

PHYTOPLANKTON PRODUCTION IN AGULHAS BANK WATERS (SOUTH AFRICA)

by

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DECLARATION

The text of the co-authored paper (Chapter 2) was written by Dr Robin Carter. I assisted with the collection of the data, the data analysis and the preparation of the figures. This paper was presented both orally (Dr Carter) and by poster (myself and Dr Carter) at the Benguela Ecology Programme Symposium at the University of Cape Town, September 1986.

The laboratory investigation of the field method of measurement of primary production (Chapter 3) was self-initiated and all laboratory work and data interpretation was primarily my own efforts.

All data presented in Chapters 4 and 5 were collected jointly with Dr Carter and C S I R physical oceanographers (V. Swart and Dr J. Largier). The interpretation and presentation of this data is my own and has not been published elsewhere, excluding the March 1986 data on the Alphard Banks (Chapter 4) which also appears in Chapter 2, here, however, in different context.

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Finally, though it is seldom done, I wish to express my gratitude for the great untamed beauty of nature, without which the questions addressed in this thesis would never have arisen.

Abstract - Carbon-14 measurements of community and size- fractionated production in continental shelf waters of the Agulhas Bank (South Africa) are presented. Auxilliary measurements included chlorophyll *a*, nitrate concentrations and thermal profiling of the water column.

During the winter and spring surveys, the mixed layer extended deeper than the euphotic zone, with nitrate and phytoplankton biomass being evenly distributed through the euphotic zone. Production maxima occurred at the 40 - 90 % surface irradiance light depths, with some evidence of surface photoinhibition. All surveys during summer months (December - March) showed a thermally stratified euphotic zone ($Z_{eu0.5\%}/Z_m = 1.1 - 2.2$), with a well defined nitracline within the thermocline. A subsurface chlorophyll maximum closely associated with the region of maximum nitrate gradient (3 - 10 % surface irradiance) was typical of summer measurements. Subsurface chlorophyll *a* concentrations were lower in western Agulhas Bank waters ($0.5 - 6 \mu\text{g.l}^{-1}$) than in eastern Agulhas Bank waters ($1 - 15 \mu\text{g.l}^{-1}$). Highest subsurface chlorophyll *a* concentrations ($15 - 40 \mu\text{g.l}^{-1}$) were measured during the late summer survey (March 1986) at the Alhard Banks station in a strongly stratified water column.

For profiles showing a very well developed subsurface chlorophyll maximum, the production maximum occurred at or slightly shallower than the depth of the chlorophyll maximum. In western Agulhas Bank waters, during surveys when a shallow (<30m) thermocline persisted, production maxima at 90 and 100% surface irradiance intensities were frequently observed. Integrated production values ranged between 70 and $1390 \text{ mgC.m}^{-2}.\text{h}^{-1}$. Minimum areal production rates were observed during winter (July), whilst maximum rates were measured during late summer (March). High euphotic zone production was also measured during the spring survey in western Agulhas Bank waters ($347 \text{ mgC.m}^{-2}.\text{h}^{-1}$), associated with the stabilising of the water column after winter mixing.

The <15 μm size-fraction was observed to account for much of total production (62 - 97%) during conditions of deep mixing in winter and a deep upper mixed layer during summer. During the spring survey and those surveys where a shallow (<35m) thermocline persisted, production was predominantly by the netplankton >15 μm size-fraction (60 - 87 %). Periods of enhanced netplankton

growth may be crucial for the sustaining of the large biomass of spawning anchovy present in western Agulhas Bank waters.

Vertical profiles, the subsurface chlorophyll and production maximum and size-fractionated production measurements are discussed with relevance to the control of phytoplankton production and potential trophic fluxes in Agulhas Bank waters.

Contents

	page
Chapter One: General Introduction	
Introduction	1
Aims of this study	1
The physical and chemical hydrology of the Agulhas Bank	2
The physical hydrology	2
Thermal stratification	3
Nutrients	4
Breakdown of stratification	5
Fish, phytoplankton and primary production	5
Anchovy distribution	5
Phytoplankton biomass	6
Phytoplankton production	8
Chapter Two: Thermocline characteristics and phytoplankton dynamics in Agulhas Bank waters	
Abstract	9
Introduction	9
Research area and methods	9
Results and discussion	12
Conclusion	16
Acknowledgements	17
Literature cited	17
Chapter Three: An evaluation of the radiocarbon technique of marine phytoplankton primary production measurement: potential errors and methodological precautions	
Introduction	19
Methods and materials	20
Materials	20
Culture species	20
Filters, scintillation vials and fluor	20
$^{14}\text{C-HCO}_3^-$ stock solution	20
Methods	21
Sample inoculation	21
Removal of inorganic carbon-14 residues	21
Filtration vacuum pressure and rinse effects	22
CO_2 -sorber addition and sample count stability	22

Results and discussion	23
¹⁴ C stock solution	23
Determination of sample initial activity	23
Sample decontamination of inorganic carbon-14 residues	23
Sample filtration and rinsing	24
Sample count stability and storage	25
The ¹⁴ C method	26
Chapter Four: Phytoplankton biomass and primary production in summer stratified waters over the Alphard Banks, Agulhas Bank.	
Introduction	30
Methods and materials	31
Results	32
Profiles: phytoplankton biomass and production	32
Water column phytoplankton chlorophyll <i>a</i> , primary production and nitrate distributions	33
Size-fractionated primary production measurements	34
Discussion	34
Chapter Five: Phytoplankton primary production in western Agulhas Bank waters	
Introduction	39
Materials and methods	40
Results	42
Vertical profiles	42
Integrated water column biomass and production rates	45
Size fractionated primary production and dominant phytoplankton species	45
Discussion	46
Seasonal variability of phytoplankton production	46
Formation of the subsurface chlorophyll maximum	49
Size-fractionated primary production and carbon fluxes in western Agulhas Bank waters	50
Chapter Six: General Conclusion	52
References	54

List of figures

	facing page
Figure 1.1. The hydrographic regime of the Agulhas Bank. (a) The location of primary production stations. (b) The physical hydrography and bottom topography of the Agulhas Bank (adapted from: LARGIER and SWART 1987). (c) The distribution of anchovy eggs in Agulhas Bank waters during a survey in November 1985 (from: HAMPTON 1987)	2
Figure 3.1. The time-course of decontamination of filter papers soaked in the vial with three different acid strengths.	23
Figure 3.2. The time-course of decontamination of 8ml filtrate sample aliquots acidified to pH 2-2.5 with 0.5 ml 0.5 N HCl.	24
Figure 3.3. The effect of vacuum pressure differential on filter count for the two algae species, <i>Chaetoceros gracilis</i> (o---o) and <i>Dunaliella primolecta</i> (x---x).	24
Figure 4.1. The geographical location of the Alphard Banks sampling station on the Agulhas Bank.	30
Figure 4.2. a - c. Vertical profiles of measurements of primary production (▲—▲), chlorophyll <i>a</i> (●---●), light (log I)(●---●), temperature (←—→) and nitrates (x---x) obtained during March 1986, (86/04), at the Alphard Banks station. % surface irradiance is given on the y-axis.	32
Figure 4.3. a - c. Vertical profiles of measurements of primary production (▲—▲), chlorophyll <i>a</i> (●---●), light (log I) (●---●), temperature (←—→) and nitrates (x---x) taken at the Alphard Banks station during the cruise 87/02/B, January 1987.	32
Figure 4.4. a - b. Vertical profiles of measurements of primary production (▲—▲), chlorophyll <i>a</i> (●---●), light (log I) (●---●), temperature (←—→) and nitrates (x---x) taken at the Alphard Banks station during the cruise 88/01/C, January 1988.	33
Figure 5.1. The locations of midshelf (QP and DP) and offshore (OFS 1 , 2, 3) primary production stations occupied during the study period.	40

Figure 5.2 a - c. Vertical profiles of euphotic zone measurements of phytoplankton production (\blacktriangle — \blacktriangle), chlorophyll *a* (○---○), light attenuation (log I)(○---○), temperature (←—→) and nitrates (x---x) during the mid-winter survey, July 1988 (88/10). 42

Figure 5.3 a - c. Vertical profiles of measurements of primary production (\blacktriangle — \blacktriangle), chlorophyll *a* (●---●), light attenuation (log I)(●---●), temperature (←—→) and nitrates (x---x) as observed during the spring survey, October 1987 (87/14/B). 42

Figure 5.4 a - d. Vertical profiles of measurements of primary production (\blacktriangle — \blacktriangle), chlorophyll *a* (●---●), light attenuation (log I)(●---●), temperature (←—→), and nitrates (x---x) for the summer 87/02/B cruise, January 1987. 43

Figure 5.4 e - h. Vertical profiles of measurements of primary production (\blacktriangle — \blacktriangle), chlorophyll *a* (●---●), light attenuation (log I)(●---●), temperature (←—→) and nitrates (x---x) for the January 88/01/C cruise (profile e) and the December 86/19/I cruise (profiles f - h). 44

Figure 5.5. Mean productivity ($\text{mgC}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$) per unit chlorophyll *a* ($\text{mgChl}a\cdot\text{m}^{-3}$) (P^B) plotted for each light depth (% surface irradiance) during winter(----), spring (-----) and summer (—). 47

Figure 5.6. The frequency plot of the observed positioning of the chlorophyll and primary productivity maximum in the euphotic zone at the different % surface irradiance incubation light depths during the stratified summer (December - January) month cruises. 49

List of tables

	facing page
Table 3.1 A and B. Comparison of treatments for the removal of inorganic ^{14}C from filter papers.	23
Table 3.2 A and B. Effect of rinsing during sample filtration on filter paper and filtrate count.	24
Table 3.3 A and B. Effect of the addition of 0.2ml of the CO_2 -sorber, Carbosorb 11 ^R (Packard), on sample count and stability of count during storage.	24
Table 3.4. Loss of counts from tightly sealed capped samples over a storage period of 16 days.	25
Table 4.1. Ranges of P^{B} , chlorophyll a and nitrates through the water column for each light depth.	33
Table 4.2. The depth of occurrence and measured value of the Chl_{max} , the P_{max} and the $\text{P}_{\text{max}}^{\text{B}}$ for all Alphard Banks stations.	34
Table 4.3. Size-fractionated primary production measurements for the 87/02/B and 88/01/C surveys. The percentage contribution of each size fraction is given in parentheses, with the cumulative percentage of the size fraction $< 15\mu\text{m}$ displayed in the last column.	34
Table 4.4. Integrated primary production and biomass (chlorophyll a) for the euphotic zone to 0.4% surface irradiance light depth. The depth of the euphotic zone (Z_{eu}), depth of surface mixing (Z_{m}), integral P^{B} and the ratio of the euphotic zone to the mixing depth ($Z_{\text{eu}}/Z_{\text{m}}$) are shown.	35
Table 5.1. A description of cruise dates, sampling frequency at station locations and average incubation conditions (incoming solar irradiation and sea-surface temperature) for the five cruises. Station locations not occupied during cruises is shown by an *.	40
Table 5.2. Ranges of summer measurements for 87/02/B, 88/01/C and 86/19/I. Where means are given, the standard deviation appears in parenthesis. Z denotes depth in the euphotic zone of the described variable. The upper mixed layer (UML) extends from sea-surface to the inflection point of the thermal trace	44

Table 5.3. Integrated phytoplankton production rates and biomass (chlorophyll *a*) for the euphotic zone to the 0.5% surface irradiance light depth. Means are given for measurements from the same station location during individual cruises. 45

Table 5.4. Mean size-fractionated production rates for the winter, spring and summer surveys. The percentage contribution to community production of each size-fraction is headed %, and the combined % contribution of the <15 µm size-fraction is presented in the last column. 45

Table 5.5. Microscopic cell count analyses and sample chlorophyll *a* values. These were used for the computations of C:Chla ratios presented in Table 5.6. The numerically dominant phytoplankton taxa observed in samples are listed. 46

Table 5.6. Phytoplankton community turnover times (doublings per day) for the well mixed euphotic zone during the winter survey (88/10) and for the UML and thermocline regions during the summer stratified survey (88/01/C). 49

Table 6.1. An overall summary of observed seasonal ranges of the physical environment and associated mean levels of phytoplankton production and biomass during winter, spring and summer in Agulhas Bank waters. Ranges about the means are given in parentheses and dominance of the assemblage by net- or nanoplankton as observed, is suggested. 52

CHAPTER ONE:

GENERAL INTRODUCTION:

Introduction

Aims of this study

The physical and chemical hydrology of the Agulhas Bank

The physical hydrology

Thermal stratification

Nutrients

Breakdown of stratification

Fish, phytoplankton and primary production

Anchovy distribution

Phytoplankton biomass

Phytoplankton primary production

INTRODUCTION

Continental shelf waters are of the most productive globally, covering less than 10% of the oceans area yet producing 99% of the world's fish catches. The productivity of a continental shelf region depends on the area covered by the shelf, the hydrological regime and the extent of wind influenced surface mixing or coastal upwelling (WALSH 1981). The efficiency of carbon transfers from the primary producers of the system to the exploitable fish resources will be determined by the proportion of primary production within size classes which are available to higher trophic orders (RYTHER 1969, MOLONEY and FIELD 1985). Phytoplankton production dynamics are primarily controlled by the physical and nutrient environment of the water column - light, mixing depth, thermal stratification, nutrient input into the euphotic zone, and secondarily by grazing losses to zooplankton and other planktivores with associated regenerated nutrient inputs (LONGHURST and HARRISON 1989). Seasonal fluctuations in levels of primary productivity of a continental shelf area may well reflect at higher trophic levels, in particular those of economic importance to man (SHANNON and FIELD 1985). Thus knowledge of the seasonal variability of phytoplankton production and abundance may provide a measure for the prediction of fluctuations in fish stocks within the system (LASKER 1978, AGENBAG *et al.* 1982).

AIMS OF THIS STUDY

The purpose of the five oceanographic sampling surveys aboard the *R. V. Meiring Naude* in Agulhas Bank continental shelf waters during the period December 1986 to January 1988 was to quantify the temporal and spatial variability of phytoplankton primary production and abundance, and to identify the controlling factors regulating primary production in these waters. We have investigated size-fractionated phytoplankton production in three areas of the Agulhas Bank: the inner eastern bank (CARTER *et al.* 1987), the midshelf (Alphard Banks) and the western shelf region, over a sampling period of four years. The locations of these sampling stations are displayed in Figure 1.1 a. The distinction of size-fractionated phytoplankton production has enabled the investigation of size related production, of relevance to trophic and nutrient pathways in these waters.

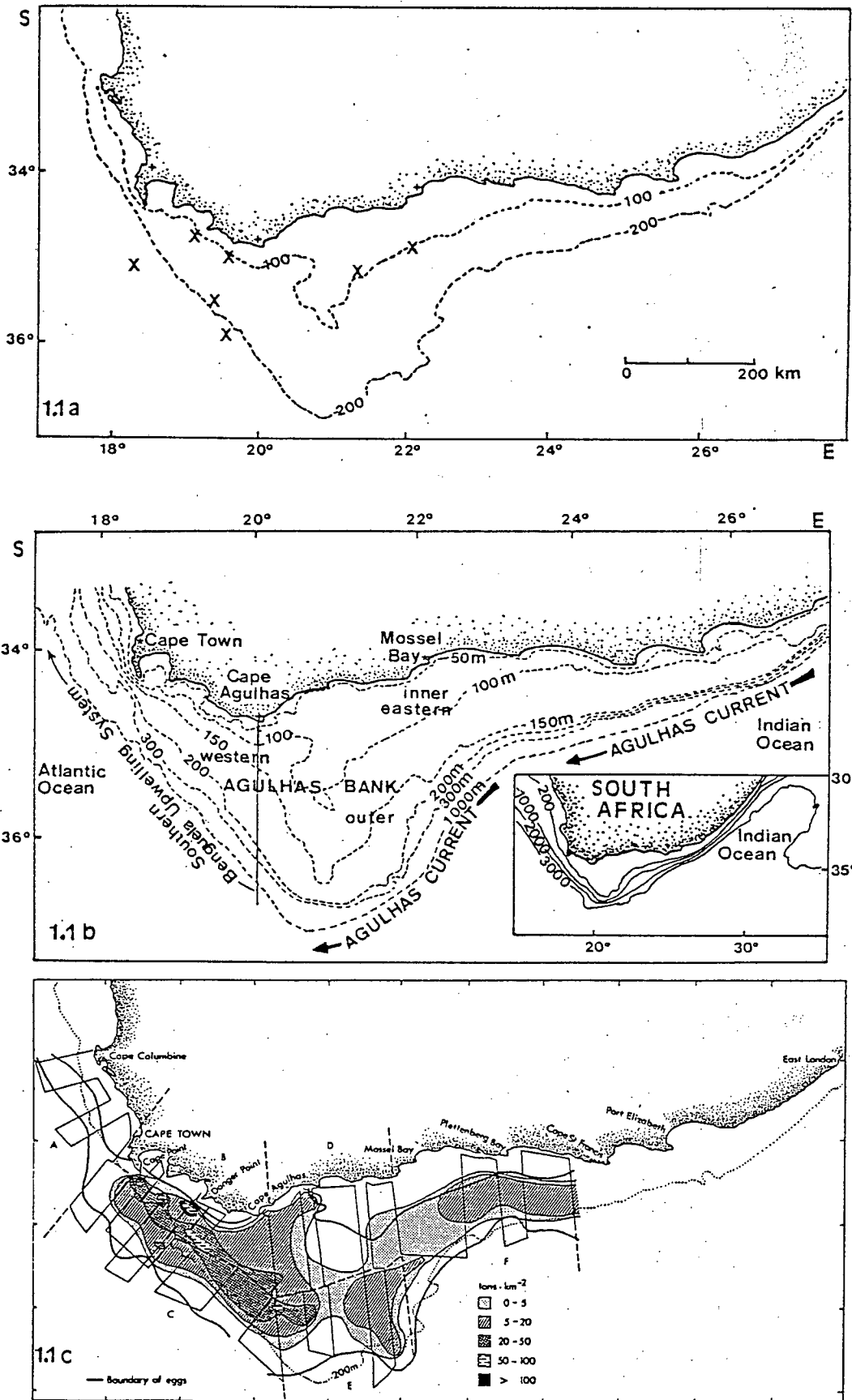


Figure 1.1. The hydrographic regime of the Agulhas Bank. (a) The location of primary production stations. (b) The physical hydrography and bottom topography of the Agulhas Bank (adapted from: LARGIER and SWART 1987). (c) The distribution of anchovy eggs in Agulhas Bank waters during a survey in November 1985 (from: HAMPTON 1987)

A brief description of the physical, chemical and biological environment of Agulhas Bank waters follows, as a general introduction to this continental shelf system.

THE PHYSICAL AND CHEMICAL HYDROLOGY OF THE AGULHAS BANK

The physical hydrology

The Agulhas Bank covers an extensive area south of South Africa (approx. 5 000 km²), stretching from Cape Point in the west to Algoa Bay in the east, and offshore south from Cape Agulhas to the 200m isobath. The size and bottom topography of the bank and its geographic positioning juxtaposed between western and eastern boundary currents, the south-west flowing warm Agulhas Current to the east and the cool west coast Benguela upwelling system to the west (Figure 1.1 b), promotes complex watermass characteristics and currents over the bank.

Sufficient hydrological evidence (HARRIS 1978, NELSON and HUTCHINGS 1987, LARGIER and SWART 1987, CATZEL 1989) now exists for the distinction of three major areas across the Agulhas Bank (Figure 1.1 b), particularly during summer months (November - March) when the water column is stratified. These regions have been defined as: (i) The western Agulhas Bank, where waters west of Cape Agulhas display continuity with the west coast Benguela upwelling region during south-easter wind driven coastal upwelling events (SHANNON *et al.* 1984). (ii) The inner eastern bank as the region east of the Cape Agulhas/Cape Infanta "divergence" (SCHUMANN and BEEKMAN 1985) but inshore of the cold water upwelling ridge which runs parallel to the coast in the east between the 100m and 150m isobath line. (iii) The outer eastern bank, consisting of east bank waters offshore of the cold ridge (LARGIER and SWART 1987).

Currents on the bank are highly variable, a combination of wind forcing, the input of bottom water onto the shelf from the east and shelf-edge upwelling, bottom topography and the intrusion of eddies from the Agulhas Current contribute further to current variability. The eddies are generated at the shelf edge and propagate westwards across the shelf (BANG 1974, HARRIS 1978, LUTJEHARMS *et al.* 1981, LUTJEHARMS and VALENTINE 1983, LARGIER and SWART 1987). Current meter deployments in

bottom waters, particularly during periods of strong south-easterly winds (SWART and LARGIER 1987, V. SWART unpublished data). Bottom topography further influences current variability.

Thermal stratification

During the summer, Agulhas Bank waters are stratified, a condition typical of temperate latitude continental shelf waters elsewhere in the world (PINGREE *et al.* 1976, CULLEN and EPPLEY 1981, MALONE *et al.* 1983, HOLLIGAN *et al.* 1984a, TRANTER and LEECH 1987). The water column resembles a two-layer structure in which the thermocline separates two watermasses of different characteristics and origins (EAGLE and ORREN 1985, SWART and LARGIER 1987, CATZEL 1989). The surface layer of the Agulhas Bank originates from mixing of waters of the Agulhas Current (Subtropical Indian Ocean Surface waters) and existing Agulhas Bank surface waters. These surface waters are wind mixed, warm ($>18^{\circ}\text{C}$) and poor in nutrients (EAGLE and ORREN 1985). The bottom water has its origins from the deep Indian Ocean Central waters, and is advected onto the shelf during shelf-edge upwelling. This bottom water is cool ($<12^{\circ}\text{C}$), nutrient-rich and is well mixed by bottom friction turbulence and tidal oscillations (CATZEL 1989). Shelf-edge upwelling and the associated input of bottom water onto the shelf due to current shear effects with the passage of the Agulhas Current past the shelf-edge (LARGIER and SWART in prep.), occurs most strongly along the eastern and southern shelf-edge. Advection of bottom water onto the shelf also occurs along the southwest edge, but appears to be of a less continuous nature and more seasonal (BANG 1974, BOYD *et al.* 1984, CATZEL 1989).

The temperature profile of the water column is the primary feature that changes between east and west bank waters during the thermally stratified summer months. The thermocline is observed to deepen and slacken in gradient with the progression from inner eastern bank region to western bank waters (LUTJEHARMS *et al.* 1981, SCHUMANN and BEEKMAN 1984, LARGIER and SWART 1987, CATZEL 1988). The thermocline in the inner east bank region is shallow (15 - 25m) and very intense, displaying temperature changes of up to 11°C between the upper mixed layer ($20 - 21^{\circ}\text{C}$) and cool bottom water ($9 - 10^{\circ}\text{C}$), with gradients of as much as 2°C.m^{-1} (SCHUMANN 1983, CARTER *et al.* 1987, CATZEL 1989). The thermal structure is highly stable in the east bank region during these months, when wind

stress is reduced (CATZEL 1989). Close proximity of the eastern bank region to the bank shelf-edge adjacent to the Agulhas Current results in the maintainance of this thermal structure by advection over prolonged periods. If the vertical structure is deepened by a mixing event, the thermocline is rapidly returned to its previous shallow position (SWART and LARGIER 1987).

In western Agulhas Bank waters, the thermocline is typically situated at greater depth in the water column (30 - 45m) and seldom achieves gradients of more than $1\text{ }^{\circ}\text{C}\cdot\text{m}^{-1}$. High variability of thermal structure in this region has been observed (SCHUMANN and BEEKMAN 1984). The appearance of $<10\text{ }^{\circ}\text{C}$ bottom water in the western shelf region during summer stratification (BOYD *et al.* 1985, EAGLE and ORREN 1985) suggests that the thermocline is still advectively maintained. However, due to the deeper water column and increased distance from the region of very active shelf-edge upwelling to the east, the thermal structure is less pronounced (LARGIER and SWART 1987).

Coastal upwelling west of Cape Agulhas is an important feature of this region during summer months (SHANNON *et al.* 1984, BOYD *et al.* 1985, LARGIER and SWART in prep.). Upwelling creates frontal regions of cold nutrient-rich inshore upwelled surface waters separated from warmer midshelf surface waters. It has been proposed that strong coastal upwelling enhances the flow of cold bottom water onto the shelf along the southwest edge of the shelf (BOYD *et al.* 1985, CATZEL 1989, LARGIER and SWART in prep.). The increased volume of bottom water over the western shelf results in uplifting of the thermocline over much of the western bank to c. 30m. However, the deep stratified condition with the thermocline situated between 35 - 45m depth appears to be more typical of this region during late summer months (January -late February).

Nutrients

Associated with the thermocline is a nutricline. Nitrates, phosphates and silicates all show depletion in the surface mixed layer during summer months and increase in concentration through the thermocline region with depth (BOYD *et al.* 1985, EAGLE and ORREN 1985, CARTER *et al.* 1987). It is generally accepted that uptake of nutrients by phytoplankton growth in the illuminated surface layer depletes

these waters of nutrients once the water column has stratified and stabilized (HARRISON *et al.* 1983, HOLLIGAN *et al.* 1984b, LONGHURST and HARRISON 1989).

Typical concentrations of nitrates are slightly higher in surface waters in the west relative to the inner eastern bank; $1 - 5 \mu\text{mol.l}^{-1}$ and $< 1 \mu\text{mol.l}^{-1}$ respectively. These concentrations increase to $> 20 \mu\text{mol.l}^{-1}$ across the nitracline.

Breakdown of stratification

During winter months (May - September), as insolation input decreases and surface waters cool, deep mixing of the surface waters by wind stress and the possible slackening of bottom water advection onto the shelf results in the deepening of the thermocline to depths $> 70\text{m}$ (PUGH 1982, CARTER pers comm.), and sometimes to the bottom (EAGLE and ORREN 1985). However, the continuous nature of shelf-edge upwelling of bottom water onto the shelf by oceanic forcing which is not seasonally controlled, maintains some thermal structure of the water column. This is more so in the eastern sector than in the west (SWART pers. comm.). Nutrients are mixed up into the surface waters during deep mixing resulting in nitrate concentrations $> 5 \mu\text{mol NO}_3\text{.l}^{-1}$ throughout the water column during the mid winter months (BOYD *et al.* 1985, EAGLE and ORREN 1985). As phytoplankton production increases in the surface waters with increased insolation and water column stabilisation during the spring months (September - November), so nutrients are depleted from the upper mixed layer.

