters and sizers) to obtain cell or particle numbers and volumes. Chemical techniques are also used to estimate biomass in terms of the carbon, nitrogen, phosphorus, sulphur and chlorophyll a (most commonly used) content of the particulate matter.

Phytoplankton productivity and growth are notoriously difficult to measure and interpret realistically (Peterson 1980). Thus at the outset it is necessary to establish what is meant by these concepts. There appears to be no rigid distinction in the literature between the terms "production" and "productivity".

However, to avoid confusion, their usage here will be according to the definitions of Strickland (1960). Primary productivity is the rate of autosynthesis of organic material by phytoplankton; gross primary productivity being the increase in plant material before any corrections for respiration or excretion are made, whereas net primary productivity includes these corrections but is not corrected for losses due to death, predation, etc. Unless specified, "productivity" will refer to net primary productivity. Strickland (1960) reserves the term "net production rate" to describe the rate of production of phytoplankton under the influence of all environmental factors and so includes losses by death, predation, etc. Net production thus appears to be equivalent to what Harris (1984) terms "population growth", which may be measured from *in situ* changes in phytoplankton biomass. Growth rates thus obtained may show differences depending on which measure of biomass is used. Productivity, on the other hand, is usually measured as photosynthetic carbon fixation or oxygen released in bottle experiments (i.e. it is a rate measured by the flux of elements), but may also be measured by the rate of increase in phytoplankton biomass in enclosed water samples (as long as predation has been eliminated).

In the present series of drogue studies the growth of phytoplankton populations (i.e. net production) in upwelled water was monitored in terms of chlorophyll *a* (see Chapter 6) and particulate volume (Olivieri *et al* 1985), while phytoplankton ^{14}C-uptake productivity measurements were conducted usually twice daily. The focus of this chapter is on the assessment of these productivity measurements. Although most commonly used for assessing productivity, ^{14}C-uptake has been severely criticised because of uncertainty regarding its interpretation (Strickland 1960, Cassie 1962, Lean and Burnison 1979, Peterson 1980). Rates of organic productivity estimated from such measurements are sometimes regarded as an index of primary productivity and not as an absolute value. Consequently in addition to the ^{14}C-uptake "light bottle, dark bottle" experiments, two completely different methods were employed to assess productivity.

Firstly, bottle experiments measuring the increase in particle volume in water samples from the 100% and 50% light depths (Cruises B-D) and from the 100%, 50% and 1% light depths (Cruise E) were conducted daily (Olivieri and Hutchings 1985a). Where 1% measurements were not made, the increase in particle volume at the 1% light depth was assumed to be zero for calculating depth-integrated estimates of productivity. Particle volume productivity estimates, as presented by Olivieri and Hutchings (1985a) in their Tables 1-4 for Cruises B-E, are reinterpreted in this report.

Secondly, primary productivity was calculated (using Redfield ratios) from changes in the nutrient and oxygen content of the water masses which the drogue followed (see Section 8.3). This approach is based on the assumption that decreases in nutrients and increases in oxygen in the water column at the drogue are solely a result of autotrophic activity, and that changes in N, Si, P and O occurred in roughly the same proportions as they are reported to occur in phytoplankton (Redfield _et al_ 1963).

In this chapter the various productivity estimates are compared with each other and with _in situ_ net production (phytoplankton growth) as reflected by the observed biomass changes along each

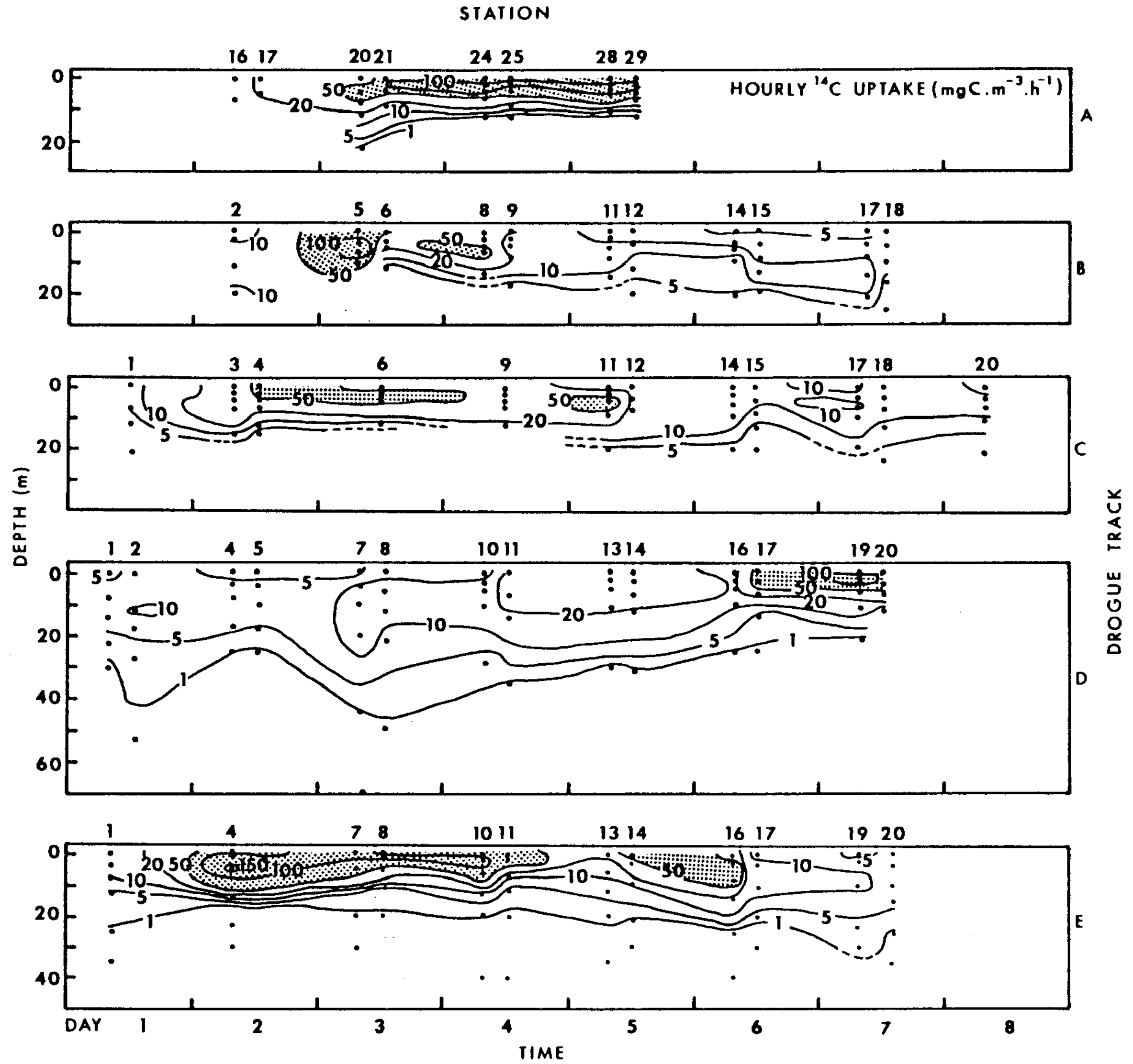


Fig.8.1: Vertical sections of hourly ^{14}C-uptake productivity measurements along Drogue tracks A-E (shading indicates rates greater than 50 mg C.m^{-3}.h^{-1}).

drogue track. An attempt is made to account for the differences and to examine the factors influencing production.

8.2 ^{14}C-uptake measurements

Detail on the procedures used in ^{14}C-uptake experiments may be found in Chapter 4. However, ^{14}C-uptake was normally measured at and above the 1% light-depth, which is assumed to be the base of the euphotic zone. Extra measurements below this depth along Drogue track E indicate that very little production did, in fact, occur below the 1% light level. Consequently productivity measurements integrated between the sea-surface and the 1% light level are considered to be representative of the total productivity occurring in the water column. On occasion, however, relatively high uptake rates were recorded at the 1% light depths, possibly because of the underestimation of the 1% light depth itself. In these cases column or depth-integrated productivity (i.e. per m^2) was calculated by extrapolating the productivity-depth profile to zero on the productivity axis, and integrating productivity to the corresponding depth.

8.2.1 Hourly productivity rates

Vertical sections of hourly estimates of primary productivity, obtained from short-term (3-4.5 h) in situ measurements of ^{14}C-uptake along each drogue track, are presented in Fig.8.1, with the maximum rates for each cruise summarised in Table 8.1. ^{14}C-uptake was not measured on Day 1 of Cruise A, however, productivity rates on Day 2 (station 16) were low (10-14 mg

TABLE 8.1: Maximum hourly rates of ^{14}C-uptake measured during each cruise

CRUISE	DAY	STATION	DISCRETE MEASUREMENTS Depth (m)	Light-depth (%)	Productivity ($mgC.m^{-3}.h^{-1}$)	INTEGRATED MEASUREMENTS Productivity ($mgC.m^{-2}.h^{-1}$)
A	5	29	2	50%	155.2	-
		28	-	-	-	753
B	2	5	3	10%	137.4*[1]	1 144
C	4	11	4	25%	82.3	577
D	7	19	3	25%	121.4	717
E	2	4	5	10%	152.2*[2]	1 465

*[1] No measurements for 50% or 25% light-depths

*[2] No measurements for 25% light-depth

$C.m^{-3}.h^{-1}$ in the upper euphotic zone), then increased rapidly to subsurface maxima of 144 and 155 mg $C.m^{-3}.h^{-1}$ on Days 4 and 5 respectively. Productivity estimates during Cruise B increased rapidly along the drogue track from about 19 mg $C.m^{-3}.h^{-1}$ on Day 2 (station 2) to peak at 137 mg $C.m^{-3}.h^{-1}$ on Day 3 (station 5), then decreased and levelled out at about 10 mg $C.m^{-3}.h^{-1}$ over Days 5-7. During Cruise C, the drogue moved from a patch of chlorophyll-poor water with a low productivity rate (less than 10 mg $C.m^{-3}.h^{-1}$) on Day 1, into a patch richer in chlorophyll *a* on Day 2. Over Days 2-5 the rate of maximum productivity ranged between 40 and 82 mg $C.m^{-3}.h^{-1}$, then decreased to about 11-21 mg $C.m^{-3}.h^{-1}$ on Days 6-8. During Cruise D the euphotic zone was deep, and productivity rates were low (7-14 mg $C.m^{-3}.h^{-1}$) on Days 1-3, but increased slowly on Days 4-6 (16-62 mg $C.m^{-3}.h^{-1}$) as the euphotic zone shallowed, then rapidly to a maximum of 121 mg $C.m^{-3}.h^{-1}$ at station 19 on Day 7. During Cruise E the rate of productivity increased rapidly from about 13 mg $C.m^{-3}.h^{-1}$ on Day 1 to 152 mg $C.m^{-3}.h^{-1}$ at station 4 on Day 2, then decreased slowly to about 10 mg C.m-3.h-1 on Day 7.

The changes in productivity rates along the five drogue tracks roughly reflected chlorophyll *a* distribution near the sea surface (see Figs 6.2 and 6.4), thus suggesting that the rate of productivity was a function of biomass. Maximum discrete productivity rates (i.e. per m^3) ranged between 82.3 (Cruise C) and 155.2 (Cruise A) mg $C.m^{-3}.h^{-1}$, and occurred relatively near the sea surface (2-5 m) at light penetration depths of 10-50%.

Depth-integrated (column) productivity (Fig.8.2) was less variable than discrete measurements as increases in productivity near the

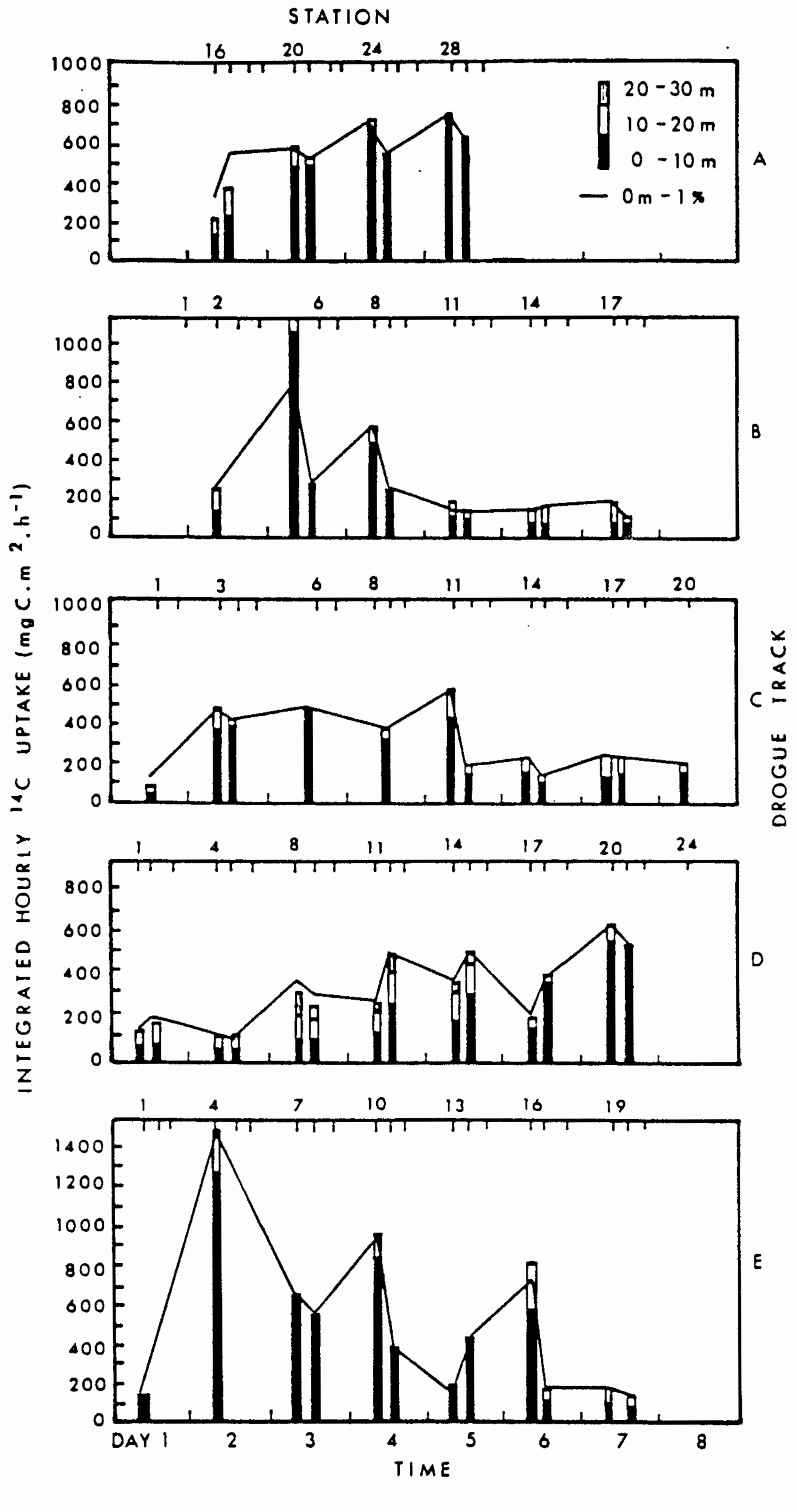


Fig.8.2: Depth-integrated measurements of ^{14}C-uptake productivity for morning and noon incubations along Drogue tracks A-E (shading indicates rates greater than 50 mg C.m^{-2}.h^{-1}).

sea surface were partly tempered by reduced euphotic zone depths due to self-shading. However, trends were similar to those for discrete productivity (Table 8.1) with maximum rates of column productivity generally occurring at the same stations as the discrete maxima. Column productivity ranged between 577 (Cruise D) and 1465 (Cruise E) mg $C.m^{-2}.h^{-1}$. The lowest rates (27-54 mg $C.m^{-2}.h^{-1}$) were recorded in very recently upwelled water before the main drogue was released during Cruise A.

Fig.8.2 also shows that most production occurred above 20 m; in fact, in highly productive waters the euphotic layer was often limited to the upper 10 m. Differences in hourly productivity rates measured during morning and noon incubations (Fig.8.2), indicate diel variation in production, morning rates usually being faster than those in the afternoon (except for Cruise D when afternoon rates were faster on 4 out of 7 occasions). The different patterns of productivity occurring during the five cruises may be related to the stability of the water column and the availablility of light and nutrients; this will be discussed in Section 8.5.

8.2.2 Daily productivity rates

The estimation of daily productivity from ^{14}C-uptake experiments is difficult for various reasons. For example, the limitations of enclosing water samples in bottles (Venrick et al 1977) are compounded for long-term (24-h) incubations (Vollenweider 1969) while the accuracy of converting hourly productivity rates (obtained from short-term experiments) into daily rates is reduced mainly by unpredictable diel variations in phytoplankton productivity (Brown and Field 1985 and Fig.8.2). Moreover, different methods of calculation give different estimates of daily productivity (Brown 1983).

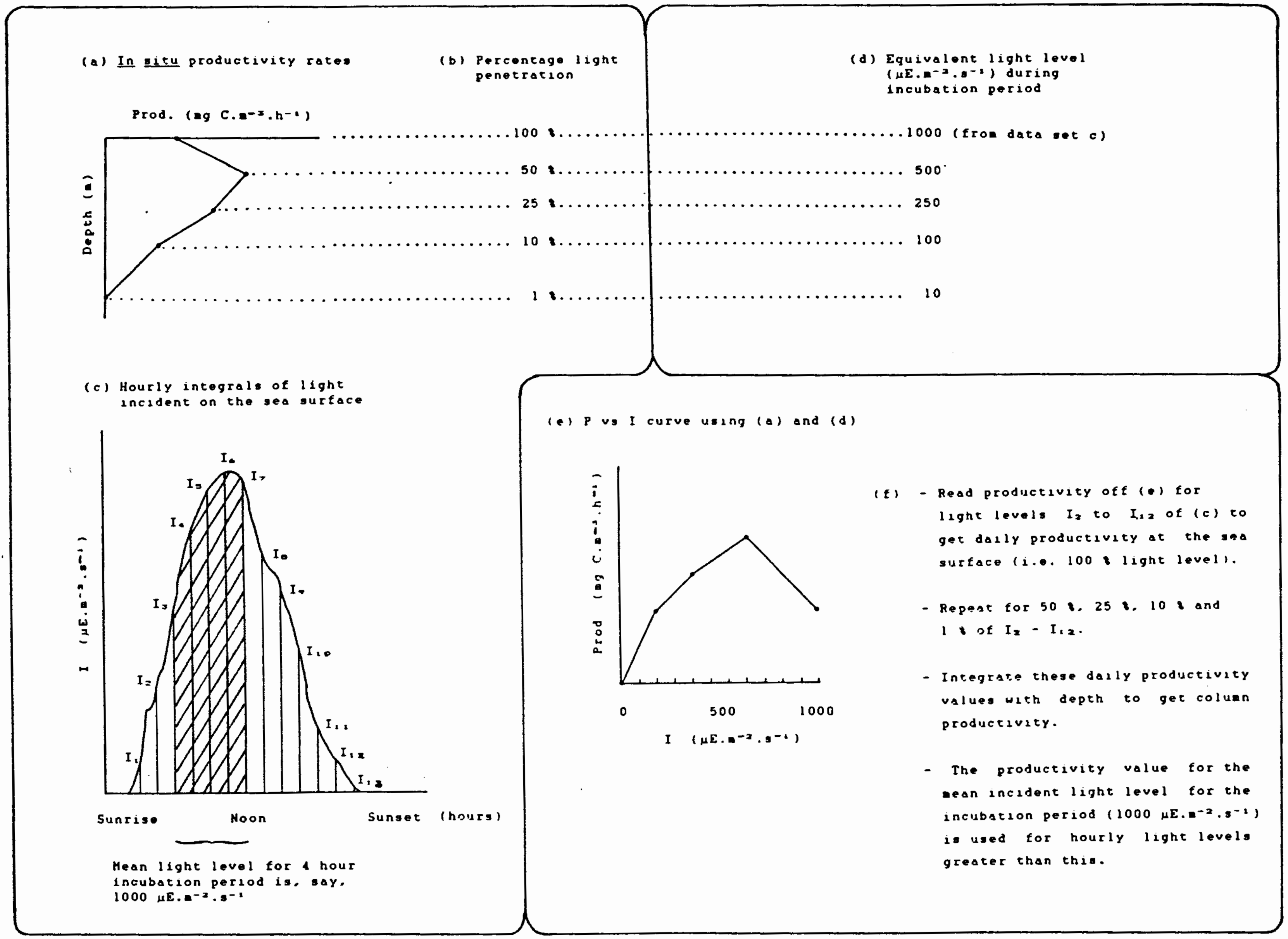
Ideally, daily productivity should be calculated by summing a series of short-term experiments spanning the whole 24-h period. The labour- and time-consuming practicalities of such an approach precluded its use in the present study. As a compromise, two short-term incubations (totalling 8-9 hours of the daylight period, 6-7 hours for Cruise A) were conducted over the middle of the day as recommended by Brown and Field (1985).

