REGIONAL ESTIMATES OF POTENTIAL NEW PRODUCTION IN THE SOUTHERN BENGUELA UPWELLING SYSTEM

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Thesis Presented for the Degree of
DOCTOR OF PHILOSOPHY
in the
Department of Oceanography, Faculty of Science
UNIVERSITY OF CAPE TOWN
December 1995

ACKNOWLEDGEMENTS

I wish to extend sincere appreciation to my supervisor, Prof. G.B. Brundrit and co-supervisor, Dr. T.A. Probyn for their insight and guidance throughout the development and preparation of this thesis.

The South African Data Centre for Oceanography, Sea Fisheries Research Institute, Satellite Applications Centre and Weather Bureau are gratefully acknowledged for their provision of archived data. The Sea Fisheries Research Institute also permitted my participation in a number of their research cruises.

I would like to express my thanks to Scarla Weeks for processing the satellite imagery and Sarah Searson and Roy van Ballegoyen for their help with the sea level record.

A special thanks is due to my parents, Roy and Ruth Waldron and my wife, Miranda, for their unstinting support.

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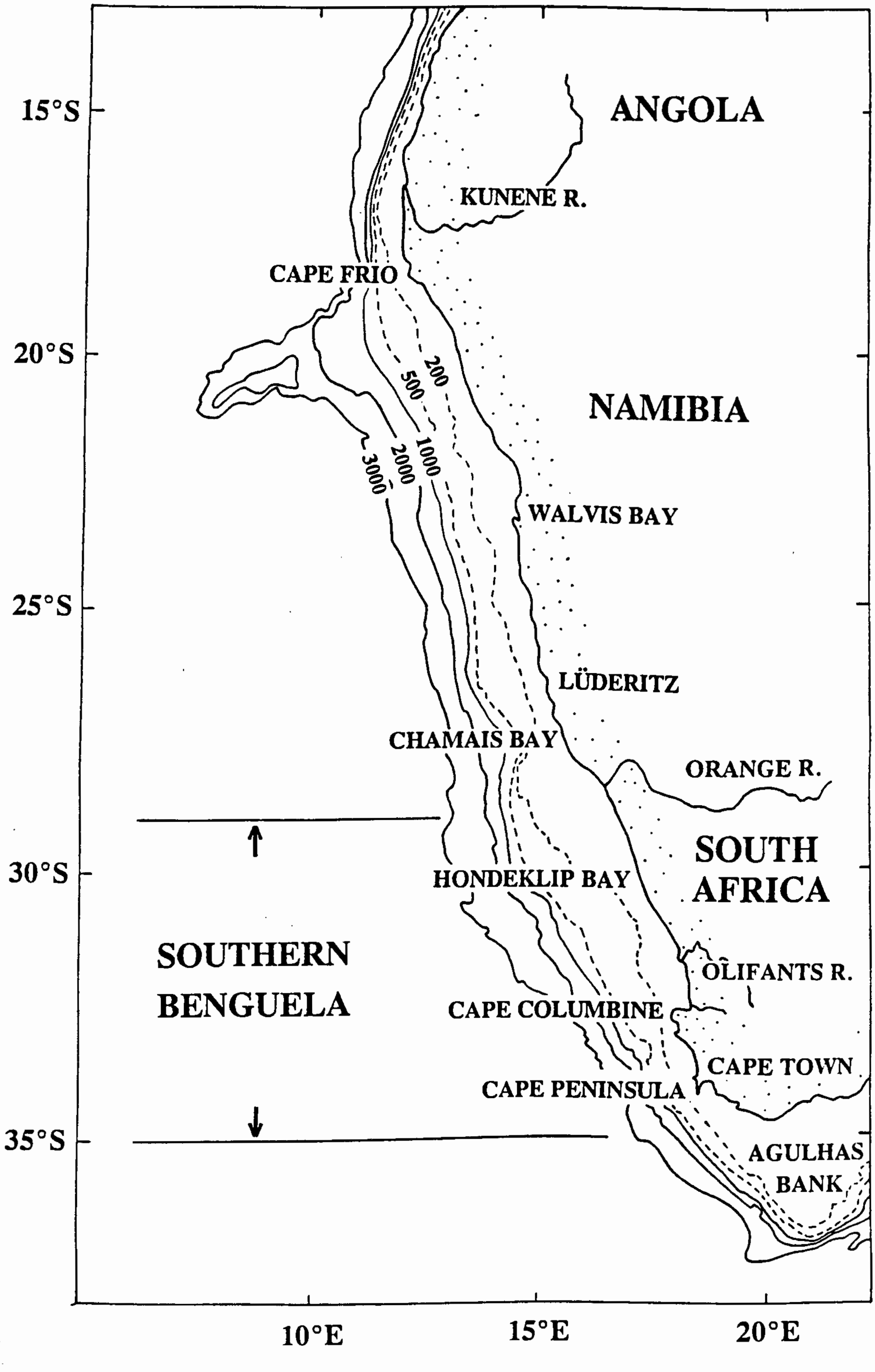


THESIS ABSTRACT

The estimation of annual potential new production at a regional scale for the decade of the 1980s provides the main focus of this thesis. New production is the proportion of total primary production which relies on the uptake of NO_3-N by the phytoplankton while potential new production assumes that all the NO_3-N available to primary producers is assimilated. The Redfield ratio between carbon and nitrogen in the marine environment was used to express rates of potential new production in terms of carbon. In order to arrive at annual estimates of potential new production it was necessary to progress from the event-scale to the annual scale. This was achieved by the adoption of two novel methods of approach. Event-scale estimates of potential new production were made by assessing the amount of NO_3-N present in the nominal euphotic zone as a result of upwelling. Remotely-sensed images of sea surface temperature (SST) coincident with or shortly after upwelling events were used in combination with a derived relationship between SST and NO_3-N concentrations integrated over the depth range of the productive surface layer in the southern Benguela region. In this way it was possible to overcome the main shortcoming of passive satellite imagery by quantifying a sub-surface variable. The event-scale estimates of potential new production were extrapolated to the annual-scale by taking into account the dynamics of the system. Sea level fluctuation at the coast preceding upwelling events was found to be related to the event-scale estimates of introduced NO_3-N and hence used as a proxy for upwelling. Using a ten year record of sea level, estimates of annual potential new production, spanning the period June to May inclusive, were made for the period 1980/81 to 1989/90. The annual period was selected so as optimise the interaction between upwelling and biology. The range of these estimates was 5.16×10^{13} to 6.19×10^{13} $gC.y^{-1}$ with a mean of 5.60×10^{13} $gC.y^{-1}$. Their validity, in terms of appropriate order of magnitude, was tested by relating them to $^{15}NO_3$-N uptake

experiments conducted in the southern Benguela over an eight year period. In addition, they were subjected to an intra- and inter-regional comparison. The reported flux of upwelling source water was found to be consistent with that necessary to sustain the estimated potential new production.

New production is recognised as being equivalent to export production when integrated over sufficiently long time scales, and hence a sink for carbon. The application of current thinking in relation to ocean/shelf/sediment interactions was used to establish a two-dimensional network of potential new production pathways relevant to the southern Benguela. The mean annual potential new production estimate was used as the starting point for assigning rates to each of the pathways in the network. It was calculated that approximately 70% of southern Benguela new production is sequestrated in shelf sediments and offshore, below the permanent thermocline, at time scales which constitute a long-term loss to the system.

The hypothesis that new production is related to tertiary production was tested by relating the estimates of annual potential new production to a number of pelagic fisheries variables. There was evidence, unsupported by statistical analysis, of a rectangular hyperbola fit between annual potential new production and fish condition (quantified as the cumulative oil:meal ratio). There was also an indication that a median amount of potential new production in the Spring and Summer period (September to February inclusive) may be beneficial to fish condition, reflected in the cumulative oil:meal ratio for the following March to July inclusive period.

A dome-shaped relationship was established between annual potential new production (x) and anchovy spawner biomass (y), demonstrating that both a paucity and surfeit of upwelling is detrimental to the fishery. The variables were related in the form of a Gaussian Area curve:

$$y = 1.90e^{[-0.5((x-5.72)/0.43)\hat{}2]},$$

making it possible to provide a first estimate of fish biomass six months in advance of existing methods. This finding could be incorporated in the suite of operational tools available to fisheries management. Scope for a similar relationship was found with respect to the anchovy recruitment biomass. The dome-shaped curve between an upwelling proxy and fish biomass was in agreement with work conducted in other Ekman-type systems.

CHAPTER 1

BACKGROUND AND THESIS OBJECTIVES

GENERAL INTRODUCTION

This thesis spans two main spheres of interest in the context of nutrient element cycles: the extent to which the ocean (in this case a major upwelling system) acts as a sink for carbon and the establishment of a quantitative link between NO_3-N available to phytoplankton and tertiary (in this case pelagic fish) production. It is therefore appropriate to give an overview of the global carbon cycle and aspects of contemporary thinking related to climate change plus the concept of "new" production and the pivotal role it plays in both the estimation of carbon sequestration and the productivity of a given marine system.

(i) CARBON CYCLE

The nutrient element cycles mentioned above refer to carbon, oxygen, nitrogen and phosphorus. This follows the categorization by TUREKIAN (1968) who divided the elements distributed in the oceans into major, nutrient and trace element groupings. The nutrient elements are included in compounds which make up plant and animal tissue in the form of proteins, fats, starches, sugars and compounds important to energy transfer (e.g. adenosine triphosphate) within organisms. Broadly speaking, the nutrient elements are available in the oceans as dissolved bicarbonate, CO_2, inorganic phosphate and nitrate (other nitrogenous nutrients will be mentioned later). Primary production occurs in the upper water column through the extraction of carbon, nitrogen and phosphorus to a depth where there is sufficient light penetration for photosynthesis. All other links in the food chain are dependent on this first step. Some of the organic particles passively sink out of the surface layer to deeper waters where bacterial decay recycles the nutrient elements. The net result of this simplified overview is a reservoir of nutrient elements underlying a nutrient-depleted euphotic zone. Transfer of nitrate and phosphorus back into the euphotic zone is essential to maintain continued production in surface waters. Bicarbonate and CO_2 are non-limiting and, in any event, their resupply can occur through air-sea interaction. This vertical transport of nutrients occurs through a combination of eddy diffusion, convection and upwelling. Steady-state profiles of the nutrient elements in the main ocean basins (e.g. SVERDRUP *et al.*, 1942) indicate an equilibrium between removal and supply.

This natural balance has been perturbed in the post-industrial era through fossil fuel combustion and deforestation which have acted in concert to increase atmospheric CO_2 levels. According to SUNDQUIST (1985), the consensus estimate of atmospheric CO_2 levels prior to the influence of man is 550 - 590 gigatonnes (Gt) and that 86 Gt were added between 1958 and 1980 (although only 50Gt are reflected in the measured atmospheric increase). The present level of fossil fuel carbon input to the atmosphere is 5 $Gt.y^{-1}$. The projected effect of increased levels of atmospheric CO_2 on global climate is well known. It is thought to be accompanied by a wide range of predicted temperature increases depending on future CO_2 input scenarios. The response of the oceans to these changes is less well known.

MOORE and BOLIN (1986) state that the CO_2 uptake of the ocean is controlled by seawater temperature, surface chemistry and biology and patterns of mixing and circulation which determine the transport of carbon from surface waters to the deep ocean. It is important to note that the actual exchange of CO_2 between the sea surface and atmosphere is driven by turbulence and diffusion at the air/sea interface governed by the sea surface wind velocity, state of the ocean surface and partial pressure difference. They also point out some features which stand out in the ocean's role with respect to atmospheric CO_2 loading consequent to the above set of interactions. These include the consumption of CO_2 in euphotic zone primary production, the decomposition and dissolution of detritus leading to enrichment of CO_2 in deep waters, sinking of surface water in polar regions, equatorial outgassing of CO_2 due to divergent upwelling and general turbulent mixing processes between intermediate and surface depths superimposed on the general meridional circulation. These processes operate on different time scales which further complicate predictions of oceanic response (SUNDQUIST, 1985). There is an event-scale exchange at the air/sea interface followed by ocean mixing on a much longer time-scale. This is mediated by the seasonal scale of biological processes. Note that the carbon removed from the euphotic zone is mostly oxidized by the time it reaches 1500m and therefore sequestration is of the order of hundreds of years.

MOORE and BOLIN (1986) touch on the issue of time scales in their consideration of the oceanic sink for excess CO_2. Water which upwells today reflects pre-industrial levels of atmospheric CO_2 owing to the century time scale of sequestration. Together with the increased concentration of atmospheric CO_2 (compared to say 200 years ago) and the assumption that the gross flux of CO_2 into present day surface waters is greater than the pre-industrial flux implies that there has been a decrease in the vertical difference of total carbon in seawater.

The complex interactions involved in maintaining global equilibrium and uncertainties about relevant processes and rates mean that the oceanic consequences of a perturbation in atmospheric CO_2 cannot be accurately predicted. LONGHURST (1991) expresses the opinion that uncertainties are so great that we do not know whether the marine biosphere will mitigate or reinforce the increase of anthropogenic greenhouse gases in the atmosphere. Moore and Bolin (1986) state that an understanding of patterns of bottom water formation and the biological pump lie at the heart of understanding the response of the ocean to climate change. Part of this thesis addresses the question of carbon pathways within a major upwelling system.

(ii) NEW PRODUCTION

The measurement of total primary production was and is achieved through the use of ^{14}C labelling techniques. Dugdale and Goering (1967) apportioned total primary production between "new" and "regenerated" production depending on the nitrogenous sources to, and its cycling within the euphotic zone. It was shown via the use of ^{15}N labelling techniques that nitrogen available to the phytoplankton could be divided between newly incorporated nitrogen (NO_3-N or N_2) and recycled nitrogen (NH_4-N or dissolved organic-N (mainly urea)). Simple budgetary considerations dictate that new nitrogen must enter the productive surface layer at a rate sufficient to equal or exceed the export of organic nitrogen in order to prevent the ecosystem running down. Primary production associated with the uptake of NO_3-N and N_2-N was called "new production" and that dependent upon NH_4-N (and urea) was termed "regenerated production."

Eppley and Peterson (1979) concurred in the necessity for replacing lost nutrients by external inputs to avoid a decline in productivity and suggested that "new" production was the driving force behind fish catch and the downward flux of organic matter. Iverson (1990) provides evidence for the control of fish (and squid) production by the amount of new N annually incorporated into phytoplankton biomass and transferred through food webs. In addition, since dissolved inorganic carbon moves upward in sympathy with NO_3-N in the Redfield ratio (106C:16N) then only the sinking flux due to new production could be identified as a biologically-mediated transport of atmospheric CO_2 to the deep ocean. In other words, new production in the euphotic zone is equivalent to the carbon sink over appropriate time scales. EPPLEY and PETERSON (1979) also coined the term f-ratio to describe the ratio of new production : total production (described by DUGDALE and GOERING (1967) as percentage new production). The f-ratio is the proportion of N assimilated by phytoplankton via new production and (1-f) is the proportion assimilated via regenerated production. Note that the number of times a nutrient element is recycled in the euphotic zone before sinking out in particulate form can be described by the expression (1-f)/f (EPPLEY and PETERSON, 1979).

Conceptualizing new production as a sink for organic carbon in the context of an upwelling system needs refinement following the work of ROEMMICH (1989). A distinction was drawn between "imported" new production and "local" new production. "Imported" new production results from the addition of NO_3-N from outside the system whereas "local" new production results from the settling of euphotic zone particulate organic nitrogen followed by oxidation and the return of NO_3-N to the surface domain. In the latter case time scales may not be appropriate to designate the initial sink as sequestration.

The main point to emphasise is that new production can be a focus for the study of fish production and carbon sequestration provided the correct N and C pathways within the system are identified. It is the objective of this thesis to address these aspects of the southern Benguela Upwelling System at the regional scale by making use of satellite imagery and a novel method of predicting potential new production supported by ground truth measurements made on a number of research cruises within the area.

(iii) BENGUELA UPWELLING SYSTEM

GEOGRAPHY AND DESCRIPTIVE BACKGROUND.

The Benguela upwelling system is situated off the west coast of southern Africa. It is one of the four major eastern boundary currents in the world ocean (others occurring off the Californian, Peruvian and N.W. African coasts) and is typical in the sense that it is characterized by equatorward winds, concomitant upwelling of cold, nutrient-rich water adjacent to the coast resulting in enhanced levels of production at all trophic levels. ANDREWS and HUTCHINGS (1980) and NELSON and HUTCHINGS (1983) provide an excellent descriptive background to the system and, read in conjunction with a tetralogy of Benguela review papers (SHANNON, 1985; CHAPMAN and SHANNON, 1985; SHANNON and PILLAR, 1986; CRAWFORD, SHANNON and POLLOCK, 1987), dealing with, 1. Evolution, physical features and processes, 2. Chemistry and related processes, 3. Plankton and 4. Major fish and invertebrate resources respectively, should comprehensively acquaint the reader with the system *per se* and pre 1985 - 1987 research. Most contemporary research undertaken relevant to the Benguela has been done under the auspices of the Benguela Ecology Programme which began in 1982 and is still continuing. The proceedings of two international conferences held in 1986 and 1991 (published as volumes 5 and 12 respectively of the South African Journal of Marine Science) give a good overview of the range of work undertaken during this period.

The publications referred to above will be used in the present case to provide a general introduction to the Benguela and thus give a relevant background to the work of this thesis.

SHELF BATHYMETRY.

The bathymetry of the system's continental shelf varies in terms of width, angle of slope and depth of shelf break. The shelf is narrow at the northern (southern Angola) and southern (Cape Peninsula) extremities (20 km and 40 km respectively) and also south of Lüderitz (75 km). It is widest in the vicinity of the Orange River where it extends to 180 km offshore. The shelf north of Walvis Bay is also relatively wide at 140 km. Between Hondeklip Bay and the Cape Peninsula the irregular nature of the coastline results in a variable shelf width. The shelf has its steepest slope in the vicinity of the Kunene margin, Lüderitz and off the Cape Peninsula. The transition between continental shelf and continental slope occurs at about 200m in the Kunene margin and 350m on average between Cape Frio and Chamais Bay. In the region of the Orange River this transition deepens from 200m to 500m in a north-south direction. South of 33°S the shelf break occurs at 500m. Compounding this apparent complexity is the existence of double shelf breaks, especially in the region of Walvis Bay (inner and outer shelf breaks at 140m and 400m respectively) and Cape Columbine (200m - 380m and 500m respectively). The morphology of the continental shelf has important implications for the physical and biological dynamics of the upwelling system. Interaction between the bathymetry and wind field governs the presence of quasi-permanent sites for upwelling cells and the shelf-edge provides a plane of generation for shoreward propagating internal waves. The width and steepness of the shelf may govern the extent to which photosynthetically fixed carbon is transported beyond the system boundary and sequestrated.

METEOROLOGY.

The Benguela is driven by the interaction between zonal shifts of the South Atlantic High Pressure System, the seasonally oscillating pressure field over southern Africa and the belt of eastward moving cyclones to the south. This results in a highly seasonal upwelling in the southern part of the Benguela (reaching a maximum during Spring and Summer (SHANNON, 1966; ANDREWS and HUTCHINGS, 1980)), a central and northern region where upwelling is perennial but with a tendency towards a Spring/Summer maximum in the former and a late Winter/Spring maximum in the latter. In the context of this thesis, which also takes into account physical considerations based on the geographical distribution of upwelling cells (LUTJEHARMS and MEEUWIS, 1987) and the biological boundary between northern and southern anchovy fish stocks (CRUICKSHANK *et al.*, 1990), it was felt appropriate to define the extent of the southern Benguela between 29°S and 35°S.

WATER MASSES AND PHASES OF UPWELLING.

Water which upwells off the west coast between the northernmost extremity of the Benguela and Cape Point is generally accepted as being South Atlantic Central Water (CLOWES, 1950; STANDER, 1964; SHANNON, 1966) formed in the Sub-tropical Convergence region by the sinking and northward spreading of mixed sub-tropical and sub-Antarctic water masses (SVERDRUP *et al.*, 1942). NELSON (1985) states that the Central water which upwells originates from a maximum depth of 200m. This places a range of values on its conservative and non-conservative properties. These have been described for the region off the Cape Peninsula over five upwelling seasons (ANDREWS and HUTCHINGS (1980). Using their values in combination with the studies of BARLOW (1982), WALDRON (1985) and ARMSTRONG *et al.* (1987) permit a broad description of the physical, hydrochemical and biological changes occurring during the active and passive phases of an upwelling cycle.

Following the onset of upwelling-favourable winds, the initial phase is characterized by a sharp thermohaline front between offshore surface waters (termed Oceanic Water) and newly upwelled water. The surface expression of Oceanic Water is typically

>18°C and >35 psu in terms of its temperature and salinity with low levels of NO_3-N (<1 mmol.m^{-3}) and chlorophyll *a* (approximately 0.5 mg.m^{-3}). Inside the front, temperatures are much lower with the possibility of the 10°C isotherm outcropping at the coast. Salinities would be in the range 34.7 psu - 34.9 psu. NO_3-N values are high (15 mmol.m^{-3} - 25 mmol.m^{-3}) and owing to the absence (as yet) of any substantial primary production, chlorophyll *a* values are low (0.4 mg.m^{-3} - 0.9 mg.m^{-3}). The cessation of equatorward winds permits the sun-warming of cold surface waters inside the upwelling front, resulting in a realignment of isotherms and a broad temperature front between water of upwelling origin and Oceanic Water. Temperature increases up to 16°C are possible during this phase. This quiescent phase is conducive to primary production with resulting increases in chlorophyll *a* (up to 20 or 30 mg.m^{-3}) and decreases in NO_3-N (to approximately 2 mmol.m^{-3}) and other phytoplankton nutrients. It is significant to note that salinity, which is a conservative property in the absence of evaporation or riverine input, is a useful tracer of post-upwelling structure across and inside the upwelling front. In addition, the approximate time elapsed since an upwelling event can be estimated from the temperature of surface waters inside the front assuming a summertime daily mean heat exchange into the sea of up to 315 W.m^{-2}. This is capable of increasing the temperature of the upper 10m of the water column by 0.65°C.day^{-1} (GUASTELLA, 1992).

COASTAL TRAPPED WAVES AND SEA LEVEL.

There has been a contemporary appreciation that local manifestations of upwelling can be effected by varying degrees through the passage of long, equatorially or coastally trapped waves (WOOSTER, 1981). Local, coastal wind stress is not therefore the only variable to consider when differentiating between a sequence of upwelling events. LEBLOND and MYSAK (1978) refer to coastal trapped waves as shelf waves. They are a type of topographic planetary wave which is highly rotational. In the southern hemisphere, the coast lies to the left of the direction of phase propagation (therefore in the case of the Benguela such a wave moves from north to south). The motion consists of a sequence of horizontal eddies of alternating sign which is confined to the shelf/slope region. Coastal trapped waves are generally thought to be generated by large-scale weather systems that move across or along the shelf. They have long wavelengths compared to the dimensions of the shelf (of order 10^3 km), low frequencies (approximately 1 week) compared to the local inertial period (22.5 hours) and small amplitudes (pressure and wind-stress fluctuations of order 5 mbar and 0.1 $N.m^{-2}$ respectively). The favoured mechanism of generation is that of wind-stress.