FISH, PHYTOPLANKTON AND PRIMARY PRODUCTION

Anchovy distribution

The anchovy, *Engraulis capensis*, is presently the major contributor to the annual commercial pelagic fish catch in South African waters (SHELTON 1984). Furthermore, since the collapse of the pilchard (*Sardinops ocellata*) stocks in west and south coast waters, pelagic predators (seabirds, sea mammals

and piscivorous fish) previously nourished by pilchards, have of necessity substituted the anchovy as their primary pelagic food resource (CRAWFORD *et al.* 1987).

Anchovy spawning takes place during the summer months (October - January) and egg and larval surveys have shown the waters of the Agulhas Bank west of Cape Point to Mossel Bay to be the main spawning grounds of the South African anchovy (SHELTON and KRIEL 1980, SHELTON and HUTCHINGS 1982). Fish surveys estimate more than a million tonnes of actively spawning anchovy (1+ year old fish) to be present in Agulhas Bank waters during the summer months (Figure 1.1 c - HAMPTON *et al.* 1985, HAMPTON 1987), making these waters of considerable biological importance to the pelagic fish resources in South African waters. The anchovy occur widespread in loose shoals over the entire bank, with the major proportion of the anchovy biomass in the region west of Mossel Bay (HAMPTON *et al.* 1985, SHELTON *et al.* 1985).

It is thought that the western Agulhas Bank spawning population is responsible for the subsequent west coast 0-year old recruitment (SHELTON *et al.* 1985). The passive transport of anchovy eggs and larvae in a jet current around Cape Point (BANG and ANDREWS 1974, NELSON and POLLITO 1987) to upwelling enriched west coast waters has been shown to be the linking mechanism between Agulhas Bank spawning and 0-year old anchovy recruitment to the west coast fisheries (SHELTON and HUTCHINGS 1982, NELSON and HUTCHINGS 1987).

General inshore and eastwards migration of adults on the Agulhas Bank occurs as waters of the mid and outer bank warm to $>21^{\circ}\text{C}$ (SHELTON *et al.* 1985). Anchovy of 2 - 3 years old are typically found in eastern Agulhas Bank waters. Although the eastern Agulhas Bank population still contains active spawners, this population appears to be of little importance to the maintenance of west coast fisheries (HAMPTON 1987), but is likely to be of great importance to east coast pelagic fish predators.

Phytoplankton biomass

Calculations of phytoplankton standing stocks from theoretical models for Agulhas Bank waters suggest that primary production may be limiting to fish yields from these waters (MOLONEY and FIELD 1985, SHANNON and FIELD 1985). However, very little is yet known of the phytoplankton standing stock

variability on the bank, both seasonally and spatially in response to the changing physical and biological (grazing) environment. Furthermore, even less is known of zooplankton secondary production in these waters, the primary food resource of anchovy (JAMES 1988). These calculations therefore remain speculative and unquantified.

A seasonally occurring and spatially continuous subsurface chlorophyll maximum associated with the thermocline-/nitracline has been observed in both east and west bank waters during stratified months (SHANNON *et al.* 1984, CARTER *et al.* 1986, 1987, MCMURRAY *et al.* in prep., HORSTMAN unpublished data). The shallow, intense thermoclines in the east support a narrow chlorophyll maximum layer (<10m thick decreasing to as little as 1m), which have been observed to persist over time periods of weeks. The more diffuse thermal gradients in the west waters support a broader (10 - 15m) subsurface chlorophyll maximum. The subsurface chlorophyll maximum attains considerably higher concentrations in east bank waters than west of Cape Agulhas, often $>10 \mu\text{g.l}^{-1}$ to as much as $45 \mu\text{g.l}^{-1}$ in the east compared to $0.5 - 5 \mu\text{g.l}^{-1}$ to the west.

Cross-shelf transects in the east display decreasing chlorophyll concentrations beyond 30 nautical miles (nm) from the coast with the highest concentration occurring midshelf, 20 -30 nm offshore (CARTER *et al.* 1986). Similar cross-shelf transects in the west bank region display variable mid-shelf subsurface chlorophyll concentrations ($1 - 3 \mu\text{g.l}^{-1}$) increasing shorewards to $>25 - 40 \mu\text{g.l}^{-1}$ in surface waters (BROWN and HUTCHINGS 1985). These high coastal chlorophyll measurements are most probably relicts of recent coastal upwelling events (SHANNON and HENRY 1983, SHANNON *et al.* 1984). During these periods of coastal upwelling along both south and west coasts, the phytoplakton assemblage of south coast nearshore waters has been shown to be continuous with species assemblages of west coast waters (DE DECKER 1979, SHANNON and PILLAR 1986). This observation presents further evidence of the physical and biological continuity between western Agulhas bank waters and west coast waters, particularly during summer months. Similar scale pulsing of coastal surface chlorophyll is not observed in east bank waters (SHANNON *et al.* 1984), where coastal upwelling is limited to small capes during easterly winds (SCHUMANN *et al.* 1982).

Phytoplankton primary production

Measurements by BROWN (1983) during November 1981 presented the first good field estimates of primary production in Agulhas Bank waters. Integrated euphotic zone values ranged between 1.46 - 2.82 $\text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in midshelf western bank waters and 0.52 - 0.81 $\text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in the east. These values differ little from integrated productivity measurements presented by MALONE *et al.* (1983) in stratified waters of the New York Bight (0.83 - 1.72 $\text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), and also those of YODER (1985) for the southeastern U.S. continental shelf during periods of nutrient-rich bottom water intrusions ($>2 \text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$). However, the Celtic Sea and Southern Californian Bight continental shelf waters appear considerably less productive than Agulhas Bank waters during stratified months. Euphotic zone productivity was shown to range between 0.26 - 0.74 $\text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ for Celtic Sea waters (JOINT and POMROY 1983) and 0.16 - 0.52 $\text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (maximal production seldom $>1 \text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) in Southern Californian Bight waters (CULLEN and EPPLEY 1981, EPPLEY and SMITH 1982).

It is well known that the biological productivity of continental shelf waters are subject to considerable temporal variability in response to the physical and nutrient environment (LONGHURST and HARRISON 1989, WALSH 1981). This study presents field measurements of phytoplankton size-fractionated production and the vertical distribution of biomass in the water column for three seasons, winter (July), spring (October) and summer (December and January). Furthermore, due to problems encountered when using the ^{14}C uptake method for the measurement of primary production, I initiated a laboratory investigation of the method. This investigation with the resultant method adopted is presented in chapter 3.

CHAPTER TWO:

**THERMOCLINE CHARACTERISTICS AND PHYTOPLANKTON DYNAMICS IN AGULHAS
BANK WATERS**

Abstract

Introduction

Research Area and Methods

Results and Discussion

Conclusions

Acknowledgements

Literature Cited

Presented by R. A. CARTER at the Benguela Ecology Programme Symposium held at the University of Cape Town, September 1986, and published in : *The Benguela and Comparable Ecosystems*, A.I. PAYNE, J. A. GULLAND and K. H. BRINK, editors. *South African Journal of Marine Science*, 5, 327 - 336. 1987

THERMOCLINE CHARACTERISTICS AND PHYTOPLANKTON DYNAMICS IN AGULHAS BANK WATERS

R. A. CARTER*, H. F. McMURRAY* AND J. L. LARGIER*

Eastern and central Agulhas Bank waters are characterized by strong, shallow thermoclines and well developed subsurface maxima of phytoplankton biomass. The thermoclines are advectively maintained and as such are dynamically stable, but they do exhibit short-term variations in absolute temperature gradients. There are corresponding variations in subsurface phytoplankton biomass maxima. The water-column phytoplankton production maxima are generally situated in the biomass maxima because these are sufficiently shallow to ensure adequate light. Self-shading becomes a limiting factor with the development of high phytoplankton biomasses. Western Agulhas Bank waters are characterized by deeper thermoclines and less intense subsurface maxima of phytoplankton biomass. Due to the depth of the thermoclines the biomass maxima are generally situated below the depth of the 1-per-cent surface light intensity and, consequently, phytoplankton production is limited. Possible mechanisms for the maintenance of these deep chlorophyll maxima are discussed.

Die water oor die oostelike en sentrale Agulhasbank word gekenmerk deur sterk, vlak termokliene en goed ontwikkelde maksima van fitoplanktonbiomassa benede die oppervlak. Die termokliene word advectief gehandhaaf en is as sodanig dinamies stabiel, maar hulle vertoon wel wisselings op die kort termyn in die absolute temperatuurgradiënte. Daar is ooreenstemmende wisselings in die maksima van fitoplanktonbiomassa benede die oppervlak. Die produksiemaksima van fitoplankton in die waterkolom is gewoonlik binne die biomassamaksima geleë aangesien hul vlak genoeg is om voldoende lig te verseker. Self-beskaduwing word 'n beperkende faktor soos hoë fitoplanktonbiomassa ontwikkel. Die water oor die westelike Agulhasbank word gekenmerk deur dieper termokliene en minder intense maksima van fitoplanktonbiomassa benede die oppervlak. Vanweë die diepte van die termokliene is die biomassamaksima gewoonlik geleë benede die diepte waar die ligintensiteit 1 persent van die aan die oppervlak is; fitoplanktonproduksie word dus beperk. Moontlike meganismes waardeur hierdie diep chlorofilmaksima in stand gehou word, word bespreek.

The Agulhas Bank forms a broad, irregularly shaped expanse of continental shelf situated south of South Africa (Fig. 1). The shelf waters are characterized by strong thermal stratification (Shannon 1966) with associated subsurface maxima of phytoplankton biomass (Brown 1981, Carter *et al.* 1986), and they are thus similar to temperate shelf seas in the northern hemisphere (e.g. Pingree *et al.* 1975, Cullen and Eppley 1981, Holligan *et al.* 1984a). The Agulhas Bank region is the primary spawning area for the Cape anchovy *Engraulis capensis* (Shelton and Hutchings 1982, Shannon *et al.* 1984) and, as such, it is crucially important to the pelagic fishery associated with the resource.

The inferred indirect dependence of anchovy spawning success on subsurface maxima of phytoplankton biomass (cf. *E. mordax* - Lasker 1975) and the dependence of the latter on thermal stratification prompted this investigation of Agulhas Bank thermoclines and plankton distributions in 1985 and 1986. The measurement programme in this investigation, entitled Agulhas Bank Coastal Dynamics Experiment (ABCDE) consisted of two components. The first was a long-time course (October 1985-March

1986) monitoring of currents and temperature structure by means of current-meter and thermistor-chain moorings, and the second was a time-series and larger scale areal coverage based on ship-borne measurements of temperature, salinity, nutrients, phytoplankton biomass and production in February and March 1986. In this report, aspects of the second component of the above, with particular reference to phytoplankton distributions in relation to thermocline depth and degree of development, are discussed.

RESEARCH AREA AND METHODS

The geographic locations of ship (R.V. *Meiring Naudé*) stations occupied for the time-series and areal survey studies are shown in Figure 1 in relation to upper mixed layer depths (from the surface to the top of the thermocline) measured during this study. At the two time-series stations (A and B) shown in the Figure, CTD profiles were made at 2-h intervals and water samples (CSIR design rosette and/or 8-l Niskin bottles) were taken at alternate CTD profiles

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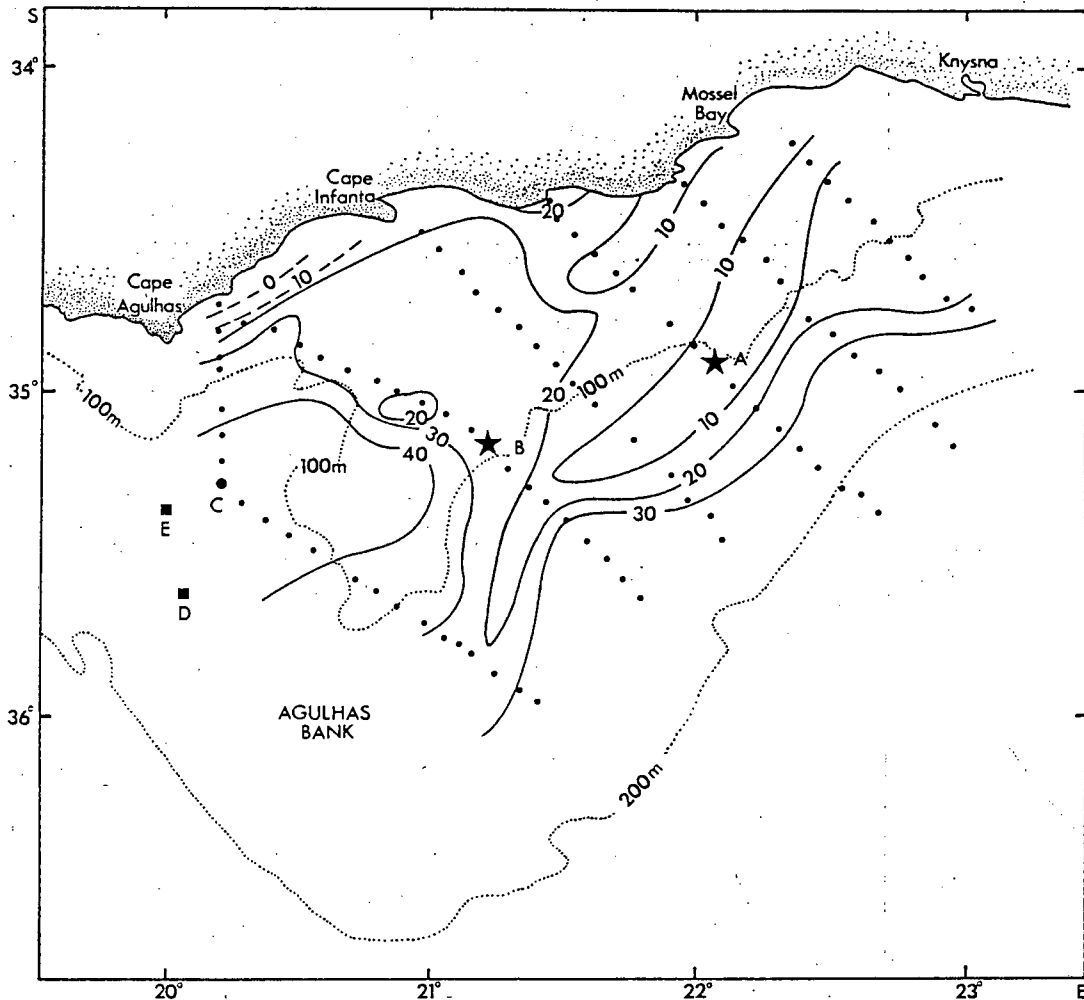


Fig. 1: Surface mixed layer depth on the Agulhas Bank in March 1986 (modified from Swart and Largier 1987). A and B indicate the locations of the ABCDE time-series investigations, and C, D and E the locations of Stations 88 (March 1986), AA 120 (December 1985) and 5 and 31 (October 1984) for which profiles are presented in Figure 5

(i.e. 4-h intervals). These water samples were immediately analysed for nitrate- and ammonia-nitrogen concentrations on a Technicon autoanalyser, and aliquots were taken and frozen at -20°C for analyses of phosphorus and silicon ashore.

Phytoplankton pigments were determined fluorometrically (Turner Fluorometer calibrated against chlorophyll *a* [Sigma Chemicals]) on 90-per-cent-acetone-extracted 250-ml samples filtered through GF/C filter papers. Further, underwater irradiance profiles were made by means of a Kahlsico under-

water irradiance meter between 09h00 and 10h30 each day, and water samples were taken for measurements of primary production and concentrations of chlorophyll and particulate organic C and N at depths corresponding to 66, 30, 12, 7, 5, 3 and 0.4 per cent of the surface light intensity.

Aliquots for primary production were decanted into three clear and one dark 125-ml glass stoppered reagent bottles, $5\ \mu\text{Ci}$ radiocarbon (as NaHCO_3) added, and incubated at their respective light levels in a water-cooled deck incubator for periods of 4-5 h

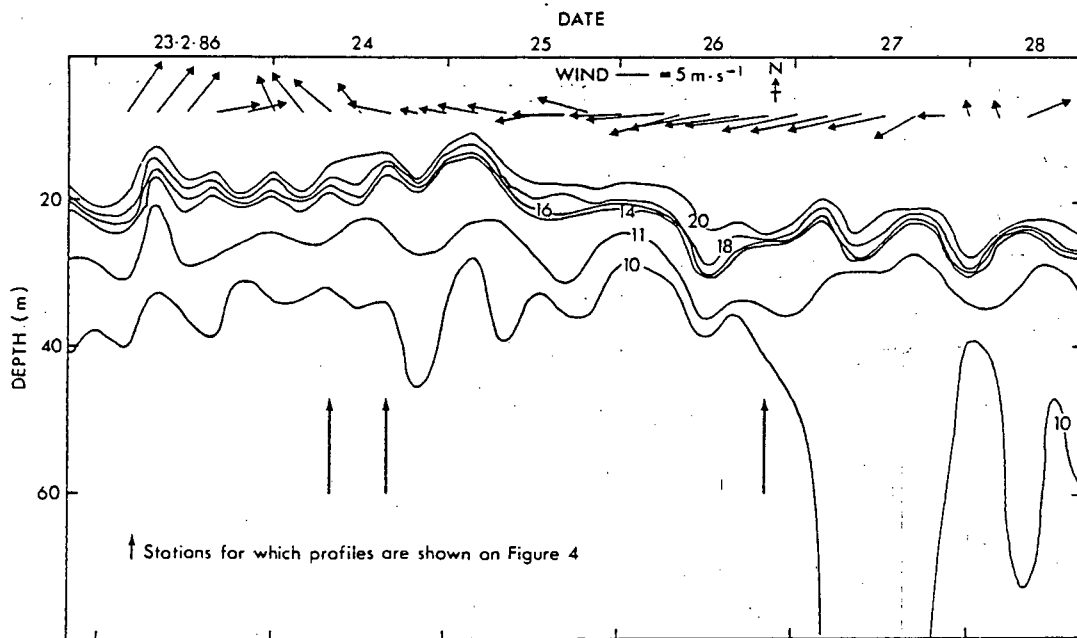


Fig. 2: Surface wind vectors and water column temperature (°C) structure from 23 to 28 February 1986 at time-series location A

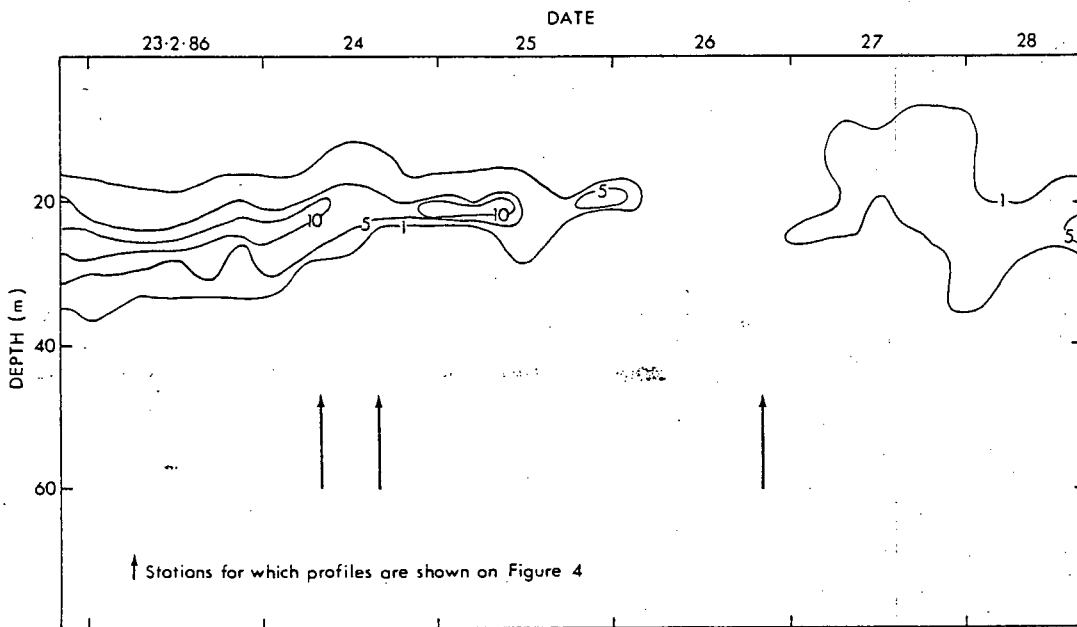


Fig. 3: Chlorophyll a ($\mu\text{g}\cdot\text{l}^{-1}$) distributions from 23 to 28 February 1986 at time-series location A

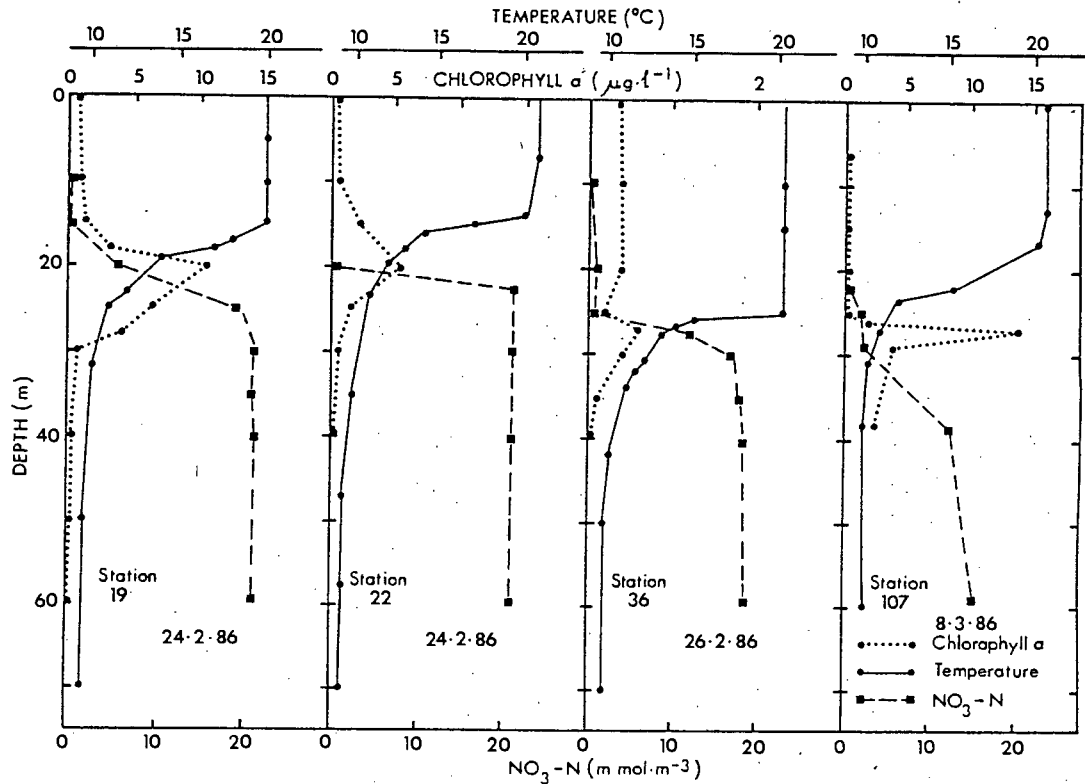


Fig. 4: Representative shallow thermocline temperature, chlorophyll a and nitrate-nitrogen profiles measured at time-series locations A (Stations 19, 22 and 36) and B (Station 107). Note that x-axis changes between panels

over local noon. Incubations were terminated by filtering onto GF/C filter papers. These papers were subsequently dried over silica gel, fumed over HCL and added to 12 ml of Beckman MP45 scintillation cocktail in glass scintillation vials. Isotope DPMs were read on a Liquid Scintillation Counter ashore and carbon fixation was calculated according to Parsons *et al.* (1984). Samples for particulate C and N analyses were collected by filtering 11 aliquots through precombusted, preweighed GF/C filter papers. Subsamples were taken from each of the filter papers for determinations of the weights of particulate matter and the C and N fractions (Carlo-Erba Elemental Analyser) of both non-combusted and combusted (450°C) samples. Organic fractions were determined by subtraction.

During the areal CTD survey (Fig. 1), the biological and chemical sampling/measurements just described were carried out daily at a station occupied between 08h00 and 10h00 irrespective of position. In

addition to these parameters, regeneration rates of nitrogen and phosphorus were measured at the surface and 0,4-per-cent surface light intensity depth. Results from the regeneration measurements are reported elsewhere (Probyn and Lucas 1987).

The western regions of the Agulhas Bank were not well covered in terms of phytoplankton distributions during the ABCDE cruises, and therefore unpublished data from previous cruises in this region are used to expand the data set. During these cruises, similar procedures to those already described had been followed. The locations of these measurements are depicted in Figure 1.