Daily productivity was calculated for each experiment using 3 methods, viz.

(i) the "time factor" and
(ii) the "light factor" methods (Vollenweider 1969) and
(iii) the in situ production versus light (P vs I) model of Wulff and Larsson (1982).

In methods (i) and (ii) the production measurement was multiplied by a "time factor" (duration of daylight divided by duration of experiment) or by a "light factor" (total irradiance per day divided by irradiance during the exposure time) respectively. Daylight duration was taken to be the number of hours for which light was recorded, minus 2.

Method (iii) was based on Fee's (1973) P vs I model for calculating daily productivity, except that water samples from the 100%, 50%, 25%, 10% and 1% light depths were incubated in situ. The model



- Read productivity off (e) for light levels I_2 to I_{12} of (c) to get daily productivity at the sea surface (i.e. 100 % light level).
- Repeat for 50 %, 25 %, 10 % and 1 % of I_2 - I_{12}.
- Integrate these daily productivity values with depth to get column productivity.
- The productivity value for the mean incident light level for the incubation period (1000 µE.m^{-2}.s^{-1}) is used for hourly light levels greater than this.

Fig.8.3: The P vs I model for calculating daily productivity from data sets (a), (b) and (c); (d) and (e) are intermediatory steps for calculating the final value in (f) (method from Wulff and Larsson 1982).

(illustrated in Fig.8.3) uses three sets of data:

(a) *in situ* productivity rates in the euphotic zone (Fig.8.1)

(b) % light penetration at the depths where production was measured, and

(c) hourly integrals of light incident on the sea surface (see Fig.5.13).

Ambient light at each incubation depth (d) was calculated for each hour of the day using data sets (b) and (c). The corresponding productivity estimates were read off a P vs I curve (e) constructed from data sets (a) and (b), and summed to give a measure of daily productivity at each depth. In turn, these data were depth integrated to obtain total daily productivity in the water column (f).

Daily productivity estimates for methods (i), (ii) and (iii) were corrected for loss of organic carbon resulting from phytoplankton respiration during the night. Because ^{14}C-uptake is thought to represent something between net and gross productivity, no correction was made for day-time respiration. Night-time respiration was calculated by multiplying hourly respiration (assumed to be 10% of hourly productivity) by the number of night hours (i.e. the number of hour intervals for which no light was recorded, plus 2).

Depth-integrated daily productivity (calculated for each station at which ^{14}C-uptake measurements were made) are summarized in Table 8.2. Daily productivity rates were lowest (0.20-0.88 g $C.m^{-2}.d^{-1}$) in the very recently upwelled water prior to the release

TABLE 8.2: Daily productivity estimates (g $C.m^{-2}.d^{-1}$) from 4-hour ^{14}C-uptake experiments for the morning and noon stations. Daily rates were calculated using the "time-factor" (tf), "light factor" (lf) and "P vs I model" (m) methods (see text)

Day	Time	Cruise A			Cruise B			Cruise C			Cruise D			Cruise E		
		tf	lf	m	tf	lf	m	tf	lf	m	tf	lf	m	tf	lf	m
1	Morn.	-	-	-	-	-	-	-	-	-	1.68	1.05	1.26	1.52	1.22	1.27
	Noon	-	-	-	-	-	-	1.31	2.24	1.56	2.46	2.73	2.24	-	-	-
2	Morn.	3.89	2.43	0.84	2.71	1.96	2.09	5.12	3.53	4.28	1.45	0.94	1.03	14.04	9.40	7.50
	Noon	6.62	4.21	1.03	-	-	-	4.55	5.88	4.70	1.32	1.44	1.15	-	-	-
3	Morn.	6.88	4.17	4.74	12.22	8.44	10.32	-	-	-	4.46	2.87	3.30	6.26	4.60	4.06
	Noon	6.19	7.46	6.25	3.01	6.25	3.85	5.20	6.16	4.92	3.65	4.48	3.35	5.30	6.85	3.82
4	Morn.	8.56	5.29	6.10	6.21	4.36	5.36	-	-	-	3.30	2.13	2.38	10.25	6.48	5.82
	Noon	6.38	6.90	5.96	2.73	4.82	2.62	4.12	4.80	3.87	6.01	7.08	5.55	4.22	6.52	3.42
5	Morn.	8.84	5.47	6.68	2.01	1.54	1.71	6.16	4.09	4.77	4.47	2.76	3.09	2.21	1.27	1.33
	Noon	7.50	6.77	6.30	1.53	2.29	1.57	1.97	2.21	1.47	6.13	7.11	5.66	5.10	9.04	4.15
6	Morn.	-	-	-	1.68	1.19	1.51	2.43	1.70	1.91	2.08	1.71	1.81	9.93	6.47	6.35
	Noon	-	-	-	1.77	2.85	1.81	1.37	1.55	1.30	3.81	7.03	5.56	2.30	2.30	1.98
7	Morn.	-	-	-	2.08	1.45	2.22	2.56	1.57	2.03	6.86	4.73	5.43	2.41	1.38	1.43
	Noon	-	-	-	1.36	2.29	1.53	2.50	3.39	2.51	5.98	10.63	7.09	1.79	2.65	1.75
8	Morn	-	-	-	-	-	-	2.16	1.31	1.46	-	-	-	-	-	-
	Noon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

of the main drogue in Cruise A (not listed), but much higher in the maturer upwelled water along Drogue tracks A-E where estimates ranged from 0.84 to 14.02 g $C.m^{-2}.d^{-1}$.

The diel variation evident in hourly productivity rates (Fig.8.2) is reflected in different daily estimates for morning and afternoon incubations (Table 8.2). The "time factor" method usually yielded higher estimates of daily productivity for morning incubations (i.e. for 18 out of 25 pairs of measurements), whereas daily estimates using the "light factor" method were usually higher for afternoon measurements (21 out of 25 times). Results from the P vs I model were higher for afternoon incubations on 14 occasions. The "light factor" method and P vs I model compensate for variable light intensity in different ways. The "light factor" method assumes productivity to be directly proportional to incident light, and therefore may over-compensate for light variations. The P vs I model takes photo-inhibition into account, and thus may give a more realistic estimate of daily productivity. To minimize the effect of diel variation on ^{14}C-uptake derived estimates of daily productivity along the drogue tracks, the mean of each set of morning and afternoon daily estimates is used in a comparison with independently derived estimates (see Sections 8.3 and 8.4).

8.3 Productivity estimates from *in situ* changes in nutrients and oxygen (Redfield productivity)

Along each drogue track large changes in the chemical properties associated with primary productivity occurred in the euphotic zone, i.e. oxygen concentrations increased and nutrient concentrations decreased (see Fig.6.4). Following Ryther et al (1971) and Herbland et al (1973), cumulative changes in nitrates, silicates, phosphates and oxygen were assumed to be roughly proportional to the organic matter produced during each study period. Because the depth of the euphotic zone (as estimated from the 1% light-depth) varied (7-63 m, mean 22.4 m), chemical changes in the upper 20 m layer were used in subsequent productivity calculations, because 0-20 m usually encompassed most of the euphotic zone and surface mixing layer (Figs 5.12 and 8.2), and the centre point of the drogue was set at 10 m.

Although it was tempting to use a deeper surface layer (e.g. 0-50 m) so as to be certain of incorporating all the effects of autotrophic activity (especially when deep mixing occurred as in Cruises B, C and D), inspection of the data showed that variability in the chemistry of the deep water sometimes precluded its incorporation into the the productivity calculations. Nelson (SFRI, pers. comm.) considers that during upwelling a relatively thin layer, a few metres to perhaps tens of metres thick, of surface water shears over the deeper layers with subsequent entrainment of variable concentrations of nutrients (see Fig.6.3 and Table 6.1).

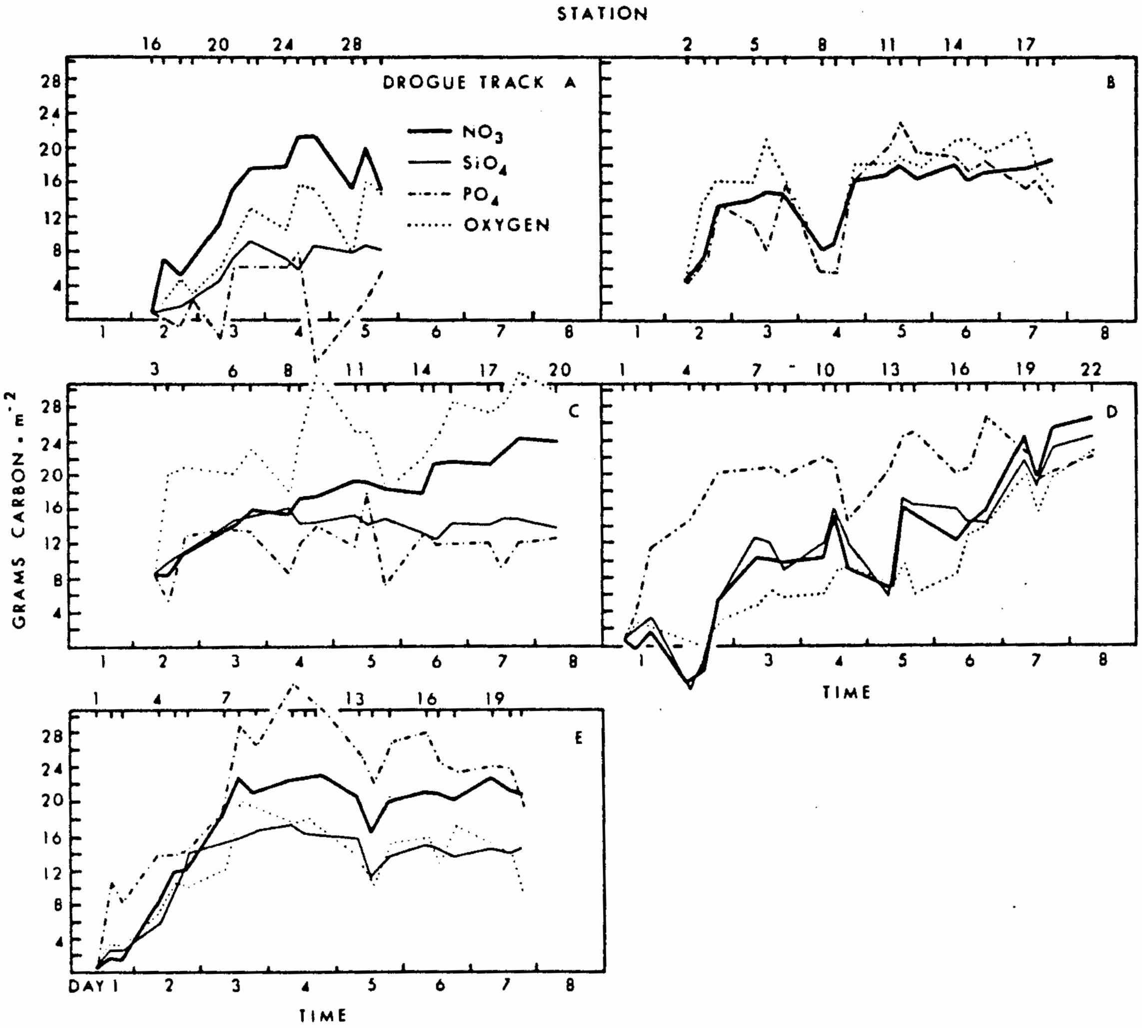


Fig.8.4: Redfield productivity (g C.m^{-2}) estimated from changes in the nutrient (nitrate, silicate and phosphate) and oxygen content of the upper 20 m layer along Drogue tracks A-E.

Differences between the initial nutrient and oxygen values (i.e. at the first station) and those observed at each successive station were converted into equivalent organic carbon (g $C.m^{-2}$) as follows:

mmol NO_3-N $.m^{-2}$ x (106/16) x 12 / 1000 for nitrate changes,
mmol SiO_4-Si $.m^{-2}$ x (106/15) x 12 / 1000 for silicate changes,
mmol PO_4-P $.m^{-2}$ x (106/1) x 12 / 1000 for phosphate changes and
dm^3 O_2 $.m^{-2}$ x 1.43 / 32 x 2 x (106/276) x 12 for oxygen changes.

Such conversions are based on the assumption that elements are taken up (or produced) in the same ratios (by atoms) as occur in phytoplankton (Flemming 1940, Richards 1958, Redfield <u>et al</u> 1963) i.e. O:C:N:Si:P = -276:106:16:15:1. Mmoles of N, Si, P and O were multiplied by the appropriate Redfield ratio (to get mmol. C), then by 12, the atomic weight of carbon (to get mg C), then divided by 1000 (to get g C). Oxygen measurements (dm^3) were first multiplied by 1.43 (to get mg); then divided by 32, the molecular weight of oxygen, and multiplied by 2, the number of atoms per molecule (to get mmol.oxygen), before being converted to carbon units. In each case, the carbon thus estimated (henceforth referred to as Redfield productivity) was added to that initially observed at the first station to produce the cumulative total (the initial carbon value was calculated from chlorophyll <u>a</u> measurements using a carbon:chlorophyll <u>a</u> ratio of 50:1; the choice of the ratio is argued in Section 8.4.1). Each series of cumulative productivity estimates was initiated at the first station at which ^{14}C-uptake measurements were made, so as to facilitate comparison of productivity estimates based on the two methods. During Cruise C, however, a large increase in chlorophyll

TABLE 8.3 Cumulative Redfield productivity estimates (g $C.m^{-2}$) based on nutrient and oxygen changes in the upper 20 m layer along each drogue track.

CRUISE	A	B	C	D	E
Calculation period					
Stations	16-29	2-18	3-19	1-22	1-19
Time (days)	3.20	5.21	5.62	7.00	6.00
Productivity estimates (g $C.m^{-2}$) from changes in:					
Nitrate	19.19	14.42	16.00	26.01	22.50
Silicate	7.92	-	6.41	24.02	14.17
Phosphate	1.90	13.62	3.61	21.59	23.88
Oxygen	15.46	11.71	23.44	22.05	14.63

a from station 1 to station 2 indicated that the drogue had moved into a different patch of water (see Chapter 6.5). In that case, productivity calculations were started at station 3 (Day 2).

Estimates of Redfield productivity along the five drogue tracks are presented in Fig.8.4. The curves are somewhat irregular, with occasional negative slopes suggesting an increase in the nutrient (or decrease in the oxygen) content of the upper 20 metres of the water column. Nutrient-rich water may have been mixed into the original patch from either below the nutricline or from an adjacent more recently upwelled patch of water (e.g. Cruise A st.28). Shoaling of the nutricline or oxycline (possibly caused by internal waves or by small errors in the depth of sampling) would have had a similar artefactual effect on productivity estimates calculated in this way (e.g. Cruise B st.8-9, Cruise D st.20, Cruise E st.20, Cruise C st.11-12; the deep trough at st.13 was caused by a single low oxygen value, 2.7 $dm^3.m^{-3}$, at 3 m).

Nonetheless, maximum estimates of cumulative productivity along the drogue tracks ranged between 14.42 g $C.m^{-2}$ (Cruise B) and 26.01 g $C.m^{-2}$ (Cruise D), with nitrate changes usually yielding the highest values (Table 8.3). Although production estimates from phosphate changes (Fig.8.4) were sometimes high (Drogue tracks D and E), they varied widely (particularly those along Drogue tracks A, C and D) probably because of erratic phosphate distribution (see Fig.6.1), which may result from phosphate being regenerated faster than nitrate or silicate. This reduces the reliability of Redfield productivity estimates based on phosphate changes. Oxygen concentrations in newly upwelled

TABLE 8.4: Estimates of daily productivity (g C.m^{-2}.d^{-1}) for the whole study period (whole) and for the period of maximum nutrient uptake (max upt) during each cruise.

CRUISE	A		B		C		D			E	
	whole	max upt	whole	max upt	whole	max upt	whole		max upt	whole	max upt
Station range	16-29	16-22	2-18	2-5	3-19	3-6	1-22	17-22	17-19	1-19	1-8
(Days)	(2-5)	(2-3)	(2-7)	(2)	(2-7)	(2)	(1-7)	(7)	(6)	(1-6)	(1-3)
Productivity method											
1) Redfield[*1], using *in situ* changes in:											
Nitrate	6.00	11.47	2.77	10.62	2.84	4.95	3.72	6.79	12.07	3.74	9.24
Silicate	2.47	5.77	-	-	1.14	5.34	3.43	5.59	8.71	2.36	6.33
Phosphate	0.59	3.71	2.61	11.62	0.64	4.72	3.08	0.82	2.48	3.98	11.60
Oxygen	4.83	8.36	2.25	6.92	4.17	9.86	3.15	5.27	8.52	2.44	7.98
2) ^{14}C- uptake[*2]											
mean	4.74	4.10	3.21	2.25	3.64	4.68	3.30	6.79	3.59	5.20	5.57
(max)$^{\text{Day no.}}$	(6.94)^{5}		(7.35)^{3}		(5.42)^{3}		(6.79)^{7}			(10.30)^{2}	
3) Particle volume increase[*3]											
mean	-	-	6.91	21.37	7.74	10.85	6.65	2.59	16.44	4.89	6.80
(max)$^{\text{Day no.}}$			(21.37)^{2}		(10.85)^{2}		(16.44)^{6}			(14.55)^{2}	

[*1] from Fig.8.4 and Table 8.3

[*2] from Table 8.2

[*3] from Olivieri and Hutchings' (1985a) Tables 1-4

waters are moderate (4-5 $dm^3.m^{-3}$), and exchange with the atmosphere was presumed to be negligible as oxygen-based productivity estimates were usually intermediate between nitrate- and silicate-based estimates. Two anomalously low oxygen measurements near the sea surface at station 3 of Cruise C, caused oxygen-based productivity for this cruise to be overestimated (see Table 8.4 and Fig.8.4).

When translated into mean daily rates, Redfield productivity estimates from nitrate changes along the drogue tracks, ranged between 2.77 and 6.00 g $C.m^{-2}.d^{-1}$ (Table 8.4). However, Fig.8.4 shows that productivity rates were higher towards the beginning of each study suggesting that, as a method of estimating productivity, the Redfield calculations are probably more successful during the early stages of bloom development, and also when the water column is stable. At a later stage of bloom development, nutrient requirements may be met by regenerated nutrients and those stored within the cell; and oxygen is lost to the atmosphere at an increasing rate because of supersaturation. Turbulent conditions can also bias results because mixing usually introduces more nutrients into the surface layer, thereby masking nutrient uptake. Daily productivity estimates calculated solely for periods of maximum nutrient uptake (Table 8.4) were, accordingly, higher than for the whole period, and ranged between 4.95-12.07 (nitrate), 5.34-8.71 (silicate), 0.64-11.62 (phosphate) and 5.27-9.86 (oxygen) g $C.m^{-2}.d^{-1}$ over the five cruises. Even though on first appearance the entire study period during Cruise D seemed suitable for such productivity calculations, close inspection of the chemical changes along the drogue track (see Chapter 6.5) shows that only between stations 17 and 22 did the drogue maintain itself in a reasonably consistent water mass. Productivity estimates for this period are presented separately in Table 8.4.