How do coastal trapped waves impact on the dynamics of the upwelling process? Their propagation as trapped waves along the coast means that the amount of upwelling depends on two factors; the local forcing and the forcing which the wave had experienced prior to its arrival at the region under consideration (GILL and CLARKE, 1974). The interplay between these factors is thought to be as follows: upwelling is produced by offshore Ekman transport resulting from local conditions. The magnitude of the upwelling, however, depends on how much the amplitude of the coastal trapped wave is increased or decreased by this Ekman transport as it progresses along the coast. The phase of the wave in relation to the wind dictates whether conditions favour an increase of amplitude or otherwise.

One of the main points from GILL and CLARKE (1974) relevant to the present study is that upward motion of the thermocline is correlated with a fall of sea level at the coast. This implies that information relating to upwelling can be obtained from tide gauges. They found that sea level changes by 1cm across the shelf for every 1.45m displacement of the thermocline.

Brink (1991) maintains that a central focus on coastal trapped wave theory is appropriate because it has proven to be a versatile approach, yielding successful predictions as well as physical insight.

AIMS OF THE THESIS.

The central thrust of this thesis is to estimate, by means of a multi-disciplinary study, the potential new production on an annual basis at a regional level. A time series of such estimates will be used to quantify carbon pathways in an ocean/shelf/sediment network and establish relationships between potential new production and the commercially important pelagic fishery. The multi-disciplinary nature of the study rests in the use of satellite oceanography, marine chemistry and dynamical oceanography to provide answers, at the system level, to questions relating to carbon transport (and sequestration) and tertiary biology.

The first step in this sequence will be to establish the relationship between sea surface temperature (SST) and NO_3-N integrated over the productive surface layer of the southern Benguela. Using this relationship, in conjunction with a series of satellite images of SST taken during upwelling events, it will be possible to quantify the amount of NO_3-N available to southern Benguela primary producers for different upwelling events. This is equivalent to the potential new production and can be converted to carbon using the Redfield ratio.

In order to investigate potential new production in relation to a system of carbon pathways and links to the pelagic fishery it is necessary to progress from the event- to the annual-scale. In this context work will be conducted into the identification of a proxy for upwelling which is related to the event-scale estimates of potential new production and, as an upwelling index, can be used to provide seasonal and annual estimates of potential new production. The dynamics of upwelling in an Ekman-dominated system dictates that sea level at the coast is one such variable. Patterns of sea level rise and fall in association with upwelling events will be examined to establish such an index and hence quantify the annual extent of potential new production. The period covered by these estimates spans the decade of the 1980s. The validity of the estimates will be tested by means of an intra- and inter-regional comparison using ambient rates of NO_3-N uptake and documented regional estimates.

It is intended to use the mean of the time series to attribute quantities to a proposed network of NO_3-N driven carbon pathways between ocean and shelf waters and sediment in the southern Benguela. This will provide an estimate of how much carbon is sequestrated at time scales sufficient to constitute a long-term loss to the system. Inter-annual variation in potential new production will then be related to the anchovy fishery in terms of fish condition (oil:meal ratios), recruitment and spawner biomass. The aim of this part of the study is to establish annual potential new production as a predictor of certain fisheries variables. The extent to which these objectives have been fulfilled and other related matters will be addressed in a concluding chapter.

CHAPTER 2

THE REGIONAL ESTIMATION OF POTENTIAL NEW PRODUCTION IN THE SOUTHERN BENGUELA UPWELLING SYSTEM ON AN EVENT SCALE.

INTRODUCTION

The recent emphasis on a global approach to oceanography has increased the importance of remote sensing in the estimation of primary production. Much of this work has focussed on total primary production estimates from surface pigment concentrations and/or light intensity (LORENZEN, 1970; SMITH *et al.*, 1982; DUPOUY *et al.*, 1986; PLATT, 1986; ENGLISH *et al.*, 1987; BALCH *et al.*, 1989; FROUIN *et al.*, 1989). SATHYENDRANATH *et al.* (1991) have estimated new production from satellite imagery by applying an appropriate f-ratio (EPPLEY and PETERSON, 1979) to their total production estimates. Also, EPPLEY *et al.* (1985) have used a multiple linear regression model to predict integral production based on the variables of chlorophyll *a*, temperature and day length.

The Benguela is one of the world's major coastal upwelling systems and is characterised by the pulsed input of cold, nutrient-rich water into the euphotic zone at specific sites (LUTJEHARMS and MEEUWIS, 1987) along the west coast of southern Africa between about 15°S and 35°S (SHANNON *et al.*, 1987). Identification, at the system level and on the event scale, of the area influenced by upwelling is discernible from satellite images of sea surface temperature.

The negatively correlated relationship between water temperature and NO_3-N concentration throughout the ocean is well established (ZENTARA and KAMYKOWSKI, 1977) and results from incident solar radiation which provides a major heat source for water temperature increase coincident with the availability of light for primary production and nutrient uptake (STRICKLAND *et al.*, 1970; KIRK, 1983). This relationship has important implications for regional studies of phytoplankton production. BISHOP *et al.* (1980) state that the inverse relationship between temperature and nutrients can be used as an index of productivity in the equatorial Pacific and in the same region, MURRAY *et al.* (1989) note the comparative uniformity of integrated NO_3-N and the implications for interpretation of remote sensing images. BROWN and HENRY (1985) suggested using the temperature NO_3-N relationship in conjunction with satellite infra-red imagery, to estimate the nutrient status of a particular environment and in the selection of an appropriate production-chlorophyll *a* regression in the estimation of primary production. WILKERSON *et al.* (1987) established a linear regression between surface temperature and integrated nitrate and silicate for the purpose of comparing El Niño and non-El Niño years.

This chapter of the thesis attempts to estimate the potential new production of the southern Benguela upwelling system for a strong upwelling event in each of the years between 1984/1985 and 1993/1994 inclusive. Note that the years run from 1 June to 31 May. This was felt to be more appropriate in terms of biological aspects of the study and the dominance of upwelling winds during the Austral summer period (which span the change of a calendar year). In general terms, this was achieved through the establishment of a significantly correlated relationship between SST and NO_3-N integrated over the biologically productive surface layer. This relationship was used in conjunction with a series of satellite images of SST (coincident with upwelling events) to quantify the amount of NO_3-N (mmol) available for new production during those periods of upwelling. It was hence possible to provide an estimate of event-scale potential new production.

METHODS

A data set of temperature (°C) *vs* NO_3-N (mmol.m^{-3}) sampled in the vertical at 423 stations in the southern Benguela was compiled from archived data at the South African Data Centre for Oceanography (SADCO) and the Sea Fisheries Research Institute. Using these data, the primary objective was to establish a significant, negatively correlated relationship between SST (°C) and NO_3-N integrated over the depth range of the nominal euphotic zone (mmol NO_3-N.m^{-2}). It was necessary to define a nominal euphotic zone because measured euphotic zone depths were not available from all stations in the data set, therefore, following the work of WALDRON and PROBYN (1992), which took into account reported values from SHANNON (1985), BROWN and HUTCHINGS (1987) and ESTRADA and MARRASÉ (1987), it was decided to use 30m as a realistic (and possibly conservative) southern Benguela euphotic zone depth or at least the depth to which NO_3-N would be available to primary producers. Where the sampling depth at a particular station did not coincide exactly with 30m a linearly interpolated concentration of NO_3-N (mmol.m^{-3}) was obtained from vertically adjacent values. Integrated values for each station were calculated and plotted *vs* SST at the same station. The correlation coefficient (r^2) of these data was also calculated.

Surface water of upwelling origin was assumed to fall within the temperature range 10°C to 16°C inclusive which takes into account sun-warming of newly-upwelled water over the course of an upwelling cycle. Typically, water ≤ 16°C is found landward of the upwelling front in the southern Benguela. One satellite image of SST occurring during a strong and relatively cloud-free upwelling event was selected for each year between 1984/1985 and 1993/1994 inclusive using 'quick-look' facilities available in the Dept of Oceanography. Financial constraints prevented the selection of a complete set of images for each year. In order to determine SST, advanced very high resolution radiometer (AVHRR) data from the TIROS/NOAA series of polar-orbiting satellites were obtained from the South African Satellite Application Centre, Hartebeeshoek. Raw AVHRR data from the visible spectral band, 0.58 - 0.68 μm, and SST calibrated data from bands four and five in the thermal infrared, 10.5 - 11.5 μm and 11.5 - 12.5 μm, were obtained for the ten selected images. The data were processed using the PC-SEAPAK software package developed at the NASA Goddard Space Flight Centre (McClain *et al.*, 1992), and transformed to an equirectangular projection having a 40 second, or approximately 1 kilometre resolution. The total area coverage extended from 14.31°E to 20.00°E and 29.00°S to 34.69°S. Cloud masking was achieved by applying a two-step thresholding algorithm to the thermal infrared wavebands, with constant 'tuning' of the threshold for each individual scene. The SST algorithm applied to the infrared data was such that these data represent SST according to the linear equation:

$$\text{SST (°C)} = (\text{digital value} * 0.127) - 0.254.$$

Remotely-sensed measurements of SST were used in conjunction with the SST *vs* integrated NO_3-N relationship (derived from observations made at sea), therefore it was necessary to assess the potential effect of the sea-surface skin-temperature deviation. The temperature of the sea surface is typically between 0.1°C and 0.5°C cooler than the temperature a few centimetres below due to the vertical heat flux (Robinson, 1985). Since this is less than the 1°C bin size, used to group the integrated NO_3-N values in the estimation of event-scale potential new production (see later), it would not impact on the results.

The data were analysed to give the area covered in the defined southern Benguela region by 10°, 11°, 12°, 13°, 14°, 15° and 16°C water (km^2). The 10°C water, for example, was defined as 10.00°C to 10.99°C inclusive.

In Waldron and Probyn (1992), the regression equation between SST and §NO_3-N was used to predict the amount of NO_3-N associated with different bands of SST in the southern Benguela during an upwelling event. In the present case, however, having obtained a statistically significant correlation between SST and §NO_3-N, the integrated NO_3-N data were grouped into 1°C temperature bins over the range 10°C - 16°C inclusive. This permitted the calculation of mean integrated NO_3-N values for each temperature bin together with standard deviation and standard error. SST *vs* §NO_3-N was then presented as a series of discrete points (with error bars) rather than a line of regression.

Using the set of ten SST satellite images and computed areas of temperature bands therein, it was possible to calculate the amount of NO_3-N (mmols) in the productive surface zone available for new production for each of those ten upwelling events. This was converted from mmol NO_3-N to grams carbon. The conversion was done as follows:

1. mmol NO_3-N * molar relationship between carbon and nitrogen in the marine environment (6.6) gives mmol C.
2. mmol C * atomic weight of carbon (12) gives mg C.
3. mg C / 1000 gives g C.

This provided an event-scale estimate of potential new production in the southern Benguela upwelling system.

RESULTS

CORRELATION BETWEEN SST (°C) AND INTEGRATED NO_3-N ($mmol.m^{-2}$) OVER THE 0 - 30m DEPTH RANGE.

The relationship between SST and integrated NO_3-N is shown in the scatter plot of these variables from the 423 stations analysed (Figure 1) and provides evidence of a negative relationship. It is a similar shaped curve to that found by ZENTARA and KAMYKOWSKI (1977), who plotted simply temperature *vs* [NO_3-N], at an equivalent southern latitude (35°S). The product-moment correlation coefficient (r) for all data was -0.70 and therefore significant at better than the 99.9% level of confidence. The temperature range of interest to this study is between 10°C and 16°C inclusive (up to 16.99°C) which allows for the sun-warming of newly-upwelled water over the time course of an upwelling cycle. The product-moment correlation coefficient of data lying within this range was -0.61 (350 observations) which is also significant at better than the 99.9% level of confidence. It is interesting to note that the relationship looks curvilinear over the entire temperature range but has a rectilinear appearance over the 10°C to 16°C range (Figure 1). The occurrence of uniformly low integrated NO_3-N values above 18°C probably forces a curvilinear shape and is not relevant in the present context.

INTEGRATED NO_3-N VALUES ASSOCIATED WITH TEMPERATURE BINS BETWEEN 10°C AND 16°C INCLUSIVE.

Having demonstrated a significant negative correlation between SST and integrated NO_3-N it was decided to group the integrated NO_3-N data into temperature bins. The mean integrated NO_3-N value was computed for each temperature bin. In addition, the confidence limit at the 0.95 level of probability was also computed for each sample mean as follows:

$$\text{Mean value} \pm (1.96 * s) / \sqrt{N}$$

Where s = standard deviation of the sample

N = number of observations in a temperature bin

The following results were obtained:

Temperature Bin (°C)	Mean integrated NO_3-N ($mmol.m^{-2}$)	± (95% level) ($mmol.m^{-2}$)
10	496.6	43.8
11	390.4	33.3
12	290.2	28.3
13	223.4	22.0
14	200.5	19.9
15	176.9	29.1
16	142.8	30.4

SATELLITE IMAGES OF SST DURING TEN UPWELLING EVENTS BETWEEN 1984/85 AND 1993/94 - AREAS ASSOCIATED WITH TEMPERATURE BINS BETWEEN 10°C AND 16°C.

As stated previously, the designated year runs from 1 June to 31 May and thus encompasses the entire upwelling season. Ten satellite images of SST covering the southern Benguela upwelling system are shown in Figures 3a to 3j inclusive. Each image represents an upwelling event for each of the years from 1984/85 to 1993/94. The computed areas (km^2) associated with the different bands of temperature are given overleaf.

From these areas of upwelling-derived water for each of the ten upwelling events it is possible to get an idea of the variability between events.

Date	10°	11°	12°	13° (km^2)	14°	15°	16°
22/02/85	1111	2955	5822	5057	11979	21949	19712
29/01/86	2772	4102	5398	9832	11040	13586	18585
08/01/87	52	294	592	1248	3835	12461	21373
02/02/88	753	1795	2296	5119	8880	9458	10781
25/03/89	172	979	2107	6707	15068	17158	14738
24/01/90	720	2518	3672	5156	8639	13110	15653
24/01/91	3388	5423	8316	7956	9180	11245	15539
05/03/92	8	137	869	4106	7610	15679	15469
14/01/93	996	1774	3105	6146	6561	7555	9061
10/12/93	2085	2804	5238	12016	12713	15476	24392

A graphical representation of the results (Figure 4) shows the total area of upwelling-derived water associated with each event and the relative percentages of "recent" and "aged" components of the upwelling-derived water. Recently upwelled water was deemed to fall within the 10°C - 13°C inclusive temperature range. It was thus possible to describe each event in terms of its magnitude (large, moderate) and stage of development (new, mature, old). These broad categorizations are given below:

YEAR	EXTENT	STAGE
84/85	LARGE	MATURE
85/86	LARGE	NEW
86/87	MODERATE	OLD
87/88	MODERATE	MATURE
88/89	LARGE/MODERATE	MATURE/OLD
89/90	MODERATE/LARGE	MATURE
90/91	LARGE/MODERATE	NEW
91/92	MODERATE	OLD
92/93	MODERATE	NEW
93/94	LARGE	NEW

This method of categorization is refined in chapter 7.

AMOUNT OF NO_3-N AND HENCE POTENTIAL NEW PRODUCTION PER EVENT.

For each upwelling event in the years 1984/85 to 1993/94 inclusive, the known relevant variables are:

1. Mean integrated NO_3-N (mmol.m^{-2}) in the biologically productive surface layer for 1°C temperature bins between 10°C and 16°C inclusive and the associated 95% confidence limits.

2. The areal coverage (km^2) in the southern Benguela of each temperature bin for each of the ten images.

From this information it was possible to calculate the amount of NO_3-N available for new production (mmols) for each of the ten upwelling images between 1984/85 and 1993/94 inclusive. The detail of these results is given in table 1 at the end of this chapter and a summary is given below.

SOUTHERN BENGUELA - AVAILABLE NO_3-N (mmols) ON AN EVENT SCALE

Event	NO_3-N (mmols x 10^{12})	New Production (gC x 10^{12})
84/85	13.624 ± 1.899	1.08 ± 0.15
85/86	14.012 ± 1.807	1.11 ± 0.14
86/87	6.616 ± 1.145	0.52 ± 0.09
87/88	7.878 ± 1.050	0.62 ± 0.08
88/89	10.739 ± 1.494	0.85 ± 0.12
89/90	9.845 ± 1.361	0.78 ± 0.11
90/91	14.039 ± 1.722	1.11 ± 0.14
91/92	7.735 ± 1.198	0.61 ± 0.09
92/93	7.407 ± 0.952	0.59 ± 0.08
93/94	15.105 ± 2.041	1.20 ± 0.16

The mmol quantities of event-scale NO_3-N have been expressed in carbon terms via the multiplication of mmol NO_3-N by the molar relationship between carbon and nitrogen in the marine environment (the Redfield ratio = 6.6) to give mmol C and the atomic weight of carbon (=12) to give mg C (converted to grams).

DISCUSSION

The interpretation of satellite imagery in the field of oceanography is often hampered by the fact that satellite equipment only senses the ocean surface. In the present study, a depth-related parameter (integrated NO_3-N) was obtained from a surface variable (SST) which permitted the NO_3-N content of the upper 30m of the water column to be quantified at the regional level on a snapshot basis. This method of estimating the event-scale potential new production of the southern Benguela upwelling system makes a direct attack via NO_3-N content of the marine surface layer rather than an algorithmically derived total production (from remotely-sensed chlorophyll *a*) in combination with a regionally appropriate f-ratio (e.g. SATHYENDRANATH *et al.*, 1991).

There are several areas of uncertainty which originate from assumptions in the method and, to a lesser extent, the underlying logic implicit in the methodology. These require critical examination. The absence of measured euphotic zone depths in the data set necessitated the designation of 30m as the lower boundary of the productive surface layer. The choice of the 0 - 30m depth range took into account the wide range of possible euphotic zone depths found in coastal areas generally, and especially those of upwelling systems (SHANNON, 1985; BROWN and HUTCHINGS, 1987; ESTRADA and MARRASÉ, 1987). In cases where the base of the euphotic zone was below 30m the NO_3-N content will have been underestimated (and therefore errs on the side of conservatism). In the opposite case it was felt that any NO_3-N which has got to within 30m of the surface will be utilised in the context of potential new production per event since vertical transport mechanisms such as wind mixing and Langmuir circulation would be superimposed on the upwelling pulse. The sensitivity of the potential new production to choice of depth range was tested in WALDRON and PROBYN (1992). It was found that using the 0 - 40m and 0 - 20m depth ranges for purposes of integration raised and lowered respectively the final estimate by 38% but did not alter the order of magnitude.

The chosen temperature range of 10°C - 16°C for upwelling-derived water was based on a combination of the work of ANDREWS and HUTCHINGS (1980) and WALDRON (1985). The former found that water lying outside the upwelling front (termed Oceanic Water) generally had temperatures >18°C. WALDRON (1985) used the quasi-conservative property, salinity, to tag upwelling-derived water (from approximately 200m depth offshore) inshore of the upwelling front and found that sun-warming had increased the temperature from 10°C to 14°C (Maturing Upwelled Water). Water temperatures up to and including 16°C formed the inshore portion of the frontal zone with associated salinities characteristic of water which had come from approximately 100m depth offshore. Most of the archived data used to establish the relationship between SST and integrated NO_3-N were collected outside the short Austral Winter period thus any seasonal bias will have been small.

Arriving at event-scale estimates of potential new production, it was assumed that all the NO_3-N available to the nominal euphotic zone as a result of upwelling was utilised by primary producers. OLIVIERI (1983) found that around 85% of NO_3-N (integrated over the euphotic zone) was utilised over a four day period. WALDRON and PROBYN (1992) found that the average interval between summer upwelling events (in 1987) was about twelve days, it is therefore likely that most of the NO_3-N forming the basis of event-scale new production calculations would be taken up within the time scale of the upwelling cycle. On a longer time scale, it is reasonable to assume that all the NO_3-N would be used. Even if this occurs outside the confines of the system following advection, it is still attributable to the potential new production of the southern

Benguela. The main caveat is the possible loss of NO_3-N through downwelling at the upwelling front, which is not easily quantified.

The approach with respect to the assessment of NO_3-N content of the surface layer in this study is slightly different to that of WALDRON and PROBYN (1992) in that mean integrated NO_3-N values have been used for the range of temperature bins between 10°C and 16°C rather than the regressed values from the SST *vs* integrated NO_3-N relationship. The question arises as to whether the integrated NO_3-N values are realistic for upwelled water in the southern Benguela. Water with a surface temperature of 10°C was found to have a mean integrated NO_3-N value of 496.6 $mmol.m^{-2}$ over the 0 - 30m depth range. Such water would be of South Atlantic Central Water (SACW) origin and recently upwelled. The integrated value equates to a concentration of 16.6 $mmol.m^{-3}$ through that depth range. JONES (1971) quotes NO_3-N concentrations in the range 10 - 15 $mmol.m^{-3}$ and HENRY (1975) found concentrations of 10 - 18 $mmol.m^{-3}$ in SACW. Upwelled water in the southern Benguela system was found to have a NO_3-N concentration signature of 20 ±4 $mmol.m^{-3}$ by ANDREWS and HUTCHINGS (1980).

Potential new production estimated for the southern Benguela at the event scale covered the range 0.52×10^{12} - 1.20×10^{12} gC. WALDRON and PROBYN (1992), who estimated potential new production for the combined northern and southern systems, obtained an estimate of 2.46×10^{12} gC from their whole system NOAA 9 image dated 22 March 1987. These findings appear to be consistent.

The ten satellite images used in the present study show a non-equivalence in terms of magnitude and stage of development. This variability is not surprising but in order to arrive at annual estimates of potential new production for each year it is necessary to identify a reliable proxy for upwelling. This work is undertaken in the following chapter.

TABLE 1.