RESULTS AND DISCUSSION

Swart and Largier (1987) show that eastern and central Agulhas Bank thermoclines are advectively

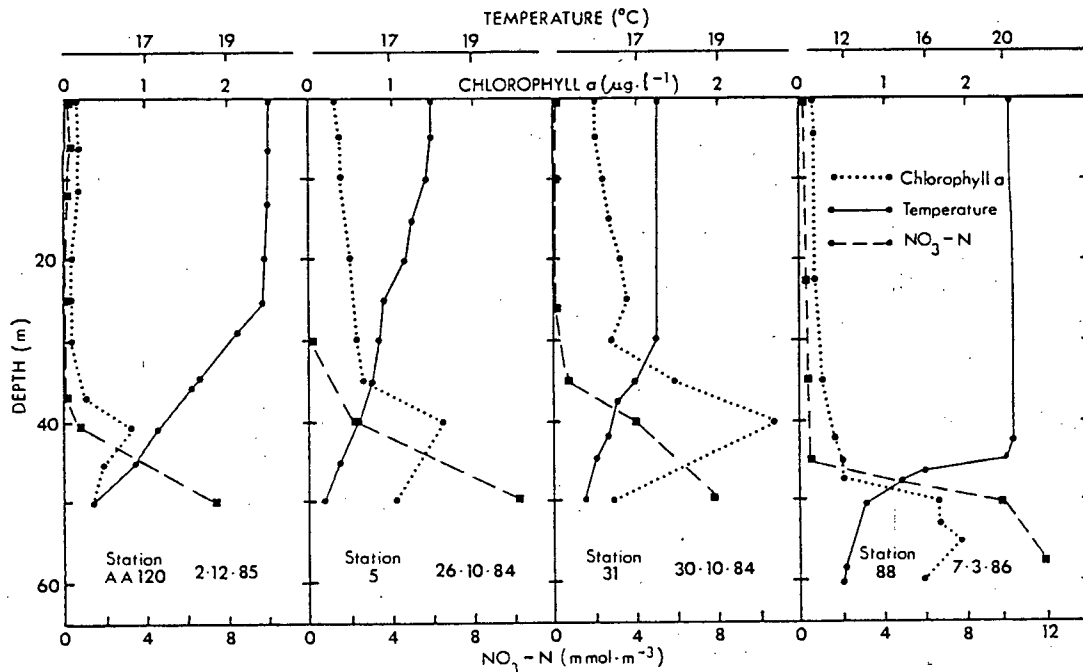


Fig. 5: Representative deep thermocline temperature, chlorophyll *a* and nitrate/nitrogen profiles measured at locations C (Station 88), D (Station AA 120) and E (Stations 5 and 31)

maintained by bottom water intrusions from the east and south-east. They further demonstrate that thermocline depth is dependent upon the "thickness" of the westward-advecting bottom water and that the temperature gradients within the thermocline are dependent upon this and the depth of the upper mixed layer. The former factor varies with longitude and water depth, declining westwards as water depths increase (Largier and Swart 1987) and consequently thermocline depths increase (Fig. 1). Similar distributions were noted for this area in March 1968 (Lutjeharms *et al.* 1981). The temporal variation in upper mixed layer depth and thermocline intensity over a 5.5-day period at time-series location A is shown in Figure 2. The structure is stable throughout the measurement period, the only change being a deepening of the surface mixed layer between 25 and 26 February 1986 associated with higher winds. However, slackening of wind speeds subsequent to the 26th was not accompanied by a decrease in depth of the surface mixed layer.

The corresponding chlorophyll *a* distributions measured during the time-series are depicted on Figure 3. The well developed subsurface maximum observed in the first half of the time-series persisted until the surface mixed layer deepened, and it began

to reappear only towards the end of the time-series. Selected profiles from the time-series are displayed in Figure 4 along with a profile (Station 107) obtained farther west, at time-series location B (Fig. 1). The profiles for Stations 19, 22 and 107 all show that the chlorophyll maximum is situated towards the base of the thermocline in close association with the nitracline. These shallow chlorophyll maxima are generally dominated by diatoms, although dinoflagellates may also contribute (De Decker 1973, Carter *et al.* 1986), and they are thus largely dependent upon diffusive processes for nitrogen supply for production within the maxima. Similar distributions of phytoplankton relative to temperature and nitrate-nitrogen have been recorded in stratified waters in the Gulf of Maine (Holligan *et al.* 1984a).

The location of the chlorophyll maxima towards the base of the thermocline indicates that they will not be disrupted by surface mixing (e.g. Fig. 2) unless this is sufficiently intense to break down the thermocline itself. The lack of a marked subsurface chlorophyll maximum during the period of deep surface mixed layers (compare Fig. 3 with Fig. 2 and Fig. 4, Station 36) is therefore interpreted as being due to advection of another water mass past the measuring station rather than to dissipation by turbulence. This inter-

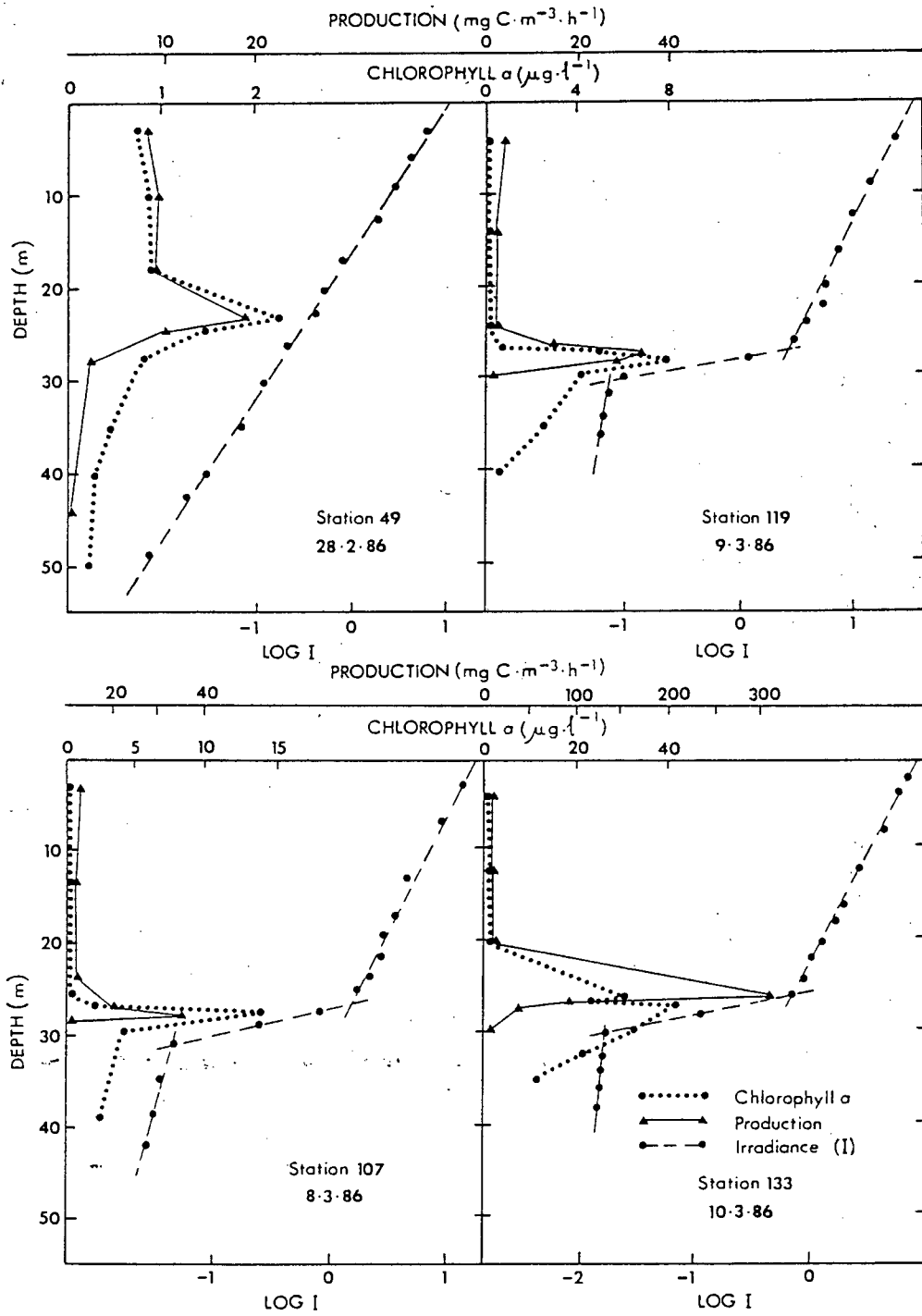


Fig.6: Chlorophyll a, primary production and underwater irradiance (arbitrary log scale) profiles measured at time-series locations A (Station 49) and B (Stations 107, 119 and 133). Note that x-axis changes between panels

pretation is supported by records of increased bottom temperatures (Fig. 2) and lower mean silicon concentrations in sub-thermocline waters for the period 26–28 February v. 24–25 February ($13.41 \text{ SD} = 4.23 \mu\text{M Si}\cdot\text{l}^{-1}$ [$n = 38$] v. $24.73 \text{ SD} = 5.53 \mu\text{M Si}\cdot\text{l}^{-1}$ [$n = 28$]; means different at $p < 0.005$, Student's t test) of the time-series. It is not clear why subsurface chlorophyll maxima were undeveloped in this water mass.

Examples of profiles measured in the deep thermocline region in the west of the CTD station grid (Fig. 1) are presented on Figure 5. Data from previous cruises are included here because this region was not extensively sampled during the ABCDE cruises. Despite relatively weak temperature gradients in three of the four profiles displayed, all show similar trends in distribution of chlorophyll and nitrate-nitrogen. These, in turn, are basically similar in structure to the shallow thermocline distributions, but it is notable that the magnitude of the chlorophyll maxima is reduced. This feature is discussed further below.

Representative distributions of phytoplankton production rates measured in shallow thermocline stations with varying development of the subsurface chlorophyll maxima are illustrated, together with the relevant light attenuation profiles, on Figure 6. It is apparent that the distribution of primary production follows that of chlorophyll, this being especially well illustrated at Station 49, where the subsurface chlorophyll maximum was not well developed and light attenuation was low ($K_d = 0.11 \cdot \text{m}^{-1}$) and regular over the water column. With increased development of the chlorophyll maxima (Stations 107, 119 and 133), light attenuation across the chlorophyll maxima increased ($K_d > 0.70 \cdot \text{m}^{-1}$) and, thus, production was limited to the upper layers of the chlorophyll maximum at these stations.

The consequences of this were marked decreases in overall biomass-specific production rates for the chlorophyll maxima and therefore increases in population turnover times (Table I). The extremely long turnover time calculated for Station 133 appears to be unrealistic because the chlorophyll maximum would probably be dissipated by entrainment into the bottom waters or depleted by zooplankton grazing within this period (Carter *et al.* 1986). Further, it is unlikely that water column stability itself has similarly long time-constants in this region of the Agulhas Bank, as is indicated by the analyses of Largier and Swart (1987). These analyses demonstrate increasing instability of thermoclines with decreasing longitude on the Agulhas Bank, supporting the records of seasonal variation in western Agulhas Bank thermocline development given by Boyd *et al.* (1985) and Eagle and Orren (1985). These factors indicate that

Table I: Phytoplankton assimilation numbers (P^B) and population turnover times for the chlorophyll maxima depicted in Figure 4. Population turnover times were calculated on a measured carbon/chlorophyll a ratio of 67 ($\text{SD} = 22.2$, $n = 17$; samples taken from shallow chlorophyll maxima) and a 10-h production day (Brown 1980)

Station	Phytoplankton assimilation number P^B		Population turnover times (d)	
	At P_{max}	At Chl_{max}	At P_{max}	At Chl_{max}
49	8.7	2.91	0.77	2.3
119	6.9	1.22	0.97	5.5
107	3.9	0.64	1.72	10.5
133	10.4	0.04	0.64	168.0

the phytoplankton would have to be growing at or near the maximum rate (Table I) to maintain the observed biomass distributions. The mechanisms for this are obscure in the data set, although it is apparent that the biomass maxima are not located at the stability maxima (cf. Holligan *et al.* 1984a). Therefore, mixing within the chlorophyll maxima may occur, exposing phytoplankton cells to the light intensities existing at the upper layers of the maxima (e.g. Fig. 6). Again, any dissipation of the maxima by turbulence or grazing would reduce the self-shading effect and thus act to increase rates of phytoplankton production.

The distribution of phytoplankton production in relation to chlorophyll and light for the single deep thermocline station at which these parameters were measured during the ABCDE cruises is shown on Figure 7. Phytoplankton production was limited to two small peaks in the upper mixed layer, zero rates being measured in the chlorophyll maximum.

The low rates of production in the upper mixed layer are due to extremely low phytoplankton biomasses, and the location of the chlorophyll maximum below the depth of 1-per-cent surface light intensity leads to the zero production rates measured there. This raises the question as to how these deep chlorophyll maxima are maintained in the face of zooplankton grazing and/or dissipation by mixing when phytoplankton production is apparently light-limited?

Largier and Swart (1987) present theoretical arguments, supported by measurements off Cape Point, west of Cape Agulhas, that indicate that the deep thermocline regions of the western Agulhas Bank are areas of significant internal wave activity, with the semidiurnal tide being the major driving force. This tide has an amplitude ranging between 5 and 15 m off Cape Point, 10-m amplitudes being common. With the distributions depicted in Figure 7 as an example, an internal wave of 10-m amplitude would lift the

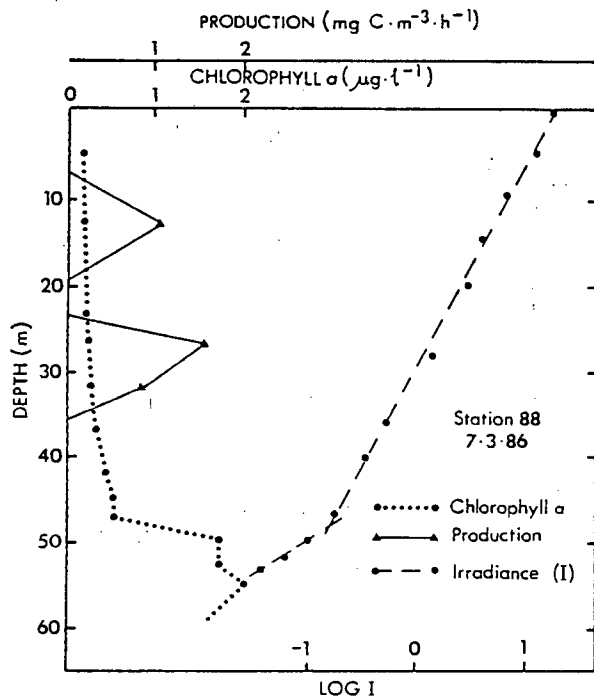


Fig. 7: Deep thermocline chlorophyll a, primary production and underwater irradiance (arbitrary log scale) profiles measured at location C (Station 88)

chlorophyll maximum from < 1 to some 4 per cent of the surface light intensity. The photosynthesis/irradiance response, measured in a Lewis and Smith (1983) photosynthetron, of a flagellate-dominated phytoplankton community (B.A. Mitchell-Innes, Sea Fisheries Research Institute, pers. comm.) sampled from the deep chlorophyll maximum depicted on Figure 5, Station AA 120, is shown in Figure 8. The response curve indicates that an increase from 0.5 to 4 per cent in light level would potentially lead to an increase in assimilation number (P^B) from c. 0.5 to 4.0, which is close to the maximum photosynthetic rate. From the carbon/chlorophyll ratio of 67 determined for diatom-dominated samples farther east (Table 1), such an increase in P^B would be equivalent to a decrease from 13.4 to 3.4 days in population turnover time. This calculation takes the diurnal nature of the tide into account, but it assumes first that the internal wave is sinusoidal in shape and second that the phytoplankton adapt rapidly to changes in the light field. Wave shape is dependent

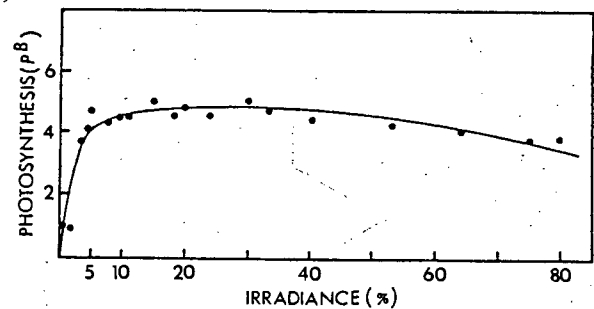


Fig. 8: Photosynthesis/irradiance (P/I) response of phytoplankton from the subsurface chlorophyll maximum at location D (Station AA 120)

upon the location of the wave interface (i.e. thermocline) relative to the bottom or surface (LeBlond and Mysak 1978, pp. 89–93). Therefore, variations in thermocline depth can cause variations in phytoplankton turnover times as a result of increased or decreased period for which phytoplankton is exposed to higher light levels.

Malone *et al.* (1983) have shown that phytoplankton P^B in subsurface chlorophyll maxima of the New York Bight increase with elevations in mean irradiance. Marra (1978a) has demonstrated that this response can be rapid, but that photosynthetic capacity is maximal early in the photoperiod and subsequently declines (Marra 1978b). The P/I curve illustrated in Figure 8 indicates a rapid response by the phytoplankton (20 min. incubation) to increased light, but it gives no indication as to the duration of this response. There are not sufficient field data yet to warrant pursuing this point further here.

CONCLUSIONS

Phytoplankton distributions in shallow and deep thermoclines on the eastern and central Agulhas Bank are similar in structure and in their relationships with temperature and nitrate-nitrogen concentration gradients, but distributions in deep thermoclines are characterized by weaker gradients. The structures observed are similar to those recorded in temperate continental shelf waters elsewhere, e.g. western approaches of the English Channel and Gulf of Maine (Holligan *et al.* 1984a, b, c), Mid Atlantic Bight (Falkowski *et al.* 1983) and southern California Bight (Cullen and Eppley 1981). However, they differ

in that they are largely maintained by an intrusive cold bottom layer rather than seasonal insolation changes. In this aspect the Agulhas Bank is similar to the south-east continental shelf of the United States (Yoder 1985). The magnitudes of the Agulhas Bank chlorophyll maxima are generally stronger than those recorded in these other regions, but it is not clear whether this is due to discrete sampling in variable profiles (e.g. Derenbach *et al.* 1979). Magnitudes of the deep chlorophyll maxima are similar to those recorded off Japan (Kishino *et al.* 1986).

In shallow chlorophyll maxima the biomass peak was also a primary production peak, very low rates being measured in the upper mixed layer. This finding differs from those in stratified waters elsewhere, where production rates in the upper mixed layer may form a large fraction of water column production (Malone *et al.* 1983, Holligan *et al.* 1984c, Joint *et al.* 1986). The coincidence of the Agulhas Bank primary production peak with the nitracline indicates that "new" production (Eppley and Peterson 1979) predominates. Rates of ammonium regeneration in surface waters are rapid (Probyn and Lucas 1987), and it is unclear from the data as to why "regenerated" production was negligible during the sampling period. The estimated turnover times of phytoplankton for the upper surface of the shallow chlorophyll maxima are rapid, implying high photosynthetic efficiency at the 3–7-per-cent surface light intensity depths (see Kishino *et al.* 1986).

Turnover times for the entire chlorophyll maxima generally agree with those calculated for the Mid Atlantic Bight by Falkowski *et al.* (1983), but they become very long (>100d) for dense maxima because of self-shading (cf. Malone *et al.* 1983). This observation implies some mixing process in the chlorophyll maxima to increase the average light levels to which the phytoplankton are exposed. The mechanism for this is obscure.

Deep chlorophyll maxima on the Agulhas Bank appear to be generally light-limited for production, and low rates of this parameter may occur in surface waters. Because of this it is inferred that the phytoplankton in the chlorophyll maxima respond to changes in the light field caused by internal waves, this response being rapid but of unknown duration.

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CHAPTER THREE:

**AN EVALUATION OF THE RADIOCARBON TECHNIQUE OF MARINE PHYTOPLANKTON
PRIMARY PRODUCTION MEASUREMENT: POTENTIAL ERRORS AND
METHODOLOGICAL PRECAUTIONS**

Introduction

Materials and Methods

Results and Discussion

The ^{14}C Method

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1. INTRODUCTION

The method of radiocarbon labelling of phytoplankton (Steemann Nielson 1952) has become the most widely applied technique of aquatic carbon production measurement, especially in waters of low productivity (Peterson 1980). To date, much of the technical detail of the original ^{14}C method has been researched and modified by others (reviewed by Hilmer 1984). However, the sensitivity of this method to error incurred during the technical procedure remains a matter of concern amongst scientists hoping for comparable data sets within similar research environments (Sakamoto *et. al.* 1984). Recent research investigations of the applied ^{14}C method include problems encountered with metal contamination of samples (Fitzwater *et. al.* 1982), alternative methods of sample treatment (Sondergaard 1985), filtration artifacts (Goldman and Dennet 1985), time duration of incubation of samples (Hitchcock 1986), light environments during incubation (Buhlmann *et. al.* 1987) and the interpretation of data obtained using the ^{14}C method (Bender *et. al.* 1987, Dring and Jewson 1982, Harris 1984, Talling 1984). The best synthesis of the precautions necessary to reduce technical error when applying the ^{14}C technique for the measurement of oceanic phytoplankton production is still that by Peterson (1980), but recent developments in the technique require that the procedural outline given by Peterson be updated.

During field measurements of phytoplankton production in continental shelf waters (Agulhas Bank, South Africa), I have experienced problems with interpretation of results obtained when using the ^{14}C method due to large variations between counts of replicate samples and difficulty in obtaining a reliable estimate of $^{14}\text{C}\text{-HCO}_3^-$ dosage of samples. This initiated the laboratory investigation of the methods used, to evaluate possible technique-associated biases and/or errors. The results of this investigation are presented here. Furthermore, the method derived from these results and which I now adopt for phytoplankton production measurements in Agulhas Bank waters is described.

2. MATERIALS AND METHODS

2.1 MATERIALS

Culture species:

Two algal species, Dunaliella primolecta (Chlorophyceae) and Chaetoceros gracilis (Bacillariophyceae), were cultured separately in the laboratory in 0.45 μm filtered seawater at room temperature (19 - 21°C) under saturating light conditions. Experimental samples were drawn from these parent cultures, inoculated with $^{14}\text{C-HCO}_3^-$ and incubated in 250ml Duran^R Schott glass bottles in the same light and temperature environment. Chaetoceros is the dominant genus occurring in Agulhas Bank waters (Shannon & Pillar 1986) and is thus a suitable test organism. The more fragile Dunaliella was chosen as representative of the lower range of "robustness" expected.

Filters, scintillation vials and fluor:

Whatman^R GF/F 25mm filter papers and glass scintillation vials with plastic screw tops were used throughout all experiments. Filters were placed in 7ml mini-vials and filtrate samples in 20ml maxi-vials. The scintillation fluor Instagel^R (Packard) is suitable for filter and aqueous samples, provided that a phase separation curve is established for high aqueous load samples (filtrate samples). For 8ml aliquot samples, the addition of 8 - 10ml fluor proved a stable mix with limited phase separation. 6ml of fluor was added to filter paper samples. Samples were counted on a Packard 1500 Tri-Carb liquid scintillation counter.

$^{14}\text{C-HCO}_3^-$ stock solution:

High activity $\text{NaH}^{14}\text{CO}_3$ ampoules were diluted in a Na_2CO_3 (AnalaR grade) solution (0.3 g.l^{-1}) to a final stock activity of $2 \mu\text{Ci.ml}^{-1}$ at a pH of 9.4 - 9.7. The stock was stored in the dark in a tightly stoppered pyrex glass flask. The pH of the stock was checked regularly and the stability of the stock count activity was monitored over a three week period at weekly intervals.

2.2 METHODS

Sample inoculation:

Two methods for determining the total activity of ^{14}C added to samples before incubation were tested. The first can be characterised as the direct method, where five replicate 1.0ml aliquots were taken from each individual sample immediately after the ^{14}C stock inoculum had been added. Total sample volume was measured with an A-grade measuring cylinder. Sample total initial activity was calculated by extrapolating the average aliquot count to total sample volume. The second method involves calibrating the ^{14}C stock and subsequently dosing all samples with an equal volume of stock. The ^{14}C stock solution was calibrated at the start of each experiment as follows: ten replicates of the stock inoculum (0.50ml) were made up volumetrically to 25.0ml in the previously described Na_2CO_3 solution, from which five aliquots (0.50ml) of each dilution were assayed for activity, i.e. 50 standard samples per experiment. All transfer instruments, e.g. repetman^R, pipetman^R, were calibrated to deliver accurate volumes. Total activity added to samples was calculated from the average standard count corrected for dilution (X50). One data set has been selected for each of the methods and the variability between counts within each set is compared.

Removal of inorganic carbon-14 residues:

Sample decontamination of inorganic ^{14}C residues by the three different methods viz. drying and fuming papers over concentrated HCl, addition of HCl directly to filters in the scintillation vial, and bubbling air through acidified aqueous samples, was examined by laboratory experimentation (methods detailed on pp. 15 (fig. 1), 16 (fig. 2) & 18 (table 1)). Samples used for these experiments were 200ml 0.45 μm pre-filtered seawater samples inoculated with 2 μCi $^{14}\text{C}\text{-HCO}_3^-$. Thus filter papers and filtrate aliquots contained only inorganic ^{14}C activity. For further investigation, filters containing organically bound ^{14}C were treated (4 filter papers per method) by either drying for one

hour and fuming over concentrated HCl for a further 1 hour, or by fuming in the vial after addition of two drops concentrated HCl for 45 minutes. Sample counts were compared.

Filtration vacuum pressure and rinse effects:

The effect of four vacuum pressure differentials viz. 50, 100, 150 and 175 mmHg on filter count was examined. Replicate sets of samples drawn from the algal cultures (four of each species) were inoculated with 2 μCi ^{14}C and incubated for three hours. Two samples, one per species, were filtered onto filter papers at each of the above described pressure differentials.

To establish the effect of a rinse administered during filtration on sample count, 250ml algal culture samples were inoculated, incubated and split into two 100 ml aliquots and then filtered at 100 mmHg vacuum pressure. One of the aliquots received a rinse during filtration, this done by the washing of the funnel walls and filter paper with 10 ml of 0.45 μm pre-filtered sea water just before the meniscus of the sample touched the filter paper. The other aliquot was not rinsed. This experiment was repeated using 4 replicate samples (250ml) of each species, two of the replicates rinsed, two not rinsed. Filter papers, filtrate and funnel wash samples were decontaminated of inorganic ^{14}C (procedures described later in report) and analysed for count.