Productivity estimates based on ^{14}C-uptake and particle volume increases for roughly equivalent periods are also presented in Table 8.4. Redfield productivity estimates based on nitrate changes over the whole period were similar to ^{14}C-uptake estimates, ie between 0.7-1.3 (mean 0.95) times the average ^{14}C estimates for the different cruises; whereas particle volume productivity for Cruises B-E was 1.3-2.7 (mean 2.07) times the Redfield estimates, and 0.9-2.2 (mean 1.81) times the ^{14}C estimates. However, for the periods of maximum nitrate uptake, Redfield estimates were considerably higher (between 1.7 and 4.7 times higher) than the equivalent ^{14}C values (except for Cruise C where they were similar), but were lower than the productivity estimates obtained from increases in particle volume. The latter (estimated for Cruises B-E only) were 1.2-2.2 times higher than Redfield estimates, and 2.3-9.5 times higher than ^{14}C estimates except for Cruise C when they were slightly lower.

The details of these results show that individual productivity estimates can be considerably different (eg during the maximum nutrient uptake period of Cruise B, the particle volume productivity estimate was 9.5 times higher than the equivalent ^{14}C estimate). However, when one considers the possible errors (methodological or otherwise) that can influence such individual estimations, it becomes apparent that a more controlled comparison is required, particularly for the ^{14}C and particle volume methods of estimating productivity. However, this rough comparison does

TABLE 8.5: Linear regression statistics for the relationships between biomass indices for the drogue studies: chlorophyll a (mg.m^{-3}), particle volume (μm^{3} x 10^{6}.ml^{-1}) and CHN carbon (mg.m^{-3})(from Olivieri 1985)

RELATIONSHIP	CRUISE	EQUATION	r	n
Carbon on chll a	B	Y = 23.8x + 482	0.54	53
	C	Y = 30.9x + 683	0.33	29
	D	Y = 54.3x + 288	0.87	33
Carbon on particle volume	B	Y = 61.2x + 385	0.52	53
	C	Y = 109.7x + 500	0.56	29
	D	Y = 149.7x + 218	0.95	33
Chll a on particle volume	A	Y = 1.5x + 0.2	0.93	86
	B	Y = 1.9x + 0.6	0.80	161
	C	Y = 1.7x + 0.2	0.89	191
	D	Y = 2.4x + 0.3	0.95	205
	E	Y = 2.5x + 0.5	0.94	194

support the commonly held suspicion that the ^{14}C method may in fact underestimate in situ productivity, but not as much as the ten-fold underestimate suggested by some workers. It should be borne in mind, however, that if Redfield productivity represents gross productivity (as losses due to respiration and excretion would not be accounted for), then the difference between Redfield and ^{14}C estimates would be less than calculated here.

8.4 A comparison of calculated biomass with *in situ* biomass

8.4.1 In situ biomass estimates

Phytoplankton biomass was monitored along each drogue track by measuring chlorophyll a concentrations (see Chapter 6, Figs 6.2 and 6.4) and particle volume (Olivieri and Hutchings 1985a) at all sampling depths. However, the rate of change of particulate organic carbon is assumed to represent the most direct measurement of "net community organic production" (Ryther et al 1971). Thus particulate carbon was measured (usind a CHN analyser) at selected depths in the euphotic zone (during Cruises B-D) to provide suitable equations for converting chlorophyll a and particle volume to carbon (assuming that the particulate matter was largely phytoplankton). Linear regressions for these biomass estimates (Olivieri 1985) are summarized in Table 8.5. Although chlorophyll a and particle volume were strongly correlated for each cruise (r = 0.80-0.95), their relationships with carbon were poor (except for Cruise D). Moreover, the carbon:chlorophyll a and carbon:particle volume ratios (i.e. the slopes of the linear regressions) varied considerably, 24.8-54.3 and 61.2-149.7 respectively. Consequently, in each case a single conversion

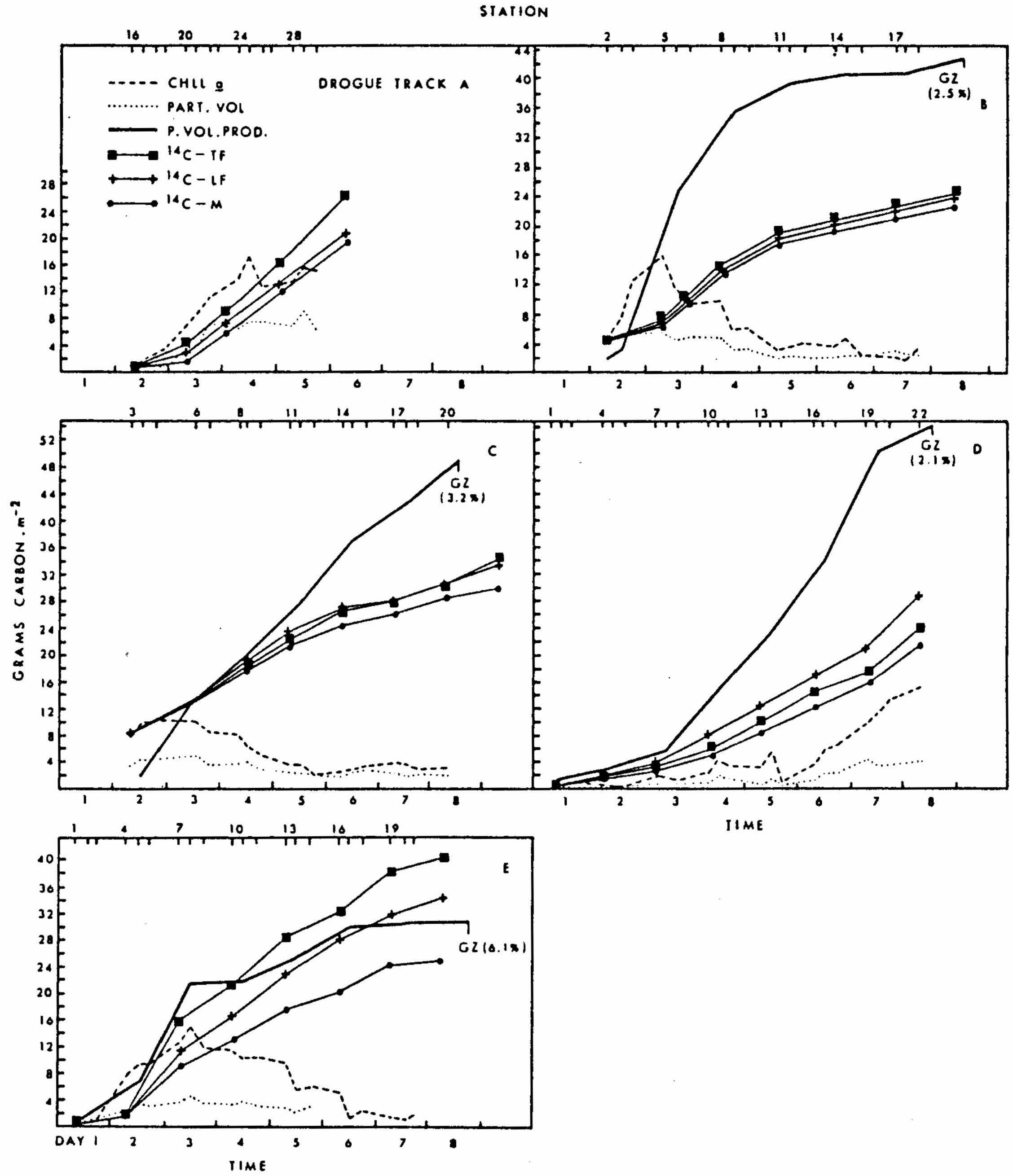


Fig.8.5: Changes in phytoplankton biomass (g $C.m^{-2}$) in the upper 20 m layer along Drogue tracks A-E, as calculated from in situ chlorophyll a (CHLL a) concentrations and particle volume (PART.VOL.) measurements; and, as predicted by cumulatively adding daily productivity estimates to the organic carbon initially present in the water column. Predicted biomass is based on particle volume productivity measurements (P.VOL.PROD.) and ^{14}C-uptake measurements using the time factor (^{14}C-TF), light factor (^{14}C-LF) and P vs I model (^{14}C-M) to estimate daily productivity.

factor was chosen from the literature so as to facilitate comparison of results amongst the cruises. The use of a single factor may be justified since the blooms covered roughly the same physiological states on each cruise.

Chlorophyll *a* was converted to carbon using a carbon:chlorophyll *a* ratio of 50:1. Although much variation is known to occur in field measurements of carbon:chlorophyll *a* (Banse 1977), 50:1 was selected partly because it was found to be most appropriate in a similar study off Peru (Ryther *et al* 1971) when the phytoplankton bloom was also dominated by diatoms, and changes in chlorophyll *a* and nutrient concentrations were similar to those which occurred here (see Chapter 6). Moreover, the only reasonable correlation ($r=0.95$) for linear regressions of organic carbon on chlorophyll *a* for the present drogue studies, was for Cruise D (Table 8.5) when the carbon:chlorophyll *a* ratio was 54.3:1 (i.e. most similar to 50:1). Also, Bailey and Chapman (1985) report a carbon:chlorophyll *a* ratio of 56:1 for the St Helena Bay area of the southern Benguela region.

Particle volume was converted to carbon using the linear regression equation of Cowles (1977) for the Peruvian upwelling area:

$$\text{carbon } (\text{mg.m}^{-3}) = 41.76 \text{ volume } (\mu\text{m}^{3}.106.\text{cm}^{-3}) + 13.38$$

as selected for this research project by Olivieri and Hutchings (1985a). They did not use the particle volume to carbon relationships obtained for Cruises B, C and D (Table 8.5) because, being so variable, they would complicate inter-cruise comparisons of carbon productivity and biomass estimated from particle volume experiments along the drogue tracks.

Biomass estimates, in terms of chlorophyll-carbon and particle volume-carbon in the upper 20 m layer along the five drogue tracks, are presented in Fig.8.5. Chlorophyll-carbon showed similar trends to the euphotic zone chlorophyll a concentrations in Fig.6.4, increasing from low biomass levels from the start of each drogue track (except for Cruise C when the drogue moved into a patch of chlorophyll-rich water on Day 2) to peak on Day 4 (Cruise A), Day 2 (Cruises B and C), Day 8 (Criuse D) and Day 3 (Cruise E). Maximum levels ranged between 10.23 (Cruise C) and 17.29 (Cruise A) g $C.m^{-2}$.

Chlorophyll-carbon estimates were considerably higher (on average between 1.6 and 2.6 times higher) than carbon estimates from particle volume measurements (Fig.8.5). At first this seems surprising because "particle volume" measurements may include heterotrophic organisms and detritus, and thus, if anything, should over-estimate phytoplankton carbon. The discrepancy may, of course, result from the use of unsuitable conversion equations, both of which are based on relationships in Peruvian upwelled waters. If a carbon:chlorophyll a ratio of 30:1 was used, as suggested by Banse (1977) for healthy growing phytoplankton populations, the two estimates of phytoplankton carbon would be more similar. On the other hand, if the slope of the regression of carbon on particulate volume in Cowles' equation (41.76) was replaced by the mean slope (106.9) for Cruises B-D (Table 8.5), the difference would also be accounted for. However, the inherent variability in the relationships between chlorophyll a or particle volume and carbon (Banse 1977, Mullin et al 1966) makes biomass conversions difficult. Furthermore, in this particular instance the carbon measurements themselves are suspect, because samples may have been contaminated during collection on the RV Africana II. The vessel, an oil-burning steam ship, periodically belched out copious volumes of sooty smoke. The high Y-intercepts on the carbon axes (218-683 mg $C.m^{-3}$) (Table 8.5) suggest background levels of carbon in the samples not accounted for by either chlorophyll a or particle volume.

Another relevant consideration in this respect, is that if the Cowles (1977) particle volume:carbon factor of 42 was replaced by the locally derived value of 107 the carbon productivity estimates obtained from particle volume bottle experiments would be relatively even higher (4-5 times higher on average) than estimates obtained from ^{14}C-uptake and Redfield calculations (see Sections 8.3 and 8.4.2).

8.4.2 Calculated biomass estimates

In Figs 8.4 and 8.5 biomass was calculated along each drogue track by cumulatively adding daily productivity estimates to the organic carbon initially present in the water column. The initial carbon was estimated from chlorophyll a measurements for ^{14}C (Fig.8.5) and Redfield (Fig.8.4) productivity estimates and from particle volume measurements for the particle volume productivity estimates (Fig.8.5).

It should be noted, however, that the ^{14}C and particle volume productivity measurements were staggered in time, and thus not directly comparable; incubation periods were different and water samples were drawn at different stations. Particle volume productivity samples were from noon stations and incubated for 24 hours with repetitive counts of 4-6 hour intervals (see Olivieri and Hutchings 1985a), whereas ^{14}C-uptake samples were drawn at morning and noon stations and incubated for about 4 hours (see Chapter 4). Subsequent productivity measurements were extrapolated to daily estimates (see Section 8.3). The mean of morning and noon daily estimates was used to calculate cumulative productivity. When plotted on a common time axis, the calculated and observed biomass estimates (Figs 8.4 and 8.5) can be compared directly.

Cumulative ^{14}C productivity estimates (Fig.8.5) calculated using the "time factor" method were generally higher than the "light factor" and "P vs I model" estimates of productivity (except for Cruise D and part of Cruise C where the "light factor" estimates were highest). However, when compared in this way (Fig.8.5), the ^{14}C estimates of productivity using different calculation methods were reasonably similar (particularly for Cruises B and C), and ranged between 16 and 39 g C.m^{-2} for the five study periods (cf. 14-26 g C.m^{-2} for Redfield estimates in Section 8.3).

In contrast, particle volume productivity estimates (39.4-52.4 g C.m^{-2}) were considerably higher (on average 2.1 times higher) than the mean ^{14}C estimates for Cruises B, C and D (Fig.8.5). For Cruise E, however, the two estimates were essentially the same (i.e. 31.1 and 32.2 g C.m^{-2} for ^{14}C and particle volume productivity respectively).

It should be borne in mind, however, that mean Redfield estimates of daily productivity based on the period of maximum nutrient uptake (see Section 8.3 and Table 8.4) were between 1.6 and 4.7

TABLE 8.6: A comparison of calculated and observed phytoplankton carbon (g C.m^{-2}) at the end of each study using chlorophyll a-carbon with ^{14}C productivity estimates (Chl-^{14}C), and particle-volume-carbon with particle volume productivity estimates (P.vol). Losses due to copepod grazing (Olivieri and Hutchings 1985b) are presented for Cruises B-E

CRUISE	A		B		C		D		E	
	Chl-^{14}C	P.vol	Chl-^{14}C	P.vol	Chl-^{14}C	P.vol	Chl-^{14}C	P.vol	Chl-^{14}C	P.vol
Calculated biomass	18.5	-	23.7	41.4	30.2	47.7	25.0	53.2	31.5	33.0
(Cumulative productivity)	(17.7)		(19.1)	(39.4)	(21.8)	(44.3)	(24.4)	(52.4)	(31.1)	(32.2)
Observed biomass	15.11	6.40	3.30	2.50	3.15	2.10	15.20	4.32	1.81	-
Shortfall	3.39	-	20.4	38.9	27.0	45.6	9.8	48.9	29.7	-
(% of cumulative productivity)	(19.2%)		(93.6%)	(87.9%)	(124%)	(103%)	(40.2%)	(93.3%)	(95.3%)	-
Cumulative grazing loss	-	-	-	0.99	-	1.49	-	1.11	-	1.82
(% of cumulative productivity)			(5.2%)	(2.5%)	(6.8%)	(3.4%)	(4.5%)	(2.1%)	(5.8%)	(5.6%)
(% of shortfall)			(4.8%)	(2.5%)	(5.5%)	(3.3%)	(11.3%)	(2.3%)	(6.3%)	-

times higher than the equivalent ^{14}C productivity estimates, whereas particle volume estimates were 1.4-2.2 times higher than the Redfield estimates.

8.4.3 Differences between calculated and observed biomass

The changes in biomass actually observed along each drogue track (Fig.8.5) represent net primary production in the patch of upwelled water being studied (any losses due to whatever cause e.g. death, sinking, grazing, advection, etc. having taken their toll). Calculated biomass, on the other hand, is based on cumulative productivity measurements, without consideration of possible loss. The cumulative productivity estimates in Fig.8.5 represent potential production, and the differences between these curves and the biomass curves represent the loss of primary productivity from the 20 m^3 water column during the course of each study.

In Table 8.6 a comparison of calculated with observed phytoplankton biomass may be made, the difference being the loss of phytoplankton carbon from the 20 m^3 water column during the study periods. This shortfall (ranging from 3.39 to 48.9 g C.m-2) is equivalent to between 19.2% (Cruise A) and 124% (Cruise C) of the primary productivity accumulated during the study periods; low percentages (Cruises A and D) resulted from calculations based on blooms which had yet to decline, whereas losses greater than 100% of cumulative productivity reflect <u>in situ</u> biomass being higher at the start of monitoring than at the end. Shortfalls for particle volume-based experiments are larger than ^{14}C-chlorophyll based experiments; this is partly because particle volume productivity estimates are higher than ^{14}C-uptake estimates, and because biomass estimates based on particle volume-carbon are lower than those based on chlorophyll-carbon. Nonetheless, in both cases much of the primary production was lost during the course of each study, and high biomass levels were maintained for only a few days.

The result of zooplankton grazing experiments by Olivieri and Hutchings (1985b) during Cruises B-E (summarised in Fig.8.5) indicate that grazing pressure on the phytoplankton was negligible. In fact, cumulative grazing over each study period (see Fig.8.5 and Table 8.6) amounted to between about 2% and 6% of the shortfall calculated from particle volume experiments (or 5-11% if the grazing results were applied to the ^{14}C-chlorophyll a experiments).

Calculated biomass roughly coincided with the observed biomass until the latter peaked, particularly for Cruises A and E when moderate wind ensured that the water column was stable and the drogue did not move far (see Table 5.1). Once the blooms started to decline, the calculated biomass curves deviated from those of the observed biomass. For Cruises B, C and D, however, this relationship was less obvious. This may be linked to the fact that during these three cruises the drogues covered large distances with phytoplankton populations being subjected to more rigorous physical environments than in Cruises A and E. Strong winds, surface mixing and possibly vertical shear may have caused physical factors to dominate over biological factors, i.e. dispersive forces, such as mixing, advection and sinking resulted in the rate of export of phytoplankton from the 20 m water column exceeding the rate of population growth, so that observed biomass levels decreased. If this is true, then one of the initial assumptions made for this study does not hold, i.e. that the patch of water being tagged was large enough for such physical factors to be unimportant. However, before discussing possible losses from the phytoplankton community in the upper 20 m, let us first consider the detailed development of the population during each cruise and the influence of relevant environmental factors.

8.5 Factors affecting phytoplankton production

Representative depth profiles of phytoplankton biomass (chlorophyll a), the hourly rate of ^{14}C productivity (P), biomass standardised productivity (P^B) and nitrate concentrations along each drogue track, are presented in Figs 8.6-8.10 together with the depths of surface mixing and the 1% light level. One set of profiles per day was selected for presentation. These data allow speculation as to what factors influence phytoplankton production in each case. It should be noted here that silicate concentrations are not presented as they show similar trends to nitrates; however, at low concentrations silicates were usually slightly higher than nitrates. The depth of "surface mixing" is taken to be the depth of the isothermal layer as assessed from BT profiles (see Chapter 5.3.2), and may vary quite considerably from day to day, particularly when the water column is only weakly stable. Each cruise is dealt with below: firstly, Cruises A and E, during which relatively stable conditions persisted (i.e. moderate winds blew, the drogue did not move far and the depth of surface mixing was shallow, seldom exeeding the 1% light depth); and, secondly, Cruises C, D and B, during which conditions were more turbulent (strong winds blew, deep mixing occurred on occasion and the drogue moved more extensively).