Computation of amount of nitrate per upwelling event (mmols x 10^{12})

MEAN VALUES

Temp. Band (°C)	84/85	85/86	86/87	87/88	88/89	89/90	90/91	91/92	92/93	93/94
10	0.552	1.377	0.026	0.374	0.085	0.358	1.682	0.004	0.495	1.035
11	1.154	1.602	0.115	0.701	0.382	0.983	2.117	0.053	0.693	1.095
12	1.690	1.566	0.172	0.666	0.611	1.066	2.413	0.252	0.901	1.520
13	1.130	2.197	0.279	1.144	1.499	1.152	1.778	0.917	1.373	2.685
14	2.402	2.213	0.769	1.780	3.021	1.732	1.840	1.526	1.315	2.549
15	3.883	2.404	2.205	1.673	3.036	2.319	1.990	2.774	1.337	2.738
16	2.815	2.654	3.052	1.539	2.104	2.235	2.219	2.209	1.294	3.483
Total	**13.624**	**14.012**	**6.616**	**7.878**	**10.739**	**9.845**	**14.039**	**7.735**	**7.407**	**15.105**

MAXIMUM VALUES (95% CONFIDENCE LIMIT)

Temp. Band (°C)	84/85	85/86	86/87	87/88	88/89	89/90	90/91	91/92	92/93	93/94
10	0.600	1.498	0.028	0.407	0.093	0.389	1.831	0.004	0.538	1.127
11	1.252	1.738	0.125	0.761	0.415	1.067	2.298	0.058	0.752	1.188
12	1.855	1.719	0.189	0.731	0.671	1.170	2.649	0.277	0.989	1.669
13	1.241	2.413	0.306	1.256	1.646	1.266	1.953	1.008	1.509	2.949
14	2.640	2.433	0.845	1.957	3.321	1.904	2.023	1.677	1.446	2.802
15	4.522	2.799	2.567	1.949	3.535	2.701	2.317	3.230	1.556	3.188
16	3.413	3.218	3.701	1.867	2.552	2.710	2.691	2.679	1.569	4.224
Total	**15.523**	**15.819**	**7.761**	**8.928**	**12.233**	**11.206**	**15.761**	**8.933**	**8.359**	**17.146**

MINIMUM VALUES (95% CONFIDENCE LIMIT)

Temp. Band (°C)	84/85	85/86	86/87	87/88	88/89	89/90	90/91	91/92	92/93	93/94
10	0.503	1.255	0.024	0.341	0.078	0.326	1.534	0.004	0.451	0.944
11	1.055	1.465	0.105	0.641	0.350	0.899	1.937	0.049	0.634	1.001
12	1.524	1.413	0.155	0.601	0.552	0.961	2.178	0.228	0.813	1.372
13	1.019	1.980	0.251	1.031	1.351	1.039	1.603	0.827	1.238	2.420
14	2.163	1.994	0.693	1.604	2.721	1.560	1.658	1.374	1.185	2.296
15	3.245	2.008	1.842	1.398	2.536	1.938	1.662	2.318	1.117	2.288
16	2.216	2.089	2.403	1.212	1.657	1.760	1.747	1.739	1.019	2.742
Total	**11.725**	**12.205**	**5.472**	**6.828**	**9.245**	**8.483**	**12.318**	**6.538**	**6.456**	**13.063**

CHAPTER 3

REGIONAL ESTIMATES OF ANNUAL POTENTIAL NEW PRODUCTION IN THE SOUTHERN BENGUELA UPWELLING SYSTEM

INTRODUCTION

In the previous chapter, the potential new production of the southern Benguela was estimated for ten upwelling events between 1985 and 1993. In order to gain a realistic insight to the southern Benguela in relation to carbon cycling and the predicted link between new production and tertiary producers it was necessary to obtain annual estimates of potential new production for the system. WALDRON and PROBYN (1992) progressed from an event-scale estimate to an annual estimate by identifying the number of discrete upwelling events which occurred during the year under review from the daily record of Meteosat images (which gave a qualitative indication of SST). The results of this subjective analysis were confirmed from the daily synoptic weather maps of southern Africa available from the Department of Environment Affairs Weather Bureau. Knowing the potential new production of an upwelling event and the number of events in that year, assuming equivalence between events, it was possible to estimate the potential annual new production of the system. This method provided a reasonable order of magnitude estimate but, due to the inevitable non-equivalence between upwelling events, would not be sensitive enough for inter-year comparisons.

A different approach has been adopted in the present study which made it possible to quantify the intensity and duration of the upwelling event coincident with the NOAA satellite image and all other events occurring in that year. This was achieved by using the fluctuation of tidally filtered and pressure-adjusted coastal sea level as a proxy for upwelling. Knowing the amount of available NO_3-N from a particular event (obtained from the NOAA image of SST), the relative strength of the event responsible and that of other upwelling events it was possible to obtain more finely tuned estimates of annual potential new production.

Tidally filtered and pressure adjusted sea level data were available for the years 1980 - 1990 inclusive and event-scale estimates have been obtained at the rate of one per year between 1984/85 and 1993/94 inclusive. These constraints have resulted in the quantification of annual potential new production between the years 1980/81 and 1989/90 inclusive.

METHODS

There are a number of linked variables in the coastal region which are of relevance in a dynamical consideration of upwelling. These variables include, *inter alia*, wind, cross-shelf currents and pressure adjusted sea level at the coast. A simplistic approach provides the following scenario: an equatorward wind is present which drives an offshore surface cross-shelf current resulting in a drop in sea level at the coast. The cumulative offshore transport during an event is thus linked to the wind strength and duration. The offshore transport equates with water upwelled into the photic zone and carries with it phytoplankton nutrients from below.

The satellite images chosen for event-scale estimates of new production were selected on the basis of an abundance of cold water off the west coast of South Africa in combination with cloud-free conditions. This subjective choice, from the images available from any given year, dictates that they represent prominent upwelling events.

The present objective is to establish a quantitative relationship between a variable which forces upwelling and a variable indicative of upwelling response. Forcing variables available are tidally filtered, pressure adjusted sea level at a point on the coast and wind strength and direction at an adjacent site. The response variable is NO_3-N content, derived from the amount of upwelling-derived water present as a result of the event.

THE SEA LEVEL DATA SET

The 1980 - 1990 sea level data set was derived from DE CUEVAS (1986), who compiled the daily mean sea level along the coast of Namibia and South Africa 1980 - 1985, supplemented by SEARSON (1994) to include the latter half of the decade. A detailed description of the data and methods used in the preparation of the data set is given in chapter 3 of SEARSON (1994) including data collection, quality control and processing. In summary, a data set of daily mean sea level, adjusted for the inverse barometer effect of atmospheric pressure (SCHUMANN and BRINK, 1990) was obtained for the coastal site of Saldanha Bay which is adjacent to a major southern Benguela upwelling centre (NELSON and HUTCHINGS, 1983) on the west coast of southern Africa. Fluctuations in sea level in such a data set can then be attributed to wind-driven processes. The time series of these data, showing the positive and negative residuals above and below the long-term mean sea level for each year between 1980/81 and 1989/90 are shown in figures 5a to 5j inclusive.

THE WIND DATA SET

Wind data for Cape Columbine were obtained from The Weather Bureau, Department of Environmental Affairs and Tourism, Pretoria 0001. These data comprised of wind speed ($m.s^{-1}$) and direction (degrees) at daily times of 08h00, 14h00 and 20h00 for the calendar years 1985 - 1990 inclusive.

THE RELATIONSHIP BETWEEN FORCING VARIABLES AND UPWELLING RESPONSE.

The ten images of prominent upwelling events were taken between 1984/85 and 1993/94 inclusive. The wind record requested from the Weather Bureau covered the period 1985 - 1990 inclusive and the sea level time series, 1980/81 - 1989/90 inclusive. Therefore the overlapping period for the purpose of establishing a relationship between forcing and response was 1984/85 - 1989/90 inclusive. The exact dates of the satellite images during this period were as follows:

22/02/85	29/01/86	08/01/87
02/02/88	25/03/89	24/01/90

These images provide quantitative information, via the SST *vs* §NO_3-N regression, of the response to the forcing mechanisms of the upwelling events; i.e. the amount of NO_3-N in upwelling-derived water. Wind patterns and sea level fluctuations were critically examined in the periods leading up to these images.

The occurrence of equatorward winds for a period prior to the upwelling images was established by plotting the southerly wind component for the relevant periods. A similar exercise was undertaken with the sea level time series with the objective of establishing links between sea level fluctuation, wind and strength of upwelling. The strength of forcing in relation to the extent of response was examined through regression and correlation analyses of these variables (ultimately, sea level fluctuation *vs* NO_3-N content per event). Having established a viable relationship, the amount of NO_3-N available from other upwelling events in any given year (estimated from the fluctuation in sea level) can be calculated and summed to provide annual estimates of potential new production. This was possible for the length of the sea level record (1980/81 - 1989/90 inclusive).

RESULTS

The southerly components of wind in the ten day periods preceding the satellite images of SST (Figure 6) clearly show the presence of equatorward and hence upwelling-favourable winds. The wind data represent measurements made at 08h00 each day. This time series was selected in order to minimise the influence of land/sea breeze effects and hence give a better picture of the underlying wind regime. The presence of dominant southerly winds in the period leading up to the satellite images supports the contention that the images of SST used to estimate the NO_3-N content of the upper part of the water column followed qualitatively identifiable upwelling events. A quantitative link between wind and upwelling is complicated by the variability in wind over time.

The record of tidally-filtered, pressure-adjusted sea level at an adjacent coastal site in the same ten day periods preceding the images (Figure 7) provides an alternative version of forcing and shows that there were fluctuations (rise/fall, fall/rise) occurring equivalent to the larger excursions shown in the annual sea level time series (Figs. 5a - 5j). Although the preceding ten days of the sea level time series are shown in figure 7, the fluctuation in sea level which acted as a forcing mechanism for the event is likely to be the most prominent excursion in sea level occurring immediately prior to the upwelling image. These can be defined as follows:

1984/85 Event: A sharp fall and rise in sea level between days 7 and 10 inclusive. Note: sea level fell after day 10.

1985/86 Event: A sharp fall and rise in sea level between days 2 and 7 inclusive.

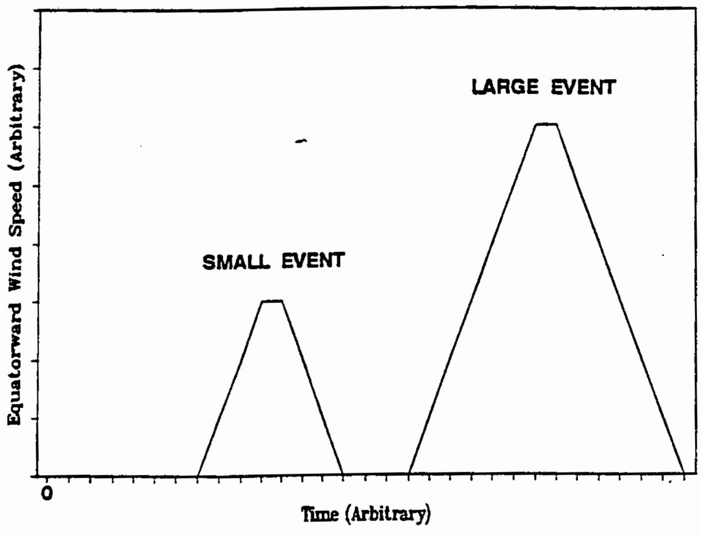
1986/87 Event: A two-step rise in sea level between days 3 and 7 inclusive followed by a fall between days 8 and 10 inclusive.

1987/88 Event: A fall and rise in sea level between days 2 and 9 inclusive with a stepped feature in the trough.

1988/89 Event: A fall and rise in sea level between days 3 and 8 inclusive. This fluctuation follows a preceding oscillation of similar amplitude.

1989/90 Event: A sharp fall and rise between days 6 and 10 inclusive. Note: sea level falls after day 10.

With the exception of the 1986/87 event, each image is preceded by a **fall** then **rise** in sea level within the 10 days prior to the image. The sequence of events driving the 1986/87 event would seem to be more complex. The question arises as to whether there is a quantitative link between some aspect of the forcing variable (sea level fluctuation) and upwelling response (NO_3-N content). In this context it is important to examine more closely the relationship between wind and sea level at the same point on the coast. In the case of wind-induced upwelling, the extent of upwelling should depend upon the intensity and duration of wind over a period of time. The harder and longer the wind event, the greater the cumulative effect on upwelling.

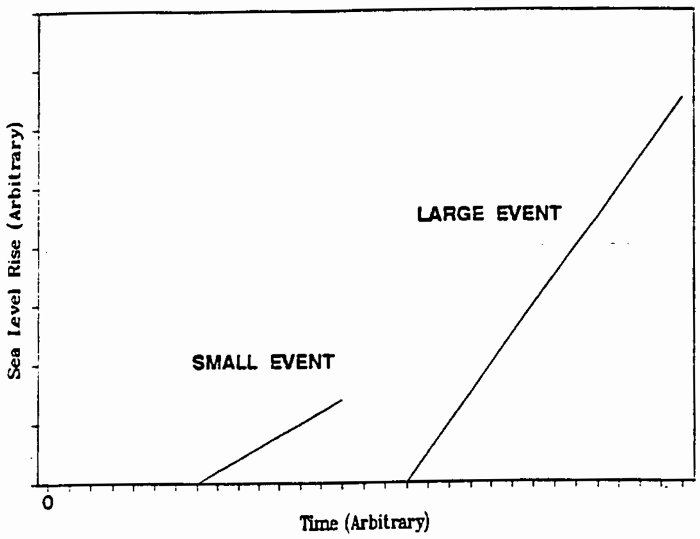


Cumulative Ekman transport (CET) is proportional to the product of the intensity of equatorward wind and the duration of the event.

CET proportional to §wind.dt

i.e. the area under the curve

Clearly this CET is directly linked to the change in sea level at the coast but it is instructive to establish the link through the wind. The stronger the wind, the more quickly will the sea level change at the coast, and the greater the duration of the wind event the greater will be the cumulative effect.



CET proportional to §slope.dt

CET proportional to §(d(sea level)l/dt).dt

CET proportional to [change in sea level]$_{event}$

From the sea level record prior to each of the upwelling images and coincident with the upwelling event, the sea level fall and rise during the large fluctuations (forcing mechanisms) have been plotted in turn against the NO_3-N content (response variable). The variables are tabulated overleaf:

Event	Rise (cm)	Fall (cm)	NO_3-N (mmol) x 10^{12}
1984/85	14	15	13.62
1985/86	16	19	14.01
1986/87	6 or 14	12	6.62
1987/88	7	8	7.88
1988/89	5	8	10.70
1989/90	8	19	9.84

Fall in sea level *vs* NO_3-N content (Figure 8) gives a correlation coefficient (r) of 0.53. This is not a statistically significant relationship (4 degrees of freedom). Rise in sea level *vs* NO_3-N content (Figure 9) gave a more encouraging picture with the exception of the rise in sea level prior to the 1986/87 image. Figure 7 shows the 1986/87 event to be unusual in that the image was preceded by a prominent rise then fall as opposed to the characteristic fall then rise of the other events. A further complication was that the rise in sea level occurred as two distinct steps separated by a day when sea level fell. The two equivocal data points for 1986/87 plotted in Figure 9 represent, (a) the total rise in sea level, ignoring the step and, (b) the second rising portion only. It can be seen that (a) provides an outlying data point and (b) is more in agreement with the other events. Given that the shape of the sea level time series for the 1986/87 event is unusual and that its rising portion is subject to alternative interpretations it was decided to exclude this data point from the regression and correlation analysis. The remaining data points give a straight line equation of the form:

$$y = 0.46x + 6.57 \ (r = 0.85),$$

which is significant at better than the 90% level of confidence (3 degrees of freedom). The standard error of the y estimate = 1.58; standard error of the x coefficient = 0.17.

This result indicates a positive correlation between the rise in sea level occurring as part of an upwelling event and the amount of NO_3-N transported into the surface layer as a result of that event. The use of the rise in sea level rather than the fall is addressed in the discussion. It thus becomes possible to estimate the amount of NO_3-N upwelled for other events in any given year from the rise in sea level which accompanies that event and hence provide annual estimates of potential new production.

Before taking this step, however, an assumption is made that there is a threshold value of forcing (sea level rise) below which the upwelling response (NO_3-N introduced to surface layer) is likely to be negligible. The regression relationship shown in figure 9 was based on variables obtained from subjectively selected large upwelling events. It is not known what regressed values of event-scale NO_3-N is obtained from low values of sea level rise. From figure 9 it would be inappropriate to extend the straight line fit to an intercept on the y-axis. Erring on the side of conservatism it was decided to regress values of NO_3-N for sea level rise excursions greater than or equal to 3 cm.

From the record of sea level between 1980 and 1990 and the regression relationship shown in figure 9 (subject to the threshold cut-off described above), the annual figures of potential new production (mmol NO_3-N.y^{-1}) and their carbon equivalents (converted as previously) are given below and shown graphically in figure 10.

Year	(mmol NO_3-N.y^{-1}) x 10^{14}	(gC.y^{-1}) x 10^{13}
1980/81	7.47	5.92 ± 1.76
1981/82	7.27	5.76 ± 1.70
1982/83	7.61	6.03 ± 1.78
1983/84	7.82	6.19 ± 1.83
1984/85	6.51	5.16 ± 1.51
1985/86	7.03	5.57 ± 1.61
1986/87	6.85	5.43 ± 1.58
1987/88	6.59	5.22 ± 1.52
1988/89	6.91	5.47 ± 1.61
1989/90	6.51	5.16 ± 1.48

These annual estimates have been resolved into their seasonal components as follows:

Winter: June, July, August.

Spring: September, October, November.

Summer: December, January, February.

Autumn: March, April, May.

The seasonal results are tabulated below in terms of carbon and shown graphically in figure 11.

Year	Winter	Spring	Summer	Autumn
		(gC.Season^{-1}) x 10^{13}		
1980/81	1.71	1.47	1.26	1.48
1981/82	1.69	1.56	1.26	1.25
1982/83	1.53	1.42	1.58	1.50
1983/84	1.69	1.46	1.54	1.51
1984/85	1.28	1.38	1.28	1.24
1985/86	1.50	1.65	1.34	1.08
1986/87	1.48	1.66	1.10	1.18
1987/88	1.36	1.43	1.03	1.40
1988/89	1.23	1.71	1.16	1.36
1989/90	1.32	1.28	1.29	1.25

The annual and seasonal estimates of potential new production are discussed below but their main impact will be addressed in chapters 5 and 6 in an attempt to address carbon pathways in the southern Benguela and the link between new production and tertiary production.

DISCUSSION

The annual potential new production estimates for the southern Benguela lay within the range 5.16 x 10^{13} gC.y^{-1} to 6.19 x 10^{13} gC.y^{-1}. The standard error of the y estimate and x coefficient resulted in a ± figure, approximately 30% of the mean predicted potential new production. The small number of data points used to derive the regression relationship in figure 9 was a constraint imposed by the number of available satellite images. It is suggested that a greater number of data points would reduce the variance but leave the mean characteristics largely unchanged. The impact of this variance is not critical in relationship to the establishment of carbon pathways in the southern Benguela (chapter 5) but introduces the potential for a broad range of potential new production in the context of pelagic fish comparisons (chapter 6).

WALDRON and PROBYN (1992) estimated annual potential new production for the whole system as 4.7 x 10^{13} $gC.y^{-1}$. This estimate compared well with other estimates of production in the Benguela, and inter-regional comparisons, but did not take into account the occurrence of upwelling events of varying intensity and duration. The combined results of this study and that of WALDRON and PROBYN (1992) indicate that estimates are robust at the 10^{13} order of magnitude.

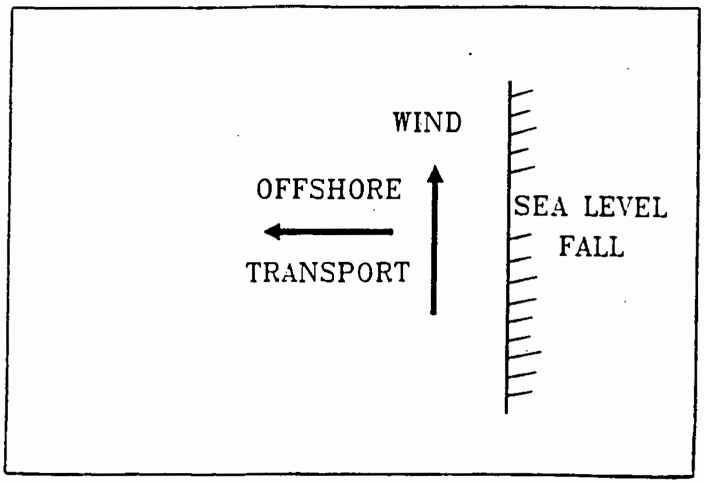
The decadal, inter-year comparison given here shows that mean estimates can vary by 20% of the mean minimum and therefore, in modelling terms, the system provides a fairly consistent carbon sink. This topic, and the possible impact of varying new production on the success of higher trophic levels, are addressed in detail in subsequent chapters.

At this stage it is possible to identify some general trends in potential new production from the decade of inter-year comparisons (Fig. 10) and seasonal differences between and within the same years (Fig. 11). Broadly speaking, potential new production in the first half of the 80s was greater than in the second with a substantial step-down occurring during 1984/85. There is a consistency between this result and certain related variables reported in SHANNON *et al.* (1992). Their annual time series of sea surface temperature anomalies showed unusually cold water (and hence more available NO_3-N) to be present in area 5 (southern Benguela coastal zone) during most of the first half of the 80s and unusually warm in the second half. A consistent picture was present in their sequences of annual averaged anomalies of equatorward pseudo wind stress and deviation from the monthly mean of the equatorward wind component at Cape Columbine lighthouse. Note that in SHANNON *et al.* (1992) a calendar year is used and data density in area 5 was low. The supportive evidence between their findings and the present study is, however, encouraging. In particular, it reinforces the use of sea level fluctuation (i.e. sea level rise) as a proxy for upwelling.

The seasonal results indicate that in the first half of the decade, the Winter provided the greatest contribution to potential new production (except marginally in 1982/83) whereas the latter half was dominated by the Spring season (note that in 1989/90 the seasonal inputs were approximately equal). Again, 1984/85 marked the transition between Winter and Spring dominance. Conventional wisdom dictates that, productively, the southern Benguela is best served by a burst of Spring upwelling which gives the system a biological "kick-start" following Winter dormance. Superimposed on this broad-based precondition is the need for quality upwelling phases which fulfil the optimal environmental window criteria of CURY and ROY (1989). These factors are discussed in a subsequent chapter dealing with new and tertiary production.

Sea level fluctuations at a point on the coast have been used as a quantitative proxy for upwelling in the estimation of potential annual new production. Specifically, a significant relationship was found between sea level rise and upwelling response (NO_3-N upwelled). The simplistic model of upwelling on the west coast of South Africa would dictate that upwelling-favourable winds are accompanied by sea level fall at the coast due to Ekman transport. This simple model assumes a uniformity around the coast of forcing wind systems and the sea level response.

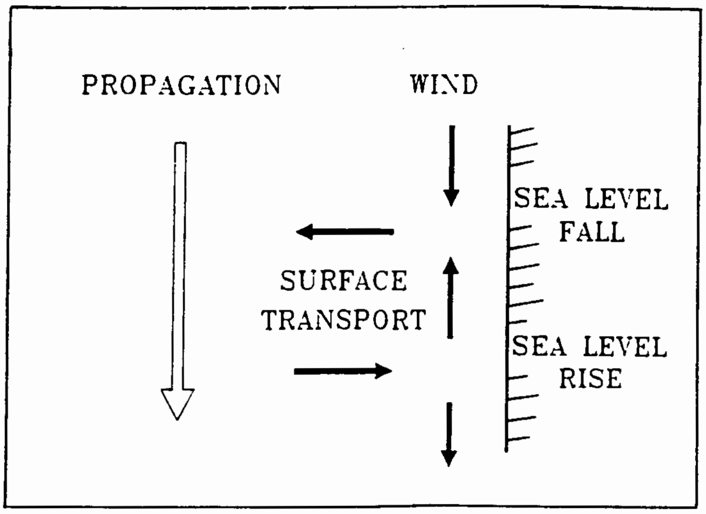
i.e.