CO₂-sorber addition and sample count stability:

Counts of equivalent pairs of stock dilution samples differing only in the addition of 0.2ml of the CO₂-sorber, Carbosorb^R II (Packard), to one of the pair were compared. Samples were recounted after one week storage to check sample count stability in the vial over time. For further examination of the rate of loss of count from capped samples during a storage period, five replicate stock dilution samples without Carbosorb addition were counted immediately after fluor addition and again after 24 hours; 6 days; and 16 days storage. Two of the five samples were dark stored.

3. RESULTS AND DISCUSSION

¹⁴C stock solution:

No decrease of count or change in the pH of the stock solution over a period of three weeks was observed. Fitzwater *et. al.* (1982) claim stability of count for up to six months when using a 0.3 g.l⁻¹ solution of Na₂CO₃. The use of chemically pure Na₂CO₃ minimizes the risk of stock contamination.

Determination of sample initial activity:

The calculated coefficients of variability for the direct method of aliquot removal from individual samples and for the method of equivalent sample dosing with a calibrated stock were 1.0% and 0.8% respectively. Although both methods are shown to be of similar precision, the additional sample handling and time requirements of the former method makes this method inappropriate for field application where large volume samples and many replicates are required. When applying the latter technique, all volumetric transfer instruments must be checked for accuracy and calibrated prior to use in the field. Inaccurate calibration of the stock ¹⁴C-HCO₃⁻ activity can be a major source of methodological error (Davies and Williams 1984).

Sample decontamination of inorganic carbon-14 residues:

Decontamination of filters by either fuming over concentrated HCl or by soaking in HCl is shown to be equally efficient (table 1A & 1B). Mere rinsing of filters removes up to 90% of the initial untreated filter count, but acid treatment is necessary to reduce ¹⁴C residues to 1% of initial contamination (table 1A). Although the data are insufficient for rigorous statistics, it appears that variability of count between replicates is lower when applying the in-vial acid soaking method (table 1B).

The time course of inorganic ¹⁴C removal from filters during in-vial acid soaking is displayed in figure 1. A minimum of 30 minutes is required for decontamination using 11N or 1N HCl. The use of 0.5N HCl is shown to be less efficient after 30 minutes

than the 1N or 11N acid additions. Although decontamination is most rapid with 11N HCl, the addition of concentrated acid to samples may cause hydrolysis of organic compounds with loss of volatile materials (Mague *et. al.* 1980).

Purging aqueous samples of inorganic ^{14}C residues requires a minimum of 30 minutes bubbling after acidification to reduce sample count to 0.03% of initial contaminant count (fig. 2). The calculation of phytoplankton organic carbon exudation and production estimates from low activity samples can be severely biased where even as little as 0.02% of initial inorganic ^{14}C count contamination remains after the decontamination procedure (Sharp 1980, Williams *et. al.* 1972). Thus inorganic ^{14}C contaminants remaining in filter and filtrate samples after the decontamination treatment must be assessed by replicate time-zero samples (representative samples filtered immediately after inoculation and acid treated) as a standard experimental procedure (Sharp 1980, Shifrin 1980, Sondergaard 1985).

Sample filtration and rinsing:

Figure 3 displays the decrease of filter count observed for both algal species with increasing vacuum pressure differential applied during sample filtration. This pressure effect is well documented (Goldman and Dennet 1985, Lean and Burnison 1979, Mague *et. al.* 1980, Shifrin 1980), where count decrease is attributed to cell breakage. It is generally agreed that pressure differentials >100 mmHg should be avoided.

The results obtained for the rinse effect experiments are very variable and show no clear trends (table 3). The high funnel wash count observed for *D. primolecta* samples suggests adherence of these organisms to the walls of the funnel and that underestimation of sample count may occur if a funnel wash/rinse is not done during filtration. When rinsing papers at the end of filtration, the rinse must be administered before the sample meniscus touches the paper. Even brief exposure of filters to air whilst under vacuum subjects the trapped algae to strong

osmotic pressure differences and cell rupture may result (Goldman and Dennet 1985). Deviations in the filtration procedure from sample to sample can cause large variations between replicates (Lean and Burnison 1979).

Sample count stability and storage:

Although sample count was increased by the addition of the CO₂-sorber, Carbosorb II, sample quench was also increased (indicated by a decrease in SIS) (table 3A) and phase separation of samples was observed. Contrary to results obtained by Wiemer et. al. (1972), addition of the CO₂-sorber did not improve loss of counts from samples during storage (table 3B). Loss of count from samples occurs at an average rate of 1.5% per week after an initial increase in count during a 24 hour period of stabilisation (table 4). Wiemer et. al. (1972) describe loss of sample count as being mainly due to the volatilization of ¹⁴C-CO₂ from the sample into the air space of the closed vial. They suggest that minimizing this air space will reduce the ultimate extent of ¹⁴C-count loss.

4. THE ^{14}C METHOD

On the basis of the above results and recommendations in the literature, the procedure outlined below is adopted for phytoplankton primary production measurements in Agulhas Bank waters:

- (i) The ^{14}C -stock solution is prepared by dilution of high activity $\text{NaH}^{14}\text{CO}_3$ ampoules (1 or 5 mCi ampoules, Amersham, England) in a 0.3 g.l^{-1} solution of analytical reagent quality Na_2CO_3 to give a nominal activity of $20\text{-}30\ \mu\text{Ci.ml}^{-1}$. The stock is stored in a tightly stoppered borosilicate flask in the dark. In each experiment carried out, aliquots of the stock solution are taken for precise calibration of its activity (see (iii) below) to calculate the amount of label added to each experimental bottle.
- (ii) All glassware is acid-washed before use (see Fitzwater *et. al.* 1982). Volumetric transfer instruments are calibrated in the laboratory prior to field use to deliver accurate volumes during field experiments. Whatman^R GF/F 25mm glass fibre filter papers are suitable for routine oceanic production measurements (Hitchcock 1986). Only glass scintillation vials are used. The scintillation fluor, Instagel^R (Packard), accommodates acidified filters and filtrate samples.
- (iii) For the calibration of the stock ^{14}C -bicarbonate activity, 50 standard samples are made up per experiment. Five 0.50ml aliquots from each of ten replicate volumetric dilutions of the sample inoculum (0.50ml stock made up to 25.0ml with Na_2CO_3) are prepared for counting (see text p.3).
- (iv) Water samples are collected in non-metallic PVC 8l Niskin sampling bottles from 7 or 8 depths in the water

column where light levels correspond to the set light regimes of the simulated in situ deck incubator. These depths range from 0.5 - 100% of surface photosynthetic active radiation (PAR). Underwater irradiance is measured with a KAHLISICO Model 268WA310 radiometric underwater irradiator.

- (v) The seawater is prescreened through 149 μm mesh when tapped from the Niskin sampler into 250ml Duran^R Schott glass bottles. Sample handling is kept to a minimum and excessive exposure to bright sunlight is avoided by tapping the samples in a darkened area (Brown 1980). During routine measurements, 3 light bottles, 1 dark bottle and a control (time-zero) sample are tapped immediately from each Niskin. Samples are kept in a darkened container.
- (vi) The samples for incubation purposes (light and dark bottles) are inoculated with an equivalent dosage (0.5ml) of the calibrated ^{14}C -stock solution using a repetman^R, or a similarly precise automatic pipette. The addition of 10-15 μCi $^{14}\text{C}\text{-HCO}_3^-$ to each sample proved necessary to avoid low count samples with high variation between replicates. Samples are incubated for 4 hours over mid-day (Brown 1980, Hitchcock 1986) at simulated in situ light levels in an on-deck incubator (obtained from J. Henry, S.F.R.I., South Africa) based on the design by J. Ryther and D. Menzel (WHO Institute, USA). Surface seawater is continuously pumped through the incubation tubes to maintain a constant temperature environment.
- (vii) Whilst sample incubation proceeds, samples for biomass (chlorophyll a), nutrients, particulate carbon, salinities and dominant phytoplankton species analyses are taken from each Niskin. Time-zero production samples are dosed with the ^{14}C -inoculum and filtered

immediately (no organic ^{14}C fixation). Filter papers and filtrate samples are decontaminated of inorganic ^{14}C contaminants following the procedures outlined in (ix) below.

- (viii) After the 4 hour incubation is complete, samples are removed from the incubator and placed in the dark. Sample filtration proceeds as rapidly as possible. Vacuum pressure differential is kept at 100 mmHg. Each sample receives a funnel wash/rinse with 10 ml of 0.45 μm filtered seawater before the sample meniscus touches the filter paper. Vacuum is removed just before the filter sucks dry.
- (ix) Papers are placed directly into the scintillation vials to which 0.5ml 1N HCl is added, and fumed for 45 minutes. If exudation measurements are included in the experimental design, filtrate samples (five replicate 8ml aliquots per filtrate) are collected at the start of sample filtration (Mague *et. al.* 1980). Aliquots are acidified to pH 2 with 0.5 ml 0.5N HCl and bubbled with air (200 - 300 ml. min^{-1}) for 30 minutes.
- (x) The scintillation fluor, Instagel^R Packard, is added after decontamination is complete. Samples are capped, well shaken and placed in a darkened container for storage. Samples should be counted as soon as possible after an initial 24 hour period of stabilization, but due to shore-based counting facilities (Packard Tri-carb 1500 LSC), samples are counted on return to shore. Samples are shaken before counting and sample quench is corrected automatically using the sample internal spectrum option (SIS).

(xi) Phytosynthetic rates are calculated according to Parsons et. al. (1984):

$$\text{photosynthesis (mgC.m}^{-3}\text{.hr}^{-1}\text{)} = \frac{(R_S - R_B) * W}{R * N}$$

where R_S : average light bottle sample count (dpm)
 R_B : dark bottle sample count (dpm)
 W : total available CO_2 (mg.m^{-3}) calculated from salinity(S) by the conversion equation:
 $W = [(S^\circ / \dots * 0.067) - 0.05] * 0.96 * 1.2 * 10^4$
 R : total activity of the ^{14}C -bicarbonate added (dpm)
 N : number of hours of incubation.

Figure 3.1: The time-course of decontamination of filter papers soaked in the vial with three different acid strengths. 200ml pre-filtered seawater samples were inoculated with $2 \mu\text{Ci } ^{14}\text{C-HCO}_3^-$ and filtered immediately. Filter papers contain no organically fixed ^{14}C material. Background count (clean filter + 6ml fluor) is 26 dpm. Only 3 time periods for 0.5N HCl (15, 30 and 60 minutes) were examined. $n = 1$

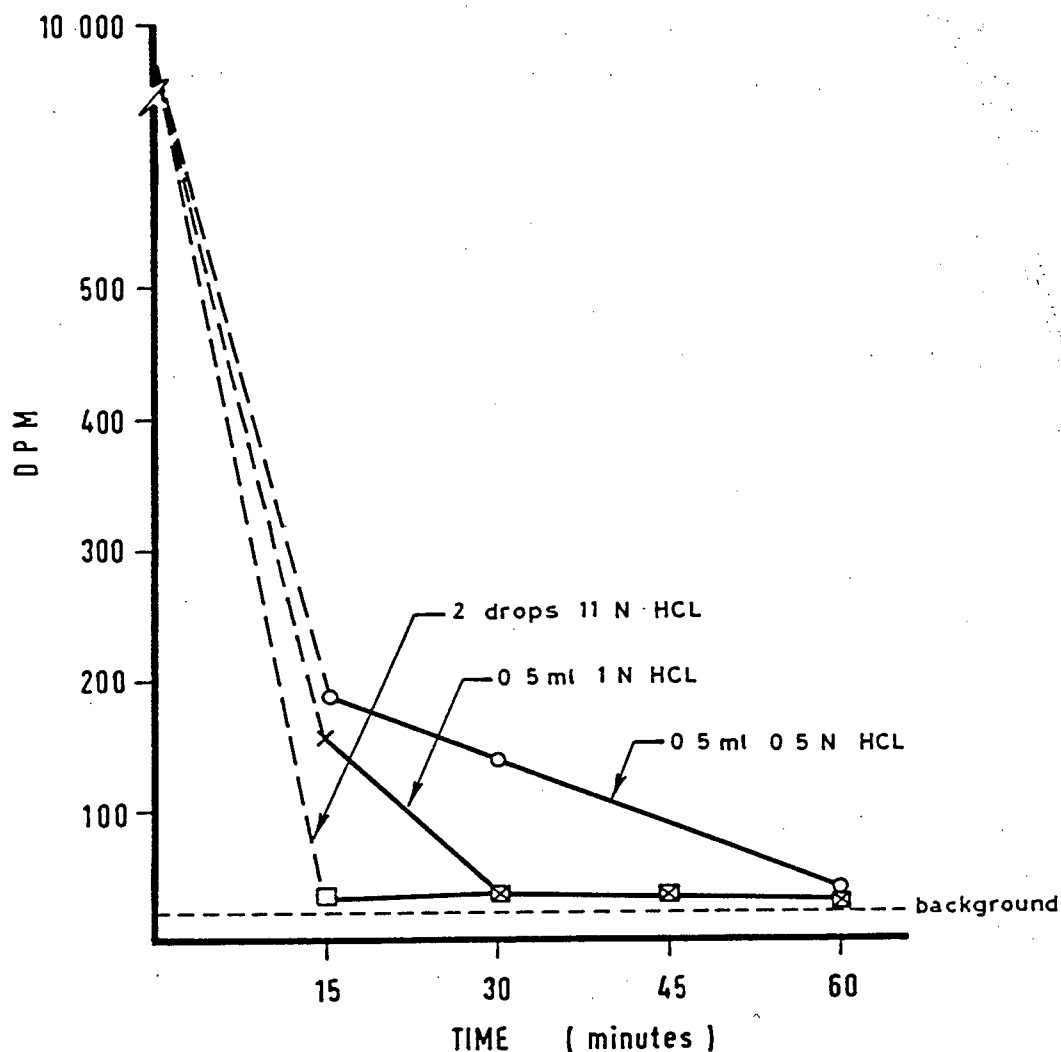


Figure 3.2: The time-course of decontamination of 8ml filtrate sample aliquots acidified to pH 2-2.5 with 0.5ml 0.5N HCl. Filtrate samples were obtained from 200ml pre-filtered seawater samples, inoculated with 2 μCi $^{14}\text{C-HCO}_3^-$ and filtered immediately. Filtrate aliquots contain no organically bound ^{14}C material. Background count (8ml pre-filtered seawater + 0.5ml 0.5N HCl + 10ml fluor) is 44 dpm. n = 3

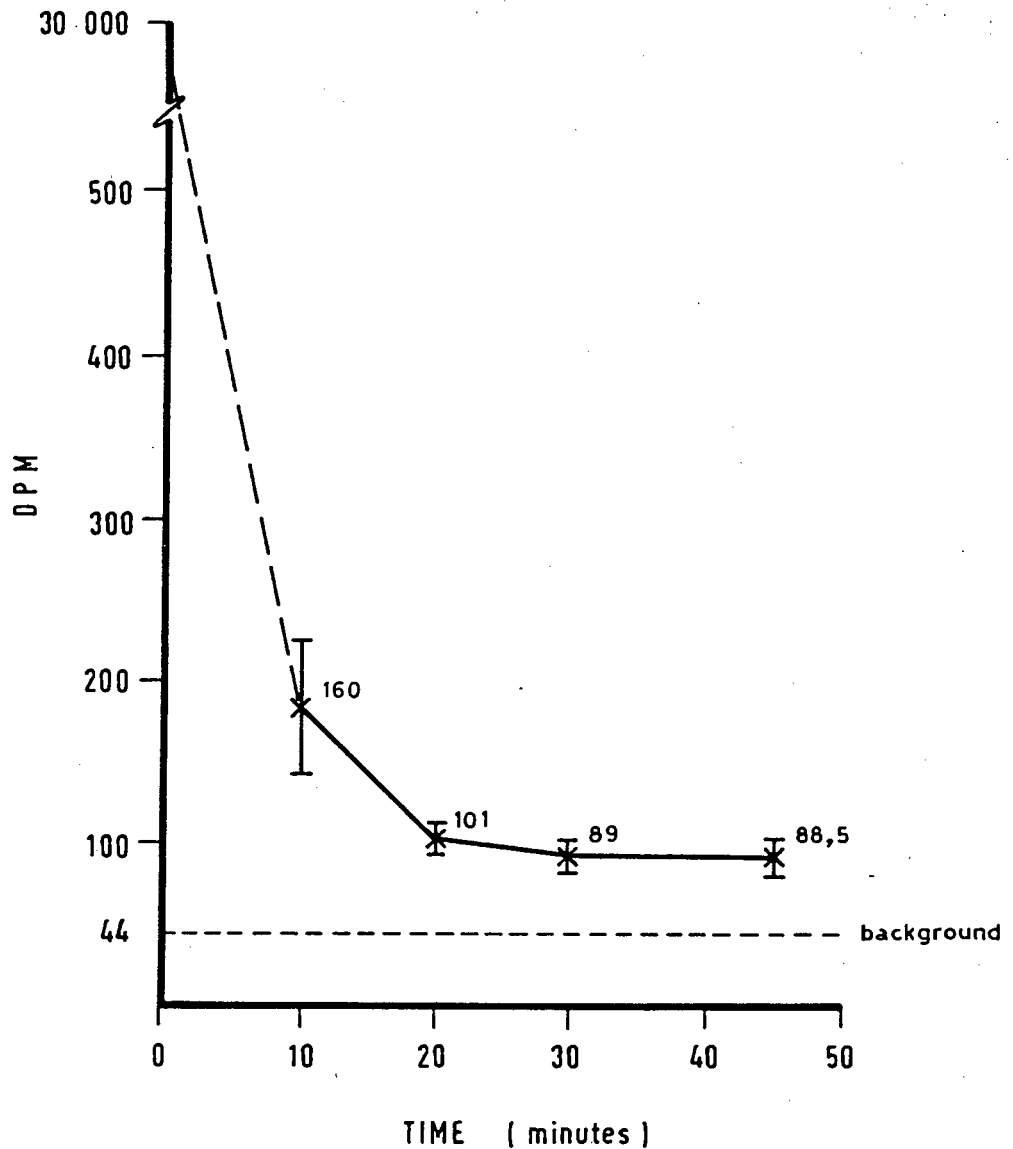


Figure 33: The effect of vacuum pressure differential on filter count for the two algae species, Chaetoceros gracilis (o----o) and Dunaliella primolecta (x----x). 200ml samples were inoculated with $2 \mu\text{Ci } ^{14}\text{C-HCO}_3^-$ and filtered after a three hour incubation period. $n = 1$

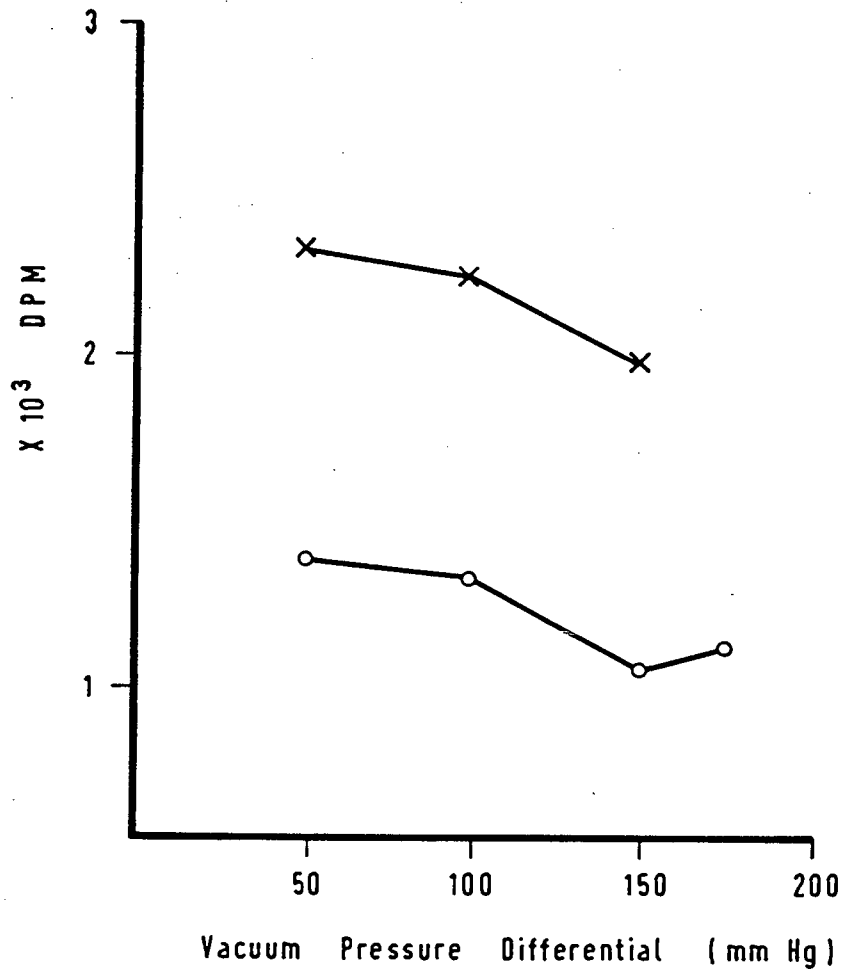


TABLE 31A: Comparison of treatments for the removal of inorganic ^{14}C from filter papers. $2 \mu\text{Ci } ^{14}\text{C-HCO}_3^-$ was added to 200ml of prefiltered seawater, which was then immediately filtered through a GF/F filter paper. The decontamination treatments are described in the table. Counts are dpm. Background count (clean filter + fluor) was 26 dpm.

TREATMENT	COUNT	RANGE
1. No treatment (\bar{x} of 3 samples)	3043	2934 - 3328
2. Filtered seawater rinse (FSW) only (\bar{x} of 3 samples)	142	115 - 219
3. FSW rinse, air dried 1 hour (\bar{x} of 2)	73	72 - 74
4. FSW rinse, air dried 1 hour, fumed over 11N HCl for 1 hour	41	
5. FSW rinse, 2 drops 11N HCl added to filter in vial, soaked for 45 minutes	31	
6. FSW rinse, 0.5ml 1N HCl added to filter in vial, soaked for 45 minutes	35	
7. FSW rinse, 0.5ml 0.5N HCl added to filter in vial, soaked for 45 minutes	67	

TABLE 31B: Comparison of counts (dpm) of filter papers containing labelled organic material and decontaminated of inorganic ^{14}C residues by methods 4 and 5 above. Replicate 200ml light bottle and dark bottle samples of C. gracilis were inoculated with $2 \mu\text{Ci } ^{14}\text{C-HCO}_3^-$, incubated for 3 hours and filtered onto Whatman^R 25mm GF/F papers. Time-Zero samples were filtered immediately after inoculation. Two samples were used for each treatment.

SAMPLE	TREATMENT	AV. COUNT	RANGE
Time-zero	4	39	36 - 42
Time-zero	5	47	45 - 47
Light bottle	4	639	571 - 707
Light bottle	5	684	678 - 690
Dark bottle	4	257	205 - 308
Dark bottle	5	213	180 - 245

TABLE 32: Effect of rinsing during sample filtration on filter paper and filtrate count. Vacuum pressure was kept constant at 100 mmHg. The two algal species samples are displayed separately. Zeros indicate that no net count remained after subtraction of the time-zero count. Counts shown are dpm.

A: Samples split prior to filtration into two 100ml aliquots; one of the aliquots receiving a rinse at the end of filtration, the other aliquot not. Count was assessed for both pre- and post-rinse filtrate of rinsed samples. Funnel wash count was only assessed for aliquots not receiving a rinse. Replicate samples (1 & 2) are shown separately.

SAMPLE	FILTER PAPER		FILTRATE			FUNNEL WASH
	rinsed	no rinse	rinsed pre-	no rinse post-	no rinse	
<u>Duanaliella primolecta</u>						
1	15614	11693	0	345	801	879
2	12340	15630	1045	574	271	849
<u>Chaetoceros gracilis</u>						
1	2861	2615	14	104	678	0
2	2251	2529	20	3	894	0

B: Four replicate 250ml samples of both species incubated for three hours after 2 μCi $^{14}\text{C-HCO}_3^-$ addition. Two samples filtered with a rinse, two samples not rinsed after filtration.

SAMPLE	FILTER PAPER		FILTRATE	
	rinsed	no rinse	rinsed	no rinse
<u>Dunaliella primolecta</u>				
	3516	3476	0	0
	3393	3364	0	69
<u>Chaetoceros gracilis</u>				
	17678	17849	0	0
	19013	18270	0	0

TABLE 33: Effect of the addition of 0.2ml of the CO₂-sorber, Carbosorb II^R (Packard), on sample count and stability of count during storage.

A: Counts of replicate sample pairs with and without the addition of Carbosorb II. Quench factor (SIS) decreases with increasing sample quench.

SAMPLE PAIR	WITHOUT CO ₂ -SORBER		WITH CO ₂ -SORBER	
	dpm	SIS	dpm	SIS
1	15343	60	16559	57
2	15223	60	16607	57
3	15225	60	16483	57
4	15216	61	16401	58
5	15235	61	16588	58

B: Loss of counts from sample pair 4 & 5 during an 8 day storage period.

SAMPLE	STORAGE TIME (days)					
	0		4		8	
	dpm	%D	dpm	%D	dpm	%D
4 : -	15216	-	15145	0.5	14960	1.7
+	16401	-	16200	1.2	16062	2.1
5 : -	15235	-	15147	0.6	15012	1.5
+	16588	-	16222	2.2	15864	4.4

%D : % decrease of count from initial (0 days)
 - : sample of pair without CO₂-sorber addition
 + : sample of pair with CO₂-sorber addition

TABLE 3.4: Loss of counts from tightly capped samples over a storage period of 16 days.

SAMPLE	STORAGE TIME (days)					
	0 dpm	1 dpm	6 dpm	%D	16 dpm	%D
1	610012	611541	603561	1.3	595710	2.6
2	599881	605587	598544	1.2	596072	1.6
3	599821	612340	600208	2.0	592491	3.2
4 *	612366	624988	610347	2.3	610530	2.3
5 *	605226	611284	606946	0.8	596839	2.4

* : dark stored samples
 %D : % decrease in sample count after an initial
 24 hours stabilization (1 day storage)

CHAPTER FOUR:

PHYTOPLANKTON BIOMASS AND PRIMARY PRODUCTION IN SUMMER STRATIFIED WATERS OVER THE ALPHARD BANKS, AGULHAS BANK.