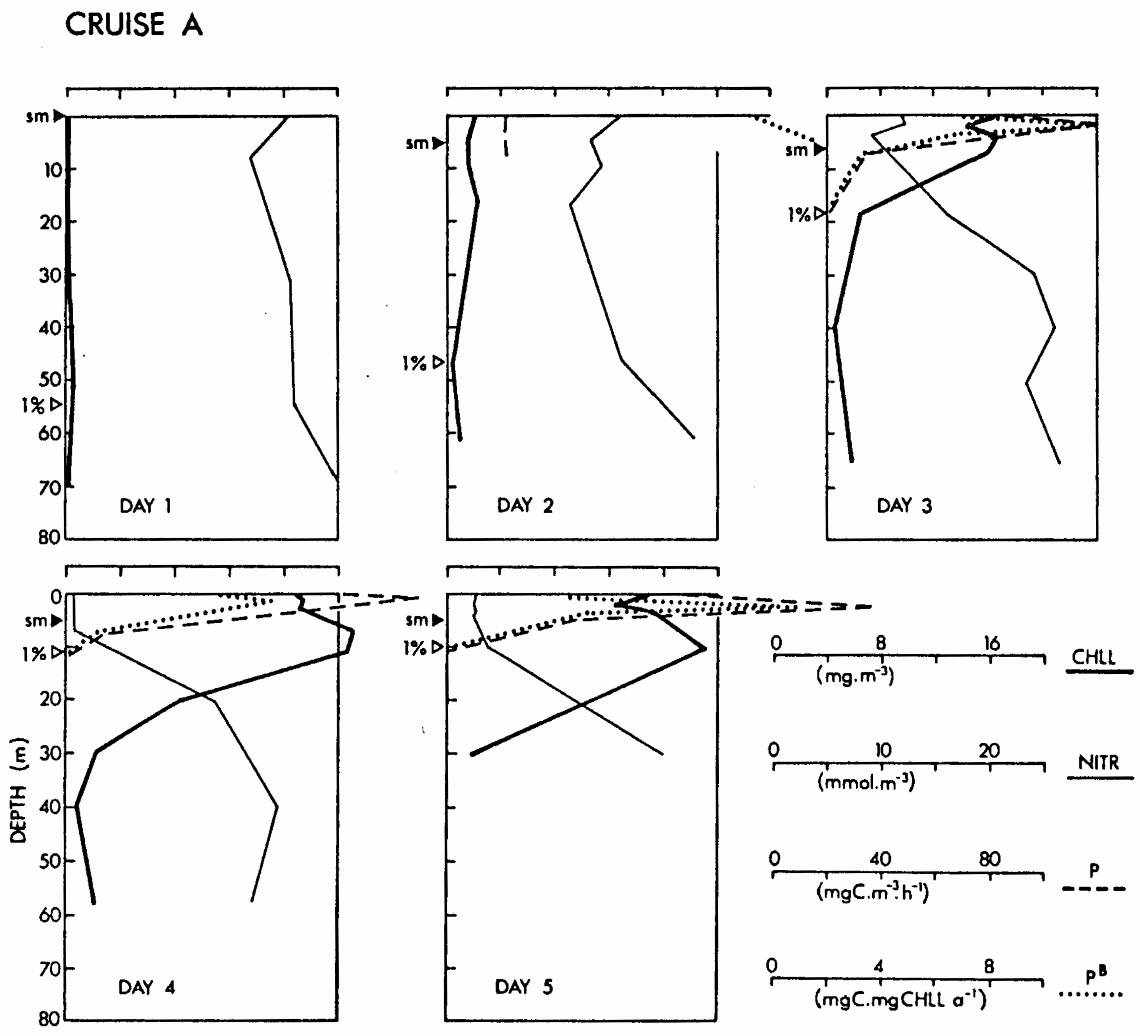


Fig.8.6: Representative depth profiles of phytoplankton biomass (CHLL), the hourly rate of ^{14}C productivity (P), biomass standardized productivity (P^B) and nitrate concentrations (NITR) with the depths of surface mixing (sm) and the 1% light level (1%) for each day of Cruise A.

Cruise A (Fig.8.6): Relatively calm conditions allowed a classic sequence of bloom build up during this cruise. Very low and uniform chlorophyll a concentrations in newly upwelled water on Day 1 increased rapidly (particularly in the euphotic zone) to maximum concentrations on Day 4 while nitrate concentrations dropped from 20 $mmol.m^{-3}$ to about 1 $mmol.m^{-3}$ in the upper euphotic zone. Productivity rates increased as chlorophyll a concentrations increased. Biomass standardised productivity (P^B) was highest at the beginning of the study. Mean P^B (above the 10% light depth) decreased from about 17 mg $C.mg\ chll\ a^{-1}.h^{-1}$ on Day 2 to 4-5 mg $C.mg\ chll\ a^{-1}.h^{-1}$ by Day 4. It is noteworthy that this decrease in P^B (at least from Day 2 to Day 3) is unlikely to be due to nutrient limitation as nitrate (5-7 $mmol.m^{-3}$) and silicate (3-4 $mmol.m^{-3}$) concentrations were still moderately high on Day 3.

The decline of the bloom was retarded by the apparent entrainment of nutrients into near-surface waters on Day 5. The stability of the water column during this cruise allowed photosynthetic products to accumulate and a bloom to develop. Production was ultimately limited, firstly, by the original nutrient content of the water mass and, secondly, by self-shading as increased biomass concentrations resulted in a decrease in the depth of the euphotic zone, thereby making the nutrients deeper down unavailable under stable conditions.

Cruise E (Fig.8.7): As in Cruise A, the phytoplankton population built up rapidly during Cruise E in the stable nutrient-rich water. Chlorophyll a increased from low concentrations to peak

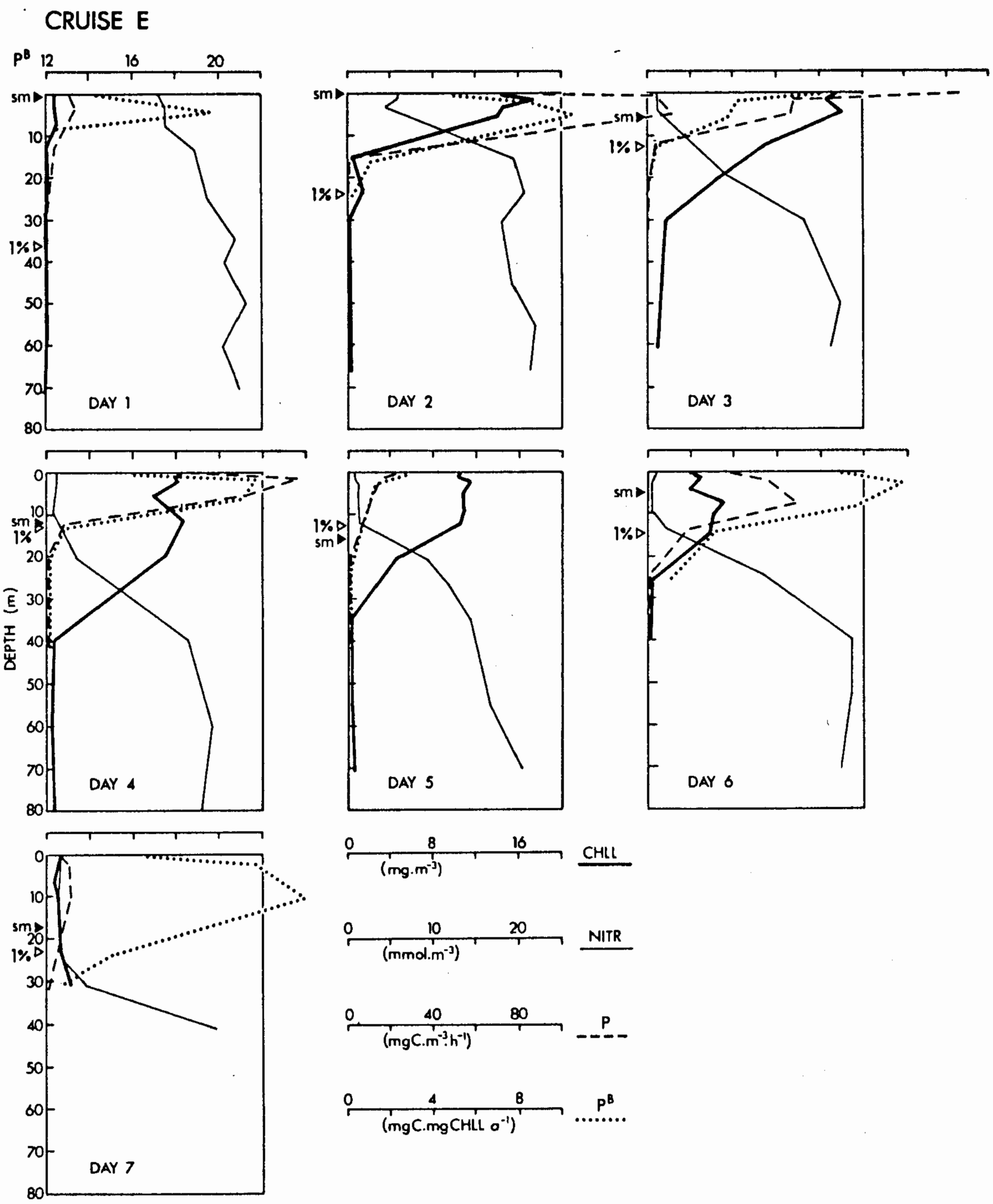


Fig.8.7: Representative depth profiles of phytoplankton biomass (CHLL), the hourly rate of ^{14}C productivity (P), biomass standardized productivity (P^B) and nitrate concentrations (NITR) with the depths of surface mixing (sm) and the 1% light level (1%) for each day of Cruise E. Note that the P^B for Day 1 has been shifted to accommodate the high values on the graph.

on Day 3, by which time nitrates in surface waters had decreased to about 1 $mmol.m^{-3}$ and (as did silicate concentrations) stayed low for the remainder of the study period. Productivity rates were high in the upper euphotic zone (over 120 $mg\ C.m^{-3}.h^{-1}$) during the biomass peak (Days 2-4) and then decreased as biomass levels fell. Comparison of chlorophyll a and productivity profiles indicate considerable light-limitation of the phytoplankton community due to self-shading. However, P^B, which may be considered an index of the physiological state of the phytoplankton (Strickland 1965), was generally quite high even at the end of the study period (i.e. about 10 $mg\ C.mg\ chll\ a^{-1}.h^{-1}$ on Days 6-7). This may have been due to regenerated nitrogen fueling production at that stage. Although P^B does not seem to be a good indicator of bloom decline, it does suggest that the phytoplankton community was not nutrient limited in a physiological sense.

Cruise C (Fig.8.8): In contrast to the relatively calm conditions during Cruises A and E, strong winds accompanied a deeply mixing water column (to between 25 and 40 m) during the first half of Cruise C. Moreover, at the start of the study, chlorophyll a concentrations were already high (about 8 $mg\ chll\ a.m^{-3}$) and the depth of the 1% light level was less than the depth of surface mixing. Despite moderately high productivity measurements (up to 70 $mg\ C.m^{-3}.h^{-1}$) and a noticeable decrease in nitrate concentrations, there was virtually no increase in chlorophyll a concentrations. Presumably this was due partly to deep mixing causing light-limitation of in situ productivity and partly to the net production being mixed downwards so that, even though total biomass may have increased, phytoplankton densities did not

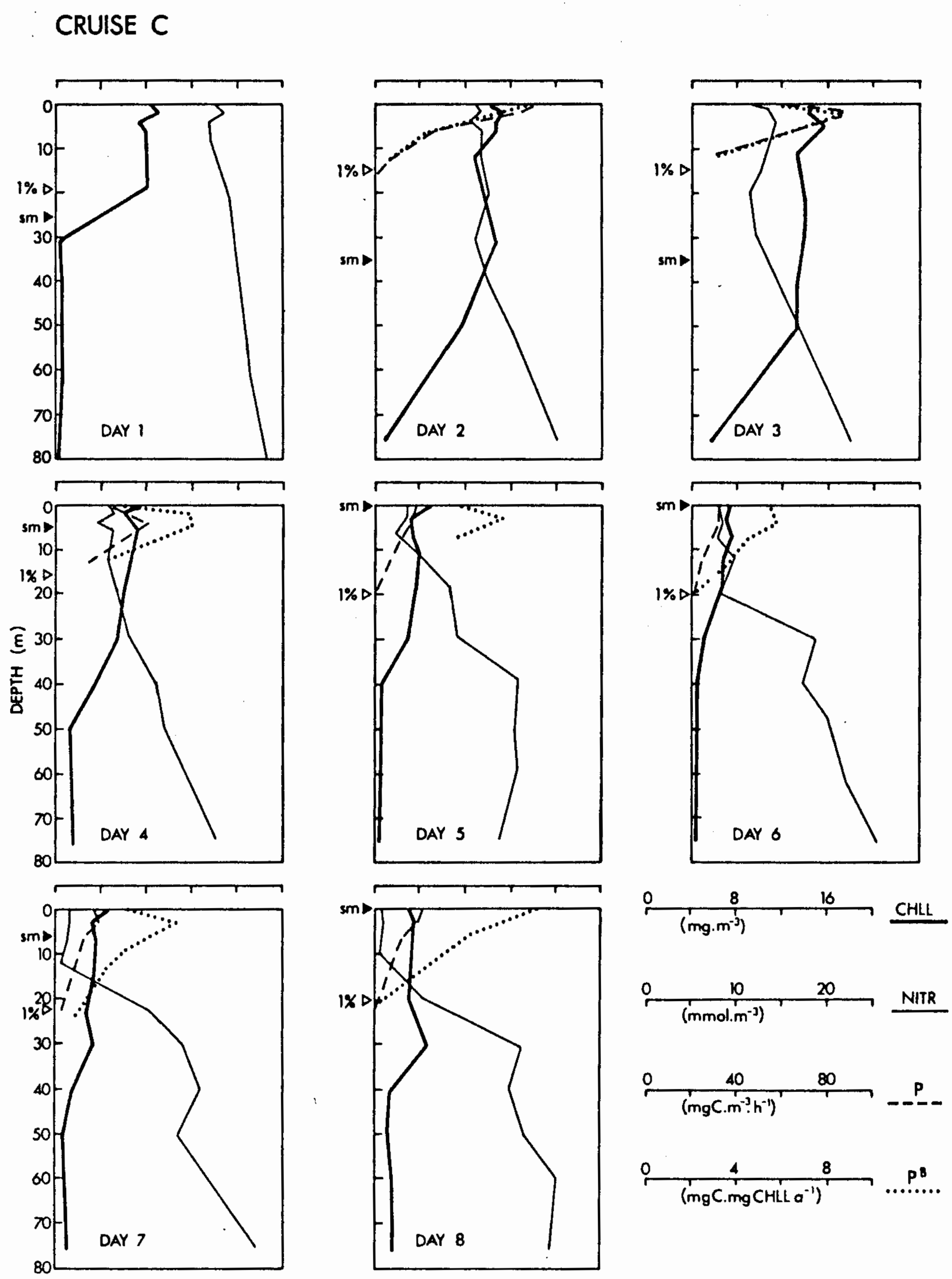


Fig.8.8: Representative depth profiles of phytoplankton biomass (CHLL), the hourly rate of ^{14}C productivity (P), biomass standardized productivity (P^B) and nitrate concentrations (NITR) with the depths of surface mixing (sm) and the 1% light level (1%) for each day of Cruise C.

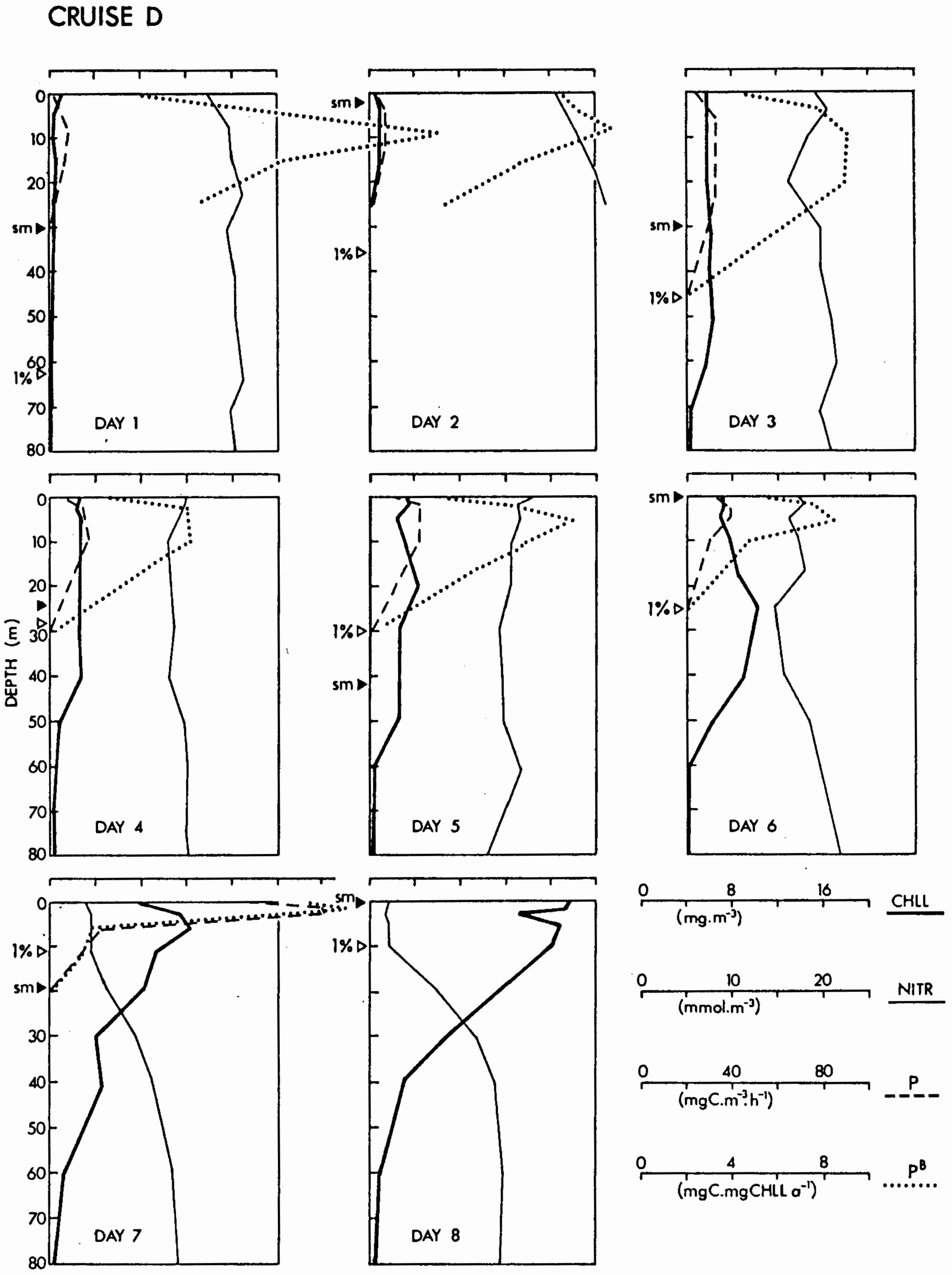


Fig.8.9: Representative depth profiles of phytoplankton biomass (CHLL), the hourly rate of ^{14}C productivity (P), biomass standardized productivity (P^B) and nitrate concentrations (NITR) with the depths of surface mixing (sm) and the 1% light level (1%) for each day of Cruise D.

increase. However, after the water column stabilized on Day 4 (station 9), chlorophyll a concentrations did not increase despite relatively high nitrate (about 5 $mmol.m^{-3}$) and silicate (about 4 $mmol.m^{-3}$) concentrations. It should be borne in mind that water column stabilization coincided with the drogue reversing direction and moving southwards (see Fig.5.4). At this point the drogue may have moved into a different patch of water, particularly as the phytoplankton species composition changed from being dominated by Nitzschia spp. to Chaetoceros spp. (Olivieri et al 1985). Nevertheless, irrespective of nutrient concentration, P^B did not vary much and ranged between 3 and 6 mg C.mg chll $a^{-1}.h^{-1}$. Bloom decline may, of course, have been caused merely by the physical dispersion of the population.