In the present study, a significant relationship was found between sea level rise and upwelling response (as evidenced by cold water events and the quantity of NO_3-N). This is contrary to the simple model described above which has clearly omitted a feature or phenomenon vital to a realistic description of coastal upwelling.

In fact, neither the forcing nor the response are uniform along the coast. Moreover, the forcing systems and response manifestations move in an anticlockwise direction around the coast (SCHUMANN and BRINK, 1990).

The diagram shown below provides a more realistic picture than the simplistic model.



At the time of peak upwelling-favourable winds at one location, there are weak winds at neighbouring locations and peak downwelling-favourable winds further away. There is a sympathetic alternation between fall and rise in sea level at the coast.

In a given time-frame, the weather system and its associated pattern of offshore (sea level fall) and onshore (sea level rise) surface transport move down and around the coast:- weather systems as a coastal trapped wave in the lower atmosphere (GILL, 1977) and surface transport patterns as a coastal trapped wave in the shelf ocean (GILL and SCHUMANN, 1974). SCHUMANN and BRINK (1990) reinforce much of this with their finding that the main generating mechanism of coastal trapped waves is the alongshore component of wind and that the weather systems (especially coastal lows in this context) generally move much faster than coastal trapped waves in the shelf ocean of the South African south coast. The complex set of interactions between forcing variables culminated in their finding that in a strongly wind-forced region, the variation in local sea level was generally more highly correlated with wind at locations in the direction from which coastal trapped waves would propagate. Therefore the peak intensity of the different aspects of forcing and response can arrive at a point on the coast with a lag between them.

Naturally, the relative speed between forcing and response systems can be different and thus the lags can vary. However, NELSON (1992) states that since the Benguela is highly productive and because of the clear evidence of coastal trapped waves it must be assumed that the correct phase relationship between upwelling-favourable winds and free waves usually obtains.

CHAPTER 4

"GROUND TRUTH" MEASUREMENTS OF NITRATE UPTAKE IN THE SOUTHERN BENGUELA UPWELLING SYSTEM.

INTRODUCTION

Regional estimates of annual potential new production have been made for the years 1980/81 - 1989/90 inclusive using a combination of satellite imagery, the relationship between SST and integrated NO_3-N and fluctuation of coastal sea level. These estimates have been presented in chapter 3. The present chapter attempts to test the validity of these estimates by comparison with stable isotope measurements of NO_3-N uptake (new production) in the southern Benguela which have been made on various research cruises over a number of years. The regional estimates cover an area of tens of thousands km^2 whereas NO_3-N uptake measurements provide an hourly or daily rate m^{-2}. This difference in scale, and hence resolution, coupled with non-synopticity, means that the NO_3-N uptake rates are not ground-truth measurements in the true sense but a non-specific means of testing whether ambient uptake rates are capable of accounting for the regional estimates. The spatial and seasonal heterogeneity typical of the southern Benguela are further complicating factors.

Four research cruises relevant to this work were undertaken between 1987 and 1995. A summary is given below and station locations are shown in figure 12.

Date	Vessel	Cruise Title	Location
March 1987	RS Benguela	Anchor Station	St Helena Bay
March 1990	RS Benguela	Filament Cruise II	Southern Benguela

Date	Vessel	Cruise Title	Location
February 1991	RS Africana	Olifants R. Tran.	32°S
February 1995	RS Africana	Drogue Study	Cape Col./ St Helena Bay

METHODS

The methodology by which NO_3-N uptake by phytoplankton was determined on the four cruises is described below.

MARCH 1987: ANCHOR STATION.

SAMPLING

Water samples for ^{15}N tracer measurements, chlorophyll *a* analyses and nutrient determinations were collected from depths corresponding to the 100%, 50%, 25%, 1% light levels and the thermocline region (<1% surface irradiance) using a rosette sampler attached to the ship's CTD system. Sampling depths were determined from a profile of downwelling irradiance measured with a Lambda LI-192S quantum light sensor and from temperature profiles. Samples for ^{15}N tracer experiments were not screened prior to incubation because of the presence of large (200 - 500 μm) *Coscinodiscus gigas* cells. Incubations were performed *in situ* on a weighted, free-floating line for 24 hours, with sample bottles attached at the appropriate depths. Bottles were mounted on a plastic wire frame for protection prior to attachment to the line. Shading by the frame was insignificant. Although 24 hour incubations are not the norm, they were performed so as to include night-time uptake of NO_3-N in the daily rate. The abundance of NO_3-N in the water would have reduced the possibility of NO_3-N limitation and the performance of separate day and night incubations would not have been logistically possible.

ANALYTICAL

NO_3-N concentrations (corrected for NO_2) were analysed on board ship with a Technicon Auto Analyser II (MOSTERT, 1983).

NITROGEN FLUX EXPERIMENTS

NO_3-N uptake rates were determined according to DUGDALE and WILKERSON (1986). Particulate nitrogen concentrations measured at the end of incubation were used in the calculation of absolute uptake rates. ^{15}N was added as $Na^{15}NO_3$ (99.6 at.%) to 1-litre samples. Labelled NO_3-N supplements were varied in concert with the measured range in ambient concentrations to keep enrichment at *circa* 10%. Incubations lasted approximately 24h with the exception of station 23 which was performed during the daylight hours (11:00 - 15:30h local time). Incubations were terminated by filtration onto Whatman GF/F filters which were rinsed with filtered seawater and stored frozen for later analysis. Enrichment of ^{15}N was measured on a Jasco N-150 ^{15}N Analyser after Kjeldahl/Rittenberg oxidation (FIEDLER and PROKSCH, 1975). This procedure also allowed calculation of particulate nitrogen concentrations. Particulate and aqueous ^{15}N enrichment in excess of natural abundance were used in all calculations.

MARCH 1990: FILAMENT CRUISE.

Total phytoplankton community NO_3-N uptake was measured in 1-litre, 200 μm screened samples spiked with 0.1 $mmolN.m^{-3}$, $Na^{15}NO_3$(99.6 at%). Samples were collected from depths corresponding to the 100, 50, 25, 10, and 1% light levels. Nitrate concentration was measured according to the method of STRICKLAND and PARSONS (1972) modified for use with a Technicon Auto Analyser II (MOSTERT, 1983). Experiments were initiated about midday local time and were run for 4h under simulated *in situ* light conditions. Experiments were terminated by filtration onto 47mm Whatman GF/F filters which were stored frozen for later analyses.

Samples were prepared according to the Kjeldahl/Rittenberg oxidation procedure (FIEDLER and PROKSCH, 1975) for ^{15}N:^{14}N isotope analysis by emission spectroscopy. Absolute rates of nitrogen uptake were calculated using particulate nitrogen concentrations measured at the end of the incubations, thereby accounting for any biomass increase that may have occurred during incubation (DUGDALE and WILKERSON, 1986; COLLOS, 1987). Particulate and aqueous ^{15}N enrichment in excess of natural abundance were used in all calculations.

FEBRUARY 1991: OLIPHANTS RIVER TRANSECT (ORT)

FEBRUARY 1995: PLANKTON DYNAMICS CRUISE (PDC)

Bulk water samples were obtained from the 100, 50, 25, 10 and 1% light depths. Samples for ^{15}N tracer experiments were pre-screened (200 μm) to exclude grazers. For each light depth a 1-litre volume was supplemented with an appropriate volume of 10 μM $Na^{15}NO_3$(99.6 at%). Labelled NO_3-N additions were varied in concert with the measured range in ambient concentrations to keep enrichment at around 10%. The spiked NO_3-N samples were incubated in 1-litre glass Schott bottles at simulated *in situ* light levels on deck. In the case of the ORT, separate day and night incubations were conducted whereas PDC samples were incubated for 24 hours. In all cases incubations were maintained at SST by continuous water flow. Uptake experiments were terminated by filtration onto 47mm GF/F Whatman filters which were frozen (ORT) or dried (PDC) and retained for later analyses of PN and ^{15}N content.

Enrichments with ^{15}N and PN concentrations were analysed by automated continuous flow analysis (OWENS and REES, 1989) through the interfacing of a Carlo Erba CHN analyser with a VG 620 mass spectrometer. NO_3-N concentrations were determined according to the method of STRICKLAND and PARSONS (1972) modified for use with a

Technicon Auto Analyser II (MOSTERT, 1983) during the ORT and manually on the PDC.

CALCULATION OF REGIONAL NEW PRODUCTION FROM NO_3-N UPTAKE MEASUREMENTS.

In order to test the validity of potential new production estimates made in chapters 2 and 3, two alternative methods of comparison have been employed addressing new production estimates on an annual and event scale. These alternative methods are aimed at establishing whether the regional potential new production estimates were of the appropriate order of magnitude rather than precise between years.

METHOD I.

This method provides an estimate of regional annual new production based on the area of water in the southern Benguela that is typically upwelling-derived, the ambient daily rate of NO_3-N uptake by the phytoplankton and an assumed duration of the productive year.

In addition to the set of daily NO_3-N uptake rates (mmol.$m^{-2}d^{-1}$) integrated over the depth range of the nominal euphotic zone available from the four research cruises, were the areas (km^2) associated with each temperature band of upwelling-derived water from the ten satellite images of SST for the southern Benguela upwelling region (chapter 2). In order to provide a regional estimate of annual new production from these data it was decided to divide the areas of upwelling-derived water between New (10 - 12°C inclusive), Mature (13 - 14°C inclusive) and Aged (15 - 16°C inclusive). From the ten images it was possible to calculate a mean area for each of the three categories. The NO_3-N uptake measurements were similarly grouped and uptake rates applicable to each category of upwelling-derived water could be applied to the temperature-defined areas giving an annual estimate of regional new production. It was decided to err on the side of conservatism, therefore the time interval used to compute annual figures of new production excluded the winter period. In addition to calculating new production for the mean areas of upwelling-derived water, new production was also calculated for the images where the areal extent of upwelling-derived water was at a maximum and minimum.

METHOD II.

The second method estimated regional new production on an event-scale and employed a conceptual model of upwelling and NO_3-N utilization. The first step was a theoretical definition of the true upwelling area based on a computation of the Rossby radii of deformation. The radius varies with latitude (i.e. Coriolis parameter, (f)), Brünt-Väisäla frequency (N) and water depth (H) according to the relationship HN/f (CHARNEY, 1955; YOSHIDA, 1967; BARBER and SMITH, 1981). The mean Brünt-Väisäla frequency was calculated according to MILLARD *et al.* (1990) and water depth was taken to be 200m. The Rossby radius was then calculated at 1° latitude intervals from 29°S to 35°S. This intrinsic scale, perpendicular to the coast, was then used to specify a theoretical area of upwelling.

This area was assumed to be inundated with newly upwelled water (10°C) at the start of the upwelling cycle. Upwelling-derived water has been defined as spanning the 10° - 16°C temperature range with New, Mature and Aged water occurring in this range. GUASTELLA (1992) found that the warming rate of waters off the west coast of South Africa was 0.65°C per day in the upper 10m. This being the case, the water upwelled into the theoretically defined upwelling area would spend approximately 4 days as New, 3 days as Mature and 3 days as Aged water. Applying the NO_3-N uptake rates typical of these water categories (Method I) for these time intervals over the theoretical upwelling area provided an event-scale estimate of new production for comparison with the estimates given in chapter 2.

RESULTS

METHOD I ESTIMATES OF ANNUAL NEW PRODUCTION

The areas (km^2) of 10, 11, 12, 13, 14, 15 and 16°C water from each of the ten satellite images were tabulated in chapter 2. Grouping these data into their New, Mature and Aged categories provided the following mean values:

Category	(km^2)
New	7 225
Mature	15 885
Aged	30 298

The largest upwelling event, in respect of areal extent of upwelling-derived water from the available record of satellite images, was in 1993/94 and the smallest was in 1992/93. The respective areas of New, Mature and Aged water from these events were as follows:

	Maximum (km^2)	Minimum (km^2)
New	10 127	5 875
Mature	24 729	12 707
Aged	39 868	16 616

Uptake rates of NO_3-N were measured over 24 hours during the Anchor Station and Drogue Study. Four hourly day-time incubations were conducted during the course of Filament Cruise II and separate day- and night-time incubations during the Oliphants River Transect. In order to get a daily (24 hour) rate of NO_3-N uptake from the latter two cruises, the ambient night-time rate from the Oliphants River Transect was added to day-time measurements. The daily rates of NO_3-N uptake from the four cruises are presented below together with their temperature-designated water categories.

Cruise	Station	NO_3 Uptake ($mmol.m^{-2}.d^{-1}$)	Category
Anchor Station	23	14.51	Mature
	32	11.21	Mature
	37	9.48	Mature
	41	9.17	Mature
Filament Cruise II	10	5.09	Aged
	14	10.02	Aged
	21	3.40	Aged
	25	12.83	Aged
	29	7.73	Aged
Oliphants R. Trans.	26	24.98	New
	30	5.06	Mature
	34	2.76	Mature
	37	6.63	Aged
	41	3.77	Aged
	45	6.21	Aged
	49	13.61	Aged
Drogue Study	1	8.67	New
	4	28.84	New
	6	61.34	Mature
	9	37.73	Mature
	14	10.06	Mature
	17	18.34	Mature
	20	1.50	Mature
	23	5.42	Mature

The mean integrated daily NO_3-N uptake rates for New, Mature and Aged water were 20.83, 15.55 and 7.70 $mmol.m^{-2}.d^{-1}$ respectively. Assuming a year in which NO_3-N uptake extends over 274 days (which excludes Winter) and converting mmol N to gC as previously, the following formula was used to calculate annual new production in $gC.y^{-1}$:

$$(\text{Water Area} * \text{Uptake Rate} * 10^6 * 6.6 * 12 * 274) / 1000$$

The results are tabulated overleaf.

Mean Areas of New, Mature and Aged Water

	Mean Area (km^2)	Uptake Rate ($mmol.m^{-2}.d^{-1}$)	No.Days	New Production ($gC.y^{-1}$) x 10^{13}
New	7 225	20.83	274	0.33
Mature	15 885	15.55	274	0.54
Aged	30 298	7.70	274	0.50
Total New Production				**1.37**

Maximum Areal Extent of Upwelling-Derived Water

	Max Area (km^2)	Uptake Rate ($mmol.m^{-2}.d^{-1}$)	No.Days	New Production ($gC.y^{-1}$) x 10^{13}
New	10 127	20.83	274	0.46
Mature	24 729	15.55	274	0.83
Aged	39 868	7.70	274	0.67
Total New Production				**1.96**

Minimum Areal Extent of Upwelling-Derived Water

	Min Area (km^2)	Uptake Rate ($mmol.m^{-2}.d^{-1}$)	No.Days	New Production ($gC.y^{-1}$) x 10^{13}
New	5 875	20.83	274	0.27
Mature	12 707	15.55	274	0.43
Aged	16 616	7.70	274	0.27
Total New Production				**0.97**

To summarize, the annual new production estimates according to Method I were:

Mean Upwelling Area - 1.37 x 10^{13} $gC.y^{-1}$

Maximum Upwelling Area - 1.96 x 10^{13} $gC.y^{-1}$

Minimum Upwelling Area - 0.97 x 10^{13} $gC.y^{-1}$

METHOD II ESTIMATE OF EVENT-SCALE NEW PRODUCTION.

A Rossby radius was calculated for each 1° of latitude between 29°S and 35°S. The Coriolis parameter (f) was calculated according to the formula $2.w.\sin\Theta$ (where $w = 2\pi/86400$, Θ = latitude) and the Brünt-Väisäla frequency (8.44×10^{-3}) from Cape Columbine data in WALDRON (1985). The Rossby radius varied between 23.94 km at 29°S and 20.23 km at 35°S giving a theoretical area of upwelling of 1.5×10^{10} m^2 (15000 km^2).

New production during New phase of upwelling cycle

NO_3-N uptake rate in New water = 20.83 mmol.m^{-2}.d^{-1}

Duration of New phase = 4 days

New Production = $(1.5 \times 10^{10} * 20.83 * 4 * 6.6 * 12)/1000$

$= 0.99 \times 10^{11}$ gC

New production during Mature phase of upwelling cycle

NO_3-N uptake rate in Mature water = 15.55 mmol.m^{-2}.d^{-1}

Duration of Mature phase = 3 days

New Production = $(1.5 \times 10^{10} * 15.55 * 3 * 6.6 * 12)/1000$

$= 0.55 \times 10^{11}$ gC

New production during Aged phase of upwelling cycle

NO_3-N uptake rate in Aged water = 7.70 mmol.m^{-2}.d^{-1}

Duration of Aged phase = 3 days

New Production = $(1.5 \times 10^{10} * 7.70 * 3 * 6.6 * 12)/1000$

$= 0.27 \times 10^{11}$ gC

The sum of new production for the 3 phases of the upwelling cycle gives an event-scale estimate of 0.18 x 10^{12} gC

DISCUSSION

The estimates of annual potential new production presented in chapter 3 and event-scale potential new production presented in chapter 2 have been tested against alternative methods of estimation using the common thread of measured rates of daily NO_3-N uptake in the southern Benguela upwelling system.

The ten estimates of annual potential new production for the 1980s gave a mean value of 5.60 x 10^{13} gC.y^{-1}. The comparative method used in this chapter provided estimates of 1.37 x 10^{13}, 1.96 x 10^{13} and 0.97 x 10^{13} gC.y^{-1} for mean, maximum and minimum areas of upwelling-derived water respectively. These results compare favourably taking into account the extrapolation to a regional scale. They indicate that 10^{13} is an appropriate order of magnitude for estimates of annual new production for the southern Benguela.

The event-scale new production estimate for a theoretically defined area of upwelling used in combination with a temperature-defined, time-based progression of NO_3-N uptake rates between New and Aged water was 0.18 x 10^{12} gC.$event^{-1}$. The ten upwelling events reported in chapter 2 gave a mean potential new production estimate of 0.85 x 10^{12} gC.$event^{-1}$. Once again, the comparative estimate was less by several factors but robust at the order of magnitude, which was encouraging. The former method, may have been expected to give a higher event-scale estimate of potential new production because of its theoretical approach. However, it uses an area of upwelling defined by the Rossby radius and Brink (1987) states that "the distance of the [upwelling] front from the coast has little to do with the internal Rossby radius length scale." Interestingly though, when the mean areas of New, Mature and Aged upwelling-derived water were subjected to their typical NO_3-N uptake rates for 4, 3 and 3 days respectively, the new production estimate was 0.16 x 10^{12} gC.event^{-1}.

Further consideration is given to the annual potential new production estimates given in chapter 3 in the context of an intra- and inter-regional and global comparison. Brown *et al.* (1991) have estimated the total (new and regenerated) production for the southern Benguela to be 7.64 x 10^{13} gC.y^{-1}. The mean estimate of annual potential new production presented in this thesis was 5.60 x 10^{13} gC.y^{-1} which provides an f-ratio (new production:total production) of 0.73. Shannon and Field (1985) reported a total production rate of 4.0 gC.m^{-2}.d^{-1} for the Cape Columbine/ St Helena Bay region from ^{14}C uptake studies. Expressing the mean chapter 3 value in the same units, using the mean area of upwelling-derived water (5.34 x 10^{10} m^2), gave a rate of 2.87 gC.m^{-2}.d^{-1} which translates to an f-ratio of 0.72. These f-ratios are at the maximum of the accepted range for the southern Benguela upwelling system (Probyn, 1992) but emphasise that potential new production as opposed to new production *per se* was being estimated. The daily new production rate of 2.87 gC.m^{-2}.d^{-1} compares well with the median rate of integrated NO_3-N uptake reported in this chapter (29.92 mmol NO_3-N.m^{-2}.d^{-1} $\equiv$ 2.37 gC.m^{-2}.d^{-1}).

Alternative comparisons are less supportive of the annual potential new production estimates given in chapter 3. When the Brown *et al.* (1991) southern Benguela estimate of total production is expressed per unit area it gives a figure of 2.01 gC.m^{-2}.d^{-1} which is less than the new production rate given here (2.87 gC.m^{-2}.d^{-1}). The Shannon and Field (1985) total production rate used in the above comparison used the figure for the Cape Columbine St Helena Bay region (4 gC.m^{-2}.d^{-1}) whereas they also quote a rate of 2.8 $gC.m^{-2}.d^{-1}$ as being typical of the southern system as a whole. Applying these comparative rates suggests that regional new production for the southern Benguela has been overestimated.

In an effort to place the southern Benguela in an inter-regional and global new production context it was compared with contemporary estimates of various oceanic regimes and the global ocean:

Source	Region	New production ($gC.y^{-1}$)
EPPLEY and PETERSON (1979)	Global	$3.4\text{–}4.7 \times 10^{15}$
CHAVEZ and BARBER (1987)	Global	8.3×10^{15}
CHAVEZ and BARBER (1987)	Eq. Pacific	$1.0\text{–}1.9 \times 10^{15}$
CHAVEZ and BARBER (1987)	E. Pacific (Coastal)	$0.8\text{–}2.0 \times 10^{14}$
This thesis (mean)	S. Benguela	5.60×10^{13}

The southern Benguela contributes between about 0.7% and 1.6% of global new production. The contribution of the equatorial Pacific to global new production lies between 12% and 56% and southern Benguela new production is between 3% and 6% that of the equatorial region.

Comparing the southern Benguela with coastal waters of the eastern Pacific (Peruvian upwelling system) shows that its new production is 43% greater than the southern Benguela at the lower end of the range. The upper value for the same system (2.0×10^{14} $gC.y^{-1}$) is about 3½ times greater than the southern Benguela. Note that CHAVEZ and BARBER (1987) obtained the lower estimate of new production for that region by applying the EPPLEY and PETERSON (1979) model to their total production figure. Any under-estimation of the f-ratio would therefore reduce their estimate of new production. The higher figure was obtained using the model of WYRTKI (1963), which estimated the upward flow across the 100m level in the coastal zone. They then converted the supply rate of NO_3-N to potential new production. The comparisons between the Benguela and Peruvian upwelling systems are in qualitative agreement with trends in fish catches of pilchard/sardine (CRAWFORD, 1987).

The intra-regional comparison is reasonable, with the proviso that certain data manipulations indicate an over-estimation of regional new production. The inter-regional and global comparisons indicate that southern Benguela estimates of annual potential new production can be successfully placed in an inter-regional and global context.

CHAPTER 5

CARBON PATHWAYS IN THE SOUTHERN BENGUELA UPWELLING SYSTEM.

INTRODUCTION

This chapter addresses the possible pathways of carbon transport in the southern Benguela upwelling system. The work draws substantially upon research reported in WALDRON *et al.* (1992) and, for the sake of completeness, certain portions of this introduction re-state aspects of the carbon cycle described in chapter 1.