Introduction

Methods and Materials

Results

Profiles: Phytoplankton biomass and production

Water column phytoplankton chlorophyll *a*, primary production and nitrate distributions

Size-fractionated primary production measurements

Discussion

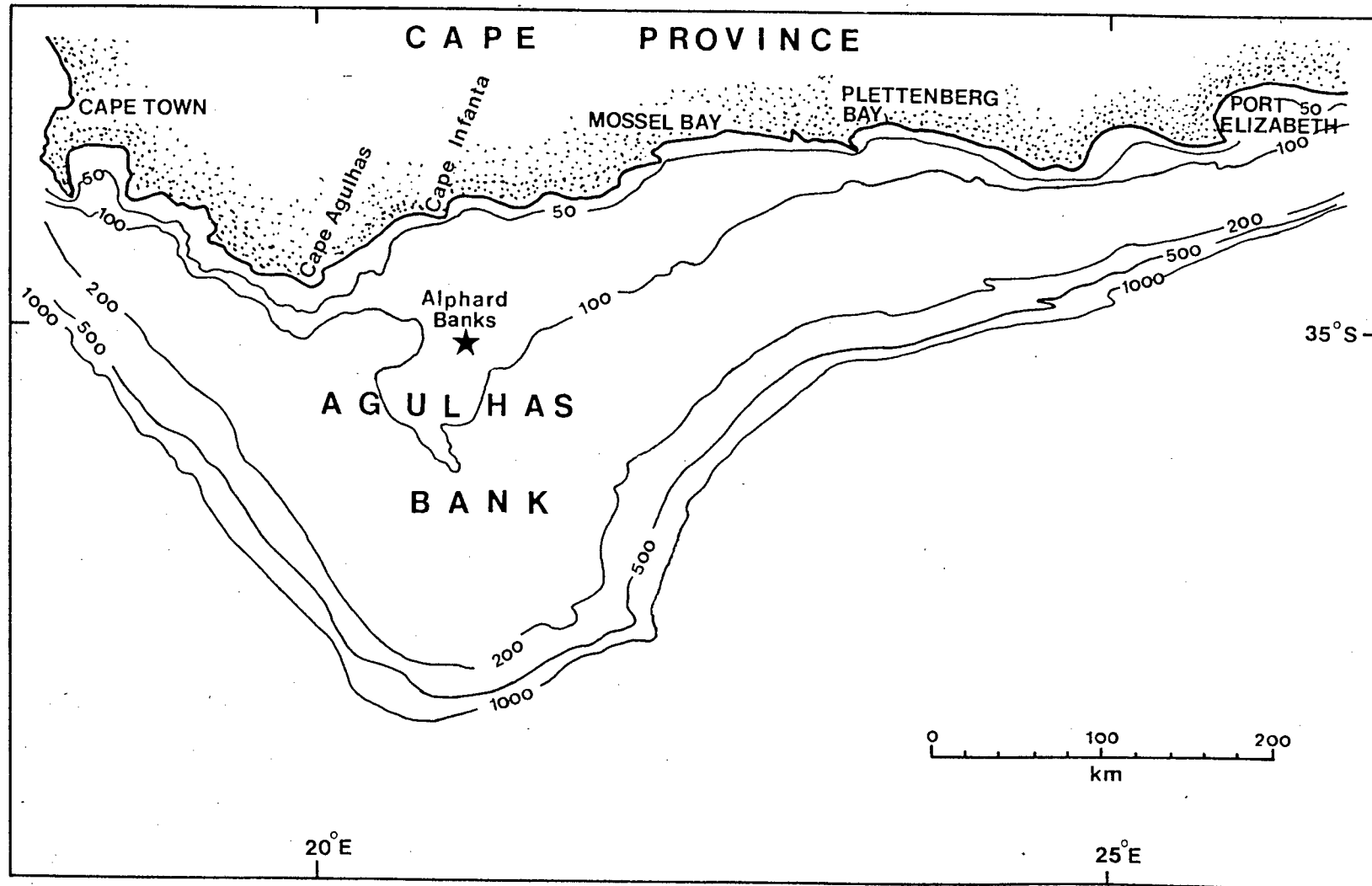


Figure 4.1. The geographical location of the Alphard Banks sampling station on the Agulhas Bank.

TABLE 4.1. Primary production, chl.a and P/B ratios for profiles on successive days in 1986, 1987 and 1988.

Cruise	%SI	Z (m)			NO ₃ - N			I ^o Production			Chl. a			P/B		
					(μ mol L ⁻¹)			(mg C m ⁻³ h ⁻¹)			(μg. L ⁻¹)					
86/04 (8-10th)	66	3	4	4	0.1	0.1	0.1	5.6	4.5	5.3	0.23	-	-	24.3	-	-
	30	14.5	14	12	0.2	0.2	0.1	2.8	1.3	4.1	0.24	-	-	11.7	-	-
	12	25	24	20.5	4.6	3.8	0.1	5.1	2.2	2.8	0.29	0.17	0.24	17.6	12.9	8.2
	7	27.5	26.5	26	4.8	2.6	12.0	6.0	14.9	319.3	0.27	0.80	30.74	22.2	18.6	10.4
	5	28	27	26.5	0.5	0.4	4.4	18.2	34.7	89.3	2.14	5.03	22.92	8.5	6.9	3.9
	3	28.5	28	27	1.8	1.1	16.7	55.0	29.4	33.0	14.10	7.96	41.17	3.9	3.7	0.8
	0.4	29	29.5	29.5	1.8	7.4	17.2	0.5	1.3	0.9	2.58	4.00	31.61	0.2	0.3	0.03
87/02/B (25-27th)	100	0	0	0	0	1.14	3.96	1.4	0.7	2.2	0.19	0.23	0.45	7.4	3.0	4.9
	30	12	12	12	1.89	1.66	0.83	2.3	17.1	6.3	0.35	0.26	0.65	6.6	65.7	9.7
	12	20.5	25	24	2.36	4.22	(9.17)	4.5	26.2	5.9	0.34	0.40	2.0	13.2	65.5	2.9
	7	26.5	32	30	9.52	4.55	1.74	5.0	26.4	13.8	-	0.47	0.36	-	56.2	38.3
	5	30.5	36	32.5	14.09	11.77	8.54	1.8	18.3	16.8	0.33	0.81	1.67	5.4	22.6	10.0
	3	40	44	37	18.21	17.17	15.21	0.9	5.6	4.5	0.34	0.28	1.67	2.6	20.0	2.7
	1	60	65	52.5	23.25	27.12	26.89	0.1	0.6	0.6	0.10	0.08	0.55	1.0	7.5	7.5
0.4	75	80	-	26.51	25.21	-	0.01	0.4	-	0.10	0.09	-	0.1	0.4	-	
88/01/C (28-29th)	90	1.5	2		0.01	0.01		2.6	1.4		0.42	0.26		6.2	5.4	
	40	9	12		0.01	0.01		3.4	1.5		0.39	0.23		8.7	6.5	
	15	20	24.5		0.01	0.01		3.4	1.6		0.36	0.18		9.4	8.9	
	10	25	30		0.04	0.01		1.0	1.2		0.27	0.16		3.7	7.5	
	6	30	36		0.02	0.03		2.4	1.1		0.51	0.12		4.7	9.2	
	2.5	39	46.5		0.16	0.08		2.8	1.1		0.88	0.54		3.2	2.0	
	1	48	58.5		14.80	14.77		0.7	1.6		0.36	0.39		1.9	4.1	
	0.5	56	67.5		22.03	23.31		0.3	0.1		0.24	0.13		1.2	0.8	

Cruise	Station	CHLOROPHYLL MAXIMUM				PRODUCTION MAXIMUM				P ^B MAXIMUM		
		%SI	Z(m)	ug.l ⁻¹	p ^B	%SI	Z(m)	mgC.m ⁻³ .h ⁻¹	p ^B	%SI	Z(m)	mgC.mgChla ⁻¹ .h ⁻¹
86/04	107	3	28.5	14.1	3.9	3	28.5	54.6	3.9	66	3	24.3
	119	3	28.0	8.0	3.7	5	27.0	34.8	6.9	7	26.5	18.6
	133	3	27.0	41.2	0.8	7	26.0	320.6	10.4	7	26.0	10.4
87/02/B	4	*	*	0.4	6.5	7	26.5	5.0	14.6	7	26.5	14.6
	11	5	36.0	0.8	22.6	7	32.0	26.4	56.6	12	20.5	66.2
	18	3	37	1.7	2.7	5	32.5	16.8	10.1	7	30	38.9
88/01/C	21	2.5	39	0.9	3.2	*	*	3.4	8.8	15	20	9.4
	26	2.5	46.5	0.6	2.0	*	*	1.6	4.0	6	36	9.0

Table 4.2. The depth of occurrence and measured value of the Chl_{max}, the P_{max} and the P^B_{max} for all Alaphard Banks stations.

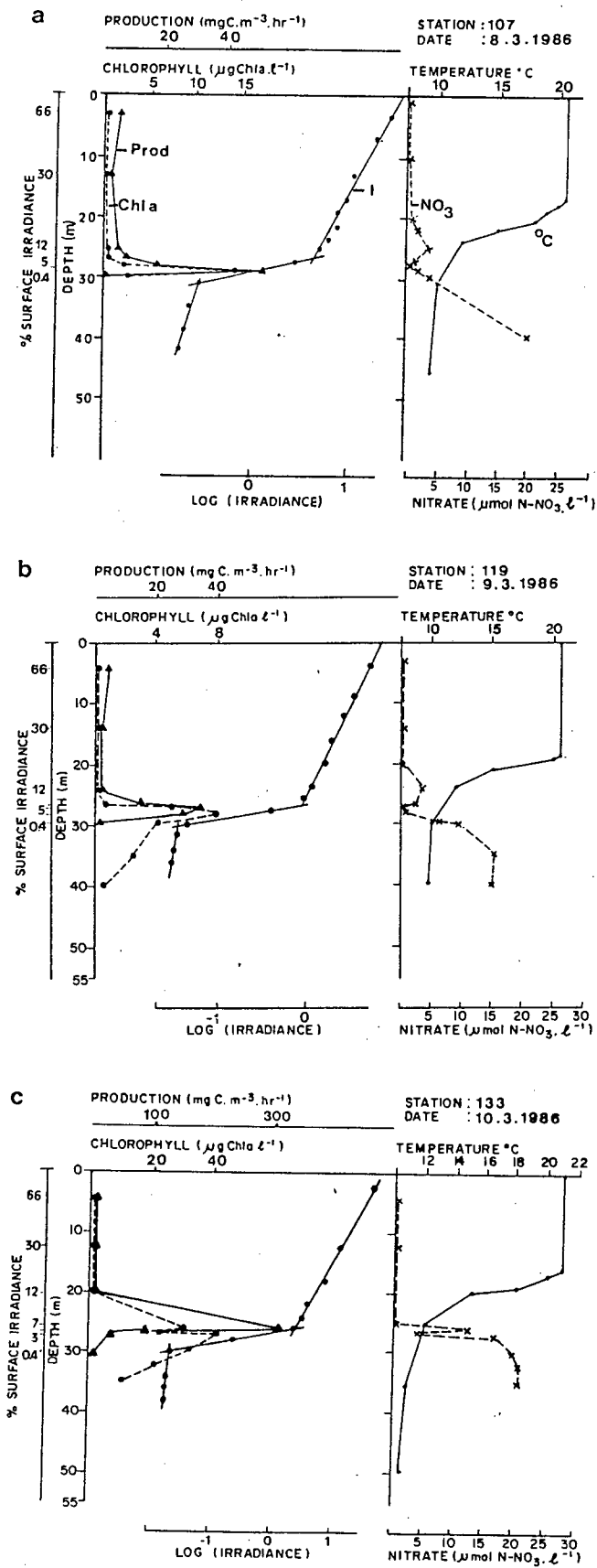


Figure 4.2. a - c. Vertical profiles of measurements of primary production (▲—▲), chlorophyll *a* (●---●), light (log I) (●---●), temperature (—●—) and nitrates (x---x) obtained during March 1986, (86/04), at the Alphard Banks station. % surface irradiance is given on the y-axis.

Cruise	Station	%SI	PRIMARY PRODUCTION				
			Total <149 μm - GF/F	<15 - 5 μm	<5 - 1 μm	<1 μm - GF/F	% of Total <15 μm - GF/F
87/02/B	4	5	4.97	0.55 (11.1)	1.47 (29.6)	0.31 (6.2)	47
	4	100	1.44	0.47 (32.6)	0.41 (28.5)	0.18 (12.5)	74
	11	5	18.31	1.10 (6.0)	1.41 (7.7)	0.47 (2.6)	16
	11	100	0.61	0.14 (23.0)	0.08 (13.1)	0 (0)	35
	18	5	16.77	4.92 (29.5)	6.71 (40.0)	3.98 (23.7)	93
	18	100	2.23	1.30 (58.3)	1.41 (63.2)	0.27 (100)	100
88/01/C	21	2.5	2.77	0.11 (4.0)	0.39 (14.1)	0.38 (14.1)	32
	21	40	3.43	0.27 (7.9)	0.89 (25.9)	1.10 (32.1)	66
	26	2.5	1.10	0.04 (3.6)	0.22 (18.6)	0.28 (25.5)	49
	26	40	1.47	0.16 (10.9)	0.36 (24.5)	0.79 (53.7)	89

Table 4.3. Size-fractionated primary production measurements for the 87/02/B and 88/01/C surveys. The percentage contribution of each size fraction is given in parentheses, with the cumulative percentage of the size fraction < 15 μm displayed in the last column.

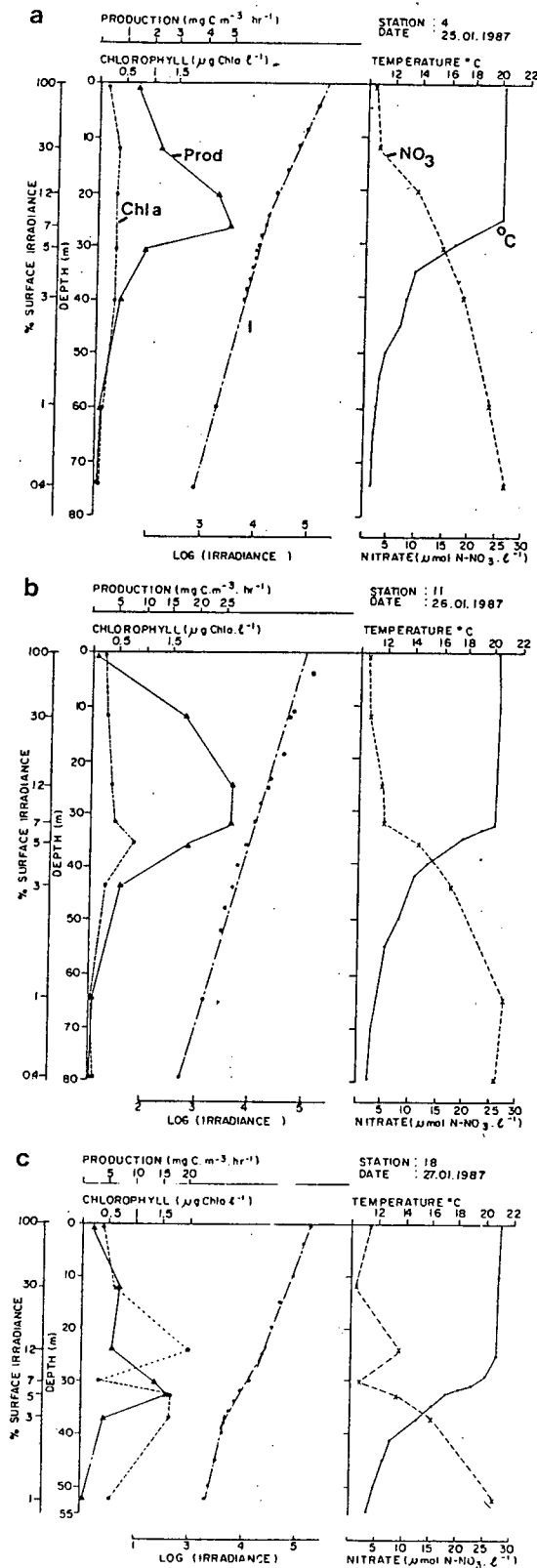


Figure 4.3. a - c. Vertical profiles of measurements of primary production (\blacktriangle — \blacktriangle), chlorophyll *a* (\bullet — \bullet), light (log I) (\bullet — \bullet), temperature (\longrightarrow) and nitrates (\times — \times) taken at the Alphard Banks station during the cruise 87/02/B, January 1987.

INTRODUCTION

The Alghard Banks are located centrally on the Agulhas Bank, South Africa, south of Cape Infanta and to the east of Cape Agulhas (Figure 4.1). An extensive survey covering a two year period has been conducted on the thermal and nutrient structure of the water column in this region by EAGLE and ORREN (1985). The regular pattern of seasonal thermal stratification and nutrient depletion in the upper mixed layer of the water column during summer and autumn months (December - April) is typical of continental shelf waters worldwide (PINGREE *et al.* 1976, CULLEN and EPPLEY 1981, MALONE *et al.* 1983). During winter months (June - August), the entire water column over the Alghard Banks is well mixed by storm events (PUGH 1982), returning nutrients to the surface waters.

EAGLE and ORREN (1985) present evidence for the mid-shelf Alghard Banks region as being intermediate between inner east bank waters, which are characterized by an intense, temporally persistent shallow thermocline and the deeper more variable water column structure to the west of Cape Agulhas during the summer stratified months (LUTJEHARMS *et al.* 1983, BOYD *et al.* 1985, LARGIER and SWART 1987, CATZEL 1989, MCMURRAY *et al.* in prep.). This proposal had been previously suggested by SCHUMANN and BEEKMAN (1985), where they refer to this region between Cape Agulhas and Cape Infanta as the "divergence zone" between east and west bank waters.

Measurements of phytoplankton biomass and production in eastern Agulhas Bank waters by CARTER *et al.* (1986, 1987), show that periods of strong, shallow thermal stratification can be suitable for the formation of very narrow layers (<5m broad) of a diatom-dominated subsurface chlorophyll maximum of high concentrations at the depth of the thermocline and nutricline. Deepening and slackening in intensity of the thermocline in western Agulhas Bank waters (LARGIER and SWART 1987) generally results in the broadening of the subsurface chlorophyll maximum in a deeper euphotic zone. The subsurface chlorophyll maximum, although still associated with the depth of the nitracline, is spread over a vertical band of 10 - 15m, and maximum concentrations are reduced relative to eastern bank

waters. The mid-shelf location of the Alphard Banks region between east and west bank waters and the variable nature of the summer thermally stratified water column, would suggest a similarly dynamic and variable biological environment in response to the changing hydrodynamics of the water column.

The sampling of an Alphard Banks station during two mid-summer (January) surveys in Agulhas Bank waters (cruises 87/02/B and 88/01/C), combined with measurements obtained at the same station in 1986 (CARTER *et al.* 1987, PROBYN and LUCAS 1987), have provided data on the vertical distribution of phytoplankton biomass and primary production associated with different vertical hydrodynamic structures. These summer stratified water column phytoplankton biomass and primary production measurements are discussed in relation to the observed water column thermal and nutrient features with an investigation of the effect of wind-mixing events.

METHODS AND MATERIALS

The geographical location of the Alphard Banks on the Agulhas Bank is shown in Figure 4.1. All sampling stations referred to in the text were carried out at this location. The materials and experimental procedures used for the measurement of downwelling light and the collection and analysis of primary production, chlorophyll *a* and nutrients samples have been previously described in chapters 2 and 3.

In addition to standard experimental primary production samples, size-fractionated production was measured during the 87/02/B and 88/01/C cruises. These measurements were included at the 5 and 100% light depth during the 87/02/B cruise and the 2.5 and 40% light depths during the 88/01/C cruise. Two replicate light bottles and one dark bottle samples were passed through a 15 μm mesh prior to incubation. After incubation, these bottles were sequentially filtered through 5 μm and 1 μm Nucleopore filters and finally onto Whatman GF/F filters. This provided productivity measurements of the 15 - 5 μm , the 5 - 1 μm and the 1 - GF/F (0.5 μm) size-fractions.

RESULTS

Profiles: Phytoplankton biomass and production

Cruise 86/04: 8 - 10th March 1986 (late summer)

Water column measurements obtained on the three sampling occasions are displayed in Figure 4.2, profiles a - c. The water column is characterized by a very stable thermal structure with a shallow upper mixed layer (15 - 20m) and an intense thermocline coincident with the 15 - 30% surface irradiance (SI) light depths. Maximum thermal gradients in excess of $4\text{ }^{\circ}\text{C}\cdot\text{m}^{-1}$ were observed. The nitracline was associated with the thermocline region and the subsurface chlorophyll maximum (Chl_{max}), with no nitrates present in the upper mixed layer. A very strong Chl_{max} situated well within the thermocline region was observed throughout the three sampling days, increasing to $>40\text{ }\mu\text{gChl}\cdot\text{l}^{-1}$ on the third day. Consistent in all three profiles is the noticeable depletion of nitrate in the upper mixed layer and at the depth of the Chl_{max} . Within the nitracline, waters above and below the depth of the Chl_{max} exhibit raised nitrate concentrations. The production maximum (P_{max}) was coincident with or slightly shallower than the Chl_{max} . Almost no production occurred in the upper mixed layer. Very fast rates of production were observed on the third day (Figure 4.2 c) ($P_{\text{max}} = 316\text{ mgC}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$), consistent with maximum chlorophyll levels. The euphotic zone was generally shallow with light being rapidly attenuated through the Chl_{max} .

Cruise 87/02/B: 25 - 27th January 1987

Figure 4.3, profiles a - c, displays measurements obtained during January 1987. Greater variability of both the physical and biological water column features was observed during this survey in contrast to the previous year. The upper mixed layer was deeper (25 - 30m) and the thermal gradients were less intense, seldom exceeding $2\text{ }^{\circ}\text{C}\cdot\text{m}^{-1}$. The thermocline region was generally located at the 7 - 12 % surface irradiance light depths. Although a nitracline was still associated with the thermocline region, considerable concentrations of nitrates were observed within the upper mixed layer. Upward advection

Cruise	Date	Station no.	1° Production (mgC m ⁻² .h ⁻¹)	Biomass (mgChla.m ⁻²)	Z _{eu} (m)	Z _m (m)	P ^B (mgC.mgChla ⁻¹ .h ⁻¹)	Z _{eu} /Z _m
86/04	9/3/86	119	168	28	30	19	6.0	1.6
	10/3/86	133	1390	289	29.5	17	4.8	1.7
87/02/B	25/1/87	4	113	9	75	26	12.3	2.9
	26/1/87	11	842	11	80	33	76.6	2.4
	27/1/87	18	296	25	52	25	11.8	2.0
88/01/C	29/1/88	21	127	31	56	35	4.1	1.6
	30/1/88	26	87	27	67.5	43	3.2	1.6

Table 4.4. Integrated primary production and biomass (chlorophyll *a*) for the euphotic zone to 0.4% surface irradiance light depth. The depth of the euphotic zone (Z_{eu}), depth of surface mixing (Z_m), integral P^B and the ratio of the euphotic zone to the mixing depth (Z_{eu}/Z_m) are shown.

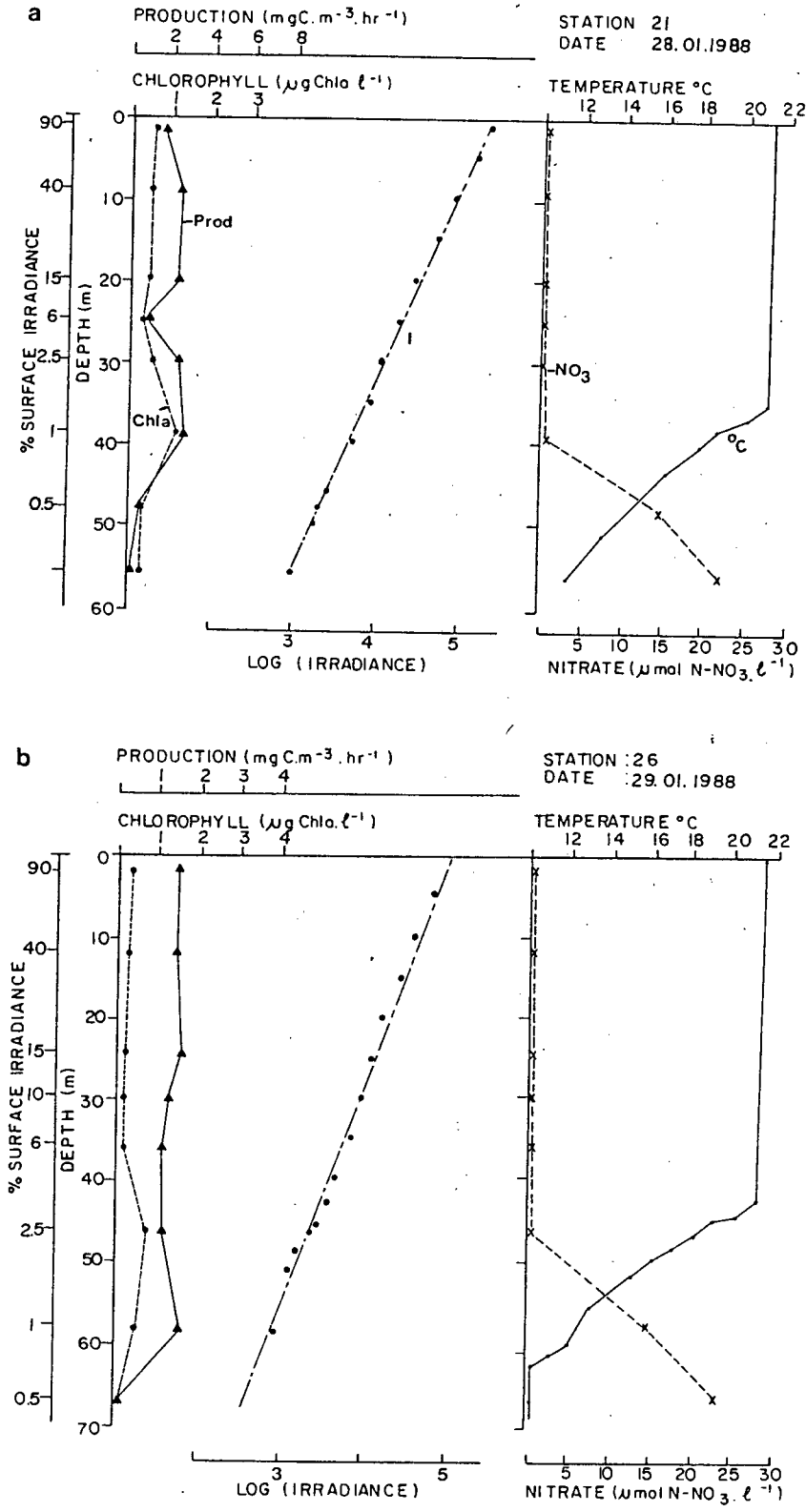


Figure 4.4. a - b. Vertical profiles of measurements of primary production (\blacktriangle), chlorophyll *a* (\bullet), light (log I) (\bullet), temperature (\longrightarrow) and nitrates (\times) taken at the Alphard Banks station during the cruise 88/01/C, January 1988.

of nitrate into the upper mixed layer was evident on the third day (profile 3 c). The vertical distribution of chlorophyll *a* was always low but very variable, being evenly distributed throughout the water column on the first day of sampling but showing a distinct subsurface Chl_{max} on the third day. Maximum chlorophyll concentrations increased over this period from 0.34 to 1.67 $\mu\text{g.l}^{-1}$. Production maxima occurred subsurface at the 5 - 7% SI light depths, but remained generally high throughout the mixed layer. A marked depression of surface production rates on all three days provides evidence of surface photoinhibition. The subsurface P_{max} was only co-incident with the subsurface Chl_{max} within the thermocline region on the third day. The euphotic zone was deep (>70m) due to low chlorophyll concentrations throughout the water column, although there was increased light attenuation on the third day due to the Chl_{max} at 25 - 30m depth.