Cruise D (Fig.8.9): The main feature of this cruise is the long time it took for the bloom to build up (8 days) even though P^B was high throughout the cruise. Close examination of the BT profiles and changes in water column chemistry indicate that the apparent "lag" was a consequence of strong winds and vigorous upwelling preventing the original patch of water from maintaining its physical integrity. It appears that turbulent advection and shear resulted in a continuum of newly upwelled water, with varying amounts of phytoplankton in it (and varying physical structure), passing the drogue until perhaps Day 6. At this stage the environment seemed to be stable enough for the bloom to build up rapidly as it did in Cruises A and E.

Cruise B (Fig.8.10): At the start of the study-period chlorophyll a concentrations were moderately high (3-4 mg $chll.m^{-3}$) and fairly evenly distributed down to about 30 m, so that throughout the

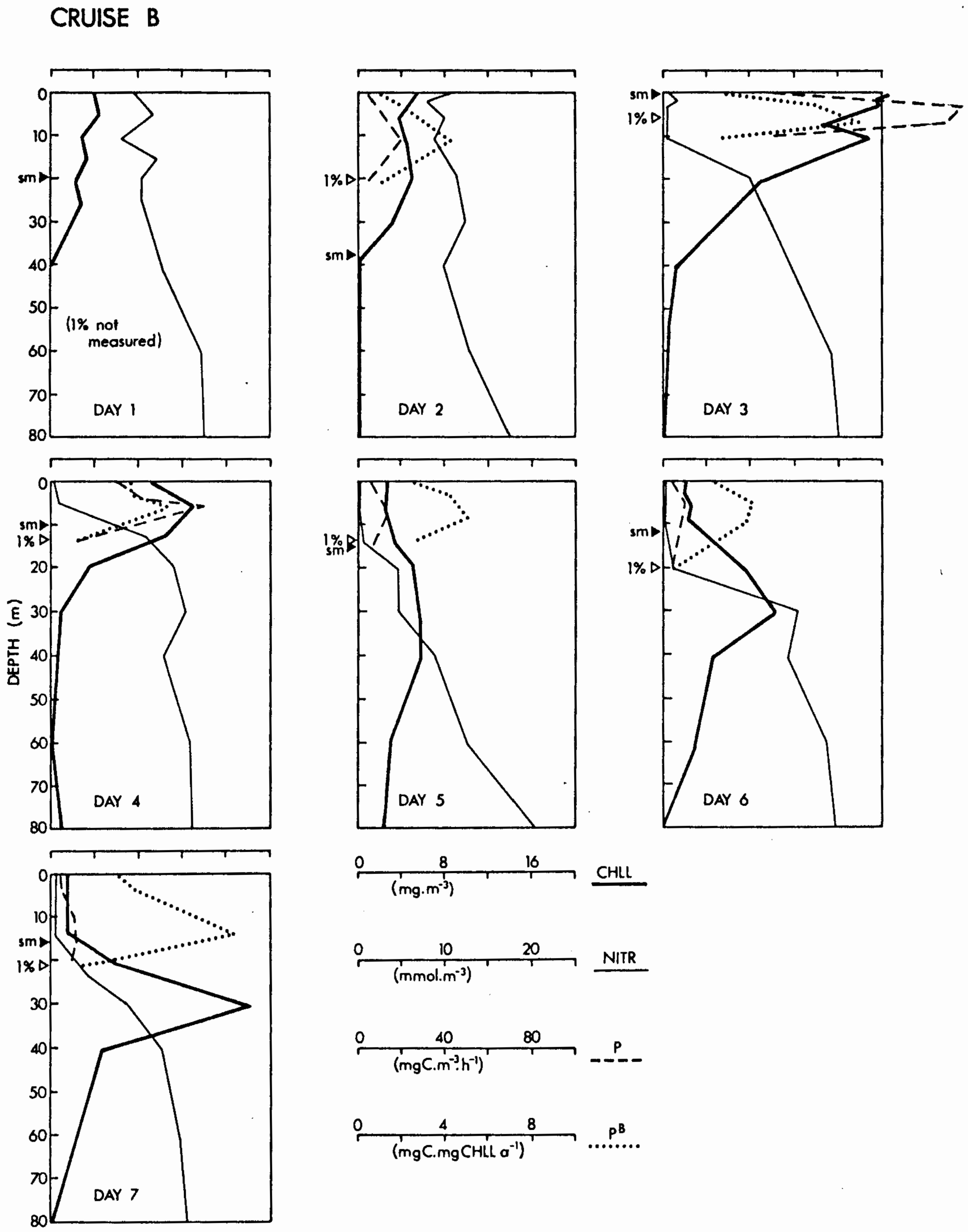


Fig.8.10: Representative depth profiles of phytoplankton biomass (CHLL), the hourly rate of ^{14}C productivity (P), biomass standardized productivity (P^B) and nitrate concentrations (NITR) with the depths of surface mixing (sm) and the 1% light level (1%) for each day of Cruise B.

cruise much of the phytoplankton community was light-limited due to self-shading. Except for Days 1-2 the surface mixing layer was shallow (mean depth 9.5 m) and phytoplankton biomass (and productivity) increased rapidly to peak on Day 3. By this stage nitrates had dropped to less than 1 $mmol.m^{-3}$ in the euphotic zone and remained low for the rest of the cruise. P^B was generally low (3-5 mg C.mg chll $\underline{a}^{-1}$) even when nitrate concentrations were high on Day 2. However, low nutrient concentrations may have caused phytoplankton to sink out of the surface layer; such sinking behaviour is observed in microcosm experiments on upwelled water, when the nutrients are stripped from the medium (G.C. Pitcher, SFRI, pers. comm.). The deepening chlorophyll a maximum (on Days 3-7) supports this suggestion, although it should be borne in mind that, if the water column was shearing vertically, the deep chlorophyll a maximum may be an accumulation of chlorophyll a from a series of such blooms during different upwelling events prior to Cruise B. Moreover, the rapid movement of the drogue up the coast may have caused some of the net production to be dispersed by horizontal turbulent advection. A decrease in surface salinity from Day 5 (see Fig.5.10) indicates that lower salinity water was probably entrained into the water around the drogue between Ysterfontein and Cape Columbine. Thus, if this low salinity water was poor in chlorophyll a, dispersive mixing could have been partly responsible for the decline in the phytoplankton population near the sea surface.

8.6 Discussion

A pertinent question now is "What happens to the organic matter which was produced during each study period?". Harris (1984)

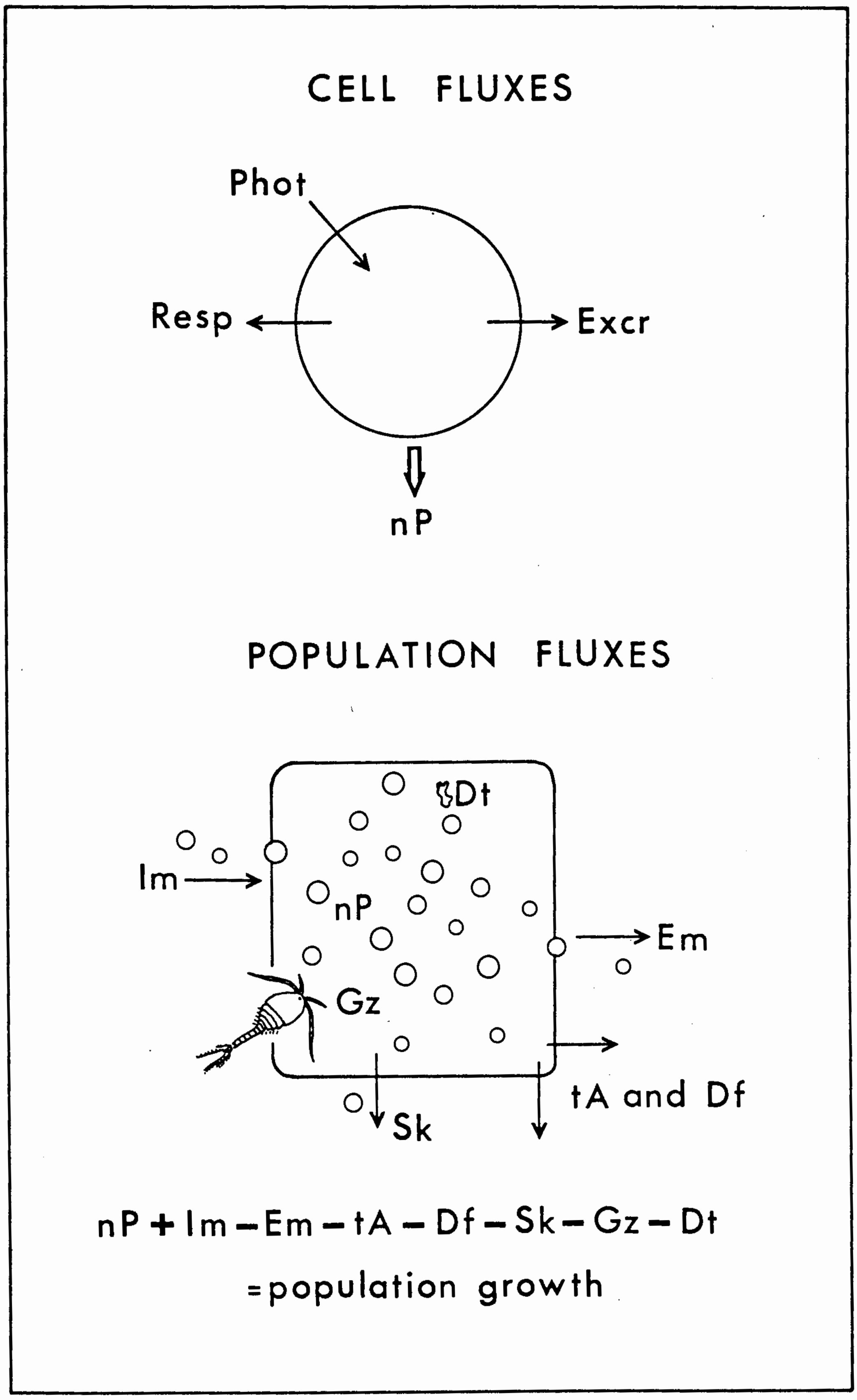


Fig.8.11: A schematic representation of the important terms in the overall balance of production and loss in surface waters. The fluxes of carbon in and out of phytoplankton cells are due to photosynthesis (phot), respiration (resp) and excretion (excr). Population fluxes result from growth due to net primary productivity (nP), immigration (Im), emigration (Em) including turbulent advection (tA) (due to shear and horizontal and vertical mixing), diffusion (Df), passive sinking (Sk), grazing (Gz) and death (Dt).

summarizes the important terms in the overall balance of production and loss in surface waters at the levels of both individual cells (photosynthesis, respiration and excretion) and the phytoplankton community as a whole (immigration, emigration, growth, grazing, sedimentation and death). The concepts, illustrated in Fig.8.11, are pertinent to both "bottle experiments" and population changes observed in the water column and may help explain the large differences between the observed and calculated biomass estimated for the five cruises in Fig.8.5.

8.6.1 Cell fluxes

Photosynthetic processes organically bind carbon within the cell in the presence of light. Some of this organic carbon is subsequently lost through cellular respiration and excretion. As the 14C-uptake productivity measurements are thought to represent something between net and gross productivity, no correction was made for the hourly day-time productivity estimates in the present study, but an arbitrary attempt was made to estimate and correct for night-time respiration (see section 8.2.2). Excretion of organic carbon was estimated in previous experiments in the same area from concentrations of radioactive organic carbon in the filtrate of productivity samples (J.L. Henry and P.C. Brown, SFRI unpublished data), and usually found to be low. Sneller (1982) also reports that the release of dissolved organic carbon by Peruvian phytoplankton communities is a small percentage (3.2-4.4 %) of the total carbon fixed; therefore its omission should not influence productivity rates unduly. In any case, phytoplankton population growth depends on particulate productivity (and not on extracelluar productivity), thus no correction was applied to productivity estimates for losses due to the excretion of organic carbon by the phytoplankton cells. The possibility does exist, of course, that more organic carbon is excreted but is "mopped up" by bacteria which may be retained on the filters and thus is not detected in the filtrates. This may account for some of the shortfall between calculated and observed biomass, but its significance is difficult to assess here, as no bacterial measurements were made during these cruises. However, Muir (1986) reports that, in the upwelling area off Cape Columbine, bacterial biomass fluctuations mirror those of phytoplankton. As the majority of marine bacteria are free-living and small (mostly rods less than 0.5 µm in length) (Muir 1986), most would have passed through the glass fibre filters used in the ^{14}C-uptake experiments. During bloom decline, however, some bacteria may be attached to detrital matter and thus retained by the filter (0.7 µm pore size) At this stage phytoplankton productivity may be overestimated. Neither respiration nor excretion corrections are necessary for particle volume productivity measurements which rely on biomass changes rather than the flux of elements.

From the view point of a cell, probably the major potential influence of the nutrient-rich upwelling environment on primary production, and consequently on bloom development, would initially be the average light intensity experienced by the cells. During deep mixing of the barely stable water column, respiratory loss of organic carbon may exceed its photosynthetic production at a cellular level, and thus retard population growth or even cause it to decline. This may have occurred on some occasions during Cruise D, and during the first half of Cruise C, when the depth of mixing was considerably deeper than the euphotic zone.

Although chlorophyll a levels did increase during Cruise C, deep mixing seemed to prevent chlorophyll a concentrations from increasing to the high concentrations attained during the other cruises.

Such influences cannot be directly accounted for by the methods used to measure productivity in this study. The "bottle experiments" artificially hold the phytoplankton at constant light depths and, thus, neglect respiration due to deep mixing. Redfield productivity based on nutrient changes reflects gross productivity thereby also omitting the loss of organic carbon by deep respiration. However, although such carbon losses would have occurred in the present study when the depth of mixing was greater than the euphotic zone depth, deep mixing was unlikely to account for bloom decline in most cases.

Another potential influence at a cellular level is that of low nutrients limiting photosynthesis. This was assessed by inspecting the biomass standardised rates of productivity, P^B (mg C.chll $a^{-1}.h^{-1}$), for each cruise (see Section 8.5). These data show no definite trends with respect to nutrient concentration and were often high when nutrient concentrations were low, thus indicating that nutrient limitation was unlikely to be operating at a physiological level. However, MacIsaac et al (1985) also found little change in P^B in sequences of phytoplankton growth in newly upwelled water in Peru, whereas they did find very definite changes in the rates of nitrogen uptake and nitrogen reductase activity. This supports Harris's (1984) suggestion that P^B should be treated with caution, as changes in P^B may be more due to shifts in species composition rather than to physiological adaptation, with minor species possibly contributing more heavily to productivity than to biomass. Perhaps indices based on nitrogen fluxes and species specific biomass estimates may be more useful indicators of the physiological response of phytoplankton to environmental changes.

8.6.2 Population fluxes

Losses from the phytoplankton community in the upper 20 m layer (Fig.8.5, Table 8.6) implicate grazing, sinking, mixing and/or dispersion as vehicles for the removal of the products of photosynthesis from the water in the vicinity of the drogue. These processes are discussed below:

Grazing: As mentioned previously (section 8.4.3) zooplankton grazing pressure on phytoplankton (as estimated by Olivieri and Hutchings 1985b) was negligible. However, the accurate estimation of in situ grazing is difficult because calculations are based on vertically migrating, patchy zooplankton populations (Hutchings 1979, 1986, Pillar 1984). Also, the omission of larger zooplankton (e.g. euphausids) and pelagic fish as potential grazers, may cause grazing pressure to be underestimated. Recent estimates of the biomass distribution of meso-zooplankton (mainly copepods and euphausids) indicate that euphausiids comprise 31.3 % of the zooplankton off the Cape Peninsula (Pillar 1986). Moreover, since WP-2 nets such as those used by Olivieri and Hutchings (1985b) do not catch large zooplankton efficiently (Pillar 1984), euphausiid biomass would have been underestimated in the drogue studies. However, as local euphausiids species are omnivores (Pillar 1984, Stuart 1986), their contribution to overall grazing pressure is probably lower than the predominantly herbivorous copepods in this area. On the other hand, while the dominant Benguela pelagic fish species (the anchovy) is also omnivorous, it is considered to be largely a zooplankton feeder (James 1986). Even if one doubled the zooplankton grazing estimate, it would still be small relative to the phytoplankton standing stock and production shown to be available in this study. However, Borchers and Hutchings (1986) show that zooplankton in the southern Benguela have a potential to remove approximately 50-60% of the annual phytoplankton production of 1.3 kg $C.m^{-2}.y^{-1}$ (Brown 1984).

Zooplankton grazing within incubation bottles (for ^{14}C-uptake and particle volume productivity measurements), may cause phytoplankton productivity to be underestimated. In this study, water samples for particle volume productivity measurements were sieved through a 200 µm mesh to remove mesozooplankton grazers from the incubation bottles; the small size of the ^{14}C incubation bottles (125 ml) would normally preclude the presence of mesozooplankton grazers (Sheldon et al 1973, Brown 1982). However, correction of such an error would only serve to increase the shortfall between calculated and observed phytoplankton biomass.

Sinking: Phytoplankton may sink out of the upper 20 metres. Although no sedimentation studies were conducted, inspection of depth profiles of biomass suggest that this may have occurred along some of the drogue tracks. Even indirectly, however, sinking losses are difficult to quantify here because of the uncertainity regarding the water column maintaining its physical integrity. If the surface layer did in fact shear over the deeper water, then deep chlorophyll a maxima (especially evident in Cruise B) may be remnants of previous events and not a direct result of phytoplankton sinking out of the surface bloom being studied. Nonetheless, sedimentation studies in the southern Benguela by Bailey (1983) and co-workers show that considerable losses of organic carbon may occur from surface waters. Sedimentation rates of up to 4.2 g $C.m^{-2}.d^{-1}$ (Bailey 1983) suggest that bloom decline may on occasion be a direct result of phytoplankton sinking out of surface waters particularly in a vertically stable water column. Pitcher (1986) has shown that while vegetative diatom cells sink slowly, resting spores form and sink rapidly from the water column. Sporulation has been observed to be initiated at the end of the exponential growth phase (Hollibaugh _et al_ 1981) with nutrient limitation being the most common causative factor triggering spore formation and rapid sinking of phytoplankton (Bienfang 1981, Pitcher 1986).

Dispersion (caused by turbulence, shear, advective mixing etc.) may also account for phytoplankton losses from the water around the drogue. By definition phytoplankton are largely passively transported from place to place by their fluid environment, thus it is not surprising that "turbulent advection plays a major role in controlling the morphology of plankton patchiness" (Mackas _et al_ 1985) and thus may also influence bloom build up and decline. Vertical turbulence can mix phytoplankton to below 20 metres (e.g. Cruises C and D), so that it is effectively lost. However, the influence of deep mixing on phytoplankton bloom ecology (Sverdrup 1953, Legendre 1981) is primarily biological. Spending long periods at low light levels in deep water results in respiration increasing relative to photosynthesis so that net productivity per cell (Section 8.6.1), and consequently population growth, are reduced.

On the other hand, the effect of horizontal turbulent advection on a bloom could be to disperse it into surrounding waters with lower cell concentrations. Species composition may even be similar in the low biomass water with the patch being defined in terms of biomass differences. Once the increase in cell numbers is exceeded by the diluting effects of turbulent advection, the bloom will decline. The intensity of the effect of turbulent advection will vary with the physical state of the environment. During calm periods after upwelling, a stable water column would favour bloom development being dominated by biological factors such as the rate of phytoplankton productivity. When nutrients become depleted and productivity is nutrient limited and possibly also light limited due to self-shading, cells may sink out of near-surface waters and/or be dispersed by even low levels of turbulence, thus resulting in the decline of the bloom.

During strong winds the shearing action of a tongue of upwelled surface water over deep layers intensifies the effects of turbulence and advective mixing particularly at the lateral and subsurface boundaries of the tongue, thus entraining water into the original parcel. The relative condition of the water being entrained (in terms of its biomass and nutrient contents) would determine its effect on bloom development.