Knowledge of the role played by the world ocean as a sink for carbon, a fundamental component of the global carbon cycle, is an essential prerequisite in the prediction of 21st century climate following anthropogenic loading of the earth's atmosphere with CO_2. In this context, the estimation of new production, as defined by DUGDALE and GOERING (1967), at the global and regional level has been the focus of much current interest (EPPLEY and PETERSON, 1979; WYRTKI, 1981; LEWIS *et al.*,1986; CHAVEZ and BARBER, 1987; ROEMMICH, 1989; WALDRON and PROBYN, 1992; WALDRON *et al.*, 1995).

According to DUGDALE and GOERING (1967), new production is the portion of a system's total primary production which utilises newly available nitrogen (e.g. NO_3-N transported advectively or convectively to the euphotic zone). The balance of total production is made up of regenerated production which results from nutrients recycled within the euphotic zone (NH_4-N and urea). EPPLEY and PETERSON (1979) stated that new production is that part of the total production which can be exported from the euphotic zone without the production system running down and LEWIS *et al.* (1986) refer to it as equivalent to the rate of export of organic carbon. The generally accepted consequence of this logic dictates that new production constitutes a long-term carbon sink, however, LEGENDRE and GOSSELIN (1989) have pointed out certain caveats based on a consideration of appropriate time and space scales, the as yet unknown magnitude of nitrogen fixation in open oceanic waters, atmospheric transport of NO_3-N and NH_4-N and concentrations of long-lived dissolved organic nitrogen in the oceans. While it has not been possible to incorporate these caveats in the results of this study, certain adjustments in approach have been necessitated by the fact that a coastal upwelling system (in this case the southern Benguela) was under consideration as opposed to the open ocean.

ROEMMICH (1989), in his study of the southern California coastal waters, made the distinction between the addition of NO_3-N from outside the system (called "imported new" production) and "local new" production which "might for example result from particulate organic nitrogen (PON) falling out of the euphotic zone, being oxidized to nitrate and then being returned by upwelling back to the surface layer." This subdivision of new production has important implications for a coastal upwelling system since it is almost inevitable that a proportion of its new production would be "local new" production and would not therefore constitute a carbon sink in the longer term. When attempting to assess the ocean's role in the moderation of greenhouse warming it is important that carbon is sequestrated on the time scale of centuries rather than the probable month or year time scale of "local new" production. This implies transport to below the permanent pycnocline in the deep ocean and incorporation in sediments in shelf systems.

This problem is addressed in the present chapter by establishing a system of possible carbon pathways between the inshore and offshore regions of the southern Benguela and between the water column and shelf sediments. It is postulated that the network of carbon pathways can be related algebraically.

METHODS

The variables relating to a network of NO_3-N (and hence new production) pathways in the southern Benguela (based on literature quoted in the Introduction) can be defined as follows:

A - "Imported new" production

B - "Local new" production

C - Southern Benguela new production

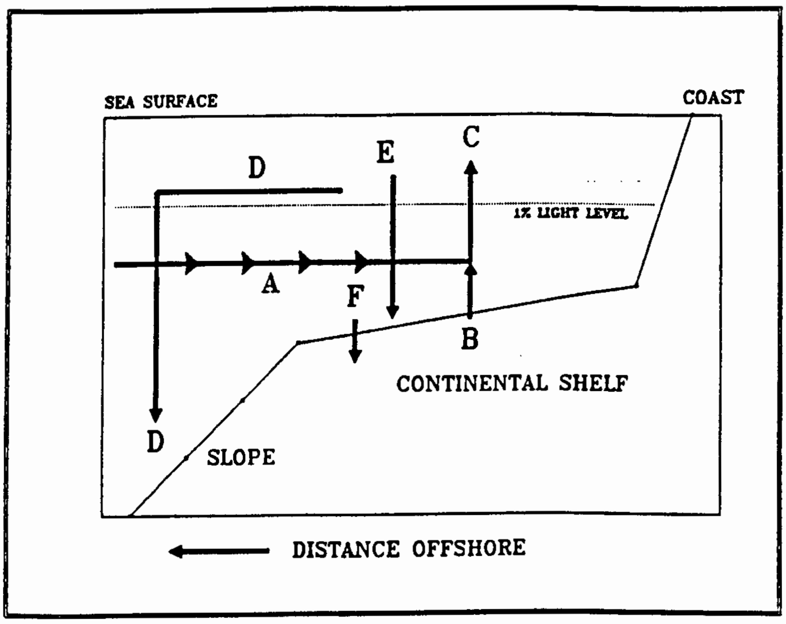
D - Southern Benguela new production exported seaward of the continental shelf break

E - Southern Benguela new production sink over the continental shelf

F - Proportion of E sequestrated in continental shelf sediments

THE PROPOSED NETWORK:

Imported new production results from the NO_3-N content of South Atlantic Central Water (SACW, the offshore source water for upwelling). This source water is supplemented with additional NO_3-N as it moves into the continental shelf domain (a result of local recycling processes). This enhancement is termed local new production. These inputs of NO_3-N combine to form the new production of the southern Benguela. This new production can be sub-divided between that which is advected offshore, beyond the continental shelf domain and the new production which sinks out locally. A proportion of the latter is sequestrated in continental shelf sediments and the remainder is recycled as local new production. These proposed pathways are shown as a two-dimensional schematic below.



From this diagram of the proposed network it was possible to identify links between certain variables.

i) S. Benguela NP = Imported NP + Local NP

ii) S. Benguela NP = S. Benguela NP exported beyond the shelf + S. Benguela NP sink over the shelf

iii) S. Benguela NP sink over the continental shelf = Proportion of NP sink sequestrated in shelf sediments + Local NP

i.e.

$$C = A + B$$

$$C = D + E$$

$$E = F + B$$

If three of the variables are known (or estimated) then solutions can be found for the remainder. Southern Benguela new production (C) has been estimated in chapter 3. It was possible to provide an estimate for local new production (B) by comparing the NO_3-N concentration in SACW with the higher concentrations found in Benguela upwelled water (resulting from its passage over the continental shelf). In this way it was possible to quantify the proportion of southern Benguela new production which was due to local NO_3-N inputs. The southern Benguela new production exported seaward of the continental shelf break (D), which is assumed to be subject to long-term sequestration, was estimated by quantifying the potential new production which occurred in upwelling-derived water seaward of a designated isobath. It was decided that 350m was an appropriate shelf-break depth, taking into account the bathymetry of the southern Benguela upwelling system. From the ten satellite images of upwelling events (chapter 2) it was possible to quantify the areas of upwelling-derived water occurring outside the 350m isobath and calculate its potential new production using the same method as that described in chapter 2. Having provided estimates of southern Benguela new production (C), local new production (B) and southern Benguela new production exported seaward of the continental shelf (D) it was possible to provide estimates of the remaining variables through algebraic substitution.

RESULTS

SOUTHERN BENGUELA NEW PRODUCTION (C)

The mean potential new production for the southern Benguela (C) was estimated to be 5.60×10^{13} gC.y^{-1} (from chapter 3).

LOCAL NEW PRODUCTION (B)

BAILEY (1985) quoted the NO_3-N concentration of SACW as 10 - 15 mmol.m^{-3} (JONES, 1971) and 10 - 18 mmol.m^{-3} (HENRY, 1975). ANDREWS and HUTCHINGS (1980) reported southern Benguela upwelled water with a NO_3-N signature of 20 ±4 mmol.m^{-3}. Taking the median value for SACW (14 mmol.m^{-3}) and the mean value for upwelled water (20 mmol.m^{-3}) implies that there has been a 43% increase in NO_3-N during its passage over the continental shelf and 30% of southern Benguela new production can be attributed to local new production. This being the case, the potential for local new production (B) has been estimated as 1.7×10^{13} gC.y^{-1}.

SOUTHERN BENGUELA NEW PRODUCTION EXPORTED SEAWARD OF THE CONTINENTAL SHELF BREAK (D)

An analysis of the ten satellite images showed that there was no 10° or 11°C water present outside the 350m isobath and that 12°C was present on only one occasion. The 1987/88 image of SST showed no upwelling-derived water seaward of 350m depth. A summary of the areas (km^2) of 12° - 16°C inclusive water occurring outside the shelf-break for each image is shown overleaf:

	Temperature (°C)				
	12	13	14	15	16
	Area (km^2)				
Year					
84/85	115	780	1341	2721	5230
85/86	0	3	210	1183	3299
86/87	0	0	4	49	274
87/88	0	0	0	0	0
88/89	0	0	230	521	1768
89/90	0	0	35	274	956
90/91	0	6	16	344	1342
91/92	0	0	28	975	2642
92/93	0	0	0	0	48
93/94	0	0	31	286	3020

Using the integrated NO_3-N (mmol.m^{-2}) values applicable to these temperature bands (chapter 2) it was possible to calculate the amount of NO_3-N in these off-shelf waters and convert (as previously) to potential new production (gC). These new production estimates were then expressed as a percentage of the event-scale new production. A summary is given below:

Year	Off-shelf NP (gC)	Event NP (gC x 10^{12})	Percentage
84/85	1.35×10^{11}	1.08	12.5
85/86	5.73×10^{10}	1.11	5.2
86/87	3.85×10^{9}	0.52	0.7
87/88	0.00	0.62	0.0
88/89	3.09×10^{10}	0.85	3.6
89/90	1.52×10^{10}	0.78	2.0
90/91	2.04×10^{10}	1.11	1.8
91/92	4.40×10^{10}	0.61	7.2
92/93	5.43×10^{8}	0.59	0.1
93/94	3.87×10^{10}	1.20	3.2

From these results it is estimated that 0 - 12.5% of southern Benguela new production per upwelling event occurs outside the confines of the continental shelf. The mean percentage for the ten events (admittedly within the context of a wide range) = 3.6%. The mean annual potential new production of the southern Benguela has been calculated as 5.6×10^{13} gC, therefore it is predicted that, on average, 2.0×10^{12} gC.y^{-1} is exported beyond the continental shelf and sequestrated below the permanent thermocline.

Having provided estimates of:

Southern Benguela new production (C) = 5.60 x 10^{13} gC.y^{-1}
Local new production (B) = 1.70 x 10^{13} gC.y^{-1}
Southern Benguela new production exported seaward of the continental shelf break (D) = 2.00 x 10^{12} gC.y^{-1},

the remaining variables in the network of new production (carbon) pathways were calculated algebraically.

Imported new production (A) = (C) - (B) = 3.9 x 10^{13} gC.y^{-1}

Southern Benguela sink over the continental shelf (E)
= (C) - (D) = 5.40 x 10^{13} gC.y^{-1}
Proportion of (E) sequestrated in continental shelf sediments (F) = (E) - (B) = 3.7 x 10^{13} gC.y^{-1}

The redrawn schematic of these carbon pathways, with annual estimates included is shown in figure 13.

DISCUSSION

The network of carbon pathways presented in this chapter is the same, in principle, as WALDRON *et al.* (1992). The values assigned to certain of the input variables, however, have been modified in the light of an adjusted estimate for carbon exported beyond the shelf (D) and the resulting algebraic knock-on effect. The new estimate for carbon exported seaward of the continental shelf is 0.20×10^{13} $gC.y^{-1}$ compared with 3.2×10^{13} $gC.y^{-1}$ in WALDRON *et al.* (1992). The primary reason for this re-appraisal stems from a belated realization that upwelling-derived water does not habitually extend as far west as was originally thought. The areal extent of the upwelling system relevant to the regional export of carbon in WALDRON *et al.* (1992) was derived from the work of LUTJEHARMS and STOCKTON (1987). Their figure 3 showed a montage of the frontal boundary of the upwelling system compiled from thermal infra-red data obtained from the METEOSAT II satellite. From this, WALDRON *et al.* (1992) designated a region where cold water of upwelling origin was present on a quasi-permanent basis and a more offshore region where the presence of such water was intermittent. A similar exercise was conducted as in the present study resulting in an estimate for off-shelf new production. The seaward extension of upwelling-derived water on a quasi-permanent and intermittent basis was found to be up to, and occasionally beyond, the 2000m isobath. The analysis performed on the ten NOAA images of SST in the current study found comparatively little water $\leq$ 16.99°C beyond the 350m isobath.

In LUTJEHARMS and STOCKTON (1987), daily METEOSAT II images in the form of photographic negatives were interpreted in such a way that the line of greatest grey-scale contrast in the South-East Atlantic Ocean was assumed to be the boundary between the cold upwelled water and the offshore South Atlantic Surface Water. This was probably the best option available in the context of METEOSAT II images but the subsequent objective analysis of temperature-defined NOAA images (albeit only ten), of prominent upwelling events seems to indicate that it had resulted in an overestimation of the extent of upwelling-derived water and a concomitant overestimation of carbon export beyond the shelf in WALDRON *et al.* (1992).

The lower estimate of carbon exported seaward of the continental shelf break (D) resulted in a higher estimate of the sink of carbon over the shelf (E) invoking the requirement for increased sequestration in shelf sediments (F) given that local new production (B) had remained much the same.

Having attempted to satisfactorily explain the main discrepancy between WALDRON *et al.* (1992) and this portion of the thesis it was thought appropriate, where possible, to test the validity of certain of the algebraically calculated variables.

The imported new production was estimated as the difference between the entire southern Benguela new production and new production due to local shelf inputs of NO_3-N. The 3.9×10^{13} $gC.y^{-1}$ calculated for this variable relied upon the NO_3-N content of SACW which has a NO_3-N concentration of $\approx$ 14 $mmol.m^{-3}$ $\equiv$ 1.1 $gC.m^{-3}$ ((14*6.6*12)/1000)). Therefore the volume of water required to account for imported new production = 3.5×10^{13} $m^3.y^{-1}$. Scaling this volume transport to a more convenient unit of oceanic flux gives a value of 1.1 Sv (over 365 days) or 1.5 Sv (over 274 days). STRAMMA and PETERSON (1989) quantified the various water transports associated with the Benguela Current Region. They found an imbalance in the transport field between 24°S and 32°S of 2 Sv, which was possibly a reflection of how much transport is associated with coastal upwelling.

The estimate given for the southern Benguela carbon sink over the continental shelf (E) was 5.40×10^{13} $gC.y^{-1}$. The dimensions of the continental shelf between 29°S and 35°S give a length of approximately 670 km and a mean width of approximately 150 km. The shelf area of 1×10^{11} m^2 invokes a sedimentation rate of 540 $gC.m^{-2}.y^{-1}$ which converts to a daily rate of 1.5 $gC.m^{-2}.d^{-1}$. BAILEY (1987), from sediment trap studies, found a sedimentation rate of 4.8 $gC.m^{-2}.d^{-1}$ in the productive St Helena Bay region and a mean rate of 3.7 $gC.m^{-2}.d^{-1}$ on the lee side of Benguela upwelling centres. The shelf average presented here (1.5 $gC.m^{-2}.d^{-1}$) seems appropriate in the present context. The remaining algebraically calculated variable (F), the proportion of (E) sequestrated in the continental shelf sediments cannot easily be verified due to a lack of independent sources of evidence. This pathway results from a high rate of sedimentation (and assumed sequestration) and may not be borne out by a comparison of, say, the organic carbon content of the sediment and the rate of deposition. This possibility opens an avenue of future research into bio-geochemichal re-cycling. It may be necessary to invoke (and investigate) a pathway for organic carbon between the continental shelf and slope similar to that proposed in the Shelf Edge Exchange Processes (SEEP) hypothesis (WALSH *et al.*, 1981). Although the hypothesis was found to be wrong in relation to the shelf off the East coast of North America, ROWE (1987) states that other shelves, especially those of upwelling systems, have a greater potential for the export of organic carbon. The dynamics of the southern Benguela means that such a study would have to take into account the possibility of spatial heterogeneity in shelf accumulation of organic carbon and sites of selective deposition in its export to the slope.

This future avenue of research notwithstanding, the main variable of interest is the amount of carbon sequestrated as a consequence of southern Benguela new production, This is equivalent to the carbon sequestrated on the continental shelf (F), a proportion of which may be subject to shelf/slope exchange, plus the new production, initially exported in the euphotic zone, beyond the shelf boundary (D) = 3.9×10^{13} $gC.y^{-1}$. The finding of the present study is that approximately 70% of southern Benguela new production is sequestrated at time scales which constitute a long-term loss to the system.

CHAPTER 6

POTENTIAL NEW PRODUCTION IN THE SOUTHERN BENGUELA UPWELLING SYSTEM AND ITS LINKS TO THE PELAGIC FISHERY

INTRODUCTION

The work of IVERSON (1990) supported an hypothesis that carnivorous fish (and squid) production is controlled by the amount of new nitrogen (NO_3-N) annually incorporated into phytoplankton biomass and transferred through marine food webs. It was decided to test this hypothesis in the context of the southern Benguela upwelling system using estimates of annual potential new production provided in chapter 3 of this thesis and locally available information relating to the pelagic fishery.

Anchovy (*Engraulis capensis*) is a major pelagic resource of South Africa. The southern stock's life history and harvesting are centred on the west coast (southern Benguela) and Agulhas Bank (lying to the south of the country). The distribution and movement of the fish at various life stages have been well established following the work of CRAWFORD (1980, 1981), SHELTON and HUTCHINGS (1982), ARMSTRONG *et al.* (1985), SHELTON (1986) and HAMPTON (1987). A summary of their findings describes a fish population which spawns between October and November in a region predominantly east of Cape Point. The ichthyoplankton is entrained west and north into the southern Benguela and is recruited into the adult population during Autumn and Winter. The adults then migrate south along the inshore part of the west coast reaching the Agulhas Bank region towards the end of their first year. JAMES (1987) found that the major component of the anchovy diet consisted of mesozooplankton, especially calanoid copepods and euphausiids. This was contrary to the prevailing view that they were non-selective filter-feeding omnivores deriving the bulk of their nutrition from diatoms. Such a finding metaphorically extends the trophic distance between new production and fish which necessitated a careful consideration of appropriate time scales when attempting to relate the two.

A simple model describing the link between new production and fish would describe a positive, linear relationship between upwelling intensity and any chosen variable relating to the fishery (e.g. stock, recruitment or oil yield). The greater the upwelling, the more NO_3-N is introduced into the euphotic zone which benefits the fishery via the phytoplankton, zooplankton food chain. This simplistic approach has been modified following the work of CURY and ROY (1989) and ROY *et al.* (1992) who described an Optimal Environmental Window (OEW)' hypothesis to accommodate the apparently contradictory evidence of both negative and positive relationships between recruitment and upwelling indices. Their hypothesis assumed a dome-shaped curve between recruitment and upwelling which considered both weak and strong upwelling intensities to be detrimental to the fishery. A zone either side of the dome apex was defined as the OEW. Wind speeds were used as a proxy for upwelling and they found the OEW to be 5 - 6 $m.s^{-1}$. MENDELSSOHN (1989), WARE and THOMPSON (1991) and ORBI *et al.* (1991) have reported supporting evidence for this hypothesis.

In this chapter, a similar approach has been adopted for the southern Benguela in order to quantitatively link the performance of the regional anchovy fishery with upwelling. In the present case, the proxy for upwelling is that of annual potential new production (i.e. amount of NO_3-N) derived from satellite imagery and rise-events in coastal sea level (chapter 3). The variables chosen to examine the performance of the fishery are condition of fish (oil:meal ratio), recruitment biomass and regional fish stocks (spawner biomass). This work has been conducted with the objective of providing predictive information of use in the management of the anchovy fishery in South Africa.

METHODS

NEW PRODUCTION AND OIL YIELD.

The oil content of fish is one of the best biological health and status indicators available (SHARP, 1987). SCHÜLEIN *et al.* (1995) have investigated the use of oil:meal ratios (obtained from commercial catch and reduction figures) as a predictor of fish recruitment. From their published data base it was possible to relate monthly and cumulative oil:meal ratios to estimates of potential new production.

On an annual basis, potential new production was plotted against the cumulative oil:meal ratio (June - May inclusive); firstly with no time lag and secondly with a lag of one year (i.e. oil $\text{yield}_{\text{year}}$ *vs* new $\text{production}_{\text{year-1}}$). An attempt was also made to relate pivotal portions of the year in respect of new production and oil:meal ratios. Potential new production in a given year occurring during summer (December - February inclusive) and Spring + Summer (September - February inclusive) were plotted in turn against the cumulative oil:meal ratio for the following March - July inclusive period. Finally, potential monthly new production estimates were plotted against monthly oil:meal ratios with a one, two and three month lag and with no lag.

NEW PRODUCTION AND RECRUITMENT.

Anchovy recruitment biomass has been measured acoustically on an annual basis each June since 1985. Previously, estimates were made using virtual population analysis (VPA) based on the age structure in commercial catches, which have subsequently been found to be unreliable. HAMPTON (1992) has tabulated the biomass of anchovy recruits measured during the May, June or July cruises of F.R.S. Africana between the maximum geographical range of Lüderitz and Mossel Bay. His figure 6 shows the distribution to be mainly related to southern Benguela waters. The recruitment tonnages for each year between 1985 and 1990 were plotted against the annual potential new production estimates for 1984/85 - 1989/90 inclusive (i.e. the twelve months preceding the surveys). An attempt was also made to link the time scales between the two variables more closely by plotting the recruitment figures *vs*:

(i) Autumn
(ii) Summer + Autumn
(iii) Spring + Summer + Autumn
potential new production estimates.

NEW PRODUCTION AND ANCHOVY SPAWNER BIOMASS.

Anchovy spawner biomass has been measured acoustically each November since 1984. The results of these research surveys have been reported in HAMPTON (1992). The annual potential new production estimates from this thesis span the period 1980/81 - 1989/90 inclusive. Prior to 1984 the total allowable catch (TAC) of anchovy was estimated from catch-per-unit-effort indices and VPA of commercial catch data. The subsequent direct survey work has rendered these data unreliable, which leaves a gap between 1981 and 1983 inclusive. DUNCOMBE-RAE *et al.* (1992) demonstrate a graphically convincing relationship between the percentage of anchovy in gannet diet and the anchovy spawner biomass (1984 - 1990 inclusive). This relationship has been extended in time and significantly regressed and correlated by CRAWFORD *et al.* (in prep.). Their regressed values of anchovy biomass between 1981 and 1983 inclusive and the acoustically measured figures between 1984 and 1990 were plotted against the annual potential new production estimates for the previous June - May inclusive periods. Note that the majority of anchovy have been subject to the southern Benguela during this period.

RESULTS

NEW PRODUCTION AND OIL YIELD.

No statistically significant relationships were obtained in any of the proposed plots between potential new production and oil:meal ratios. In two cases there was qualitative evidence worth noting. The relationship between annual potential new production (June - May) and cumulative oil:meal ratio (June - May) with no lag between years (Figure 14) was indicative of a rectangular hyperbola fit. Additionally, when the cumulative oil:meal ratio for the period March to July inclusive was plotted against the preceding Spring and Summer potential new production (Figure 15), a median range of potential new production was seen to be beneficial to fish condition. These qualitative indications notwithstanding, the lack of statistical significance in the data precluded further discussion.

NEW PRODUCTION AND RECRUITMENT

Plotting seasonal permutations of new production preceding the June recruitment measurements gave relationships of no statistical significance.