Cruise 88/01/C: 28 - 29th January 1988 (mid-summer)

Water column measurements during this survey are presented in Figure 4, profiles a and b. The upper mixed layer was deeper (35 - 40m) and thermal stratification weaker ($<1^{\circ}\text{C/m}$) than for either of the previous surveys. The thermocline region fell well below the 5% surface irradiance light depth. Nitrates were completely depleted in the surface layer and the nitracline was sharp and closely associated with the bottom of the upper mixed layer. A slight increase in chlorophyll concentrations occurred at the depth of the nitracline but remained always below 1 $\mu\text{g.l}^{-1}$. No distinctive production maximum could be discerned. Rates remained at between 1 and 3 $\text{mgC.m}^{-3}.\text{h}^{-1}$ throughout the euphotic zone except at very low light levels (0.5% SI). Light penetration was deep (55 - 68m) and evenly attenuated through the euphotic zone.

Water column phytoplankton chlorophyll a, primary production and nitrate distributions:

The vertical distribution of primary production, P^{B} , *chl**a* and NO_3 for the three cruises is displayed in Table 1. High P^{B} ratios were observed for samples from well illuminated depths (>5% SI), but specifically when co-incident with average nitrate concentrations $>5 \mu\text{mol.l}^{-1}$ at these depths. Lowest

CHAPTER FIVE:

PHYTOPLANKTON PRIMARY PRODUCTION IN WESTERN AGULHAS BANK WATERS

Introduction

Materials and Methods

Results

Vertical profiles

Integrated water column biomass and production rates

Size-fractionated primary production and dominant phytoplankton species

Discussion

Seasonal variability of phytoplankton production

Formation of the subsurface chlorophyll maximum

Size-fractionated primary production and carbon fluxes in western Agulhas Bank waters

chlorophyll *a* concentrations and biomass specific primary production rates were obtained for nitrate depleted surface layer samples in a deep stratified water column (Tables 1 and 2). The subsurface Chl_{max} was generally situated at the 3% light depth, deeper than the P_{max} (5 - 7% SI), which again was located deeper than maximum P^{B} ratios (Table 4.2). The P/B values >25 should be considered erroneous since values greater than this exceed theoretical maxima. This is particularly so for the profile on the 26th of the 87/02/B cruise. The excessively high P/B value probably reflect erroneous production measurements rather than Chl.a measurements.

Size-fractionated primary production measurements:

Size-fractionated production measurements from the 87/02/B and 88/01/C surveys are presented in Table 3. Similar measurements were not made on the 86/04 survey. Considerable variability in the contribution of the <15 μm nano-plankton size-fraction was observed, particularly during the 87/02/B survey. Here contributions by the size-fraction <15 μm showed both maximum (100% of total production) and minimum values (16%). Some spatial separation of the total contribution of the net- and nano-plankton size-fractions is apparent. The net-plankton size-fraction was responsible for most of the production at depths corresponding to the thermocline region (5 and 2.5% surface irradiance) whilst the nano-plankton size-fraction accounted for the greater proportion of total production for samples from depths within the upper mixed layer (40% surface irradiance).

DISCUSSION

Distinct differences in the vertical structure of both physical and biological features were observed between the three sampling surveys. Integrated production rates and chlorophyll concentrations are presented in Table 4. Areal biomass and production values ranged from high values of $>1 \text{ gC}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ in March 1986, associated with rich subsurface diatom concentrations (CARTER *et al.* 1987), to levels comparable to mid-summer minima in western Bank waters ($<0.1 \text{ gC}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) associated with a deep stratified water column. The concept that the thermal structure and stratification of the water column determines the vertical distribution of phytoplankton is well known (PINGREE *et al.* 1976, IGNATIADIS 1979, HAFFNER *et al.* 1980, HARRIS *et al.* 1980, LEGENDRE 1981, PARKER 1986, VANDELDELDE *et al.*

1987). Any changes in the thermal structure of the water column due to mixing events or prolonged periods of surface heating will be reflected in the vertical distribution of the phytoplankton assemblage. Furthermore mixing events introduce nutrients, in particular 'new' nitrates into the generally nitrate poor surface mixed layer (KING and DEVOL 1979, WROBLEWSKI and RICHMAN 1987), promoting changes in water column productivity and initiating species successions of the phytoplankton assemblage characteristic of "stabilisation - destabilisation" cycles (PINGREE *et al.* 1978, LEGENDRE 1981).

It is recognized that the three surveys are temporally discontinuous and therefore limited in any definitive description of a time-series sequence of water column changes. Certain features are however remarkably consistent with proposed successional changes of the vertical distribution of phytoplankton obtained by modelling mixing events in stratified water columns (PARKER 1986, TETT *et al.* 1986, WROBELSKI and RICHMAN 1987). If the water column environment as observed in January 1988 (Figure 4.4) is taken as a starting point of the time-series, the progression to a recently post-mixing (Figure 4.3, January 1987) and an "aged" post-mixing (Figure 4.2, March 1986) phytoplankton community is evident.

Analysis of wind data from shore based automatic wind stations adjacent to the sampling area (Cape Agulhas and Mossel Bay) for the month of January 1988, indicates that the sampling site experienced moderate winds with very little variation in direction (south and south westerlies) or strength (10 - 25 knots) for two and a half weeks prior to the January 1988 cruise. The absence of nitrates in the upper mixed layer and the sharp nitracline at the depth of the thermocline is evidence of a prolonged period of nitrate removal from the surface waters (BROWN and HUTCHINGS 1987). Water column 'new' production was likely to be nitrate limited in the upper mixed layer (UML) and light limited at the depth of the nitracline (MALONE *et al.* 1983). The high percentage contribution by the <15 µm nano-plankton size-fraction to primary production measurements (66 - 89%), particularly in the UML, suggests that a considerable proportion of primary production was being driven by regenerated nitrogen sources (PROBYN *et al.* 1989).

Coastal wind data prior to the January 1987 cruise describe a westerly storm event of a four day period of strong to gale force (20 to 45 knots) winds subsiding two days prior to the survey. It is quite

conceivable that surface mixing associated with these wind speeds would be sufficient to cause considerable erosion of the thermocline (PUGH 1982, DENMAN and GARGETT 1983, LARGIER and SWART 1987) and result in the injection of nitrates into surface waters. The appearance of high nitrate concentrations in the surface mixed layer during this survey (Table 4.1) is indeed strong evidence of a recent mixing event (WROBLEWSKI and RICHMAN 1987).

The initial apparent response of the phytoplankton assemblage to the mixing event is greatly enhanced primary production and associated elevated P^B ratios in the nitrate enriched upper mixed layer relative to January 1988 rates. By the second day of sampling (Figure 4.3 b), the Chl_{max} was established and production was dominated by the net-plankton $>15 \mu m$. Phytoplankton standing stocks were observed to increase with high euphotic zone production resultant of continuing nitrate availability (KING 1986), consistent with expectations of limited grazing of phytoplankton at this early stage in successional progressions (WROBLEWSKI and RICHMAN 1987).

Our measurements from the third day of sampling (Figure 4.3 c) are difficult to interpret without knowledge of water mass movements past the sampling station. It is possible that a new, 'younger' body of water was advected past the sampling station, as the pulse of nitrate and complete change in the relative importance in primary production by the net-plankton size-fraction from $>60\%$ to almost zero is more consistent with the first rather than the second sampling day's water column.

Considering a time period of relaxed surface mixing with stabilisation of the water column, empirical models of phytoplankton growth in stratified seas (PARKER 1986, TETT *et al.* 1986) describe the removal of nitrates from the UML and the formation of a subsurface Chl_{max} dominated initially by net-plankton. Wind data records for the two weeks prior to the March 1986 survey, describe a four day period of strong (20 - 30 knots) south easterly winds followed by a week of calm to light (<10 knots) wind speeds in the study area. The March 1986 measurements are thus representative of an 'aged' water column environment following a wind-mixing event.

The intensification of thermal stratification of the water column during March relative to January months is in agreement with observations of EAGLE and ORREN (1985), SWART and LARGIER (1987) and CATZEL (1989) in these waters. SWART and LARGIER (1987) propose that the thermocline during

the late summer months is typically shallow (<25m) and if deepened by a mixing event will be returned to its original shallow position by bottom water advection shortly after the cessation of surface wind-mixing. Furthermore, a seven day period of relaxed surface mixing and a shallow nitracline appear to have been favorable for the development of the very dense subsurface Chl_{max} observed. Water column production and biomass attained maximum levels, but P^{B} ratios were reduced relative to the January 1987 situation which followed more immediately on a mixing event (Table 4.4). The dominance of the Chl_{max} by diatoms (CARTER *et al.* 1987, PROBYN and LUCAS 1987) is consistent with expected vertical distributions of photosynthetic net-plankton after a growth phase in surface waters followed by accumulation of sinking cells in the thermocline region at the depth of the nitracline (PARKER 1986).

Of considerable interest and somewhat contrary to expectations, was the presence of nitrate in and above the Chl_{max} and P_{max} , and the dramatic increase of biomass in the thermocline region on the third day of sampling. The increased phytoplankton biomass is strongly suggestive of considerable ungrazed 'new' production in the euphotic zone (KING 1986, MICHAELS and SILVER 1988). This is possible if phytoplankton production and zooplankton grazing with associated enhanced heterotrophic regeneration activity can assume steady state conditions (EPPLEY *et al.* 1979, WROBLEWSKI and RICHMAN 1987). PROBYN and LUCAS (1987) have shown that more than 50% of the primary production in this system is driven by regenerated nitrogen sources (NH_4^+ and Urea), thus the removal of phytoplankton by grazing and sinking does not reduce overall standing stocks, whilst biomass accumulation in the Chl_{max} can in fact exceed biomass removal rates with 'new' production utilising available nitrates advected across the thermocline (SWART and LARGIER 1987). That nitrogen is non-limiting to P_{max} in this system is supported by the accumulation of nitrate above the Chl_{max} . Light therefore becomes the major limiting factor for primary production within the Chl_{max} due to self-shading (CARTER *et al.* 1987) and the increased biomass in the subsurface Chl_{max} will mainly be a result of P_{max} above the subsurface Chl_{max} .

Clearly then, the floristic composition of the phytoplankton assemblage and the maximum concentrations achieved in the Chl_{max} are strongly dependant on the depth of the upper mixed layer and the thermocline intensity. A shallow Z_m (15 - 25m) (Table 4.4) and a tight thermal structure

supports narrower layers of high concentrations of net-plankton, similar to observations by NAPP (1987) in stratified waters of the Southern Californian Bight. However, the temporal stability of these high concentrations of phytoplankton in the subsurface maximum are likely to persist only as long as the stability of the water column is undisturbed by a mixing event.

INTRODUCTION

The continental shelf waters of the Agulhas Bank between Cape Point and Cape Agulhas and south to the 200m isobath form the southern boundary of the Southern Benguela upwelling system (SHANNON 1985). The physical and biological oceanographic features linking western Cape and south coast waters have been identified by DE DECKER (1973), BANG and ANDREWS (1974), HARRIS (1978) and SHANNON *et al.* (1984). Most significantly, the Agulhas Bank region between Cape Point and Mossel Bay constitutes the major spawning grounds of the commercially exploited anchovy, *Engraulis capensis* (CRAWFORD *et al.* 1980, SHELTON and HUTCHINGS 1982, ARMSTRONG *et al.* 1983, HAMPTON *et al.* 1985).

Acoustic fish surveys conducted on the Agulhas Bank estimate between 0.8 - 1.6 million tonnes of spawning adult anchovy to be present in these waters during the peak anchovy spawning months, October to January (HAMPTON *et al.* 1985, HAMPTON 1987). The regular annual recruitment patterns observed for anchovy in Western Cape waters are sustained by seasonally recurring environmental processes. Of these, most crucial are physical mechanisms of passive transport of eggs and larvae by currents (SHELTON and HUTCHINGS 1982, NELSON and HUTCHINGS 1987), phytoplankton production and zooplankton production in the spawning and recruitment waters (LASKER 1972, JAMES 1988).

It has been suggested that an understanding of the seasonal variability of primary production and phytoplankton biomass distributions may provide auxiliary information necessary for improved assessments of fish stock fluctuations, movements and perhaps even annual fish yields (LASKER 1978, AGENBAG *et al.* 1981, SMITH and EPPLEY 1982, SHANNON and FIELD 1985, SHELTON *et al.* 1985). Despite the location of the anchovy spawning grounds in the continental shelf waters of the Agulhas Bank, phytoplankton dynamics within this region remain poorly described. The only estimates of primary production that exist for these waters are scattered time-series measurements of limited temporal coverage (BROWN 1983, SHANNON and FIELD 1985), or calculated estimates based on measurements of surface chlorophyll concentrations by satellite remote sensing (SHANNON and HENRY

1983, SHANNON *et al.* 1984). This latter method has been shown to be of doubtful value in waters where a deep subsurface chlorophyll layer is present (HAYWARD AND VENRICK 1982), as has been observed in western Agulhas Bank waters during summer stratified conditions (SHELTON *et al.* 1984, CARTER *et al.* 1986, CARTER *et al.* 1987, HORSTMAN unpublished data).

The three year survey of phytoplankton primary production presented here involved the field measurement of community and size-fractionated phytoplankton production rates in mid and outer western Agulhas Bank shelf waters during five separate cruises of short-duration (6 - 8 days each). Phytoplankton production measurements are presented in relation to the observed vertical distribution of temperature, light, nutrient (nitrate) and phytoplankton biomass in the water column, for the identification of the possible factors controlling primary production in these continental shelf waters. The distinction of phytoplankton size-fractions is of relevance to the evaluation of potential trophic and nutrient pathways within the system (PROBYN *et al.* 1989). The size structure and activity of the planktonic community has considerable bearing on whether there is an efficient transfer of carbon to higher trophic orders or whether carbon is recycled or respired within the system and thus not available for export from the system (VEZINA and PLATT 1988).

MATERIALS AND METHODS

The locations of the study sites occupied during five oceanographic cruises in western Agulhas Bank waters aboard the research ship *Meiring Naude*, are shown in Figure 5.1. A brief description of each cruise *viz.* cruise dates, the frequency of sampling at each location, average insolation during the experimental incubation period and average sea surface temperature, is presented in Table 5.1. Frequency of sampling was highest at station QP (34.9°S, 16.5°E), chosen for sampling emphasis due to its central positioning in western Agulhas Bank midshelf waters. Spatial coverage of the western bank region extended to a midshelf station (DP) west of QP, and three offshore stations (OFS1, 2, 3) south-west and south of QP.

The standard daily procedure for water column profiling and primary production measurements is described in chapters 2, 3, and 4, but some auxiliary methods and definitions will be expanded upon.

The extinction of down-welling photosynthetically active radiation (PAR) through the water column was measured using a Kahlsico underwater irradiance meter. Samples were taken from light depths corresponding to set light levels in the incubation tubes. These varied slightly from cruise to cruise, but generally numbered eight light depths ranging from 0.4 or 0.5% Surface Irradiance (SI) to 90 or 100% SI. The euphotic zone depth ($Z_{eu0.5\%}$) is defined as the depth of the deepest sample, either 0.4% or 0.5% SI.

Chlorophyll *a* was measured fluorometrically on a Turner 111 model fluorometer after extraction in 90% acetone, as described in PARSONS *et al.* (1984). The fluorometer was calibrated against measurements on a Beckman DU spectrophotometer of a pure chlorophyll *a* extract (Sigma Chemical Co., U.S.A.) in 90% acetone solution, determined according to the SCOR/UNESCO (1966) trichromatic equations. Chlorophyll *a* values presented in the results have not been corrected for phaeopigments.

Subsamples for nitrate analysis were frozen at -20°C prior to analysis on a Technicon autoanalyser using standard methods modified by MOSTERT (1983).

Samples for species identification were preserved with formalin (1% v/v), and stored in the dark. Two stations were selected from each of two cruises (88/10 and 88/01/C) for phytoplankton species identification and cell counts. Samples were counted by inverted light microscopy using a Rose Bengal stain. Cell carbon equivalents were calculated from measured cell volumes according to STRATHMAN (1967).

The regression of chlorophyll *a* against cell carbon estimates for two stations of the mid-winter cruise 88/10 (July) provided chlorophyll *a* : carbon ratios for the winter well-mixed water column. This regression is not valid for summer stratified water column data (TETT *et al.* 1986) and here chlorophyll *a* : carbon ratios were obtained from the ratios of average values of chlorophyll *a* and cell carbon from the thermocline region and the upper mixed layer, respectively.

RESULTS

Vertical profiles

Because of strong seasonal changes observed on different cruises, winter, spring and summer measurements are treated separately.

Mid-winter measurements: 15 - 19 July 1988 (Cruise 88/10)

Figure 5.2 a - c displays water column measurements obtained at mid- and outer-shelf sampling locations (QP, DP and OFS3).

The euphotic zone at all stations was isothermal throughout. Surface water temperatures were similar for midshelf stations at 15.2 - 15.5 °C (Figure 5.2 a and b), but increased in the outer-shelf waters to 16.8 °C (Figure 5.2 c). Typically, the mixed layer extended to between 65 to 75m, with a weak thermocline at this depth. Nitrate-nitrogen was present in moderate concentrations (4 - 5 $\mu\text{mol NO}_3\text{I}^{-1}$) throughout the euphotic zone.

The 0.5% light depth ($Z_{\text{eu}0.5\%}$) showed little daily variability, with a mean depth at 51m (s.d.=3.5m;n=4). The average mixing depth (Z_{m}) was therefore considerably deeper than the $Z_{\text{eu}0.5\%}$, with the $Z_{\text{eu}}/Z_{\text{m}}$ ratio ranging between 0.51 - 0.66.

Chlorophyll *a* was evenly distributed throughout the euphotic zone. Maximum values ranged between 0.5 - 1.5 $\mu\text{g.l}^{-1}$. Maximum production rates (P_{max}) were measured at the 40 % and 85% light depths and ranged between 2.5 and 6 $\text{mgC.m}^{-3}.\text{h}^{-1}$. Negligible production was observed at light intensities below 2% surface irradiance. Surface photo-inhibition of production rates was indicated in two of the four profile measurements (Figures 5.2 b and c).

Spring measurements: (24 - 29 October 1987) (Cruise 87/14/B)

Water column measurements at the mid-shelf station QP are displayed in Figure 5.3 a - c. The vertical structure of physical and biological features closely resemble those of the winter profiles, but differ considerably in the absolute values of measurements.

The euphotic zone was isothermal throughout, showing some warming by *ca.* 1 °C to 16.5 - 16.8 °C from winter measurements. The surface mixing depth extended to between 50m and 65m, with a more strongly developed thermocline relative to the winter water column. Euphotic zone nitrate-nitrogen concentrations were very low throughout the sampling period, often below detectable levels and always $<0.5 \mu\text{mol.l}^{-1}$.

The $Z_{\text{eu}0.5\%}$ was shallower than measured during winter months, averaging at 42m (s.d.=10.6m;n=3). Little change was observed in the $Z_{\text{eu}}/Z_{\text{m}}$ ratio, which ranged between 0.5 - 0.8.

Maximum chlorophyll *a* and production rates were twice to three times those observed during the winter July months, and ranged between 1.8 - 2.5 $\mu\text{gChl}a.\text{l}^{-1}$ and 9.2 - 18.6 $\text{mgC}.\text{m}^{-3}.\text{h}^{-1}$.

Summer measurements: 23-29 January 1987 (Cruise 87/02/B)

22-29 January 1988 (Cruise 88/01/C)

2-6 December 1986 (Cruise 86/19/I)

Profiles of the summer water column measurements are presented in Figure 5.4 a - h.

The series of profiles 5.4 a - d obtained at QP between 28.01.1987 and 31.01.1987 characterize the deeply stratified water column environment of the western Agulhas Bank in summer. A marked thermocline with an associated nitracline was a constant feature between 37m and 47m depth. The top of the thermocline averaged at 40m (s.d.=2.2m;n=4). The depth of maximum nitrate gradient occurred below the base of the upper mixed layer at an average depth of 43m (s.d.=3.2m;n=4). Nitrate concentrations were considerably reduced in the upper mixed layer ($<4 \mu\text{mol.l}^{-1}$) in comparison to those in and below the nitracline (>5 and $> 20 \mu\text{mol.l}^{-1}$ respectively).

The 0.4% surface irradiance light depth was at all times deeper than 70m with a maximum depth of 83m. The very deep $Z_{\text{eu}0.4\%}$ resulted in a $Z_{\text{eu}}/Z_{\text{m}}$ ratio of 1.7 - 2.2.

A subsurface chlorophyll *a* maximum (Chl_{max}) persisted for all four sampling days within the thermocline region at the depth of maximum nitrate gradient, varying only slightly in concentration (0.5 - 0.8 $\mu\text{gChl}a.\text{l}^{-1}$) and thickness (10m - 15m). Similar temporal continuity was observed in the daily measurements of water column primary production rates. A subsurface P_{max} was always coincident

CRUISE	DURATION	LOCATION sampling frequency					Mean total isolation during incubation E . m ⁻² (s.d.)	Incubation (Sea surface) Temperature °C	
		QP	DP	OFS	1	2 / 3		Midshelf	Offshore
86/19/I	1/12/86 - 6/12/86	2	1	*	1	1	7.91 (6.1)	18.5 - 18.7	19.6
87/02/B	24/1/87 - 31/1/87	4	*	*	*	*	17.121 (0.9)	20.8 - 21.4	*
87/14/B	22/10/87 - 31/10/87	3	*	*	*	*	7.095 (2.6)	16.6	*
88/01/C	23/1/88 - 30/1/88	5	1	*	*	*	13.802 (5.3)	20.7 - 21.0	*
88/10	13/7/88 - 20/7/88	1	1	1	*	1	4.688 (3.0)	15.1	16.8
	TOTAL	15	3	1	1	2			

Table 5.1. A description of cruise dates, sampling frequency at station locations and average incubation conditions (incoming solar irradiation and sea-surface temperature) for the five cruises. Station locations not occupied during cruises is shown by an *.