Because spatial investigations were not usually conducted simultaneously with the drogue "temporal" studies, little can be said with confidence regarding the effects of horizontal turbulent advection in this study, except perhaps for Cruises A and E. During December 1979 (Cruise A) SFRI conducted aerial surveys over the Cape Peninsula to map sea-surface temperatures (SST) (Taunton-Clark

1982). SST maps for the two days prior to the release of the main drogue and for Days 1, 4-5 of Cruise A are reproduced by Olivieri (1983) with the midday position of the drogue. These data indicate that the drogue did in fact move along the axis of the upwelling tongue until Day 5 when it veered towards the shore while the tongue continued in a north-northwesterly direction. This is consistent with the suggestion that the parcel of water during this cruise more or less maintained its physical integrity until Day 5 when the increase in nutrients (Fig.8.6) and deepening of the surface mixing layer (Fig.5.12) suggested that more recently upwelled water was entrained into the original patch.

SST maps for October 1981 (Taunton-Clark 1982) indicate that the strong thermal front typical of the upwelling season had not yet developed during Cruise E. Holden (1981) made daily transects across the path of the drogue recording current profiles on either side (see Fig.5.7) and Boyd (1982) made rough estimates of dispersion and shear using a number of small drogues set at 2, 10 and 20 m in the immediate vicinity of the main drogue. Boyd's study suggests that horizontal shear may cause considerable dispersion of a bloom. Holden (1981), on the other hand, found juxtaposed northerly and southerly currents in the vicinity of the drogue. These may have resulted in turbulent advection in the shear zone between the currents dispersing the population.

During Cruises A and E the water column was relatively stable and the drogue did not move far. However, during the other three cruises (B, C and D) conditions were generally more unstable, both vertically and horizontally, so that physical dispersive forces may have influenced bloom development to a greater extent than during Cruises A and E. While the quantification of such processes is beyond the scope of this study, consideration of co-occuring environmental conditions and a knowledge of the hydrography which usually accompany these, allowed some presumptive speculation as to possible physical influences on bloom development in Section 8.5. These surveys lacked adequate measures of physical stratification and turbulence due to the limitations of only mechanical bathythermographs and bottle casts being available.

Nevertheless, the use of drogues provided greatly improved information on the time scale of events following upwelling; it provides a new perspective on the spatial and temporal scales previously available only from the less direct transect approach of Andrews and Hutchings (1980). Moreover, the comparison of independent methods of estimating primary productivity lends some confidence to the ^{14}C-uptake productivity measurements. Mixing of new and matured upwelled water is a characteristic feature of this dynamic region, and the contrast between the results of Drogues A and E (with low wind speeds and little drogue movement) and Drogues B, C and D provides some insight into the complex ways in which the surface layers are enriched during the upwelling process.

CHAPTER 9: CONCLUSIONS

9.1 The physical destination of a "patch" of upwelled water
9.2 Nutrient changes in upwelled water
9.3 Redfield ratios and the estimation of primary productivity
9.4 Phytoplankton biomass and productivity estimates
9.5 Phytoplankton bloom development
9.6 General

The drogue study (Part II) describes the short-term fate of water after upwelling off the Cape Peninsula, with emphasis on phytoplankton bloom development in recently upwelled water. In this chapter, the major conclusions from the five surveys will be drawn; and the study will be put into perspective in terms of the whole coastal upwelling system described in Part I.

9.1 The physical destination of a "patch" of upwelled water

Although drogue movement is limited in its ability to reflect the physical destination of any particular body of water (especially in a highly dynamic and pulsed upwelling system), here it indicates that upwelling water off the Cape Peninsula tends to move towards the N-NW (Cruises B, C and D) but may also be diverted southwards before moving offshore (Cruise D), move towards the coast (Cruise A) or move back and forth in a limited area (Cruise E) depending on prevailing winds and currents. Such varied movement is consistent with simulation models of drogue movements off the Cape Peninsula by G. Nelson (SFRI, pers. comm.). The models show that small temporal or spatial variation in drogue deployment may result in considerable variation in drogue tracks because of the notably unstable meteorological and circulation patterns in the area.

A "patch" of upwelled water is more likely to maintain its physical integrity with time under stable conditions such as were found during Cruise A. Vertical and horizontal instabilities resulting from deep mixing, shear, turbulent advection, slippage of water past the drogue etc., may disperse the upwelling water thereby preventing the initiation of a phytoplankton bloom and biasing a time-series study on a particular body of water, as the water in the vicinity of the drogue would be continuously displaced (e.g. first half of Cruise D). A series of measurements under such conditions reflects a continuum of different water bodies, rather than changes due only to biological activity in a single body. However, once conditions stabilized, biological and chemical changes suggest that the water body near the sea surface maintained some integrity.

9.2 Nutrient changes in upwelled water

Nutrient concentrations in upwelling source water were high (mean concentrations for nitrate, silicate and phosphate were 20.8, 16.6 and 1.88 $mmol.m^{-3}$ respectively), while oxygen (4.0 $dm^{3}.m^{-3}$) and chlorophyll a (0.6 $mg.m^{-3}$) concentrations were low. Nutrients decreased rapidly (and oxygen and chlorophyll a increased) with nitrates sometimes reaching concentrations of less than 1 mmol. m^{-3}. When the water samples collected along the drogue tracks were categorized into "newly upwelled", "mature" and "aged" upwelled water types, the changes in the mean nutrient atomic ratios of occurrence in the euphotic zone ranged from 11.17 to 3.12 to 1.69:1 for N:P and 8.66 to 3.57 to 5.75:1 for N:Si, suggesting that nitrate was used up fastest and thus, in agreement with the findings of Andrews and Hutchings (1980), is most likely to limit phytoplankton growth. Regressions of nitrate on silicate and calculations of nutrient depletion times, however, indicate that silicate may sometimes be depleted before nitrate. As regenerated nitrogen (ammonia and urea) was not measured, total nitrogen depletion was not estimated. Thus, as diatoms require silicon and the rate of silicate regeneration is slower than that of nitrogen (Dugdale 1972), the possibility of silicon limitation in the southern Benguela should not be disregarded on the grounds that nitrates were reduced to lower concentrations than silicates.

9.3 Redfield ratios and the estimation of primary productivity

The mean atomic ratios of nutrient utilization and oxygen production (_P:_N:_Si:_O), as estimated from regression analyses (1:16.3:12.8: -283) and elemental changes along the drogue tracks (1:15.7:13.8: -206), were roughly similar to the equivalent Redfield ratios (1:16:15:-276). Individual values, however, varied quite substantially from the mean ratios. Nonetheless, the calculated ratios of utilization suggest that phytoplankton in upwelled water utilize nitrate-N, silicon-Si and phosphate-P and produce oxygen in roughly the same proportions in which these elements are reported to occur in phytoplankton. Thus elemental changes in N, Si, P and O in the upper 20 metres along the drogue tracks were converted to carbon (using Redfield ratios) in an attempt to estimate rates of primary organic production without enclosing water samples in bottles (as is required by the ^{14}C-uptake and particle volume methods of measuring productivity rates).

Comparison of productivity estimates obtained using these three methods, shows that Redfield estimates (based on the whole study period) were similar to ^{14}C-uptake estimates, whereas particle volume productivity was about twice the ^{14}C and Redfield estimates. However, during the periods of most rapid nutrient uptake,

Redfield productivity estimates were on average about $2^1/_2$ times higher than the ^{14}C-uptake estimates and about $^3/_4$ of the particle volume productivity estimates. The important point to note is that, as commonly suspected, ^{14}C-uptake measurements probably do underestimate true productivity, but not by as much as the suggested "order of magnitude" (Sheldon and Sutcliffe 1978, Schulenberger and Reid 1981).

9.4 Phytoplankton biomass and productivity estimates

Biomass (chlorophyll a) and productivity (^{14}C-uptake) estimates for this study are summarised in Table 9.1. On average, about half of the biomass in the upper 50 metres occurred below the 1% light depth indicating that low light, due to self-shading, is an important factor limiting the primary productivity of the system. However, the rate of biomass standardised productivity, P^B, was usually quite high in the upper euphotic zone (mean 7.2 mg C.mg chll $a^{-1}.h^{-1}$). Although the significance of this is uncertain, it may be interpreted as meaning that the phytoplankton community was not strongly nutrient limited in a physiological sense. However, from an ecological perspective, total phytoplankton productivity is undoubtedly nutrient (N and/or Si) controlled in terms of the gross amount of nutrients which upwell, as is the case for most other upwelling systems studies (Dugdale 1983). A possible change in phytoplankton community structure from a diatom-dominated bloom (adapted to high nutrient concentrations) to phytoplankton species which are adapted to ammonia uptake and do not require silica, may explain the high P^B sometimes found at the end of the bloom when nitrate and silicate levels are low but ammonia may be available.

Column productivity rates ranged between 0.94 and 14.01 g $C.m^{-2}.d^{-1}$ (or 122-1465 mg $C.m^{-2}.h^{-1}$) with a mean rate of 3.80 g $C.m^{-2}.d^{-1}$ (or 407 mg $C.m^{-2}.h^{-1}$). These data are similar to values obtained previously for two nearshore sites off the Cape Peninsula (mean 4.05 g $C.m^{-2}.d^{-1}$) (Brown 1984); they are more variable and, on average, higher than productivity rates reviewed by Minas et al (1982) for Northwest Africa (individual values 0.56-7.6 g $C.m^{-2}.d^{-1}$; mean values 2-2.4 g $C.m^{-2}.d^{-1}$), except for the measurements made during two studies near Cape Timiris (Herbland et al 1973, Herbland and Voituriez 1974), when they were similar (mean 3.9 g $C.m^{-2}.d^{-1}$). Barber and Smith (1981) report lower mean productivity estimates for the upwelling areas off Northwest Africa (1.96 g $C.m^{-2}.d^{-1}$) and Peru (1.89 g $C.m^{-2}.d^{-1}$). Ryther et al (1971) measured similar daily rates for their drogue study off Peru (15°) (3.14-11.74 g $C.m^{-2}.d^{-1}$), while values by Beers et al (1971) (mean 1.17, range 0.83-1.79 g $C.m^{-2}.d^{-1}$) and Strickland et al (1969) (mean 1.60, range 0.25-4.10 g $C.m^{-2}.d^{-1}$) for Peruvian upwelling areas were considerably lower than in the present study. Productivity rates by Schultz (1982) for Northwest Africa (mean 1.14, range 0.18-3.58 g $C.m^{-2}.d^{-1}$) and for the northern Benguela area off Namibia (Southwest Africa) (mean 1.76, range 0.3-5.5 g $C.m^{-2}.d^{-1}$) were also lower.

9.5 Phytoplankton bloom development

The initiation of blooming appears to be controlled by the physical state of the water column, a certain level of stability (vertical and horizontal) being required. The "low physiological rates" observed by MacIsaac et al (1985) in very newly upwelled water off Peru, were not identified in the present study. This

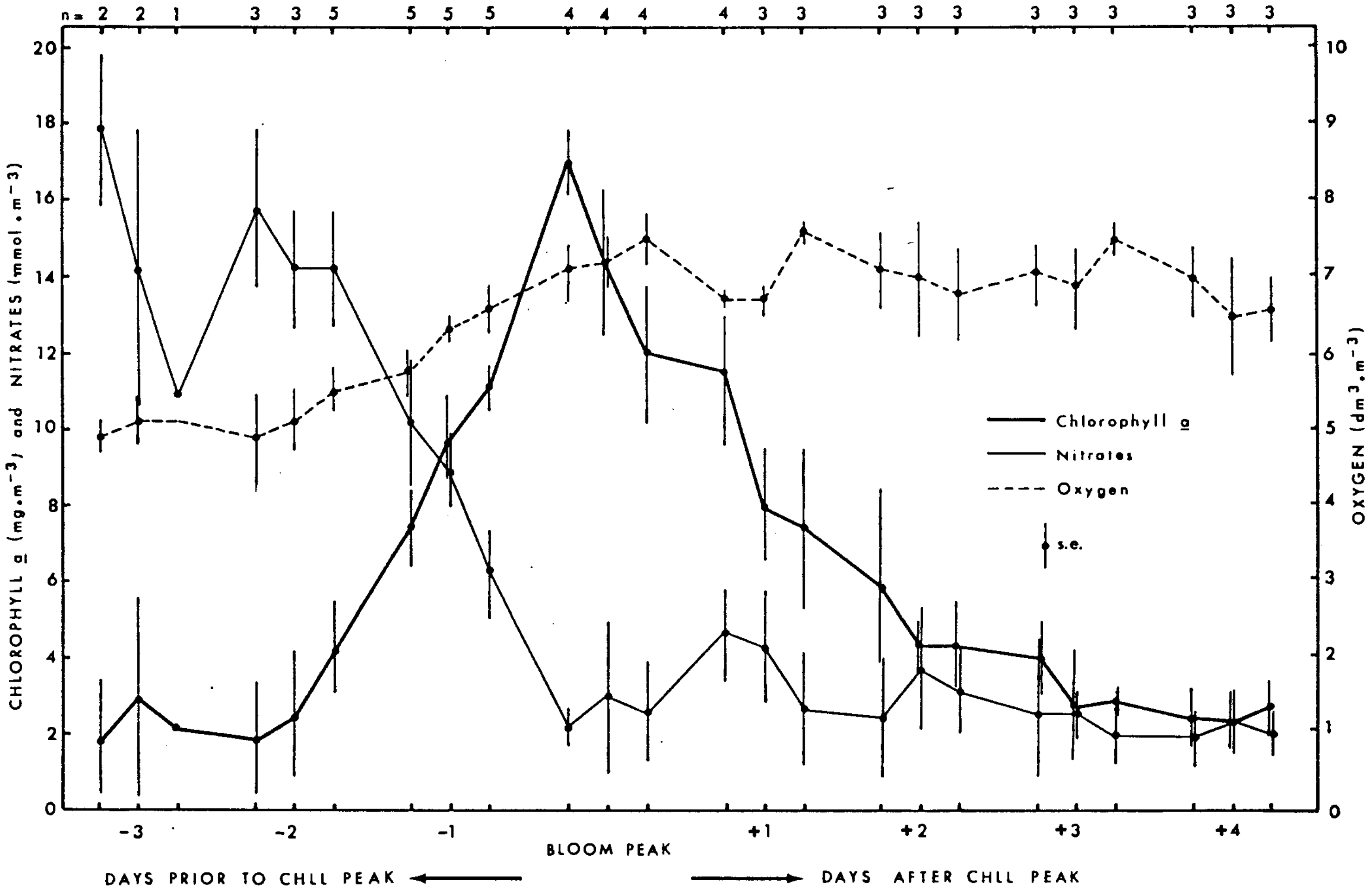


Fig.9.1: A simple model of phytoplankton bloom development in upwelled water showing changes in chlorophyll *a*, nitrate and oxygen concentrations with time. These curves were obtained by superimposing the chlorophyll *a* peaks (see Fig.6.4) along the five Drogue tracks (A-E) and calculating mean values for chlorophyll *a*, nitrate and oxygen during the build up and decline of the bloom (n is the number of data from which each mean value is calculated and s.e. is the standard error).

should not be interpreted as indicating that such a biological "lag" phase does not exist locally. At the commencement of each study period, the presence of at least a weak thermocline (see Fig.5.12) and the relatively lower nutrient and higher chlorophyll _a_ and oxygen concentrations at the sea surface (see Table 6.3), suggest that surface water had been in the euphotic zone long enough for at least some photosynthesis to occur. Thus the population may already have adapted to the high light levels in the euphotic zone and reached the MacIsaac _et al_ (1985) "shift-up" stage characterized by rapid growth. Even if it does exist, such a biological "lag" is unlikely to have a major effect on the productivity of the southern Benguela upwelling zone as whole, as the areas of intense vertical transport are relatively small (Taunton-Clark 1985). Once conditions stabilize sufficiently for the products of photosynthesis to accumulate, chlorophyll _a_ concentrations increase from low levels to peak within a few days and then decrease almost as rapidly. Phytoplankton bloom development in upwelled water is summarized in Fig.9.1. This simple empirical model was constructed by superimposing the chlorophyll _a_ peaks from the five time-series presented in Chapter 6 (Fig.6.4), and by calculating mean chlorophyll _a_, oxygen and nitrate concentrations in the euphotic zone during the build up and decline periods of the blooms. The whole cycle of bloom development is completed within about six to eight days (see Table 6.4 and Fig.9.1). Nitrates (and silicates) are rapidly stripped from the water column during the build up of the bloom, while oxygen concentrations increase and then level off as it declines.

Mean daily productivity estimates (using the ^{14}C-uptake, particle volume and Redfield methods) during the build up and decline of

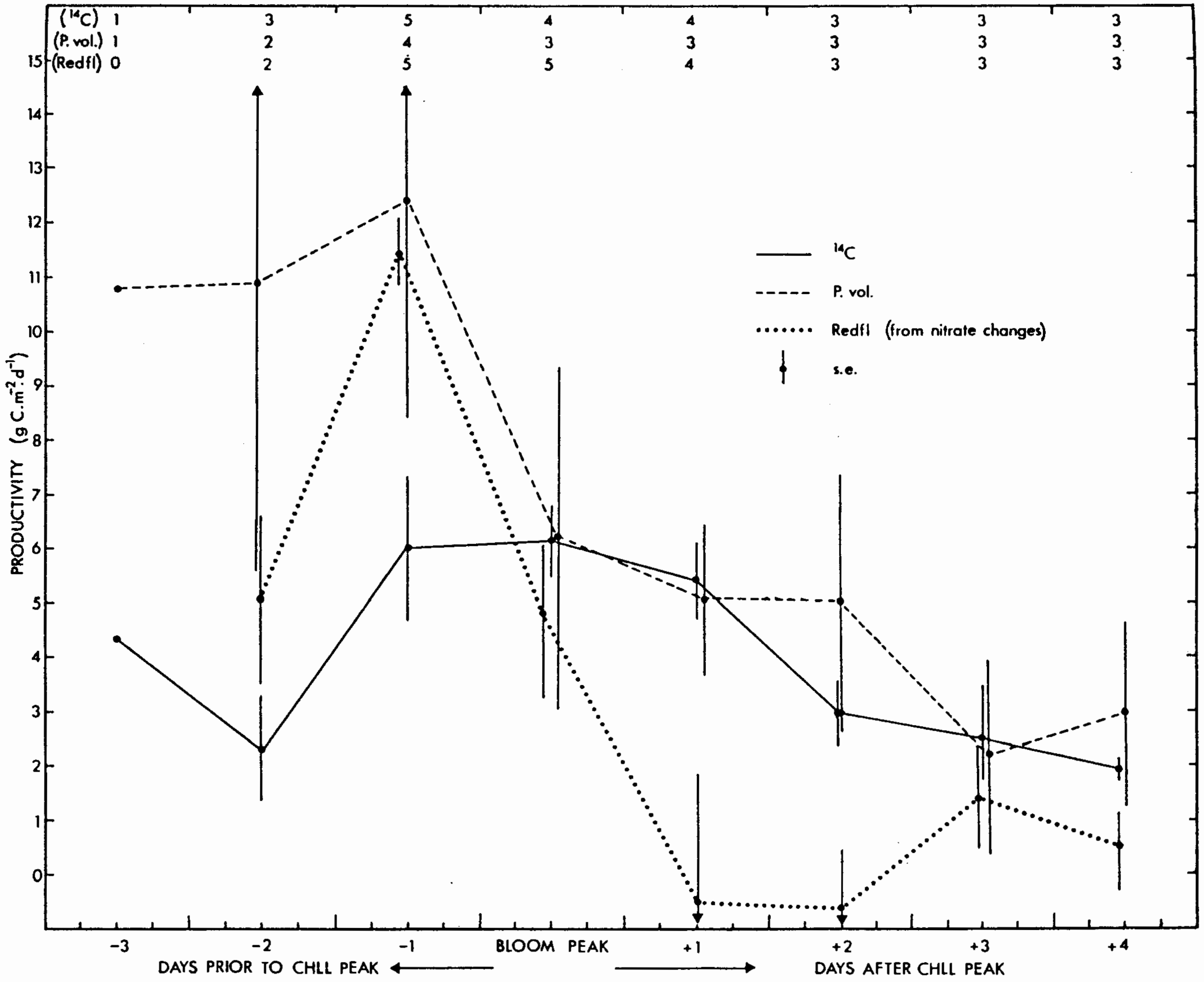


Fig.9.2: Mean productivity estimates, using the ^{14}C-uptake (^{14}C), particle volume (P.vol) and Redfield (Redfl) methods, during the build up and decline of a phytoplankton bloom using data for Cruises A-E (n is the number of data from which each mean is calculated and s.e. is the standard error). The "bloom peak" and days prior to and after the peak coincide with those in Fig.9.1.

the "model" bloom (Fig.9.1) are presented in Fig.9.2. These data may give some indication of the relative importance of "new" and "regenerated" (Dugdale and Goering 1967) productivity. As Redfield productivity was calculated from changes in the nitrate content of the upper 20 metres, it represents "new" gross productivity (i.e. including particulate, excreted and respired carbon) whereas ^{14}C and particle volume estimates approximately represent total (i.e. "new" plus "regenerated") particulate net productivity. Standard errors (Fig.9.2) for the particle volume productivity means are generally greater than those for ^{14}C and Redfield mean estimates. Fig.9.2 shows that, prior to the bloom peak, Redfield productivity falls between particle volume and ^{14}C estimates. After the bloom peak, ^{14}C and particle volume estimates are similar while Redfield estimates are low, suggesting that regenerated production becomes more important during bloom decline. However, negative estimates (with wide confidence limits) of Redfield productivity indicate that the nitrate content of the upper 20 metre layer increased (presumably due to the entrainment of "new" nutrients on some occasions e.g. Day 5 of Cruises A and E, see Fig.8.4) thus complicating Redfield productivity calculations. Nonetheless, the subsequent increase in Redfield productivity reflects the "new" production due to this input of new nutrients after the primary bloom in newly upwelled water. The difference between the Redfield estimates and the mean of ^{14}C-uptake and particle volume estimates on Days +3 and +4 (Fig.9.2) depicts the relative importance of "new" and "regenerated" productivity after bloom decline, with regenerated productivity contributing about 60% of total productivity at this stage. During bloom build up, however, "new" productivity probably accounts for some 100% of the total productivity (the total being calculated as the mean rate for Days -2 and -1 of both particle volume and ^{14}C methods), while during the "bloom peak" it accounts for about 80% of total productivity. Thus "regenerated" production probably forms between 0% and 60% of total production in Benguela coastal upwelled waters at different stages of bloom development and decline. Probyn (1985), using 15N-uptake experiments, reports that "regenerated" productivity accounts for about 30% of total productivity in the Benguela shelf area.