Annual estimates of potential new production in the year preceding recruitment *vs* recruitment gave some indication of a dome-shaped relationship (Figure 16) provided the 1989 coordinate is excluded. The small number of data points means that the scatter plot should be viewed in conjunction with figure 17 (New Production *vs* Spawner Biomass) to appreciate the appropriateness and potential for a dome-shaped fit. More importantly, is there any justification for excluding the 1989 recruitment and 1988/89 new production coordinate? DUNCOMBE-RAE *et al.* (1992) isolated the well documented recruitment collapse (ANON., 1989, 1991) to a period between June and July 1989 from a sudden change in the diet of gannets. The collapse could not be attributed to fishing, predation or a clear-cut change in environmental variables but coincided with the interaction of Benguela frontal waters with an Agulhas Ring which extracted a large volume of upwelling-derived water over a period of 2 - 3 months. It was their contention that this dynamic interaction removed anchovy larvae and pre-recruits from the Benguela system at a scale sufficient to affect the overall population. Such an event would not be reflected in the annual estimate of potential new production and would hence be outside its predictive capability in the present case. In the absence of a longer data set it is only possible to state that there may be a dome-shaped relationship between the annual potential new production in the year which precedes the measurement of recruitment biomass.

NEW PRODUCTION AND ANCHOVY SPAWNER BIOMASS.

The relationship between annual potential new production for the June - May inclusive period of each year between 1980/81 and 1989/90 inclusive and anchovy spawner biomass regressed and acoustically measured during the November following provides the most convincing evidence of a dome-shaped curve supporting the OEW hypothesis (Figure 17). Again, a case could be argued for the exclusion of the 1989 biomass figure on the same basis as previously (although in this case it is not a prerequisite to the argument). The proportion of one year old fish in the anchovy spawner stock between 1984 and 1990 (the years for which such data were available) varied between 0.62 and 0.95 (B.A. Roel, Pers. Comm.). The lowest proportion was in 1989, the year of a crash in recruitment, when fewer one year olds would be expected. The mean proportion, excluding 1989, was 0.87. Since almost all the spawners biomass consisted of one year old fish, it was not necessary to apportion *pro rata* the potential new production over the number of year classes in the spawner biomass estimate. A Gaussian area curve has been fitted to the data (excluding 1989) . The curve has an $r^2 = 0.90$ and its equation is as follows:

$$y = 1.90e^{[-0.5((x-5.72)/0.43)^\wedge 2]}$$

DISCUSSION

The results of this part of the study demonstrate a combination of probable and possible links between potential new production in the southern Benguela and key variables in the pelagic fishery relating to anchovy biomass and fish condition.

The relationship obtained between annual potential new production and spawner biomass of anchovy (Figure 17) provided strong support for the OEW hypothesis. It is unusual for independently derived variables to give such a clear picture or signal in the study of natural systems. The estimates of annual potential new production were made from remotely-sensed SST and the relationship between SST and integrated NO_3-N, extended to the annual scale via the fluctuation of sea level at the coast. To plot these findings against estimates of spawner biomass and view the result vis-à-vis the OEW hypothesis of CURY and ROY (1989) and ROY *et al.* (1992) was of some surprise. It was fortunate that the decade of the 1980s was a period of such variability (SHANNON *et al.*, 1992) thus providing data points over a large portion of the dome-shaped curve. The potential new production estimates are essentially an index of upwelling, expressed in terms of the amount of NO_3-N made available to the southern Benguela. Figure 17 clearly shows that too little or too much upwelling is ultimately detrimental to the anchovy biomass.

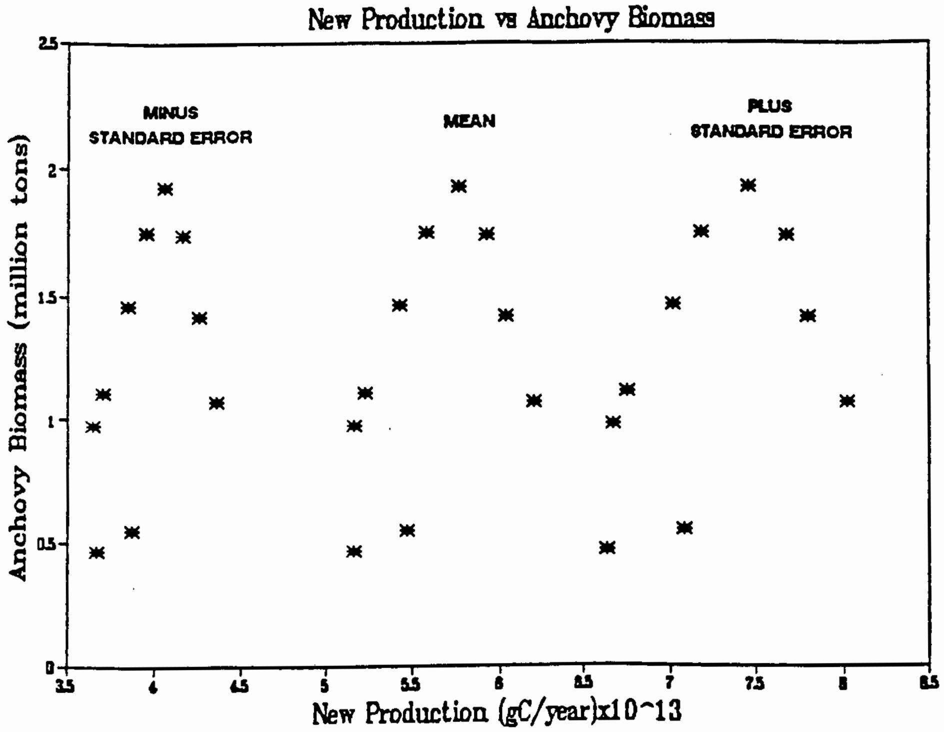
It is appropriate at this point to address the question of attributing error bars to the data points in figure 17. The standard error relating to estimates of spawner biomass have been calculated by HAMPTON (1992), however, the question of error bars in relation to the estimates of annual potential new production needs careful consideration in order to avoid a misrepresentation of the data.

The estimates of annual potential new production made in chapter 3 had an associated standard error of ± 30% based on the alternative equations of regression. Plotting this variance on figure 17 in the form of error bars would be misleading. It is important to establish that the dome-shaped relationship between annual potential new production and spawner biomass is robust to the inclusion of variance in the potential new production estimates. The regression equation used to predict potential new production was:

$$y = 0.46(\pm 0.17)x + 6.57(\pm 1.58)$$

i.e. It has the form: $y = ax + b$. If the years are ranked in terms of increasing annual potential new production then the ranking is fixed provided the value of "a" is positive (which is the case). This means that a prediction of annual potential new production at some point on its error bar constrains the other predictions to analogous points on their respective error bars and maintains the dome shape of the curve.

This is shown diagrammatically overleaf where the mean and extreme predictions of annual potential new production have been plotted against anchovy biomass.



This line of argument permits the prediction of spawner biomass from the mean estimate of annual potential new production using the equation of the Gaussian curve.

$$\text{i.e. } y = 1.90e^{[-0.5((x-5.72)/0.43)^\wedge 2]}$$

A subjective positioning of the OEW seems to indicate that an annual potential new production of between 5.4 and 6.1 x 10^{13} $gC.y^{-1}$ is required for best results in the fishery.

The ranking of annual potential new production estimates by year has been used in figure 18, which includes the standard error bars for spawner biomass and provides an alternative, non-parametric (concerning annual potential new production) method of predicting spawner biomass.

A pivotal feature of the relationship obtained between these variables, using either figure 17 or 18, is that it provides a means of predicting the anchovy spawner biomass at the end of May in any given year. This is six months in advance of the spawner biomass acoustic surveys, which take place in November. This aspect should prove to be of use in the management of the fishery.

With respect to recruitment (measured in June each year since 1985), the data set is too short to establish a dome-shaped relationship against potential new production (Figure 16). If the exclusion of the 1989 recruitment datum point is acceptable, there seems to be an indication that a similar shaped curve to that of figure 17 may evolve. It is interesting to note the broad agreement between the relative positions of data points for coincident years in the two figures. It is hoped that future data will establish the OEW hypothesis in respect of potential new production and anchovy recruitment. This would lead to a predictive capability one month in advance of the acoustic recruitment surveys.

CHAPTER 7

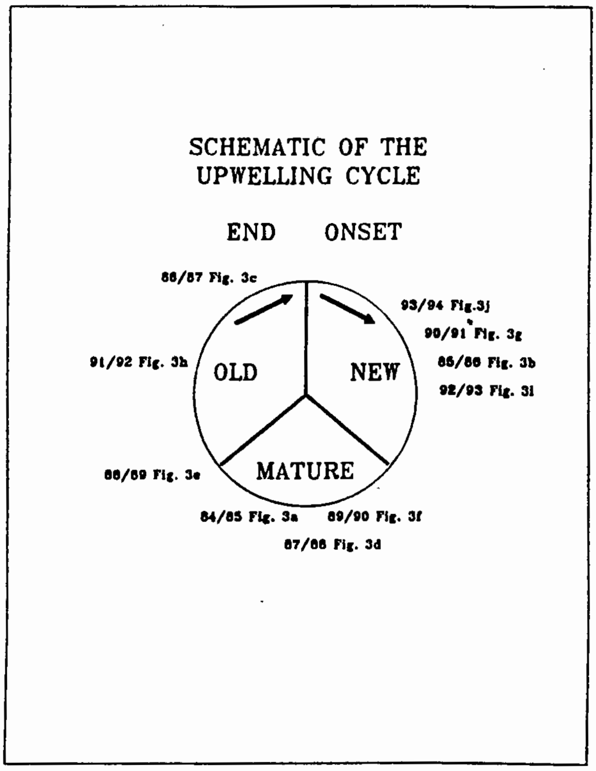
DISCUSSION AND CONCLUSIONS

This chapter will discuss the extent to which the objectives and hypotheses underpinning the thesis have been fulfilled. In addition, various aspects of the work which did not form part of the central theme of the thesis, but have emerged as having implications for the dynamical and/or biological study of the southern Benguela upwelling system will be addressed.

A method has been described which can be successfully used to estimate potential new production at the event scale. It used a depth-related variable (integrated NO_3-N) in conjunction with satellite images of SST. This approach circumvented the main limiting factor of satellite imagery (the inability to "see" below the surface) and was first reported in WALDRON and PROBYN (1992).

The methodology has been modified subsequently as part of the present study. Having established a statistically significant relationship between SST and NO_3-N integrated over the nominal euphotic zone, the NO_3-N data were grouped into 1°C temperature bins spanning the range of upwelling-derived water (10 - 16°C). The means of these temperature bins were then used to predict amounts of NO_3-N associated with the areas of different temperature bands on the satellite image, giving the amount of NO_3-N per upwelling event.

The satellite images of SST (Figs. 3a - 3j inclusive) can yield useful information over and above the estimation of NO_3-N content in different temperature bands. It was also possible to assess them in terms of the biological stage of development of the upwelling event. This was done objectively in chapter 2 by quantifying the areal extent of recently upwelled water (10°C - 13°C inclusive) and aged upwelled water (14°C - 16°C inclusive). In this way, each event was categorized as New, Mature or Old. A visual inspection of each image (subjective approach) and the intuitive positioning of them on a schematic diagram of the upwelling cycle (see below) reinforced this objective assessment.



It was felt, however, that further investigation may provide a better insight to the cycle of upwelling with respect to dynamical forcing. Information relating to the wind regime leading up to the satellite images was available for 1984/85 - 1989/90 inclusive (Fig. 6). In addition, the orientation of upwelling cells (e.g. Cape Peninsula, Cape Columbine) with respect to the coast provides a good indication as to whether upwelling is in an active state or experiencing a period of relaxation. This phenomenon is apparent in the case study approach of Jury *et al.* (1985). Taking the Cape Peninsula upwelling cell as an example, when upwelling is actively taking place, the base line of the upwelling cell forms a sharp angle with the coast. During a period of relaxation the base line and the coast form an angle close to 90°. The shape of the latter is consistent with the southward propagation of the forcing mechanism (coastal low/coastal trapped wave) which is responsible for the rapid decay of upwelling (JURY, 1986). Note that a comparison between the Cape Columbine and Cape Peninsula upwelling cells in terms of cell angle and "squeezing" southward of cold water is also useful in the interpretation of upwelling event dynamics over the southern system.

A comparison of the satellite images with wind data in the 10 days beforehand was only possible for the period 1984/85 - 1989/90. Referring to the schematic upwelling cycle above, images had been categorised according to the relative areas of different temperature water and visually as follows:

New: 1985/86
Mature: 1984/85, 1987/88, 1989/90
Mature/Old: 1988/89
Old: 1986/87

The preceding winds and orientation of upwelling cells gave clear agreement with this categorization in respect of the New and Old events. In the former case, there had been a strong wind reversal four days before the image followed by three days of upwelling-favourable winds (Fig. 6). The orientation of the Cape Peninsula and Cape Columbine upwelling cells (Fig 3b) was also indicative of active upwelling. In the latter event, there had been no upwelling-favourable wind in the four days leading up to the image although there had been six days of equatorward winds prior to that (Fig. 6). The Cape

Peninsula upwelling cell had a base orientated at approximately 90° to the coast which supports the case for a relaxation phase in upwelling (Fig. 3c).

The presence of relict upwelled water in the coastal region made those events categorized as Mature and Mature/Old more difficult to reconcile in the context of a dynamical approach, which takes into account upwelling cell morphology and a southward propagating mechanism of forcing. The 1987/88 event had been preceded by two days of upwelling-favourable wind before which there had been no wind for one day (Fig. 6). The image itself (Fig. 3d) shows evidence for the recent onset of upwelling in terms of the angle of the Cape Columbine and Cape Peninsula upwelling cells and coastal patches of 10°C and 11°C water. The 1989/90 upwelling event (Fig. 6) also had upwelling-favourable winds present coincident with the timing of the image. The coastal belt of cold water north of 31°S (Fig. 3f) and the orientation of the Cape Columbine upwelling cell indicated an active phase as did the northerly tip of the Cape Peninsula cell; note, however, its flat base. For 1989/90 it is possible that following a relaxation and re-establishment of upwelling, the weather system generating upwelling-favourable winds had not yet propagated to the most southerly part of the system. In both cases (1987/88 and 1989/90), active upwelling was taking place but with enough older (warmer) present to merit a mature categorization. The 1988/89 event was preceded by a period of sustained but variable equatorward wind (Fig. 6). Most of the cold water was present in the southern part of the system (Fig. 3e) and the Cape Peninsula upwelling cell had a flat base. Cold water was also present to the east of Cape Point. It seems likely that although upwelling had been persistent during this period, it had latterly been limited to the southerly part of the system and coincided with the southward propagation of a coastal-trapped wave. This contention is supported by the coastal belt of warm water between 31°S and 32°S, weak expression of Cape Columbine upwelling cell and flat base to the Cape Peninsula upwelling cell.

The remaining images from 1990/91 - 1993/94 were unsupported by wind data but an attempt can be made to interpret them on the basis of their upwelling cell morphology. The 1990/91, 1992/93 and 1993/94 images (Figs. 3g, 3i and 3j respectively) had been categorised as New. In figures 3g and 3j the evidence strongly supported the contention that active upwelling was present. Figure 3i (1992/93 event) appeared more complex. Regions of active upwelling were present at 30°S and at Cape Columbine but were separated by a coastal intrusion of warm water at 31.5°S. The Cape Peninsula cell was fragmented and had a flat base but with evidence of active upwelling at its northern extent. This sequence seems to show a banding of active and relaxation phases in the upwelling cycle along the meridional extent of the system giving a coastal snapshot of upwelling dynamics. There was strong evidence of relaxation in the 1991/92 image (Fig. 3h) giving credence to its Aged category.

The approach adopted above highlights the difficulty in trying to classify an upwelling event at the system level. Different stages of an upwelling cycle may be present across its spatial extent, further complicated by the abundant presence of mature upwelled water irrespective of upwelling phase. It is proposed that a system of upwelling classification for the southern Benguela be adopted which primarily takes account of the dynamics, thus providing a supplementary interpretative tool. It was evident from the series of images that there were three main sites of upwelling:

1. Broad northerly band between 29°S and 31°S (approx.).
2. Cape Columbine
3. Cape Peninsula

The dynamics of an upwelling cycle were seen to operate on a shorter time-scale than the biological cycle and thus two stages would be more appropriate than the New, Mature and Aged categories described previously. It is suggested that each of the above upwelling sites could be categorized as Active or Relaxed. The categorization would depend on the presence of cold water, morphology of the upwelling cells and the extent to which cells are separated by intrusions of warm water. This system of classification takes into account the southward propagation of mechanisms which force both phases of the cycle and provides a snapshot of the system's dynamical state.

The original method of classification, which takes into account the relative amounts of recently upwelled and sun-warmed water over the spatial extent of the system, is still appropriate for studies addressing aspects of biological development. The additional criteria used in the dynamical approach, which includes southward propagating forcing mechanisms and upwelling cell morphology, has highlighted the shorter time-scales and latitudinal variation of active and relaxed phases of the upwelling cycle. Metaphorically placing the biological and dynamical systems of classification side by side allows for a mismatch between the two impacting on the southern Benguela's ability to achieve its biological potential at some stage in the food chain (*sensu* HUTCHINGS, 1992).

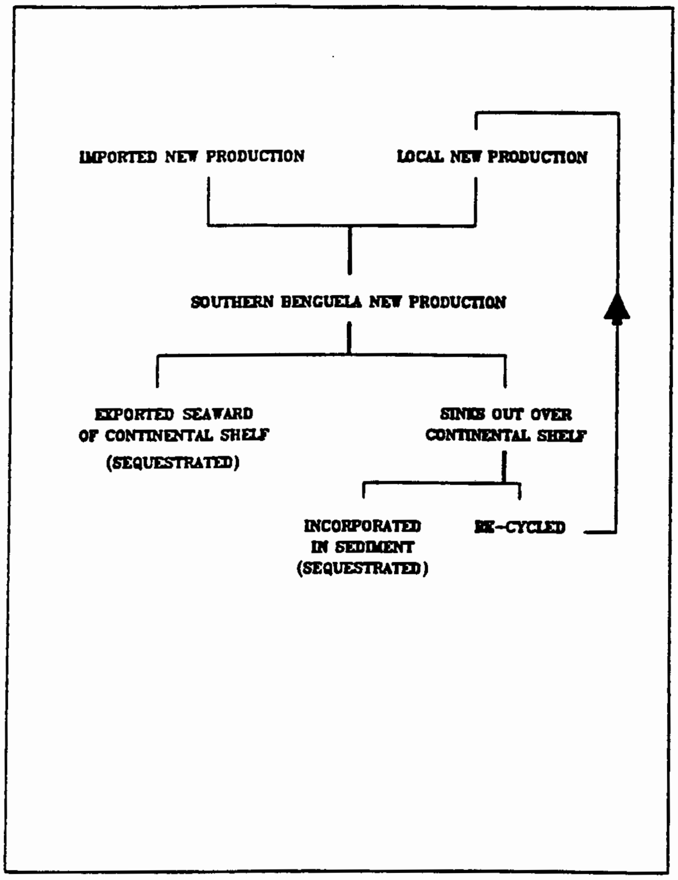
In chapter 3, the event-scale estimates of potential new production were extended to annual estimates, cumulatively, by the compilation of an upwelling index based on sea level fluctuation at the coast. This cumulative approach was possible because the southern Benguela is a pulsed upwelling system, responding to a series of relatively short events, as opposed to seasonally-forced temperate shelf systems which are dominated by a Spring and, to a lesser extent, Autumn phytoplankton bloom. It would be tempting, but unwise, to replace the estimates of annual potential new production with values of cumulative sea level rise since the estimates of potential new production made it possible to make comparative tests of their validity.

The methodology used to obtain annual potential new production estimates is novel and, to my knowledge, reported for the first time in this thesis. The relationship between rise in sea level per event and NO_3-N per event (Fig. 9) was based on relatively few data points and, if the resulting estimates of annual potential new production had to stand unsupported, my attitude would have been one of circumspection. What evidence was provided to establish the validity of these estimates?

The intra- and inter regional comparisons confirmed that annual estimates were made at an appropriate order of magnitude. Certain of the comparisons implied that the estimates were generally too high, however, this may have resulted from the fact that the estimates were those of **potential** new production. This means that **all** available NO_3-N was assumed to have been assimilated and could lead to estimates at the upper limit of any comparative range. This was the case when results were translated to f-ratios (as part of chapter 4). Ratios of 0.73 and 0.72 are towards the maximum for the southern Benguela (PROBYN, 1992) and would not be present on a system-wide basis. Potential new production, however, would reflect the maximum. Strong support for the mean estimate of annual potential new production was provided by the derived flux of upwelling water necessary to sustain annual estimates of imported potential new production (chapter 5). STRAMMA and PETERSON (1989) reported a rate of 2 Sv compared with between 1.1 and 1.5 Sv calculated as part of this study. Interestingly, this latter piece of comparative evidence points to an underestimation of potential new production.

The variability in the estimates of annual potential new production over the ten year period agreed well with general trends in related variables over the same period e.g. SST anomalies, annual averaged anomalies of equatorward pseudo wind stress and deviation of equatorward wind component (SHANNON *et al.*, 1992). These factors, together with the existence of a dome-shaped relationship between estimates of annual potential new production and anchovy spawner biomass in accordance with the Optimal Environmental Window hypothesis of CURY and ROY (1989), provided compelling evidence that the variability in estimates of annual potential new production was not spurious. This evidence notwithstanding, the range of annual potential new production estimates for the southern Benguela was relatively narrow over the ten year period. Their validity was established on the basis of order of magnitude robustness, comparison with other system-wide estimates and agreement with trends in related variables. Given that the validation exercise was unable to confirm the estimates in absolute terms, on a year by year basis, their use, in absolute terms, should be regarded as developmental.

The mean estimate of annual potential new production was used in chapter 5 for the purpose of quantifying the proposed network of carbon pathways. Note that the carbon pathways are dependent on NO_3-N. They were converted to carbon for the sake of consistency. Imported new production, contained in South Atlantic Central Water, combines with local new production (arising from short-term shelf re-cycling) to give the new production of the southern Benguela. This new production is divided between that which is advected seaward of the continental shelf boundary (and assumed to be sequestrated) and that which sinks out locally. A proportion of the latter is recycled in the form of local new production, with the remainder being sequestrated in shelf sediments. For the purpose of this discussion these pathways are presented diagrammatically overleaf.



The exercise in attributing annual rates to these pathways was made possible by the algebraic linkages existing between them in the context of the two dimensional model. It was necessary to provide estimates for three of the pathways:

i) Southern Benguela new production

ii) Local new production

iii) Southern Benguela new production exported seaward of the continental shelf boundary,

in order to calculate rates for the remaining network components.