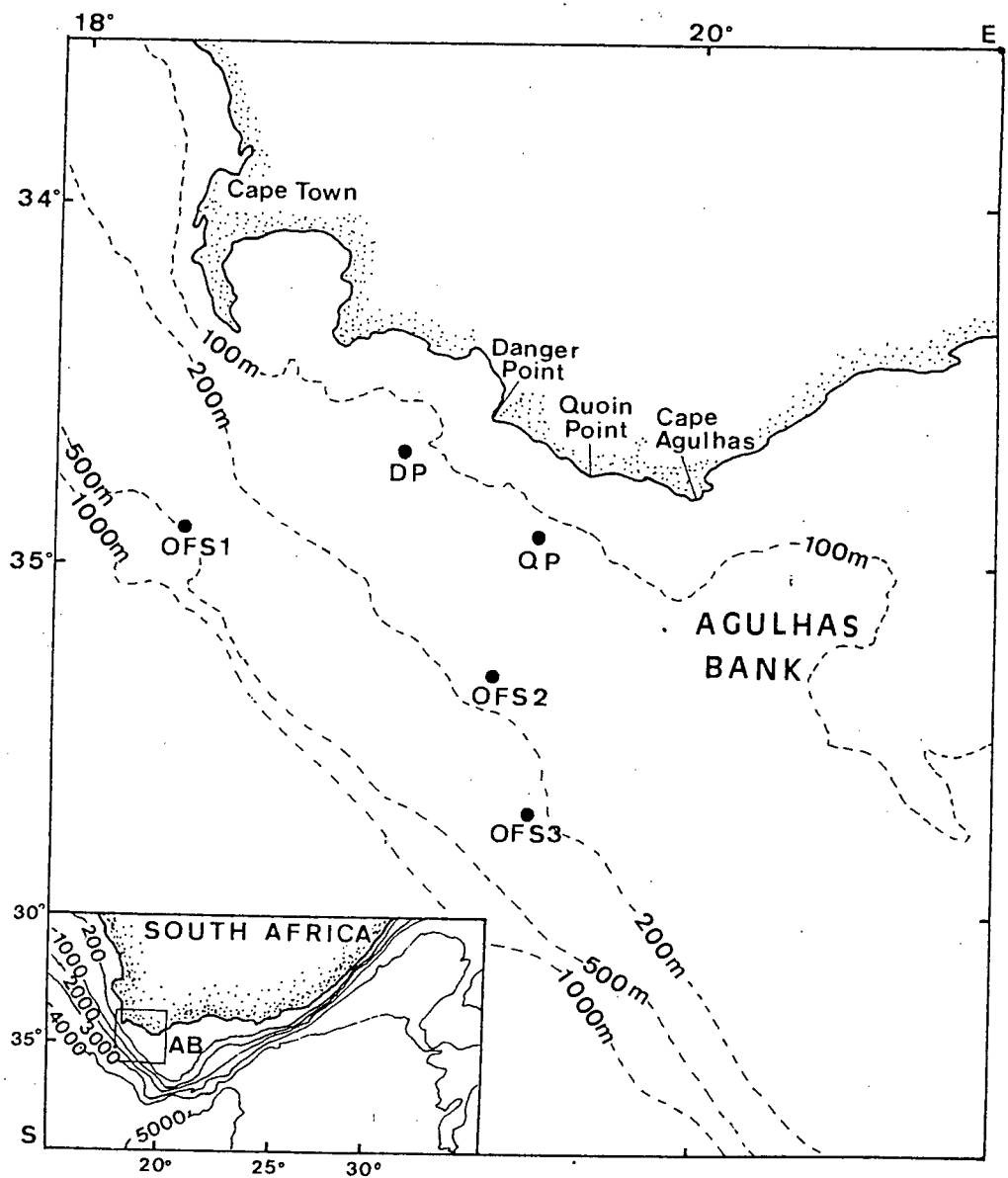


Figure 5.1. The locations of midshelf (QP and DP) and offshore (OFS 1 , 2, 3) primary production stations occupied during the study period.

CRUISE	87/02/B Midshelf	88/01/C Midshelf	Midshelf	86/19/1 Outer shelf
<u>PRODUCTION MAX:</u>				
mgC.m ⁻³ .h ⁻¹	3.51 - 5.12	2.6 - 18.72	4.02 - 19.1	1.91 - 3.99
Z (metres)	38 - 45	1.5 - 40	17.5 - 24	surface
Z (% light)	7 - 5	90 - 2.5	7	100
<u>CHLOROPHYLL MAX:</u>				
mgChla.m ⁻³	0.50 - 0.78	0.58 - 6.14	1.03 - 1.81	0.62 - 0.75
Z (metres)	38 - 53	12 - 47	32.5 - 39	32 - 33.5
Z (% light)	3 - 7	15 - 1	3 - 0.4	7 - 5
<u>p^B MAX:</u>				
mgC.m ⁻³ .h ⁻¹				
mgChla.m ⁻³	6.93 - 17.17	7.03 - 20.1	11.52 - 29.1	6.30 - 7.28
Z (% light)	30 - 100	15 - 100	7	100
<u>NITRATES:</u>				
Z nitracline (m)	30 - 47	28 - 44.5	24	33.5 - 42
Average NO ₃ ^{-j} n				
UML (μmol.l ⁻¹)	0.74 - 2.50	0.01 - 0.15	0.97 - 2.39	1.39 - 2.27
<u>THERMOCLINE:</u>				
Z UML (metres)	32 - 42	22 - 50	22 - 37	25 - 47
Average °C/M	0.3 (0.07)	0.5 (0.2)	0.8 (0.58)	0.2 (0.2)
<u>EUPHOTIC ZONE:</u>				
Z 0.5% (metres)	72 - 83	33 - 61	30 - 39	65 - 72
AVERAGE Z _{eu} /Z _{uml}	2 (0.2)	1.7 (0.4)	1.4 (0.1)	2.2 (1.0)
Number of Stations	4	6	3	2

Table 5.2. Ranges of summer measurements for 87/02/B, 88/01/C and 86/19/I. Where means are given, the standard deviation appears in parenthesis. Z denotes depth in the euphotic zone of the described variable. The upper mixed layer (UML) extends from sea-surface to the inflection point of the thermal trace

5.2a

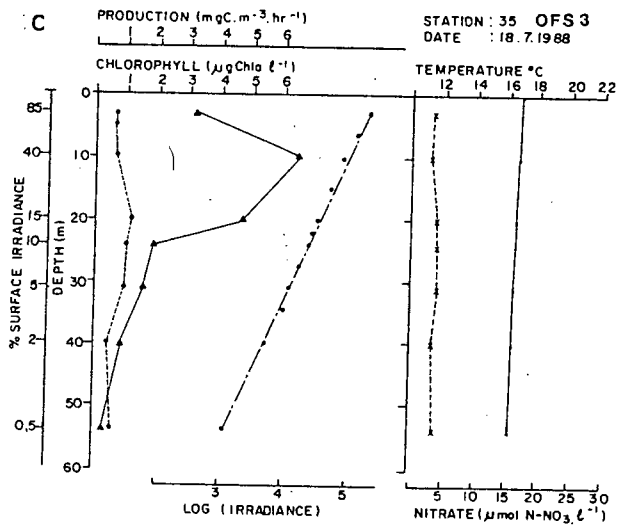
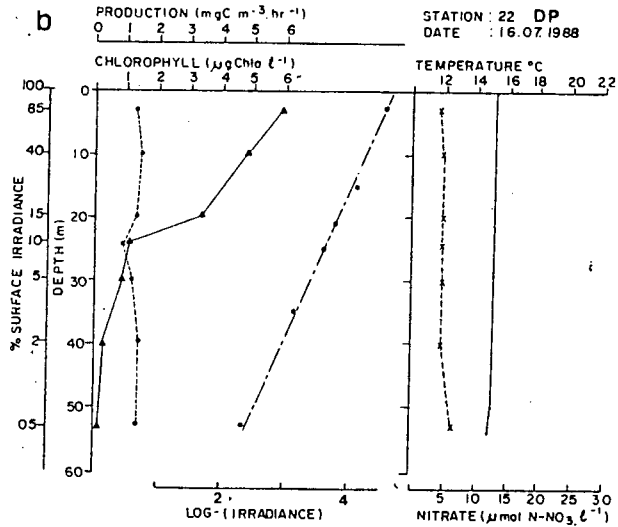
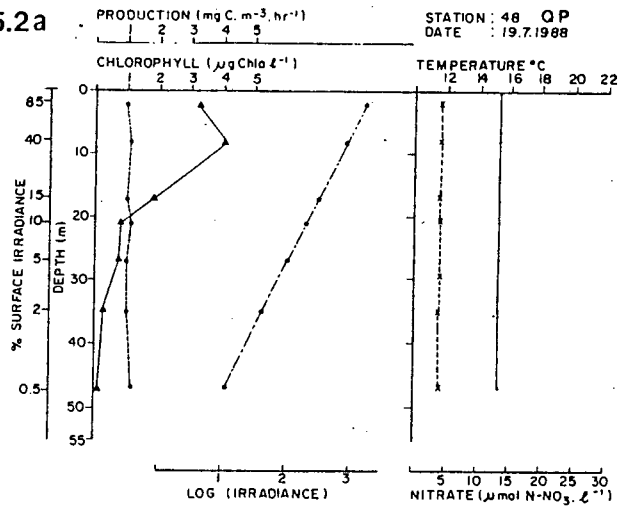
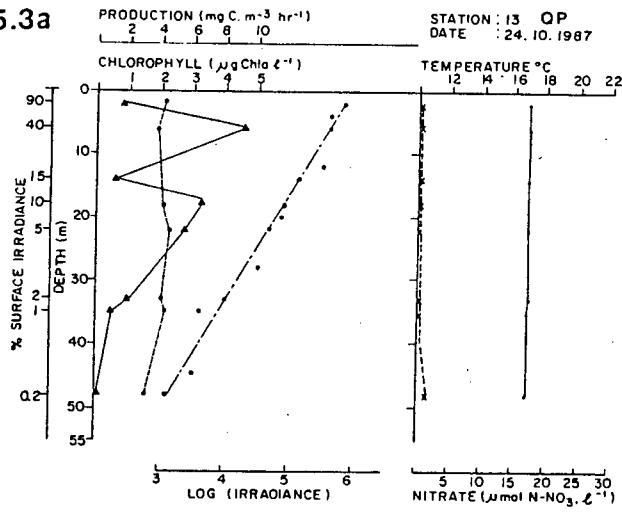


Figure 5.2 a - c. Vertical profiles of euphotic zone measurements of phytoplankton production (\blacktriangle — \blacktriangle), chlorophyll *a* (\circ — \circ), light attenuation ($\log I$) (\circ — \circ), temperature (\bullet — \bullet) and nitrates (\times — \times) during the mid-winter survey, July 1988 (88/10).

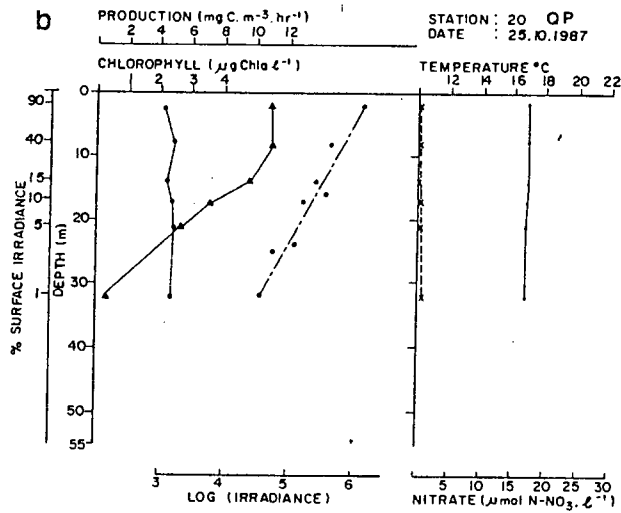
SAMPLING LOCATION	CRUISE	NUMBER OF STATIONS n.	INTEGRATED PRODUCTION (mgC.m ⁻² .h ⁻¹)		INTEGRATED PIGMENT (mgChl _a .m ⁻²)		DEPTH OF EUPHOTIC ZONE (m) 0.5% SI	
			mean	(s.d.)	mean	(s.d.)	mean	(s.d.)
<u>Mid-winter</u>								
QP	88/10	1	70.3		47.8		53	
DP	88/10	1	119.7		68.0		47	
OFS	88/10	2	108	(49.2)	35.4	(8.0)	47	(8.5)
<u>Spring</u>								
QP	87/14/B	3	243.9	(95.1)	100.6	(28.1)	44	(10.6)
<u>Summer</u>								
QP	86/19/I	2	289	(201.1)	34.5	(3.2)	42.5	(17.7)
	87/02/B	4	117	(35.3)	10.6	(3.6)	77.8	(4.5)
	88/01/C	5	195.6	(53.7)	58.6	(26.9)	55.7	(17.2)
DP	86/19/I	1	86.2		21.1		39.0	
	88/01/C	1	131.7		58.5		44.5	
OFS	86/19/I	2	80.7	(29.5)	30.9	(11.9)	68.5	(4.9)

Table 5.3. Integrated phytoplankton production rates and biomass (chlorophyll *a*) for the euphotic zone to the 0.5% surface irradiance light depth. Means are given for measurements from the same station location during individual cruises.

5.3a



b



c

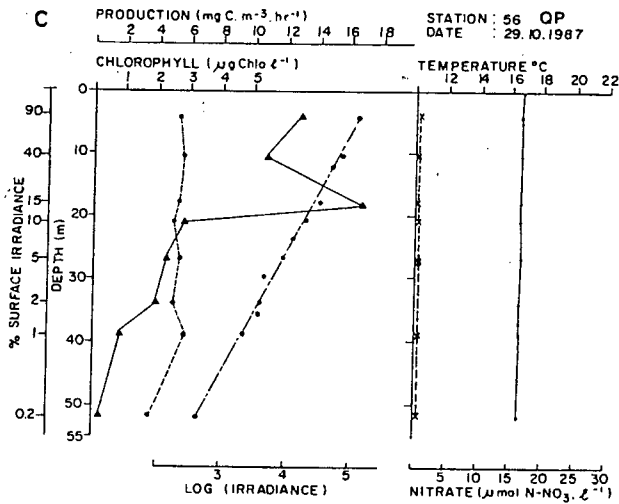


Figure 5.3 a - c. Vertical profiles of measurements of primary production (▲—▲), chlorophyll *a* (●---●), light attenuation (log I) (●---●), temperature (—) and nitrates (x---x) as observed during the spring survey, October 1987 (87/14/B).

CRUISE	DEPTH %SI	PRODUCTION (mgC.m ⁻³ .h ⁻¹)								
		TOTAL 149 μm - GF/F mean (s.d.)		15 μm - 5 μm mean (s.d.) %			5 μm - GF/F mean (s.d.) %		% of TOTAL <15 μm	
Mid-Winter										
88/10	5	0.91	(0.55)	0.65	(0.6)	71	0.23	(0.18)	26	97
n = 4	40	5.19	(0.99)	2.94	(1.7)	57	0.56	(0.17)	11	68
Spring										
87/14/B	5	5.05	(0.74)	0.48	(0.41)	10	0.97	(1.02)	19	29
n = 2	40	10.09	(1.2)	2.53	(2.12)	25	1.22	(0.41)	12	37
Summer										
87/02/B	5	3.70	(1.41)	0.71	(0.48)	19	1.60	(1.86)	43	62
n = 4	100	1.02	(1.06)	0.42	(0.39)	41	0.22	(0.30)	21	62
88/01/C	2.5	3.33	(1.89)	0.35	(0.3)	10	0.26	(0.13)	8	18
n = 6	40	5.03	(3.06)	0.56	(0.62)	11	0.92	(0.31)	18	29

Table 5.4. Mean size-fractionated production rates for the winter, spring and summer surveys. The percentage contribution to community production of each size-fraction is headed %, and the combined % contribution of the <15 um size-fraction is presented in the last column.

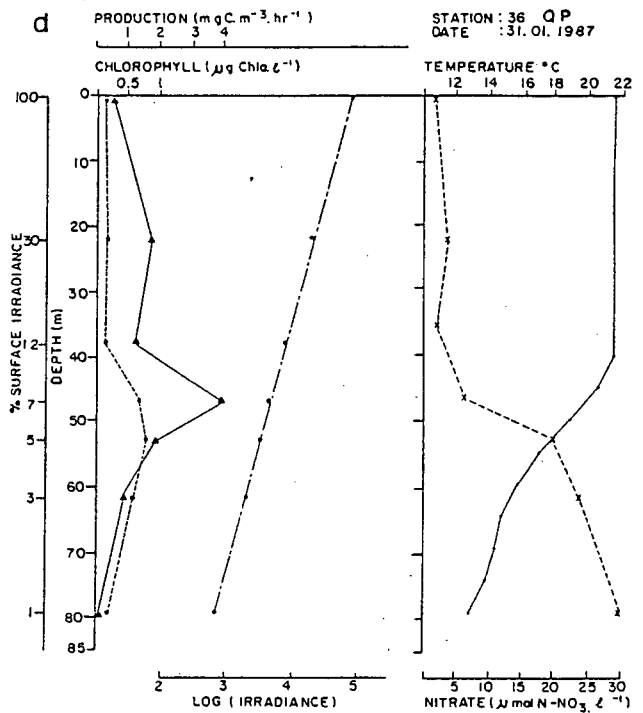
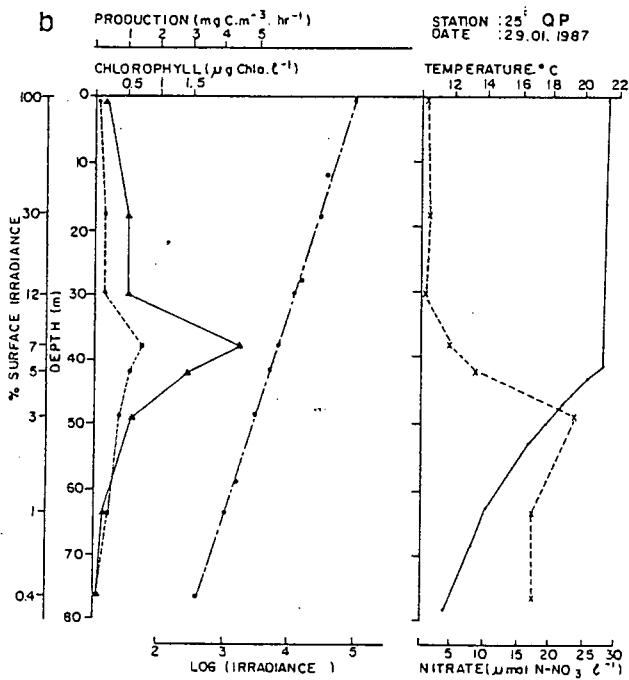
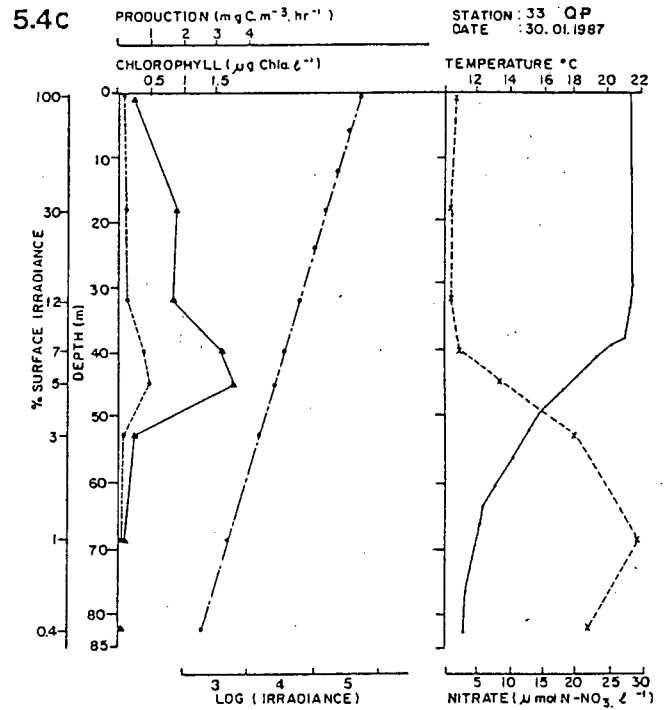
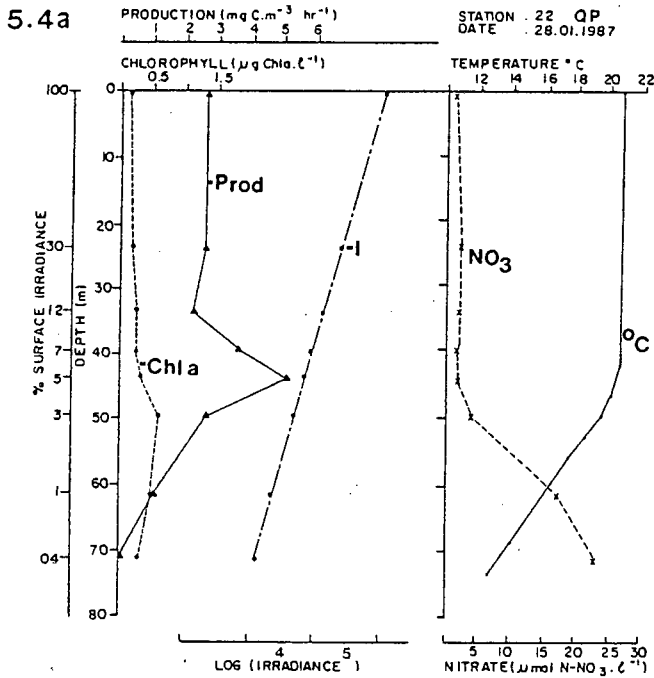


Figure 5.4 a - d. Vertical profiles of measurements of primary production (▲-▲), chlorophyll *a* (●-●), light attenuation (log I)(●-●), temperature (◄-►), and nitrates (x--x) for the summer 87/02/B cruise, January 1987.

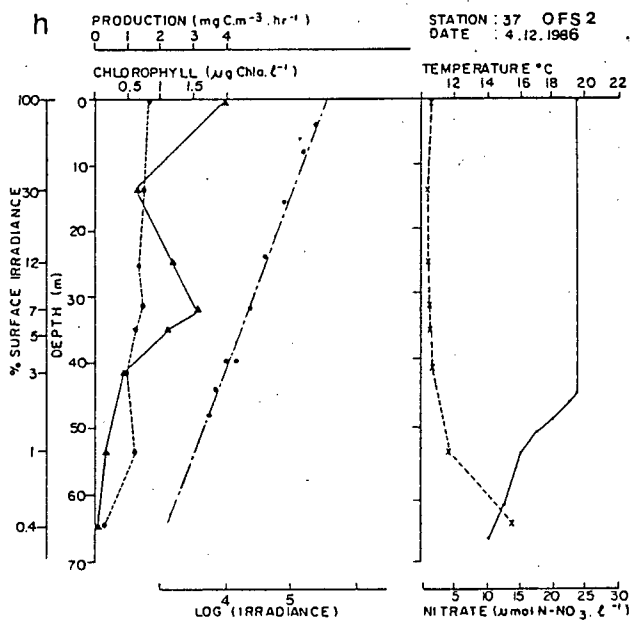
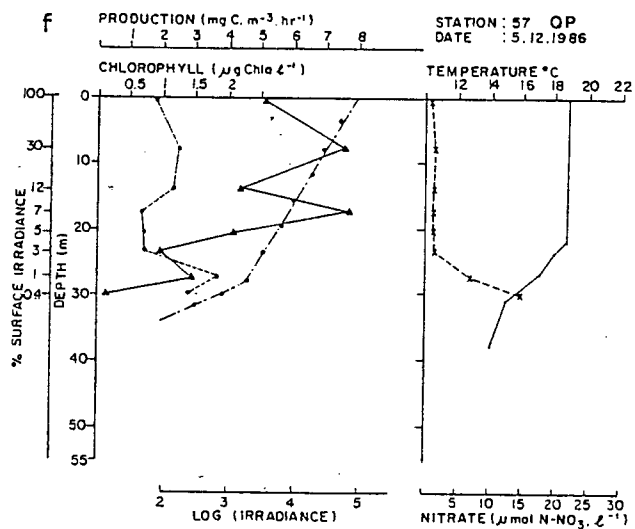
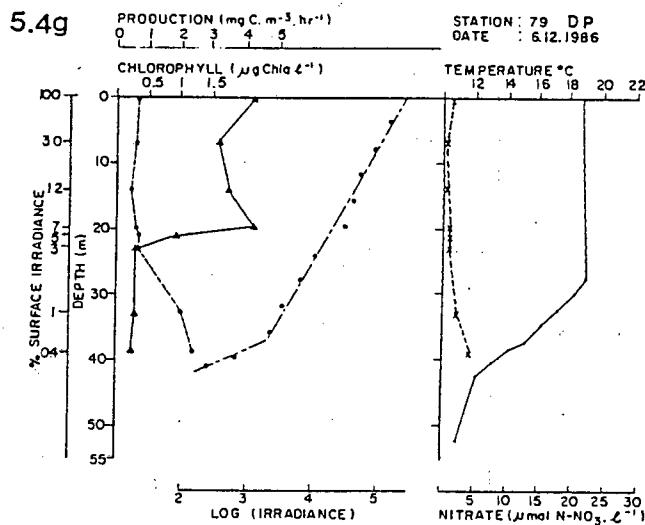
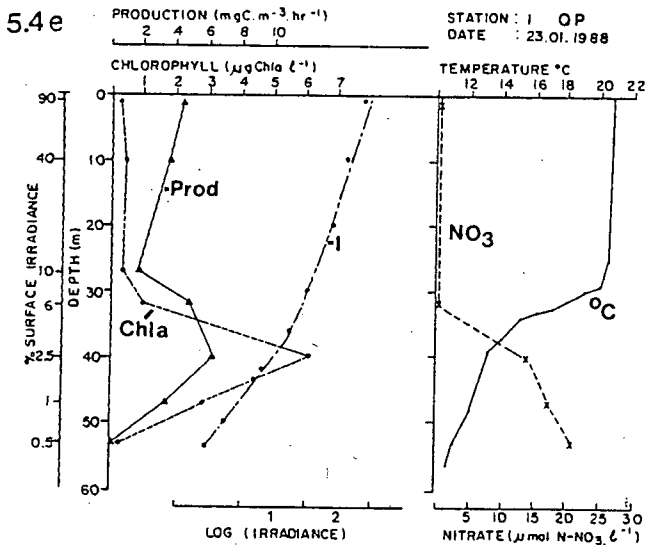


Figure 5.4 e - h. Vertical profiles of measurements of primary production (\blacktriangle), chlorophyll a (\bullet), light attenuation ($\log I$) (\bullet), temperature (\bullet) and nitrates (\times) for the January 88/01/C cruise (profile e) and the December 86/19/I cruise (profiles f - h).