Although bloom decline is strongly associated with low nitrate concentrations, biomass-standardized productivity measurements give little indication of growth being nutrient limited. This suggests that the rapid "stripping" of nitrates and silicates from the euphotic zone may be a sinking "trigger" so that phytoplankton adapted to high nutrient concentrations sink either slowly as vegetative cells (until perhaps they encounter high nutrients at the nutricline) or, rapidly as resting spores which may form in response to adverse environmental conditions (Pitcher 1986). Low nutrients may also induce cell death. Although cell death is difficult to quantify (Harris 1984), or even qualitatively substantiate in this study (the phytoplankton samples were poorly preserved), the possibility should not be ignored. In any case, biomass levels in the upper water column would decrease and the bloom would decline, leaving a smaller biomass comprised of phytoplankton types better adapted to lower nutrient conditions typical of old upwelled water. The phytoplankton which sinks out of the euphotic zone may be consumed by meso-zooplankton and/or enter the microheterotrophic food web either in the water column or on the sea bed (Lucas et al 1986). The release of organic matter by living cells during photosynthesis or by dead cells, provides suitable organic nutrients for the small free-living bacteria common in the euphotic zone, whereas the phytoplankton detritus provides a substrate for attached bacteria which are more prevalent near the end of a bloom and below the euphotic zone (Muir 1986). Resting spores, on the other hand, may remain viable on the sea bed to form the seed material which may be upwelled back into the euphotic zone to initiate another phytoplankton bloom, and thus maintain local communities of diatom species in the coastal zone (Pitcher 1986).

Bloom decline may also result from turbulent advection. Blooms may be dispersed by mixing with chlorophyll- and nutrient-poor water adjacent to the tongue. However, should nutrient-rich water be entrained, the bloom may be diluted, but the nutrient enrichment would promote further growth and thus prolong the bloom (e.g. Cruise A). On the other hand, light limitation due to deep mixing may also cause bloom decline when carbon loss by respiration exceeds photosynthetic production.

Comparison of phytoplankton biomass estimates calculated from productivity measurements, with observed changes in the standing stocks (Fig.8.5) gives some indication of the loss of primary organic matter during the monitoring periods. As the influence of zooplankton grazing on this "excess production" was found to be low (almost negligible), losses were attributed either to phytoplankton sinking out of the upper 20 m once nitrates were stripped from the surface layers, and/or to physical processes dispersing the bloom. Surface waters shearing over deeper waters may move phytoplankton in the upper euphotic zone away from the drogue, while turbulent advection may dilute the bloom with phytoplankton-poor water and/or cause light limitation of production by deep mixing.

Therefore, pulsed and strongly three-dimentional upwelling in the southern Benguela region does not necessarily result in discrete parcels of water moving offshore with blooms developing and declining intact. Strong shearing motions, vertical turbulence and horizontal advection may cause considerable mixing of new and old upwelled water, which influences the expected pattern of bloom development. Thus, although a constant sequence of events occurs after stabilization, there are marked discrepancies between the potential and actual *in situ* standing crops.

9.6 General

Satellite imagery indicates that tongues and filaments of cool, chlorophyll-rich water extend downstream from upwelling centres (Shannon *et al* 1985). These near surface features can alter rapidly as winds change from offshore to onshore. Wind clearly plays a dominant role in the duration and location of phytoplankton blooms arising from upwelling; this is not surprising considering the relatively shallow euphotic zone common in this area, where the bulk of the primary production occurs within the upper 10-20 metres and the thermocline depth is generally less than 25 m (Nelson 1985). From this perspective, the southern Benguela region probably falls between upwelling areas off Northwest Africa, where deep mixing is reported to be an important factor limiting primary production, and Peru, where the depth of mixing seldom exceeds 20 m (Huntsman and Barber 1981, Barber and Smith

1981, Dugdale and Wilkerson 1985).

Many of the phytoplankton blooms in the southern Benguela region are dominated by chain-forming spiny diatoms (e.g. Chaetoceros) which are not easily consumed by copepods (G. Paffenhoffer pers.comm.), yet these "weed" blooms can remove much of the new nutrient from inshore surface waters. On sinking, however, these diatoms may provide a suitable organic base for the microheterotrophic foodweb (Lucas et al 1986) in the form of dissolved or particulate organic matter on which free-living or attached bacteria may feed (Muir 1986). The bacteria may be consumed by micro-zooplankton organisms such as tinntinids, ciliates, flagellates or other protozoans which, in turn, may form suitably-sized food particles for various stages of zoo- and ichthyoplankton (Beers and Stewart 1969, Hargraves 1981, Houde and Lovdal 1984). This "alternative route" in the pelagic food web suggests that food production is not limited to the euphotic zone and consumers be provided with a greater variety of shapes, sizes and types of food. However, losses between trophic levels may limit the significance of this pathway. It is certainly not the "short food chain" that Ryther (1969) described for upwelling regions.

Much of the area inshore of the oceanic front is remote from the near-shore upwelling centres and the tongues in which the "primary blooms" develop. In spite of this, relatively high chlorophyll a concentrations are found right up to the oceanic front, i.e. way beyond the offshore limit of drogue movement in this study. Regenerated nutrients may, of oourse, support a moderate and more stable biomass of phytoplankton in aged upwelled waters, the succeeding species possibly being a more suitable base for the zooplankton-pelagic fish food chain. However it is also likely that turbulence, due to wind mixing (which may increase with distance from shore) (Kamstra 1985), shear (resulting from the wind dragging surface water offshore), internal waves, shelf-edge upwelling, etc. may entrain nutrients into the euphotic zone. These new nutrients would help fuel primary productivity at a level necessary to maintain both the dominance of diatoms in the shelf region (D. Horstman, SFRI, unpublished data) and the relatively high chlorophyll concentrations apparent over the outer shelf in satellite images and extensive ship surveys (Andrews and Hutchings 1980, Shannon <u>et al</u> 1984). Suitable conditions for phytoplankton growth in this system after the "primary bloom" may thus be provided by alternation of turbulent and stable water columns (Legendre 1981), and by nutrient regeneration by micro- and meso-heterotrophic organisms.

Realization of the potential phytoplankton crop and its partitioning into different trophic pathways is clearly a major deficit in our knowledge of food chain dynamics in the Benguela region. Attention is presently being channelled in this direction. This study has focussed on the initial stages of the production cycle, to provide realistic values of primary production and phytoplankton bloom development in a wide variety of conditions, and has provided greatly improved insight into the mechanism whereby injections of new nutrients at discrete upwelling sites are disseminated as phytoplankton particles in the coastal waters of the southern Benguela. For any realistic ecosystem budget to be drawn up, however, a larger area needs to be considered. Spatial and temporal (short-term and seasonal) distribution patterns of chlorophyll pigments (apparent in satellite imagery), should be combined both with the nutrient (or possibly temperature) status of the upper water column and the measurements of primary productivity rates reported in this thesis, to provide more realistic estimates of total primary production in the Benguela ecosystem. The classical approach of estimating primary productivity from the total amount of nutrients available to the phytoplankton for photosynthesis in the euphotic zone (and from the increase in dissolved oxygen), has been combined with "bottle" techniques, based on ^{14}C-uptake and increases in particle volume, to obtain independantly derived estimates of phytoplankton production in newly upwelled water. Moreover, the study has been repeated five times to gain some insight of the variation in primary production and phytoplankton bloom development in upwelled water in the southern Benguela region.

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LITERATURE CITED

ANDREWS, W.R.H. and D.L. CRAM 1969 - Combined aerial and shipboard upwelling study in the Benguela current Nature, Lond. 224(5222): 902-904.

ANDREWS, W.R.H. and L. HUTCHINGS 1980 - Upwelling in the Southern Benguela Current. Prog. Oceanogr. 9(1): 81 pp.

BAILEY, G.W. 1983 - Pilot study of the vertical flux of P.O.C. and P.O.N. in St Helena Bay. S. Afr. J. Sci. 79(4): 145-146.

BAILEY, G.W. and P. CHAPMAN 1985 - The nutrient status of the St Helena Bay region in February 1979. In South African Ocean Colour and Upwelling Experiment. Shannon, L.V. (Ed.). Cape Town; Sea Fisheries Research Institute: 125-145.

BANG, N.D. 1973 - Characteristics of an intense ocean frontal system in the upwelling regime west of Cape Town. Tellus 25: 256-265.

BANG, N.D. and W.R.H. ANDREWS 1974 - Direct current measurements of a shelf-edge frontal jet in the southern Benguela system. J. Mar. Res. 32(3): 405-417.

BANSE, K. 1977 - Determining the carbon-to-chlorophyll ratio of natural phytoplankton. Mar. Biol. 41: 199-212.

BARBER, R.T., DUGDALE, R.C., MacISAAC, J.J. and R.L. SMITH 1971 - Variations in phytoplankton growth associated with the source and conditioning of upwelling water. Inv. Pesq. 35(1): 171-193.

BARBER, R.T. and R.L. SMITH 1981 - Coastal upwelling ecosystems. In Analysis of Marine Ecosystems. Longhurst, A.R. (Ed.). London; Academic Press: 31-68.

BARLOW, R.G. 1982a - Phytoplankton ecology in the southern Benguela current. I. Biochemical composition. J. Exp. Mar. Biol. Ecol. 63: 209-227.

BARLOW, R.G. 1982b - Phytoplankton ecology in the Southern Benguela current. III. Dynamics of a bloom. J. Exp. Mar. Biol. Ecol. 63: 239-248.

BARLOW, R.G. 1984a - Dynamics of the decline of a phytoplankton bloom after an upwelling event. Mar. Ecol. Prog. Ser. 16: 121-126.

BARLOW, R.G. 1984b - Physiological responses of phytoplankton to turbulent and stable environments in an upwelling region. J. Plankt. Res. 6(3): 385-397.

BEERS, J.R., STEVENSON, M.R., EPPLEY, R.W. and E.R. BROOKS 1971 - Plankton populations and upwelling off the coast of Peru, June 1969. Fish. Bull. U.S. 69: 859-876.

BEERS, J.R. and G.L. STEWART 1969 - Micro-zooplankton and its abundance relative to the larger zooplankton and other seston components. Marine Biology. 4: 182-189.

BEERS, J.R. STEWART, G.L. and K.D. HOSKINS 1977 - Dynamics of microzooplankton populations treated with copper: Controlled ecosystem pollution experiment. Bull. Mar. Sci. 27: 66-79.

BIENFANG, P.K. 1981 - Sinking rate dynamics of *Cricosphaera carterae* Braarud: effects of growth rate, limiting substrate and diurnal variations in steady state populations. J. Exp. Mar. Biol. Ecol. 49: 217-333.

BLACH, N., BOYD, M. and M.M. MULLIN.1978 - Large-scale tower tank systems. Rapp. P.- v. Réun. Cons. Int. Explor. Mer 173: 13-21.

BORCHERS, P. and L. HUTCHINGS 1986 - Starvation tolerance, development time and egg production of *Calanoides carinatus* in the Southern Benguela Current. J. Plankt. Res. 8(5): 855-874.

BOYD, A.J. 1982 - Small-scale measurements of vertical shear and rates of horizontal diffusion in the southern Benguela current. Fish. Bull. S. Afr. 16: 1-9.

BOYD, A.J. 1983 - Intensive study of the currents, winds and hydrology at a coastal site off central South West Africa. Investl Rep. Sea Fish. Res. Inst. S. Afr. 126: 1-47.

BRINK, K.H. 1983 - The near-surface dynamics of coastal upwelling. Prog. Oceanog. 12: 223-257.

BROWN, P.C. 1982a - A note on the effect of bottle size on phytoplankton production measurements. Fish. Bull. S. Afr. 16: 21-24.

BROWN, P.C. 1982b - Phytoplankton production measured *in situ* and under simulated *in situ* conditions in the southern Benguela upwelling region. Fish. Bull. S. Afr. 16: 31-37.

BROWN, P.C. 1982c - The effect of temporary exposure of phytoplankton to mid-day irradiances on *in situ* production estimates in the southern Benguela upwelling region. Fish. Bull. S. Afr. 16: 39-44.

BROWN, P.C. 1983 - Evaluation of the "time factor" and "light factor" methods for estimating daily phytoplankton production at the sea surface. S. Afr. J. mar. Sci. 1: 139-143.

BROWN, P.C. 1984 - Primary production at two contrasting nearshore sites in the southern Benguela upwelling region, 1977-1979. S. Afr. J. mar. Sci. 2: 205-215.

BROWN, P.C. and J.G. FIELD 1985 - Diel variation in production rates of natural phytoplankton populations in the southern Benguela upwelling region. Botanica Marina 28: 201-208.

BROWN, P.C. and J.G. FIELD 1986 - Factors limiting phytoplankton production in a nearshore upwelling area. J. Plankt. Res. 8 (1): 55-68.

BROWN, P.C. and J.C. HENRY 1985 - Phytoplankton production, chlorophyll a and light penetration in the southern Benguela region during the period between 1977 and 1980. In South African ocean Colour and Upwelling Experiment. Shannon, L.V. (Ed.). Cape Town; Sea Fisheries Research Institute: 211-218.

BROWN, P.C. and L. HUTCHINGS 1985 - Phytoplankton distribution and dynamics in the Southern Benguela Current. Int. Symp. Upw. W Afr., Inst. Inv. Pesq., Barcelona 1985. 1: 319-344.

CARPENTER, E.J. and J.S. LIVELY 1980 - Review of estimates of algal growth using ^{14}C tracer techniques. In Primary Productivity in the Sea. Falkowski, P.G. (Ed.). Plenum Press, New York: 161-178.

CASSIE, R.M. 1962 - Microdistribution and other error components of ^{14}C primary production estimates. Limnol. Oceanogr. 7(2): 121-130.

COWLES, T. 1977 - Copepod feeding in the Peru upwelling system. Ph.D. thesis, Duke University: 173 pp.

CURRIE R.I. and P. FOXTON 1956 - The Nansen closing method with vertical plankton nets. J. mar. biol. Ass. U.K. 35(3): 483-492.

CUSHING, D.H. 1953 - Studies on plankton populations. J. du Conseil 19(1): 3-22.

CUSHING, D.H. 1971 - Upwelling and fish production. Adv. Mar. Biol. 9: 255-334.

DE DECKER, A.H.B. 1970 - Notes on an oxygen-depleted subsurface current off the west coast of South Africa. Investl Rep. Sea Fish. Inst. S. Afr. 122: 1-24.

DE DECKER, A.H.B. 1973 - Agulhas Bank Plankton. In Ecological Studies. Analysis and synthesis. Vol. 3. Zeitschel, B. (Ed.). Springer Verlag. Berlin. Heidelberg. New York: 189-219.

DUGDALE, R.C. 1972 - Chemical oceanography and primary productivity in upwelling regions. Geoforum 11: 47-61.

DUGDALE, R.C. 1983 - Effects of source nutrient concentrations and nutrient regeneration on production of oceanic matter in coastal upwelling centres. In Coastal Upwelling, Part A. Suess, E. and J. Thiede (Eds). Plenum Publ. Corp.: 175-~182.

DUGDALE, R.C. and J.J. GOERING 1967 - Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol. Oceanogr. 12: 196-206.

DUGDALE, R.C. and F.P. WILKERSON 1985 - Primary production in the Cap Blanc region. Int. Symp. Upw. W Afr., Ist. Inv. Pesq., Barcelona,1985. 1: 223-243.

EPPLEY, R.W., KOELLER, P. and G.T. WALLACE JR 1978 - Stirring influences the phytoplankton species composition within enclosed columns of coastal sea water. J. exp. mar.Biol. Ecol. 32: 219-239.

FEE, E.J. 1973 - Modelling primary production in water bodies: A numerical approach that allows vertical inhomogeneities. J. Fish. Res. Board Can. 30(10): 1469-1473.

FLEMMING, R.H. 1940 - The comparison of plankton and units for reporting populations and production. Proc. 6th Pac. Sci. Congr., Calif. 1939. 3: 535-540.

GILLBRICHT, M. 1969 - Calculations in marine planktology. Practical and theoretical problems. Int. Revue ges. Hydrobiol. 54(5): 645-660.

GOLDMAN, J.C., McCARTHY, J.J. and D.G. PEAVEY 1979 - Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature, Lond. 279: 210-215.

GRICE G.D. and M.R. REEVE 1982 - Marine Mesocosms. In Biological and Chemical Research in Experimental Ecosystems. Springer Verlag, New York. 430 pp.

GRILL, E.V. and F.A. RICHARDS 1964 - Nutrient regeneration from phytoplankton decomposing in seawater. J. Mar. Res. 22(1): 51-69.

HALLEGRAEFF, G.M. 1977 - A comparison of different methods used for the quantitative evaluation of biomass of freshwater phytoplankton. Hydrobiologia. 55(2): 145-165.

HARGRAVES, P.E. 1981 - Seasonal variations of tintinnids (Ciliophora: Oligotrichida) in Narragansett Bay, Rhode Island, U.S.A. J. Plank. Res. 3(1): 81-91.

HARRIS, G.P. 1978 - Photosynthesis, productivity and growth: The physiological ecology of phytoplankton. Arch. Hydrobiol. Beih. Ergeb. Limnol. 10: 1-171.

HARRIS, G.P. 1980 - The measurement of photosynthesis in natural populations of phytoplankton. In The Physiological Ecology of Phytoplankton. Morris, I. (Ed.). Uni. of Calif. Press, Berkeley: 129-187.

HARRIS, G.P. 1984 - Phytoplankton productivity and growth measurements: past, present and future. J. Plankt. Res. 6(2): 219-237.

HARRISON, W.G. 1983 - Uptake and recycling of soluble reactive phosphorus by marine microplankton. Mar. Ecol. Prog. Ser. 10: 127-135.