The rate of southern Benguela potential new production used in the network was the mean of a fairly narrow range of estimates made over a ten year period. Local new production was calculated from differences reported in the literature between the NO_3-N concentration of South Atlantic Central Water and water which upwells after its passage over the continental shelf. It is felt that these estimates (and by extension that relating to imported new production) would be consistent between years. Southern Benguela new production exported seaward of the continental shelf was obtained from a series of ten satellite images of SST during upwelling events. From these, the proportion of potential new production which occurred outside the 350m isobath was quantified. A range of between 0 and 12.5% of the southern Benguela new production was found to occur seaward of the shelf boundary. The mean value (3.6%) was used for this pathway in the network, amounting to 0.2×10^{13} $gC.y^{-1}$. The possible range, however, was between 0 and 0.7×10^{13} $gC.y^{-1}$. Given the assumed statistical consistency of southern Benguela new production and local new production, variation in new production exported beyond the shelf will algebraically affect the sink of new production over the continental shelf and the proportion of this pathway which is sequestrated in shelf sediments. Within the limits of the possible range, the former will vary between 4.9 and 5.6×10^{13} $gC.y^{-1}$ and the latter between 3.2 and 3.9×10^{13} $gC.y^{-1}$.

The complexity of carbonate chemistry (which lies outside the scope of this thesis), different methods of approach and a shift from two to three dimensions may result in subsequent research re-defining the pathways and/or attributing different rates within the network. This has been the case in the present study when compared to WALDRON *et al.* (1992). Modification of the method used to quantify new production exported beyond the continental shelf has resulted in a greatly increased local sink of new production with greater sequestration in shelf sediments. The intention in chapter 5 was to establish a working hypothesis, thus providing a template which can be reinforced, disproved or refined as a result of future work. Essentially, it was felt that the results of chapter 5 were plausible and stood up well to verification (e.g. the sediment trap work of BAILEY, 1987 and STRAMMA and PETERSON's, 1989 imbalance in the transport field), however, they allow for the advancement of knowledge in this field through the mechanism of future, more elaborate, studies. It should be emphasised that the carbon pathways and their attributed rates relate to the transport of NO_3-N converted to carbon. The status of the upwelling system as a net source or sink of CO_2 has not been addressed. Recent studies (P. Monteiro, Pers. Comm.) point to the southern Benguela as a net source, attributed to the superimposition of non-organic pathways within the system. This being the case, the pathways described here only act to biologically offset the system's carbon status.

The results obtained in chapter 6, which showed possible links between annual potential new production, fish condition (in terms of oil:meal ratio) and the recruitment biomass of anchovy as well as a convincing relationship between annual potential new production and anchovy spawner biomass, are of scientific importance and could have implications with regard to the management of the fishery. It should be emphasised that the nature of the data in the 1980s was fortuitous to the study. Especially with respect to spawner biomass, variability was such that a spread of data was available to describe the dome-shaped relationship. The findings improve our understanding of the interlinked physical and biological functioning of the southern Benguela upwelling system. Sea level fluctuation at the coast (as a proxy for upwelling) was ultimately related to certain aspects of the tertiary biology. Alternative proxies for upwelling, (SHANNON *et al.*, 1986) e.g. wind, SST or currents, would be expected to yield similar results. Too little or too much upwelling was found to be detrimental to the fishery, in agreement with the Optimal Environmental Window hypothesis of CURY and ROY

(1989), but using a different independent variable. Quality of upwelling as opposed to upwelling *per se*, whilst having been the subject of local conjecture, has now been shown as relevant to the southern Benguela.

The Sea Fisheries Research Institute, as part of the Department of Environmental Affairs and Tourism, is responsible for the setting of anchovy fishing quotas to the industry. It is currently a two-stage process, primarily governed by the results of acoustic surveys, and designed to accommodate some of the industry's operational constraints. A total allowable catch (TAC) is set at the beginning of a calendar year following the acoustic survey of anchovy spawner biomass in the preceding November. The TAC may be revised following the anchovy recruitment survey in the May/June following. At this stage, the findings of chapter 6 are at the research rather than operational level. A future scenario is possible, however, whereby anchovy spawner biomass (and recruitment) may be predicted at a time coincident with the May/June acoustic survey and six months in advance of the November survey. It is felt that such predictions should not replace but supplement the present management procedure for anchovy. They could be of benefit in providing an early warning of biomass fluctuations and hence reflected in the planning of surveys. It would be expected that such predictions could add confidence to the acoustic estimates and be incorporated in a suite of operational methods for the setting of anchovy quotas.

The starting point for the work conducted in chapter 6 was the IVERSON (1990) hypothesis, that carnivorous fish (and squid) production is controlled by new production which is transferred through marine food webs. It was assumed that this implied linearity, so the emergence of a dome-shaped relationship in respect of spawner biomass and the potential for the same with respect to anchovy recruitment required an understanding of CURY and ROY's (1989) Optimal Environmental Window hypothesis to place the findings in context.

They attributed the non-linearity of the curve in Ekman-type upwelling systems to the impact of two limiting factors. Using wind speed as a proxy for upwelling, they stated that on the left side of the curve, wind mixing is weak and the limiting factor is the production of food due to the low intensity of upwelling. On the right side of the curve, upwelling is strong and turbulence is then the limiting factor. These conclusions stem from the "match-mismatch" hypothesis of CUSHING (1975) and the "stability" hypothesis, e.g. LASKER (1975) respectively. The left side of the curve permitted the aggregation of food organisms in the frequent absence of dynamical physical processes and the right side of the curve resulted in the desegregation of aggregations of food due to turbulence when there was a surfeit of dynamical physical processes. It is felt that other factors may also have an effect. On the right side of the curve, in addition to turbulence having an impact on food availability, there would be strong advection resulting in enhanced offshore transport. This would also affect food availability. Another factor may have been revealed by this study which is unrelated to the dome-shaped curve: dynamical interaction of coastal waters with adjacent systems. The 1989 data point in figures 16 and 17 was justified as an outlier on the basis that recruitment had "crashed" as a result of the dynamical processes described in DUNCOMBE-RAE *et al.* (1992). The physical removal of recruits or their food source from the system by prolonged interaction with an Agulhas ring would not be apparent in the proxy for upwelling and could not therefore form part of the predictive process. It is a factor resulting from the unique proximity of eastern and western boundary currents; its rare occurrence should be appreciated if not foreseen.

The stated objective of this thesis was to estimate the annual potential new production of the southern Benguela by means of a multi-disciplinary research study. This was achieved by progressing from the event-scale to the annual-scale by means of an upwelling proxy using a combination of satellite oceanography, marine chemistry and dynamical oceanography. Having provided annual estimates of potential new production for the decade of the 1980s, it was possible to quantify carbon pathways in a proposed ocean/shelf/sediment network. This work estimated how much carbon is sequestrated due to the biology at time scales sufficient to constitute a long-term loss to the system. The annual potential new production estimates were also related to the pelagic fishery with the aim of making it a predictor of certain variables in the tertiary biology. Links were found with the condition of fish and recruitment biomass. Furthermore, a relationship was established between annual potential new production and anchovy spawner biomass which has a predictive capability.

In conclusion, it has been a rewarding experience to write a multi-disciplinary thesis spanning aspects of satellite oceanography, marine chemistry and dynamical oceanography in order to provide answers relating to the carbon cycle and pelagic biology of the southern Benguela upwelling system. Small scale studies into esoteric aspects of a particular oceanographic discipline are of recognised value in increasing the detailed base of knowledge necessary to the subject but it is my belief that no single branch of oceanography can stand in isolation. Since the ocean is a natural system, larger scale answers rely on the interdependence of its physics, chemistry and biology. A dynamical consideration of sea level fluctuation at the coast, in conjunction with remotely sensed SST, the concentration of NO_3-N and its assimilation by phytoplankton, so that questions relating to carbon sequestration and the pelagic fishery may be addressed, has been in recognition of this belief.

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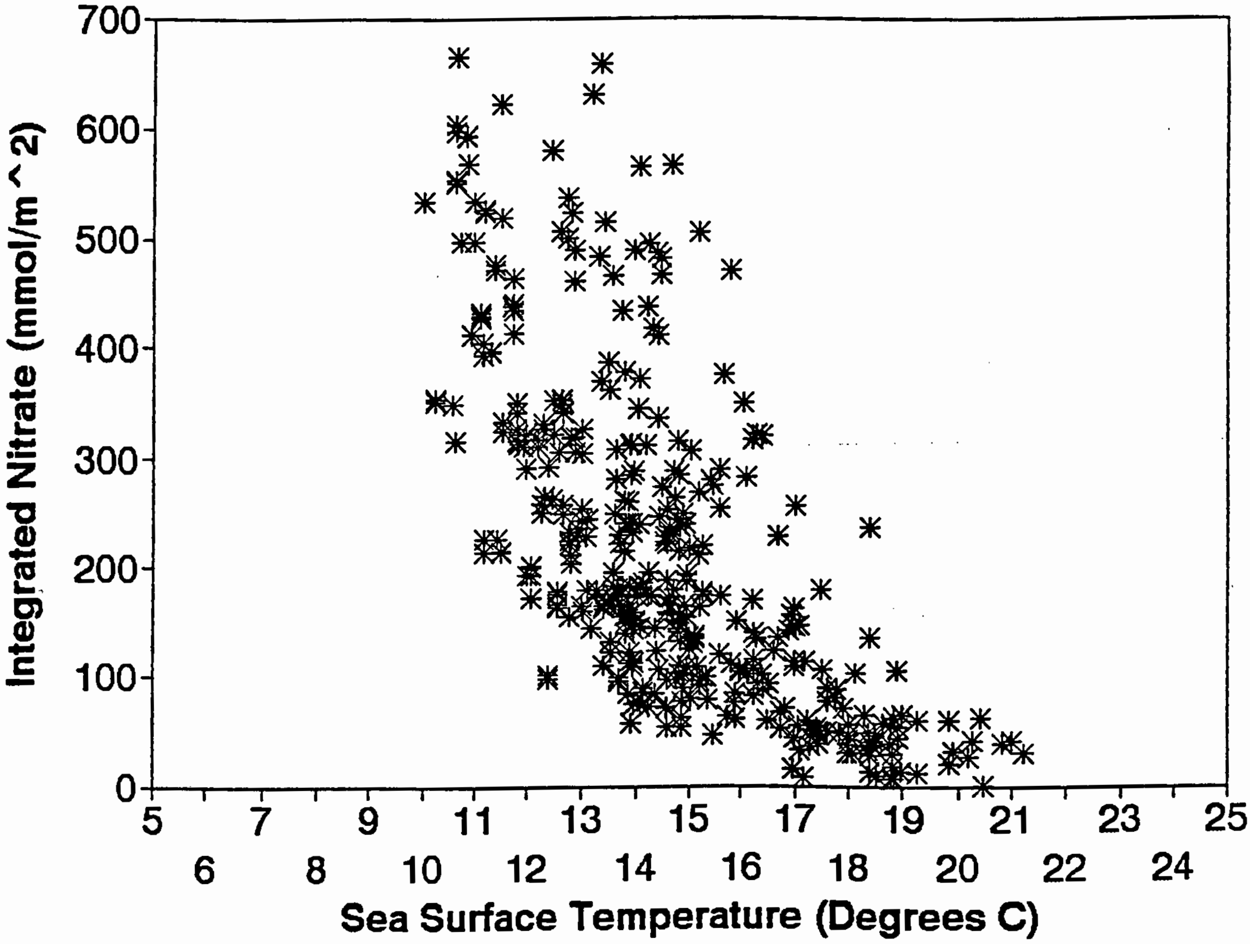


Figure 1. The negatively correlated relationship between sea surface temperature and nitrate integrated over the upper 30m of the water column in the southern Benguela (All data: r = -0.70, n = 423; Temp. range 10-16°C: r = -0.61, n = 350. Relationship is significant at better than the 99.9% level of confidence in both cases).

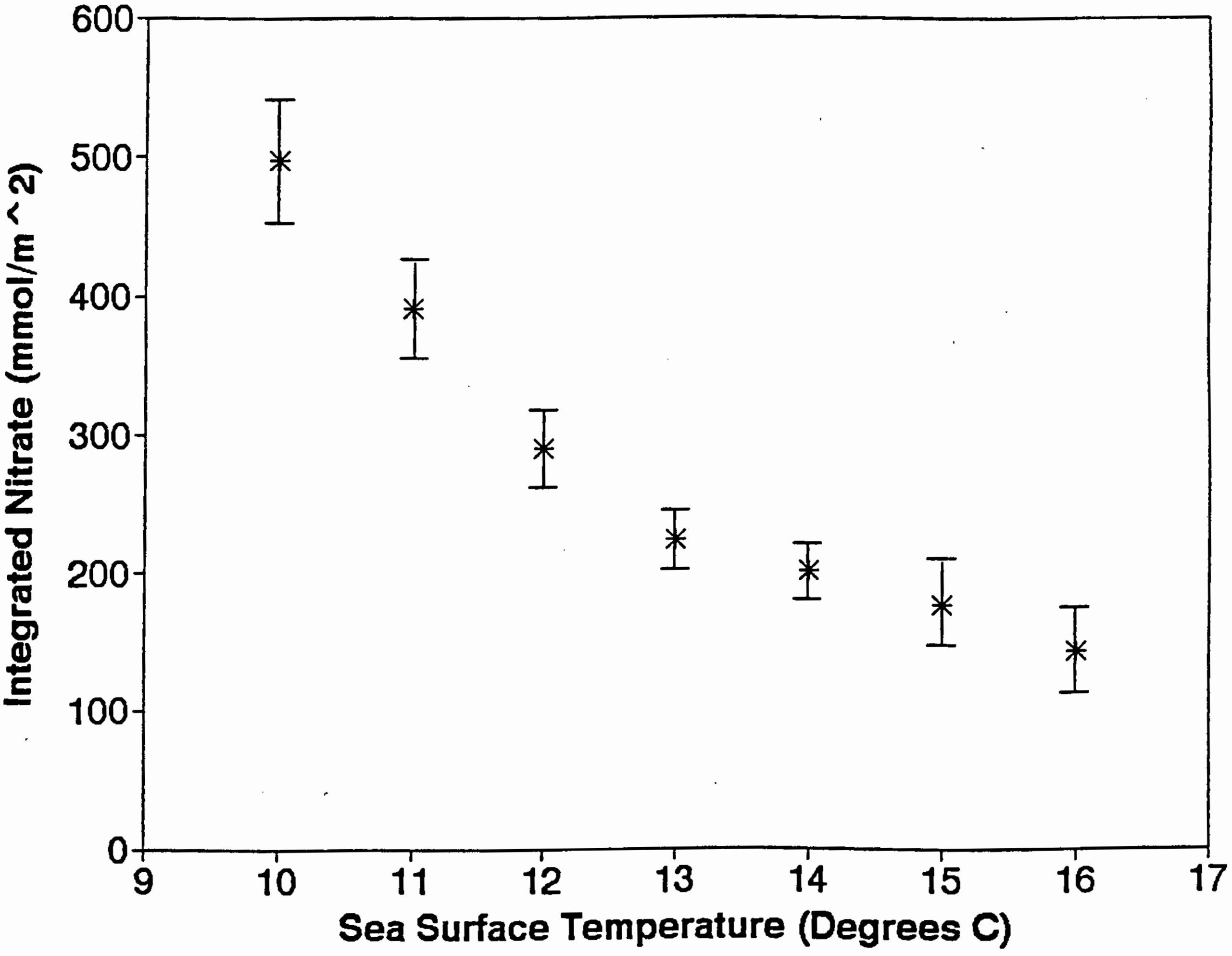
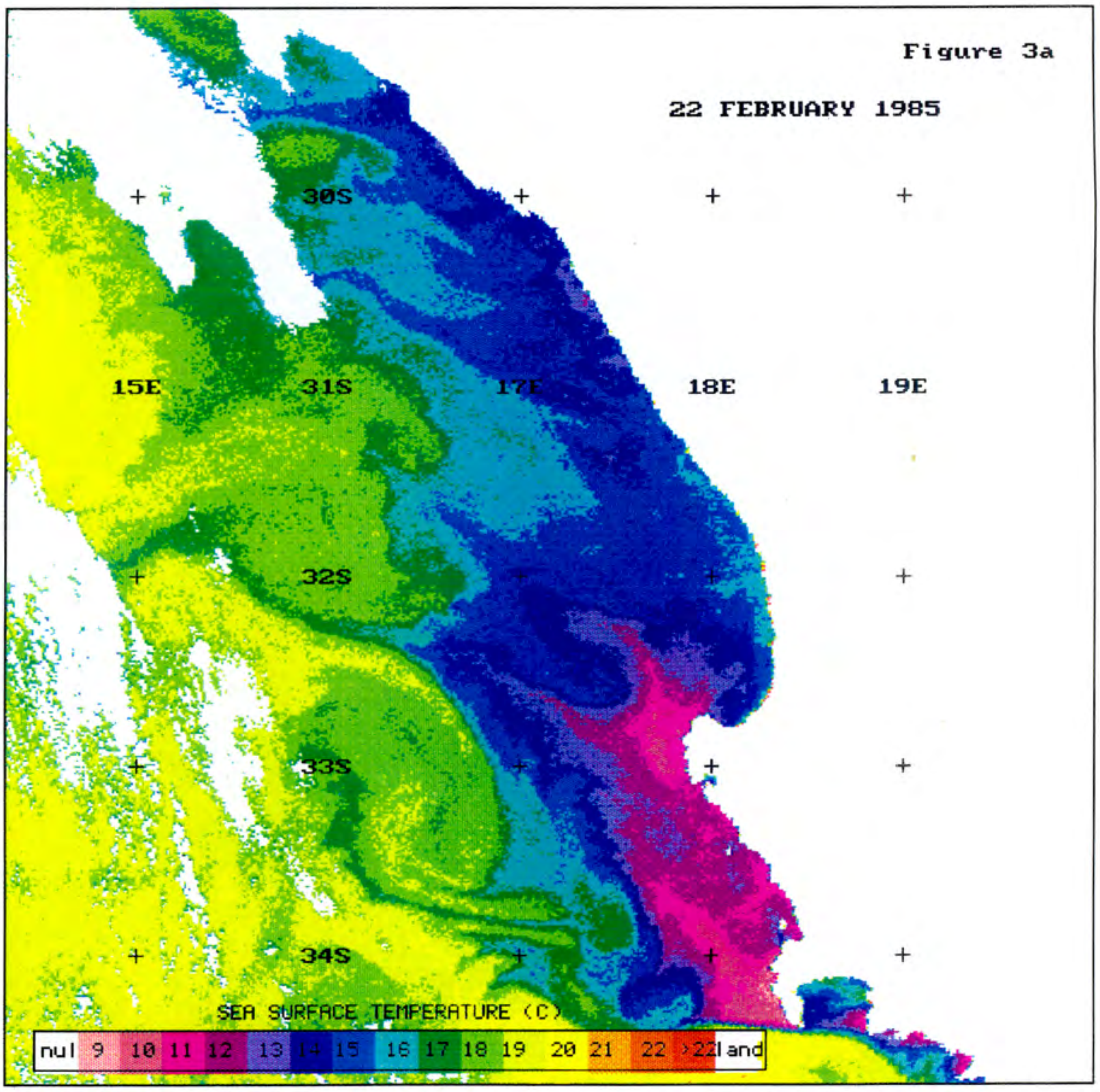


Figure 2. Mean integrated NO_3-N values for each sea surface temperature bin between 10 and 16°C (Asterisks). The error bars represent the upper and lower confidence limits at the 0.95 level of probability.



Figures 3a - 3j inclusive. TIROS/NOAA series AVHRR sea surface temperature images of ten upwelling events in the southern Benguela upwelling system.