CRUISE	STATION		DEPTH		PIGMENT µgChl a.l ⁻¹	BIOMASS mgC.l ⁻¹				DOMINANT SPECIES
	No. (Date)	Location	m	%SI		Total	Diatoms	Dino- flagellates	Flagellates	
88/10	22 (16/7/88)	DP	39.5	2	1.45	62.76	1.19	12.62	48.96	Microflagellates <15 µm
			30	5	1.22	43.05	3.28	3.85	35.92	"
			20	15	1.32	52.59	1.63	4.27	46.69	"
			10	40	1.46	59.25	2.16	4.61	52.47	"
	35 (18/7/88)	OFS3	40	2	0.46	17.49	1.15	0.04	16.31	Microflagellates <15 µm
			31.5	5	0.97	30.98	1.25	3.30	26.43	"
			20	15	1.12	41.90	1.05	1.65	39.20	"
			10	40	0.69	17.40	0.69	0	16.70	"
88/01/C	1 (23/1/88)	QP	47	1	2.81	49.69	44.74	1.13	3.82	Chaetoceros Sp.
			40	2.5	6.01	151.91	132.03	10.76	9.12	Nitschia
			27	10	0.37	46.75	42.67	1.61	2.47	Bacteriastrum
			10	40	0.45	54.35	35.15	8.57	10.64	Chaetoceros/Nitschia
	4 (24/1/88)	QP	28	1	1.81	54.49	20.34	23.04	11.11	Chaetoceros Sp.
			23	2.5	1.65	83.71	28.20	12.30	43.21	Microflagellates <15 µm
			12	15	2.41	52.79	39.02	5.83	7.84	Nitschia/Bacteriastrum
			6	40	0.93	48.09	11.37	25.40	11.32	Dinoflagellates <15 µm

Table 5.5. Microscopic cell count analyses and sample chlorophyll *a* values. These were used for the computations of C:Chl *a* ratios presented in Table 5.6. The numerically dominant phytoplankton taxa observed in samples are listed.

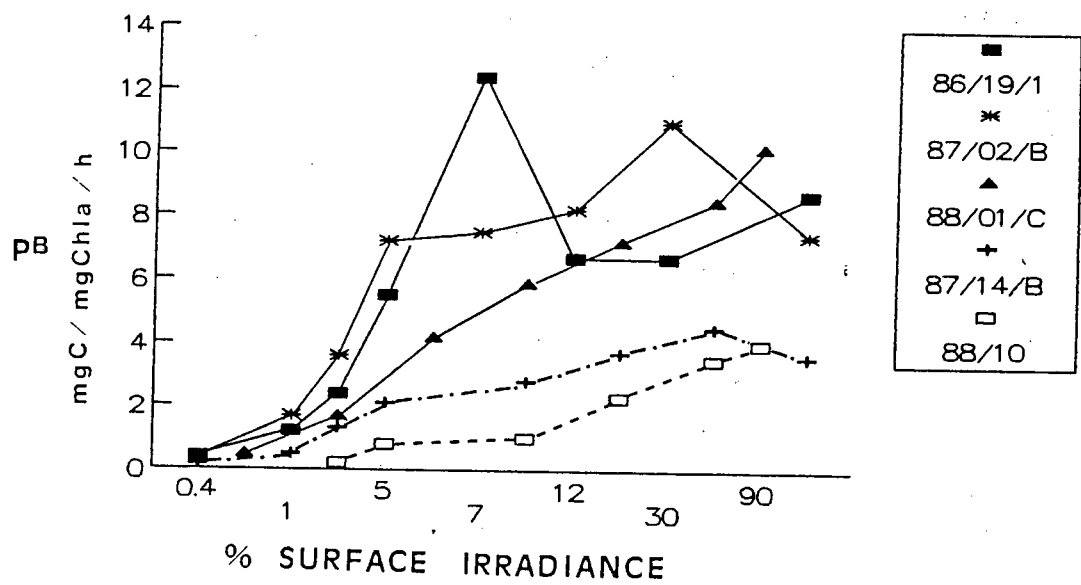


Figure 5.5. Mean productivity ($\text{mgC}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$) per unit chlorophyll *a* ($\text{mgChla}\cdot\text{m}^{-3}$) (P^B) plotted for each light depth (% surface irradiance) during winter(----), spring (— · — · —) and summer (—).

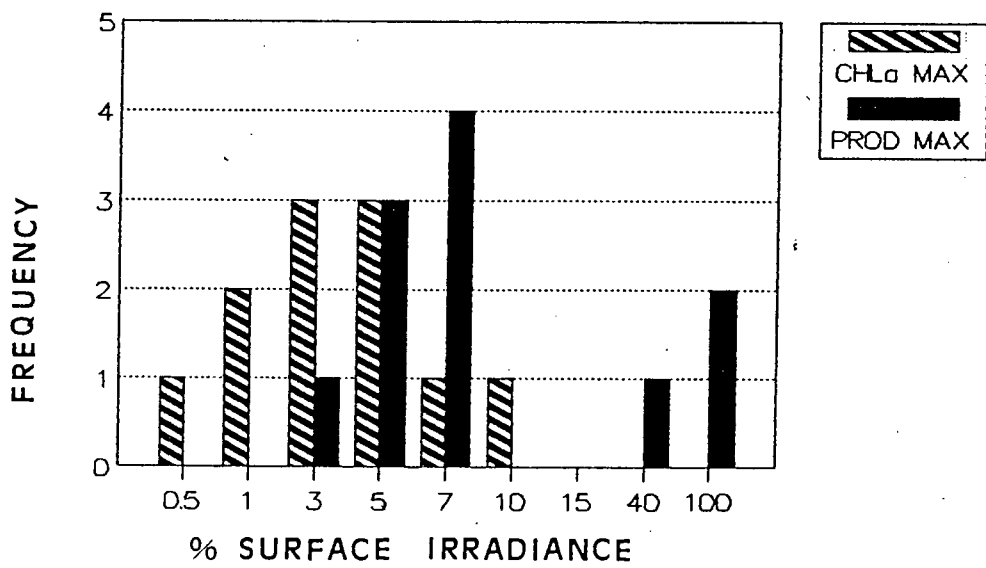


Figure 5.6. The frequency plot of the observed positioning of the chlorophyll and primary productivity maximum in the euphotic zone at the different % surface irradiance incubation light depths during the stratified summer (December - January) month cruises.

CRUISE	88/10			88/01/C					
				CHLOROPHYLL MAX			UML		
	mean	(s.d.)	n	mean	(s.d.)	n	mean	(s.d.)	n
C/Ch1a	47 (regression)		8	27	(10.2)	3	88	(56.3)	5
P/Ch1a	1.7	(0.2)	2	7.1	(2.8)	6	8.5	(1.6)	7
Doublings. Day ⁻¹	0.4			3.2			1.2		

Table 5.6. Phytoplankton community turnover times (doublings per day) for the well mixed euphotic zone during the winter survey (88/10) and for the UML and thermocline regions during the summer stratified survey (88/01/C).

with or slightly shallower (5 - 7% light depth) than the subsurface Chl_{max} (3 - 7 % light depth). Production rates at the P_{max} ranged between 4.51 and 5.12 $\text{mgC}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$. However, substantial production still occurred throughout the upper mixed layer and the overall contribution of the subsurface production maximum to total water column production was relatively low.

In contrast to the consistency of the January 87/02/B data, it is clear that the oceanographic regime is not always as stable. The large daily variability of water column measurements during the January 88/01/C and December 86/19/I sampling periods is reflected in the large ranges of values, particularly of biological parameters (Table 5.2). An important feature of the midshelf profiles during these cruises was the shoaling of the thermocline in the water column to an average depth of 32m (s.d.=9.6m;n=9) (Figure 5.4 e - g) and an intensification of the thermal gradient between surface and bottom waters (Table 5.2). The nitracline remained associated with the thermocline, and was co-incident with the depth of the subsurface Chl_{max} .

Increased chlorophyll *a* concentrations throughout the water column ($> 1 \mu\text{gChl}a\cdot\text{l}^{-1}$) caused the rapid extinction of downwelling light, particularly below the subsurface Chl_{max} , resulting in a decrease in the euphotic zone depth. This is reflected in the decreased values of $Z_{\text{eu}}/Z_{\text{m}}$ (Table 5.2). Excluding those sampling occasions when a very well developed subsurface Chl_{max} was observed (Figure 5.4 e), P_{max} was frequently obtained at light depths shallower than the 10% light depth or even at the surface (Figure 5.4 f and g).

Profile 5.4 h displays the water column measurements at an outer shelf station (OFS2) during the December 86/19/I cruise. The thermocline deepened with distance offshore, eventually breaking down beyond the 200m isobath. At this offshore station, both the chlorophyll *a* and production profiles showed little vertical structure and primary production was spread throughout the euphotic zone with P_{max} ($2 - 4 \text{mgC}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$) at the surface.

Integrated water column biomass and production rates

Computed values of areal chlorophyll *a* and primary production to the 0.5% surface irradiance light depths are presented in Table 5.3. Measurements from the same location are averaged for each cruise. Euphotic zone chlorophyll *a* ranged between 10.7 and 58.6 mg.m⁻² and production rates between 70 and 289 mgC.m⁻².h⁻¹. Measurements of euphotic zone phytoplankton production by BROWN (1983) during November 1981 in the nearshore and midshelf western Agulhas Bank waters (DP), provide very comparable estimates of 268 and 121 mgC.m⁻².h⁻¹ respectively.

Minimum integrated primary production values were obtained for the mid-winter (July) survey, whilst maximum euphotic zone production occurred consistently during the spring (October) sampling period (347 mgC.m⁻².h⁻¹) associated with maximum integrated phytoplankton biomass (130 mgChl*a*.m⁻²).

Mid-summer integrated values displayed considerable variability, both between cruises and during cruises, in particular during the 86/19/I cruise. Areal values of biomass and production were highest when the euphotic zone was shallow. A deep euphotic zone (87/02/B) was characterized by little integrated biomass (6 - 14.7 mgChl*a*.m⁻²) and associated low production (87.7 - 168.5 mgC.m⁻².h⁻¹). Integrated rates were observed to decrease at outer-shelf stations relative to midshelf stations (Table 5.2).

Size-fractionated primary production and dominant phytoplankton species

Size-fractionated production measurements are presented in Table 5.4. Production by nano-plankton (<15 µm) was found to account for more than 60% of total production during the mid-winter survey. Similarly the nano-plankton size-fraction dominated community production during the deeply stratified summer sampling period (cruise 87/02/B). The spring (87/14/B) and summer 1988 (88/01/C) surveys however, displayed considerable production by net-plankton, with maximal net-plankton production observed during the spring survey (83% of community production).

Contributions by the net- and nano-plankton size-fractions are consistent with the species identification analyses and biomass distribution data given in Table 5.5. Micro-flagellates <15 µm dominated the phytoplankton biomass and were present in very large numbers ($1 - 4 \cdot 10^6$ cells.l⁻¹) during the 88/10 cruise when production in the <15 µm size-fraction was as much as 97 % of total production. Conversely, when diatoms (*Nitzschia delicatissima*, *Asterionella glacialis*, *Bacteriastrum delicatulum* and *Chaetoceros* spp.) dominated the phytoplankton biomass during the 88/01/C cruise, the <15 µm size-fraction contributed least to total production (18 - 29 %).

DISCUSSION

An understanding of the dynamics of carbon fixation by the primary producers of a system is a prerequisite to understanding particulate fluxes, food-webs and the potential carrying capacity of that system (SMITH and EPPLEY 1982, VEZINA and PLATT 1988). It has been our aim during this study to quantify spatial and temporal variability of primary production in western Agulhas Bank waters in response to environmental changes, so providing some insight into carbon fluxes in these waters.

Seasonal variability of phytoplankton production

During winter months, the combination of low solar insolation energy and deep mixing (Table 5.1) results in reduced water column productivity and biomass, dominated by microflagellates <15 µm. Average assimilation numbers are low (Figure 5.5), and the population turnover time is less than 0.5.day⁻¹ (Table 5.6), characteristic of slow growth rates associated with nano-plankton dominated assemblages (MALONE 1977, FURNAS 1982). These measurements confirm the proposal by BOYD *et al.* (1985) that moderate concentrations of nitrates in western Agulhas Bank surface waters during the winter months resultant of winter mixing of the water column, are not depleted during these months due to seasonal limitation of phytoplankton growth.

During the spring survey (October), the physical environment of reduced mixing depth in midshelf waters and increased solar radiation was favourable for the net-plankton bloom observed, a well documented feature of shelf seas elsewhere (e.g. PINGREE *et al.* 1976, MALONE *et al.* 1983, WALSH 1981, HOLLIGAN *et al.* 1984a, FEVRE 1986). In spring, integrated production and biomass attained maximum values, with the major fraction of production in the net-plankton. The complete removal of nitrates from the euphotic zone and low average P^B throughout the water column (Figure 5.5) suggests we observed the bloom in the late stage of its development, at the onset of nutrient limitation (MALONE *et al.* 1983, BROWN 1986, BROWN and HUTCHINGS 1987).

Two distinctly different stratified water column environments were observed during summer surveys. One, a temporally stable water column with warm (>21 °C) surface waters and a deep (45m - 55m) thermocline/nitracline, persisting throughout the late January 1987 survey. Phytoplankton production was characterized by a subsurface production maximum (P_{max}) at the depth of or slightly shallower than the subsurface chlorophyll maximum (Chl_{max}), closely associated the depth of the nitracline. Integral phytoplankton biomass and production was very low relative to all other sampling periods. More than 60% of production was due to the nano-plankton (<15 μ m) size-fraction, typical of a mid-summer stratified continental shelf water column (MALONE *et al.* 1983, JOINT and POMROY 1983). Secondly, a very variable environment, where the thermocline depth was always shallower than 35m and occasionally as shallow as 25m. This was observed during the December 1986 and January 1988 surveys. The increase of net-plankton, dominated by diatoms *Chaetoceros*, *Bacteriastrum* and *Nitzschia* sp, in the euphotic zone was dramatic. The Chl_{max} attained concentrations of 6 - 7 μ gChl l^{-1} and was associated with the depth of maximum nitrate and thermal gradients in the thermocline region.

It is apparent, however, that although increased euphotic zone chlorophyll is due primarily to increased subsurface phytoplankton concentrations within the thermocline region, increased water column primary production is predominantly a result of enhanced production in the upper mixed layer rather than at the depth of the Chl_{max} . The frequent occurrence of P_{max} at or near surface irradiance intensities suggests that phytoplankton are well adapted to high average light levels and thus not subject to marked photo-inhibition (GOLDMAN and DENNET 1984).

The contrasting summer profiles suggest that considerable fluctuations occur in water column productivity in midshelf western Agulhas Bank waters during these months, possibly somewhat contrary to expectations of more stable conditions (CULLEN and EPPLEY 1981, MALONE *et al.* 1983, TRANTER and LEECH 1986). YODER (1985) has shown that the intrusion of nutrient rich bottom water across the South Eastern U.S. continental shelf, co-incident with shelf-edge upwelling processes, results in 'events' of enhanced subsurface phytoplankton growth. Increased flow of bottom water over the Agulhas Bank has been related to oceanic driven shelf-edge upwelling and coastal upwelling events associated with strong coastal south-easterly winds (BOYD *et al.* 1985, LARGIER and SWART 1987). Bottom water intrusion would account for the observed shallowing of the thermocline/nitracline by 10 - 20 metres to light depths between 7 and 30 % surface irradiance. This would result in nitrate availability at light depths optimum for diatom growth (CARTER *et al.* 1987), and the subsequent enhancement of midshelf net-plankton production. It is not unlikely that the enhancement of water column net-plankton production occurs on an 'event' scale, overlying the more temporally persistent nano-plankton dominated deep stratified water column environment, as observed by YODER (1985).

That the phytoplankton assemblage continues to display high average production rates in the upper mixed layer during these 'events' despite the depletion of nitrates to often below detectable levels during the spring and summer surveys, may be attributed to the utilisation of regenerated nitrogen sources (MALONE AND CHERVIN 1979, HARRISON *et al.* 1983, HOLLIGAN *et al.* 1984b, PROBYN 1985, COCHLAN 1986). PROBYN and LUCAS (1987) have shown that, in strongly stratified nitrate depleted eastern Agulhas Bank waters, although overall upper mixed layer phytoplankton growth may be nitrogen limited, production rates are not and are supplemented by regenerated nitrogen. It is conceivable that mixing processes in the thermocline region *e.g.* internal wave activity (LARGIER 1987, LARGIER and SWART 1987) and surface driven wind mixing (CATZEL 1989), may allow for the resuspension of nitrate-enriched cells from the thermocline region back into the shallow upper mixed layer. The similarity of the species assemblage throughout the water column (Table 5.5), supports this hypothesis. Thus the proportion of 'new' or 'regenerated' production in the upper mixed layer will be determined by the recent history of the individual cells (MORRIS 1981, HARRIS 1986).

Formation of the subsurface chlorophyll maximum

The depth of the nitracline, determined by phytoplankton uptake of nitrate and advection rates across the thermocline (KING 1986, TETT *et al.* 1986), was consistently observed to be within the thermocline region at light depths of between 3 - 10% surface irradiance. The close association of the depth of the Chl_{max} with the depth of the nitracline, and increased population doubling times in the chlorophyll maximum relative to the upper mixed layer (Table 5.6), is evidence for enhanced growth of phytoplankton in the region of greatest vertical stability and nitrate availability (DERENBACH *et al.* 1979, HERBLAND and VOITUREZ 1979, HOLLIGAN *et al.* 1984b, TETT *et al.* 1986). The rapid increase in averaged P^B ratios with increasing irradiance through the Chl_{max} region for all three summer cruises (Figure 5.5), is indicative of light limitation of phytoplankton production below and even within the Chl_{max} (MALONE *et al.* 1983). Possible self-shading within the Chl_{max} is reflected in the spatial separation of the subsurface P_{max} shallower than the Chl_{max} (Figure 5.6).

The low C:Chl ratios for samples from the chlorophyll maximum relative to ratios obtained for surface layer samples (Table 5.6) indicates physiological adaptation of phytoplankton cells in the chlorophyll maximum to low light intensities. Increased cellular chlorophyll in response to low light regimes where ambient nitrate concentrations are high is a well documented observation (FALKOWSKI and OWENS 1980, CULLEN 1982). Physiological increases in cellular chlorophyll would be facilitated by prolonged residence times in the vertically stable thermocline layer, as suggested by temperature gradients in this region (DENMAN and GARGETT 1983, VANDEVELDE *et al.* 1987).

It has furthermore been shown that in a stratified water column, the accumulation of diatoms in the thermocline shear zone prior to sinking out of the euphotic zone is likely to occur during periods of net-plankton dominance of the species assemblage (PARKER 1986, VANDEVELDE *et al.* 1987).

With these considerations, it is thus likely that the formation and maintenance of subsurface chlorophyll maxima in stratified western Agulhas Bank waters is a combination of enhanced phytoplankton growth at the depth of the nitracline, the physiological adaptation by phytoplankton to

low light levels in the thermocline/nitracline region, and the accumulation of sinking cells at the density interface between warm surface and cold bottom waters. Little can be said as to the contribution of active swimming by phytoplankters in the formation of the chlorophyll maximum, but as the chlorophyll maximum was observed to be dominated by relatively immotile species, there is nothing in our data that supports this as a contributing factor of subsurface chlorophyll maximum formation (CULLEN and EPPLEY 1981).

NAPP et al. (1988) have shown that the subsurface chlorophyll maximum observed during summer thermal stratification of southern California Bight waters is a region of improved primary food resource availability and quality. There is little reason not to assume the same holds true for the subsurface chlorophyll maximum of western Agulhas Bank waters, and that these layers would therefore represent optimum foraging depths for both herbivores and secondary consumers.

Size-fractionated primary production and carbon fluxes in western Agulhas Bank waters

Marine systems where photosynthetic nano-plankton constitute the majority of the species assemblage, are characterized by the utilisation of regenerated nitrogen sources for primary production and inefficient transfer of carbon to higher trophic levels. In such a system, limited 'new' production is available for consumption by organisms sized beyond the 'microbial loop', or for export from the system by sinking (MOLONEY and FIELD 1985, NEWELL and TURLEY 1987, MICHAELS and SILVER 1988, PROBYN *et al.* 1989). Alternatively, net-plankton dominated systems display rapid production rates with a strong dependence on 'new' nitrate-nitrogen sources (DUGDALE and GOERING 1967, EPPLEY and PETERSON 1979), and the efficiency of trophic transfers to large organisms is greatly increased. Export of 'new' production from the system by grazing, sinking and ultimately the removal of fish by fisheries will be high for such systems (TILZER 1984, MICHAELS and SILVER 1988, PLATT *et al.* 1989).

It appears that deep mixing and low insolation levels during winter months limit diatom growth in Agulhas Bank mid- and outer-shelf waters, despite the availability of nitrate ($4 - 5 \mu\text{mol.l}^{-1}$) throughout

the euphotic zone. Microflagellates have been shown to be adapted for growth under reduced light conditions (FURNAS 1982) and may well be thus advantaged during these conditions. Little primary production is expected to be available for export from western Agulhas Bank waters during winter in terms of either fish production or sinking out of the water column.

The emerging paradigm for the Southern Benguela upwelling region is that smaller nano- and pico-plankton are grazed largely by microzooplankton, while the larger net-plankton are important to the meso-zooplankton (PROBYN *et al.* 1989). It is now known that the Cape anchovy, although an opportunistic forager, feeds preferentially on meso-zooplankton (JAMES 1988) and cannot subsist for any length of time by filter-feeding on phytoplankton alone. The appearance of one-year old spawning anchovy in western Agulhas Bank water coincides with the onset of the spring net-plankton bloom (NELSON and HUTCHINGS 1982, HAMPTON *et al.* 1985, SHELTON *et al.* 1985). During early summer, 'events' of net-plankton growth by the raising of the thermocline may be frequent (BOYD *et al.* 1985), and carbon fluxes through net-plankton production into meso-zooplankton, although of a pulsed nature, is potentially high. This would sustain the resource requirements of the anchovy spawning which continues until late January.

It has been shown that a close coupling of regenerated nano-plankton primary production and micro-zooplankton grazing is generally true for thermally stratified systems with a well defined subsurface chlorophyll maximum (MALONE and CHERVIN 1979, FALKOWSKI *et al.* 1983, MALONE *et al.* 1983, HOLLIGAN *et al.* 1984a). Thus if meso-zooplankton production in western Agulhas Bank waters is limited during late summer months by nano-plankton domination of the deep thermocline system, food resources may become limiting for anchovy production. These observations are consistent with documented anchovy distributions, where anchovy are observed to move inshore and eastwards across the bank once surface temperatures exceed 21 °C (SHELTON *et al.* 1985).

CHAPTER SIX:

GENERAL CONCLUSION

SEASON	EUPHOTIC ZONE THERMAL STRUCTURE	DEPTH OF MIXING (m)	AV. DEPTH OF EUPHOTIC ZONE (m)	AV. INTEGRAL 1^0 PRODUCTION ($\text{mgC}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$)	AV. INTEGRAL PIGMENT ($\text{mgChl}a\cdot\text{m}^{-2}$)	DOMINANT SIZE CLASS (μm)	LIGHT DEPTH OF P _{MAX} %SI
MIDWINTER	Isothermal	65-75	45-50	95 (35)	58 (15)	<15	40 - 90
SPRING	Isothermal	50-60	45	244 (95)	101 (28)	>15	40 - 90
SUMMER	Stratified: Deep	35	70	125 (45)	35 (20)	<15	3 - 7
	Shallow	25-35	40-55	190 (100)	45 (14)	>15	3 - 100

Table 6.1. An overall summary of observed seasonal ranges of the physical environment and associated mean levels of phytoplankton production and biomass during winter, spring and summer in Agulhas Bank waters. Ranges about the means are given in parentheses and dominance of the assemblage by net- or nanoplankton as observed, is suggested.

The seasonal changes of the vertical distribution of phytoplankton and water column primary production in Agulhas Bank waters are typical of temperate latitude continental shelf seas elsewhere in the world. A summary of average water column primary production and phytoplankton biomass (chlorophyll *a*) associated with different physical (temperature) structures is presented in Table 6.1.

Net-plankton (> 15 μm) primary production is light limited during winter months (May - September), and nutrient limited during summer months (December - March) once the water column has stabilized and the thermocline/nutricline has been established. Nano-plankton were observed to be dominant during winter conditions of reduced light levels and deep mixing. A net-plankton bloom was observed during the spring (October) survey, associated with increased insolation input and reduced water column mixing, but prior to the establishment of a shallow thermocline. During the early summer months phytoplankton abundance and euphotic zone primary production appears to vary considerably, particularly in western Agulhas Bank waters. Our measurements suggest that a large proportion of production during these months is due to net-plankton, associated with a shallowing of the thermocline in the water column. These 'net-plankton events' are likely to be of importance in sustaining the biomass of spawning anchovy present in these waters during the early summer months.

The summer stratified water column is characterized by a spatially continuous subsurface chlorophyll maximum at the depth of the thermocline and nitracline. Enhanced phytoplankton production at the depth of nitrate availability, the physiological adaptation of cellular chlorophyll to reduced light levels in the thermocline region and the accumulation of sinking cells at the density interface between surface and bottom waters are likely mechanisms for the sustaining of the subsurface chlorophyll maximum. As surface waters warm with the progression of summer, the thermal structure of the western Agulhas Bank region deepens with the thermocline and associated nutricline situated deep in the euphotic zone at light levels <3% surface irradiance. The system then becomes nano-plankton dominated, light limited in the thermocline/nitracline region and with surface layer production minimal and dependant on regenerated nutrient sources.

In eastern Agulhas Bank waters, however, where the thermocline is typically shallower than in western bank waters, the transport of nitrate across the thermocline to well illuminated depths appears to be adequate for the sustaining of large concentrations of net-plankton (diatoms) in very narrow layers within the thermocline. During these conditions, self shading in the chlorophyll maximum will be the primary limiting factor for phytoplankton growth at depths of nitrate availability.

Wind-mixing of the water column plays an important role in the advection of nitrates into the surface nitrate-depleted layer, initiating the successional re-establishment of the subsurface chlorophyll maximum after erosion of this structure by storm mixing. Phytoplankton production in nitrate enriched surface waters is greatly increased and predominantly by net-plankton. As the water column stabilises and nitrates are depleted from the surface waters, the subsurface production maximum associated with, but slightly shallower than, the chlorophyll maximum becomes the dominant feature of the production profile. The frequency of wind-mixing events will determine the degree of development of the subsurface chlorophyll maximum. The subsurface chlorophyll maximum was observed to be well developed during the late summer months (March) in inner eastern Agulhas Bank waters.

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