HARRISON, W.G., EPPLEY, R.W. and E.H. RENGER 1977 - Phytoplankton nitrogen budgets, and observations on copper toxicity : Controlled ecosystem pollution experiment. Bull. Mar. Sci. 27: 44-57.

HENDRIKSON, P., SELLNER, K.G., DE MENDIOLA, B.R., OCHOA, N. and R. ZIMMERMAN 1982 - The composition of particulate organic matter and biomass in the Peruvian upwelling region during ICANE 1977 (Nov.14-Dec.2). J. Plankt. Res. 4(1): 163-186.

HERBLAND, A., LE BORGNE, R. and B. VOITURIEZ 1973 - Production primaire, secondaire et regeneration des sels nutritifs dans l'upwelling de Mauritanie. Doc. Scient. Centre Rech. Oceanogr. Abidjan. Orstom 4(1): 1-75.

HERBLAND, A. and B. VOITURIEZ 1974 - La production primaire dans l'upwelling de Mauritanie en mars 1973. Cah. ORSTOM, sér. Océanogr. 12: 187-201.

HOBSON, L.A., MORRIS, W.J. and K.T. PIRQUET 1976 - Theoretical and experimental analysis of the ^{14}C technique and its use in studies of primary production. J. Fish. Res. Bd. Can. 3: 1715-1721.

HOLDEN, C.J. 1981 - Current profiling cruise, 20-27 October 1981. Data Report. Sea Fisheries Research Institute, Internal Report No. 91.

HOLDEN, C.J. 1985 - Currents in St Helena Bay inferred from radio-tracked drifters. In South African Ocean Colour and Upwelling Experiment. Shannon, L.V. (Ed.). Cape Town; Sea Fisheries Research Institute: 97-109.

HOLDEN, C.J. 1986 - Low frequency currents and continental shelf waves along the west coast of South Africa. Paper at Intl Symp. on Population and Community Ecology in the Benguela Upwelling Region and Comparable Frontal Systems. Cape Town, S. Afr., September 1986.

HOLLIBANCH, J.T., SEIBERT, D.L.R. and W.H. THOMAS 1981 - Observations on the survival and germination of resting spores of three Chaetoceros (Bacillariophyceae) species. J. Phycol. 17: 1-9.

HOLM-HANSEN, O. 1974 - Review and critique of primary productivity measurements. Calif. Coop. Ocean. Fish. Invest. 17: 53-56.

HOUDE, E.D. and J.A. LOVDAL - Seasonality of occurrence, foods and food preferences of ichthyoplankton in Biscayne Bay, Florida. Estuarine, Coastal and Shelf Science. 18: 403-419.

HUNTSMAN, S.A. and R.T. BARBER 1977 - Primary production off northwest Africa: the relationship to wind and nutrient conditions. Deep-Sea Research. 24: 25-33.

HUTCHINGS, L. 1979 - Zooplankton of the Cape Peninsula upwelling region. Ph.D. thesis, University of Cape Town: 206 pp.

HUTCHINGS, L. 1985 - Vertical distribution of mesozooplankton at an active upwelling site in the southern Benguela current, December 1969. Investl Rep. Sea Fish. Res. Inst. S. Afr. 129: 1-67.

JAMES, A.G. 1986 - Trophic ecology of Engraulis capensis in the southern Benguela region. Paper at Intl Symp. on Population and Community Ecology in the Benguela Upwelling Region and Comparable Frontal Systems. Cape Town, S. Afr., September 1986.

JONES, B.H. and D. HALPERN 1981 - Biological and physical aspects of a coastal upwelling event observed during March-April 1984 off northwest Africa. Deep-Sea Research 28A: 71-81.

JURY, M.R. 1980 - Characteristics of summer wind fields and air-sea interactions over the Cape Peninsula upwelling region. M.Sc. thesis, University of Cape Town: 131 pp.

JURY, M.R. 1985 - Case studies of alongshore variations is wind-driven upwelling in the southern Benguela region. In South African Ocean Colour and Upwelling Experiment. Shannon, L.V. (Ed.). Cape Town; Sea Fisheries Research Institute: 29-46.

KAMSTRA, F. 1985 - Environmental features of the southern Benguela with special reference to the wind stress. In South African Ocean Colour and Upwelling Experiment. Shannon, L.V. (Ed.). Cape Town; Sea Fisheries Research Institute:13-27.

KREMER, J.N. and S.W. NIXON 1978 - A Coastal Marine Ecosystem, Simulation and Analysis. Springer Verlag, New York. 217 pp.

LEAN, D.R.S. and B.K. BURNISON 1979 - An evaluation of errors in the ^{14}C method of primary production measurement. Limnol. Oceanogr. 24(5): 917-928.

LEGENDRE, L. 1981 - Hydrodynamic control of marine phytoplankton production: The paradox of stability. In Ecohydrodynamics. Nihoul, J.C.J. (Ed.). Elsevier Scientific Publishing Company, Amsterdam: 191-207.

LUCAS, M.I., PROBYN, T.A. and S.J. PAINTING 1986 - Microplankton interaction in carbon flows and nitrogen regeneration in upwelling waters. Paper at Intl Symp. on Population and Community Ecology in the Benguela Upwelling Region and Comparable Frontal Systems. Cape Town, S. Afr., September 1986.

MACISAAC, J.J., DUGDALE, R.C., BARBER, R.T., BLASCO, D. and T.T. PACKARD 1985 - Primary production cycle in an upwelling centre. Deep Sea Res. 32(5): 503-529.

MACKAS, D.L., Denman, K.L. and M.R. Abbott 1985 - Plankton patchiness: Biology in the physical vernacular. Bull. Mar. Sci. 37(2): 652-674.

MENZEL, D.W. and J. CASE 1977 - Concept and design : Controlled eco-system pollution experiment. Bull. Mar. Sci. 27: 1-7.

MINAS, H.J., CODISPOTI, L.A. and R.C. DUGDALE 1982 - Nutrients and primary production in the upwelling region off Northwest Africa. Rapp. P.-v. Réun. Cons. int. Explor. Mer 180: 148-183.

MONTEIRO, P.M.S. 1986 - The potential for the use of high performance liquid chromatography in marine research. Trans. Roy. Soc. S. Afr. 46(1): 15-26.

MOREL A. and R.C. SMITH 1974 - Relation between total quanta and total energy for aquatic photosynthesis. Limn. Oceanogr. 19(4): 591-600.

MORRIS, I. 1980 - Paths of carbon assimilation in marine phytoplankton. In Primary Productivity in the Sea. Falkowski, P.G. (Ed.). Plenum Press, New York: 161-178.

MOSTERT, S.A. 1983 - Procedures used in South Africa for the automatic photometric determination of micronutrients in seawater. S. Afr. J. mar. Sci. 1: 189-198.

MUIR, D.G. 1986 - Bacterial populations and their activities in the Benguela upwelling system. Ph.D. thesis, University of Cape Town. pp.

MULLIN, M.M. and P.M. EVANS 1974 - The use of a deep tank in plankton ecology. 2. Efficiency of a planktonic food chain. Limnol. Oceanogr. 19: 902-911.

MULLIN, M.M., SLOAN, P.R. and R.W. EPPLEY 1966 - Relationship between carbon content, cell volume and area in phytoplankton. Limnol. Oceanogr. 11(2): 307-311.

NELSON, D.M. and J.J. GOERING 1978 - Assimilation of silicic acid by phytoplankton in the Baja California and North West Africa upwelling system. Limnol. Oceanogr. 23: 508-517.

NELSON, G. 1985 - Notes on the physical oceanography of the Cape Peninsula upwelling system. In South African Ocean Colour and Upwelling Experiment. Shannon~, L.V. (Ed.). Cape Town: Sea Fisheries Research Institute: 63-95.

NELSON, G. and L. HUTCHINGS 1983 - The Benguela upwelling area. Prog. Oceanogr. 12(3): 333-356.

OLIVIERI, E.T. 1983 - Colonization, adaptations and temporal changes in diversity and biomass of a phytoplankton community in upwelled water off the Cape Peninsula, South Africa, in December 1979. S. Afr. J. mar. Sci. 1: 77-109.

OLIVIERI, E.T. 1985 - Feasibility of estimating phytoplankton size and biomass in fresh and preserved samples from the Benguela current with a Coulter counter. S. Afr. J. mar. Sci. 3: 99-110.

OLIVIERI, E.T. and L. HUTCHINGS 1985a - Volumetric estimates of phytoplankton production in newly upwelled waters of the southern Benguela Current. In Phytoplankton growth and zooplankton grazing in the southern Benguela current. Ph.D. thesis, University of Cape Town: 146 pp.

OLIVIERI, E.T. and L. HUTCHINGS 1985b - The role of herbivorous mesozooplankton on newly developed phytoplankton blooms in the southern Benguela Current. In Phytoplankton growth and zooplankton grazing in the southern Benguela current. Ph.D. thesis, University of Cape Town: 146 pp.

OLIVIERI, E.T., HUTCHINGS, L., BROWN, P.C. and R.G. BARLOW 1985 - The development of phytoplankton communities in terms of their particle size frequency distribution, in newly upwelled waters of the southern Benguela Current. In Int. Symp. Upw. W Afr., Inst. Inv. Pesq., Barcelona 1985. 1: 345-371.

PARSONS, T.R. 1978 - Controlled ecosystem experiments. Introduction. Rapp. P.- v. Réun. Cons. Int. Explor. Mer 173: 5-6.

PARSONS, T.R., TAKAHASHI, M. and B. HARGRAVE 1977 - Biological Oceanographic Processes. 2nd Ed. Pergamon Press. Oxford. New york. Toronto. Sydney. Paris. Frankfurt. 332 pp.

PARSONS, T.R., TAKAHASHI, M. and B. HARGRAVE 1984 - Biological Oceanographic Processes. 3nd Ed. Pergamon Press. Oxford. New york. Toronto. Sydney. Paris. Frankfurt. 330 pp.

PETERSON, B.J. 1980 - Aquatic primary productivity and the ^{14}C-CO$_2$ method: A history of the productivity problem. Ann. Rev. Ecol. Syst. 11: 359-385.

PETTERSON, H. 1939 - The plankton shaft. In Large-scale plankton cultures. Petterson, H., Gross, F. and F. Koczy (Eds). Götenborg's K. Vetensk. Vitterh. Samh. Handl., Ser. 5B 6(13): 1-24.

PILLAR, S.C. 1984a - Diel variation in the vertical distribution of some common zooplankton species off the west coast of South Africa. S. Afr. J. mar. Sci. 2: 71-80.

PILLAR, S.C. 1984b - A comparison of the performance of four zooplankton samplers. S. Afr. J. mar. Sci. 2: 1-18.

PILLAR, S.C. 1984c - Laboratory studies on the larval growth of Euphausia lucens (Euphausiacea). S. Afr. J. mar. Sci. 2: 43-48.

PILLAR, S.C. 1986 - Temporal and spatial variations in Copepod and Euphausiid biomass off the southern and south-western coasts of South Africa in 1977/78. S. Afr. J. mar. Sci. 4: 219-229.

PILSON, M.E.Q., OVIATT C.A., VARGO G.A. and S.L. VARGO 1979 - Replicability of MERL microcosms: Initial observations. In Advances in Marine Environmental Research. Jakoff, F.S. (Ed.). EPA-600/9-79-035, U.S. EPA, Environ. Res. Lab., Narragensett, R.I.: 359-381.

PITCHER, G.C. 1986 - Sedimentary flux and the formation of resting spores of selected Chaetoceros species at two sites in the southern Benguela system. S. Afr. J. mar. Sci. 4: 231-244.

POMEROY, L.R. 1974 - The ocean's food web, a changing paradigm. Bioscience. 24(a): 499-504.

POND, S. and G.L. PICKARD 1978 - Introductory Dynamic Oceanography. Oxford; Pergamon Press: 81-133.

PROBYN, T.A. 1985 - Nitrogen uptake by size-fractioned phytoplankton populations in the southern Benguela upwelling system. Mar. Ecol. Prog. Ser. 22(3): 249-258.

REDFIELD, A.C., KETCHUM, B.H. and F.A. RICHARDS 1963 - The influence of organisms on the composition of sea-water. In The Sea. Vol. 2. The composition of sea water. Hill, M.N. (Ed.). Interscience Publishers, John Wiley and sons. New York. London: 26-77.

RICHARDS, F.A. 1958 - Dissolved silicate and related properties of some western North Atlantic and Caribbean waters. J. Mar. Res. 17: 449-465.

RYTHER, J.H. 1969 - Photosynthesis and fish production in the sea. The production of organic matter and its conversion to higher forms of life vary throughout the world ocean. Science 166: 72-76.

RYTHER, J.H., MENZEL, D.W., HULBURT E.M., LORENZEN C.J. and N. CORWIN 1971 - The production and utilization of organic matter in the Peru coastal current. Inv. Pesq. 35(1): 43-59.

SCHULTZ, S. 1982 - A comparison of primary production in upwelling regions off Northwest and Southwest Africa. Rapp. P.- v. Réun. Cons. int. Explor. Mer 180: 202-204.

SELLNER, K.G. 1981 - Primary productivity and the flux of dissolved organic matter in several marine environments. Mar. Biol. 65: 101-112.

SHANNON, L.V. 1985a - The Benguela ecosystem. Part I. Evolution of the Benguela, physical features and processes. Oceanogr. Mar. Biol. Ann. Rev. 23: 105-182.

SHANNON, L.V. (Ed.) 1985b - South African Ocean Colour Experiment. Cape Town; Sea Fisheries Research Institute: 270 pp.

SHANNON, L.V., AGENBAG, J.J. and M.E.L. BUYS 1986 - Interactions between the Angola and Benguela systems. Paper at Intl Symp. on Population and Community Ecology in the Benguela Upwelling Region and Comparable Frontal Systems. Cape Town, S. Afr., September 1986.

SHANNON, L.V., HUTCHINGS, L., BAILEY, G.W. and P.A. SHELTON 1984 - Spatial and temporal distribution of chlorophyll in southern African waters as deduced from ship and satellite measurements and their implications for pelagic fisheries. S. Afr. J. mar. Sci. 2: 109-130.

SHANNON, L.V., MOSTERT, S.A., WALTERS, N.M. and F.P. ANDERSON 1983 - Chlorophyll concentrations in the southern Benguela current region as determined by satellite (Nimbus-7 coastal zone colour scanner). J. Plankt. Res. 5(4): 565-583.

SHANNON, L.V., NELSON, G. and M.R. JURY 1981 - Hydrological and meteorological aspects of upwelling in the southern Benguela current. In Coastal and Estuarine Sciences I. Coastal Upwelling. Richards, F.A. (Ed.). Washington, D.C.; American Geophysical Union: 146-159.

SHANNON, L.V. and S.C. PILLAR 1986 - The Benguela Ecosystem. Part III. Plankton. Oceanogr. Mar. Biol. Ann. Rev. 24: 65-170.

SHANNON, L.V., WALTERS, N.M. and S.A. MOSTERT 1985 - Satellite observations of surface temperature and near surface chlorophyll in the southern Benguela region. In South African Ocean Colour Experiment. Shannon, L.V. (Ed.). Cape Town; Sea Fisheries Research Institute: 183-210.

SHELDON, R.W. and W.H. SUTCLIFFE 1978 - Generation times of 3 h for Sargasso Sea microplankton determined by ATP analysis. Limnol. Oceanog. 23: 1051.

SHELDON, R.W., SUTCLIFFE, W.H., Jr. and A. PRAKASH 1973 - The production of particles in the surface waters of the ocean with particular reference to the Sargasso Sea. Limnol. Oceanogr. 18(5): 719-733.

SHELTON, P.A., BOYD, A.J. and M.J. ARMSTRONG 1985 - The influence of large-scale environmental processes on neritic fish populations in the Benguela current system. CalCOFI Rep. 26: 72-91.

SHULENBERGER, E. and J.L. REID 1981 - The Pacific shallow oxygen maximum, deep chlorophyll maximum, and primary productivity, reconsidered. Deep Sea Res. 28a: 901.

SOURNIA, A. 1974 - Circadian periodicities in natural populations of marine phytoplankton. Adv. Mar. Biol. 12: 325-386.

SOURNIA, A. (Ed.) 1978 - Phytoplankton Manual. UNESCO Monographs on Oceanographic Methodology 6: 337 pp.

STRATHMANN, R.R. 1967 - Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. 12 (3): 411-418.

STRICKLAND, J.D.H. 1960 - Measuring the production of marine phytoplankton. Bull. Fish. Res. Bd Can. 122: 172 pp.

STRICKLAND, J.D.H. 1965 - Production of organic matter in the primary stages of the marine foodchain. In Chemical Oceanography. 1: 477-610. Riley, J.P. and G. Skirrow (Eds). Academic Press, London: 712 pp.

STRICKLAND, J.D.H., EPPLEY, R.W. and B.R. DE MENDIOLA 1969 - Phytoplankton populations, nutrients and photosynthesis in Peruvian coastal waters. Bol. Inst. del Mar del Peru 2: 37-45.

STRICKLAND, J.D.H. and T.R. PARSONS 1972 - A practical handbook of seawater analysis, 2nd Ed. Bull. Fish. Res. Bd Can. 167: 310 pp.

STRICKLAND J.D.H. and L.D.B. TERHUNE 1961 - The study of *in situ* marine photosynthesis using a large plastic bag. *Limnol. Oceanogr.* 6: 93-96.

STUART, V. 1986 - Feeding and metabolism of *Euphausia lucens* (Euphausiacea) in the southern Benguela current. *Mar. Ecol. Prog. Ser.* 30: 117-125.

SVERDRUP, H.U. 1953 - On conditions for the vernal blooming of phytoplankton. *J. Cons. int. Mer.* 18: 287-295.

SVERDRUP, H.U., JOHNSON, M.W. and R.H. FLEMMING 1942 - *The Oceans, their Physics, Chemistry, and General Biology.* Prentice-Hall Inc., New York: 1087 pp.

SWART, M.J. and R.G. BARLOW 1981 - Analysis of chlorophyll *a* in particulate matter. *Fish. Bull. S. Afr.* 14: 95-97.

TAUNTON-CLARK, J. 1982 - CUEX ART sea surface temperatures. Sea Fisheries Research Institute, Internal Report No. 81: 175 pp.

TAUNTON-CLARK, J. 1985 - The formation, growth and decay of upwelling tongues in responce to the mesoscale wind field during summer. In *South African Ocean Colour and Upwelling Experiment*. Shannon, L.V. (Ed.). Cape Town; Sea Fisheries Research Institute: 47-61.

TETT, P., HEANEY, S.I. and M.R. DROOP 1985 - The Redfield ratio and phytoplankton growth rate. *J. mar. biol. Ass. U.K.* 65: 487-504.

TILZER, M.M. 1984 - Estimation of phytoplankton loss rates from daily photosynthetic rates and observed biomass changes in Lake Constance. *J. Plankt. Res.* 6(2): 309-324.

VACHON, W.A. 1980 - Drifters. In *Air-sea interactions, instruments and methods*. Dobson, F., Hasse, L. and R. Davis (Eds). Plenum Press, New York: 201 pp.

VENRICK, E.L., BEERS, J.R. and J.F. HEINBOKEL 1977 - Possible consequences of containing microplankton for physiological rate measurements. *J. Exp. Mar. Biol. Ecol.* 26: 55-76.

VOLLENWEIDER, R.A. (Ed.) 1969 - *A Manual on Methods for Measuring Primary Production in Aquatic Environments - Including a Chapter on Bacteria.* Oxford; Blackwell: 213 pp.

VON BODUNGEN, B., VON BROCKEL, K., SMETACEK, V. and B. ZEITZSCHEL 1976 - The plankton tower. I. A structure to study water/ sediment interactions in enclosed water columns. *Mar. Biol.* 34: 369-372.

WALDRON, H. 1985 - Influences on the hydrology of the Cape Columbine/St. Helena Bay region. M.Sc thesis, University of Cape Town: 100 pp.

WULFF, F.W. and U. LARSSON 1982 - Model calculations of daily primary production from short-term *in situ* ^{14}C-measurements. (Unpublished document, Askö Laboratory, Stockholm).