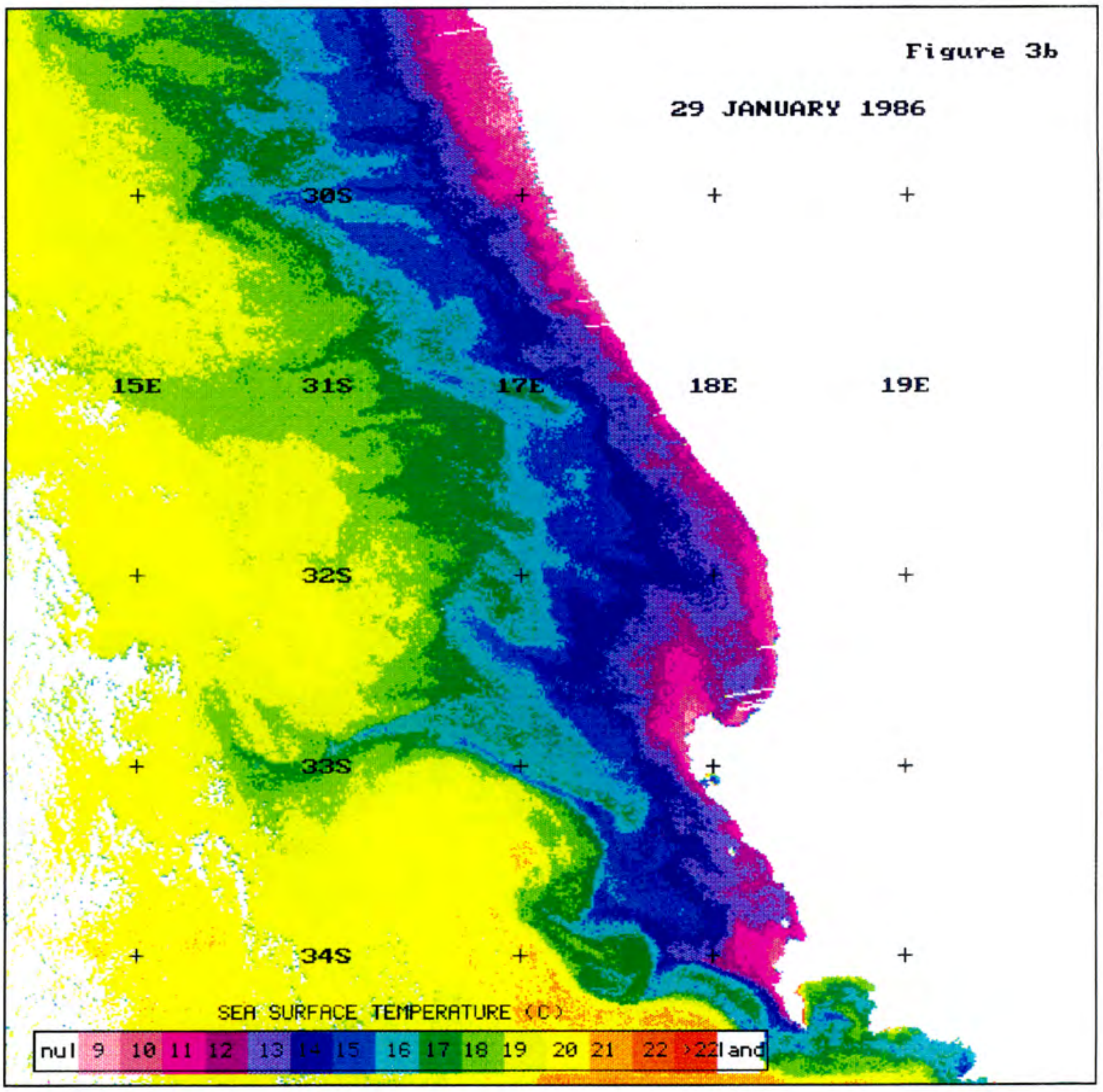


Figure 3b

29 JANUARY 1986

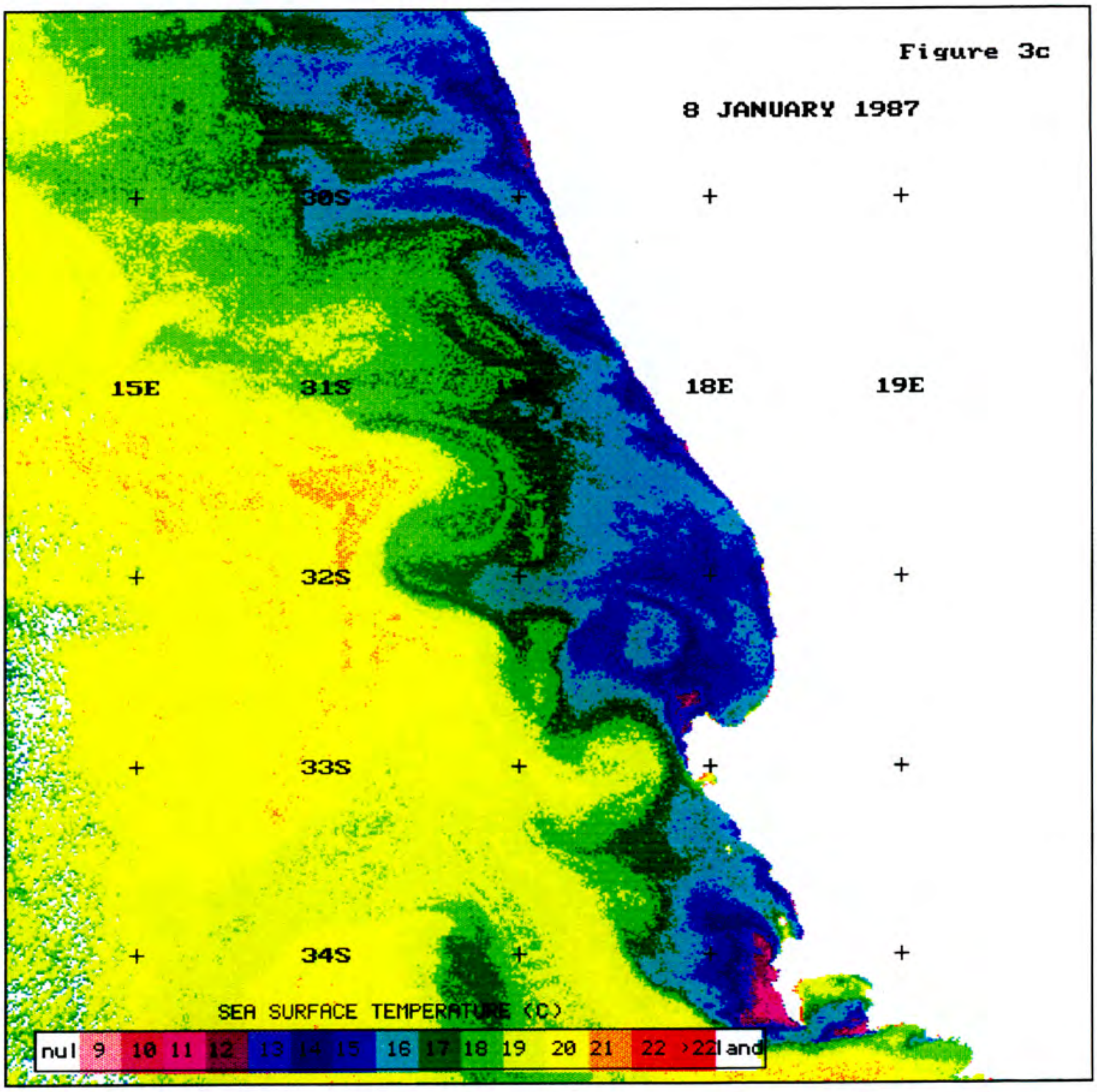


Figure 3c

8 JANUARY 1987

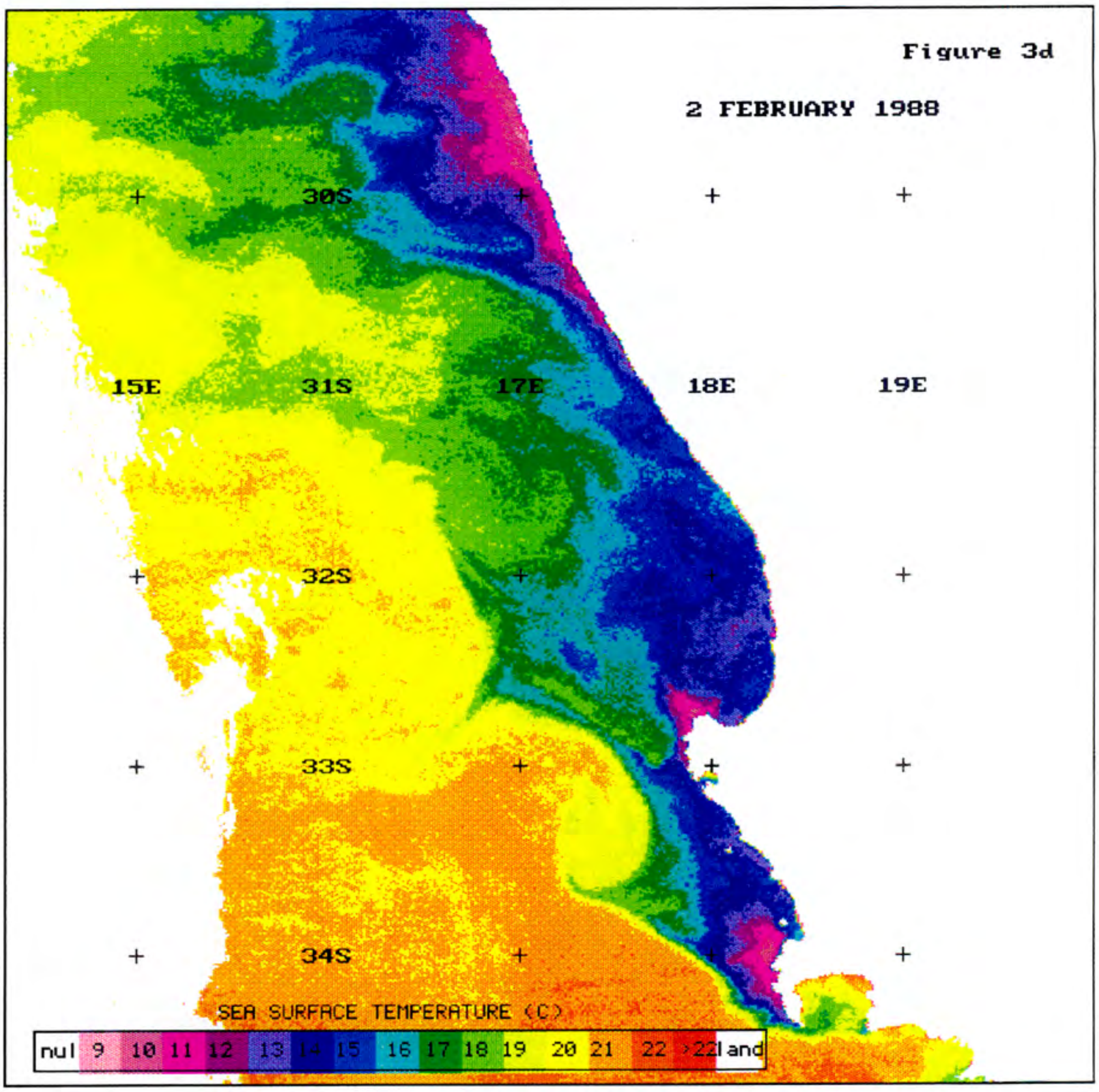
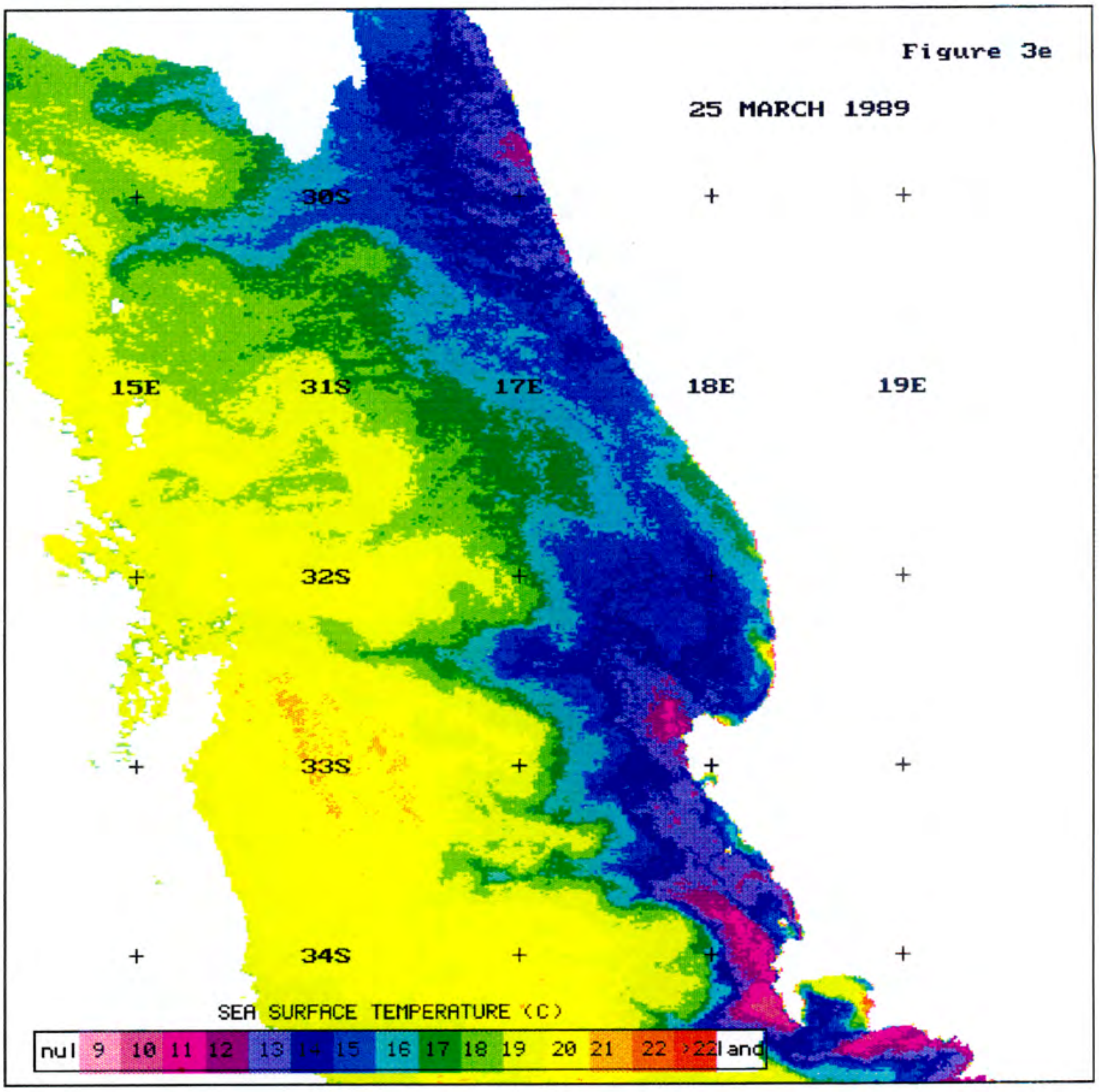


Figure 3d

2 FEBRUARY 1988



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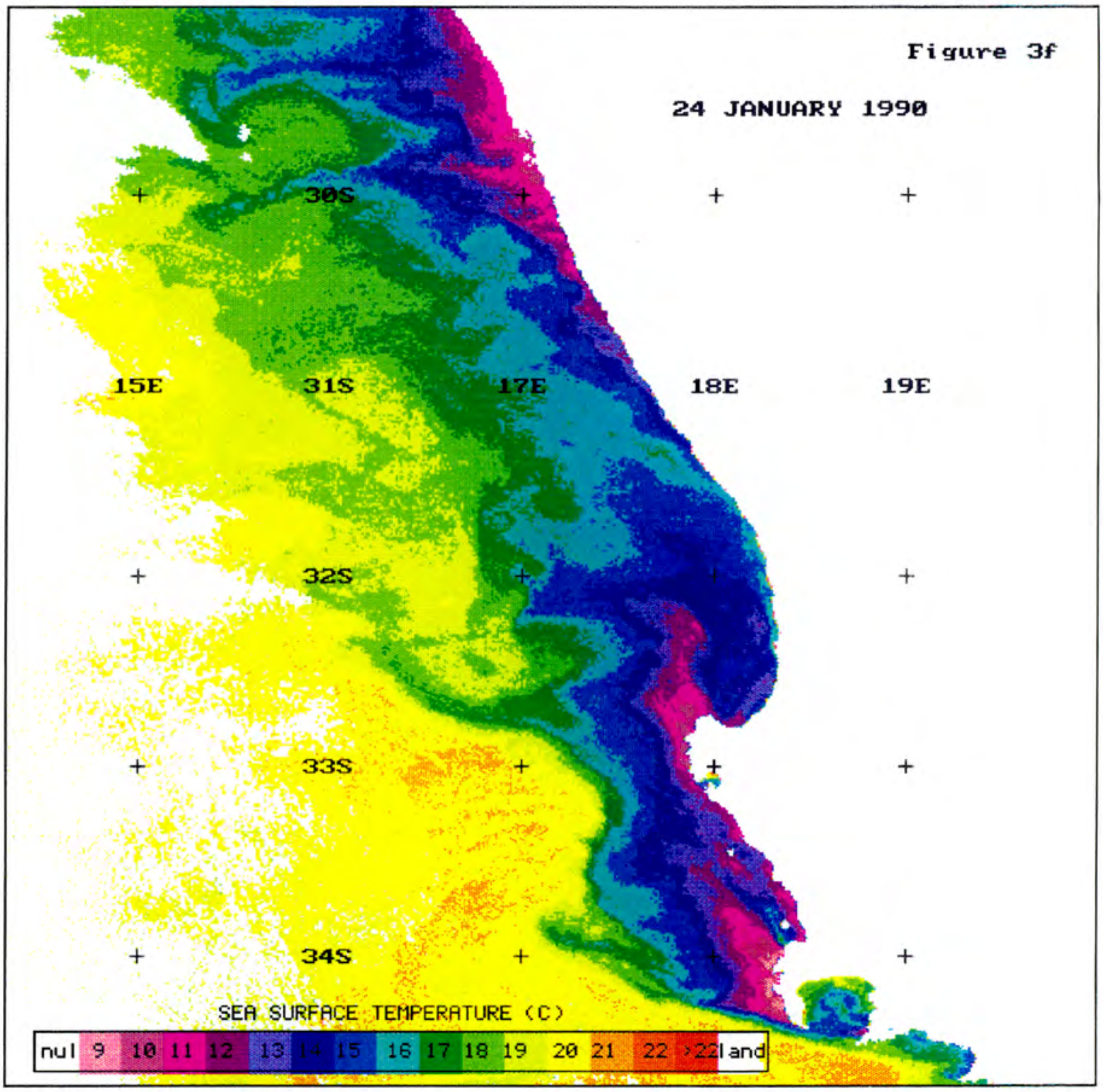
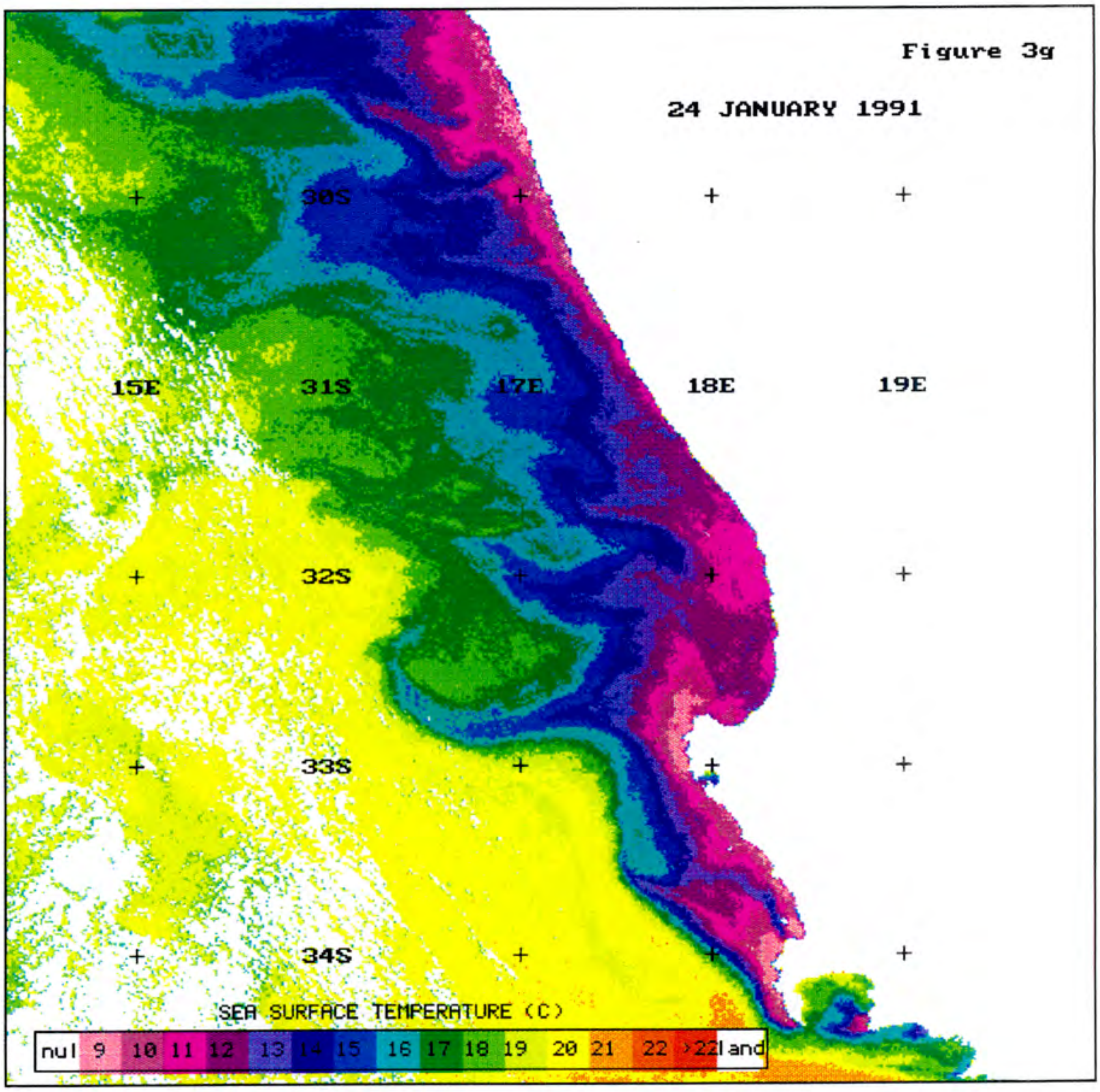


Figure 3f

24 JANUARY 1990



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24 JANUARY 1991

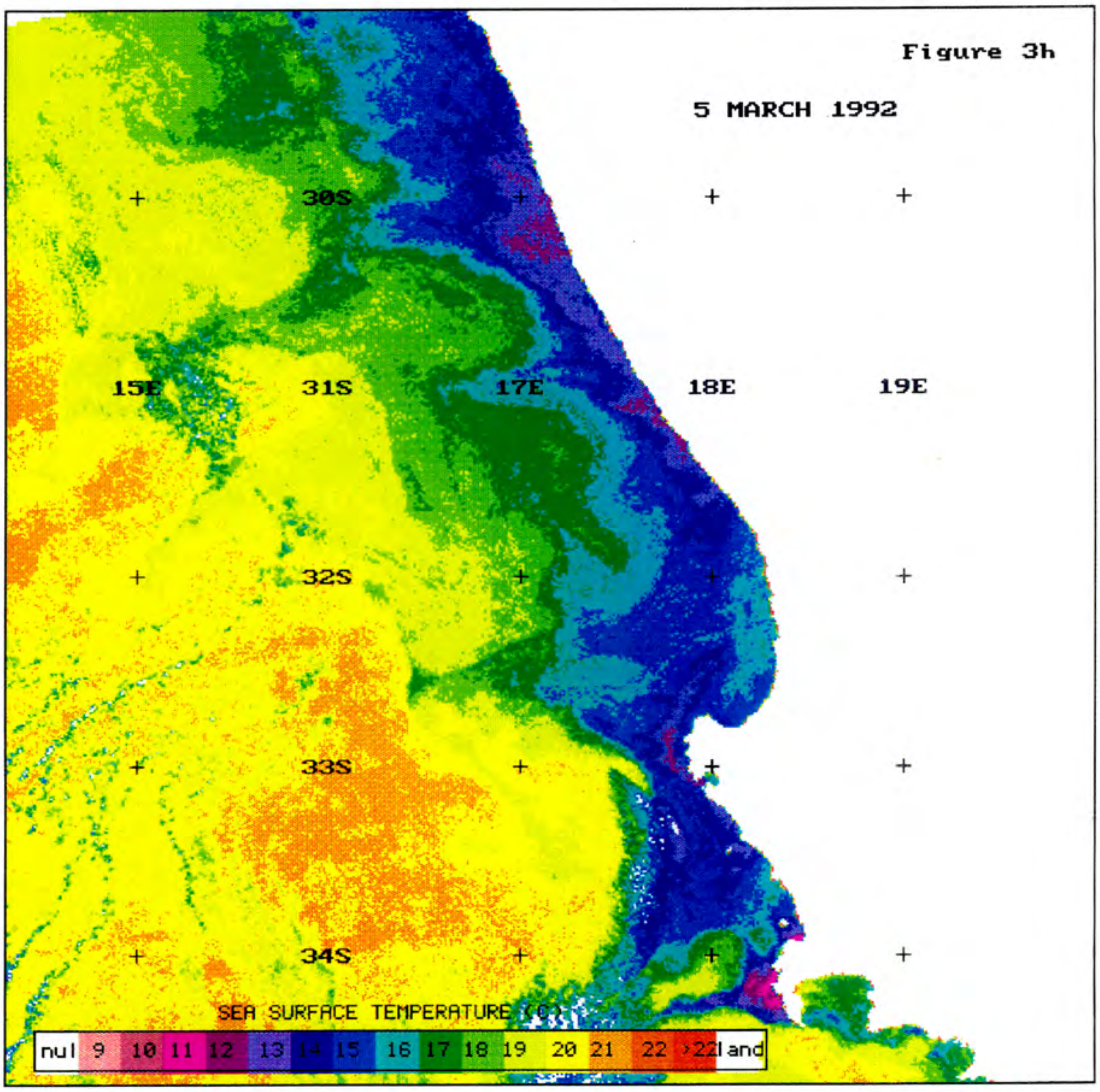


Figure 3h

5 MARCH 1992

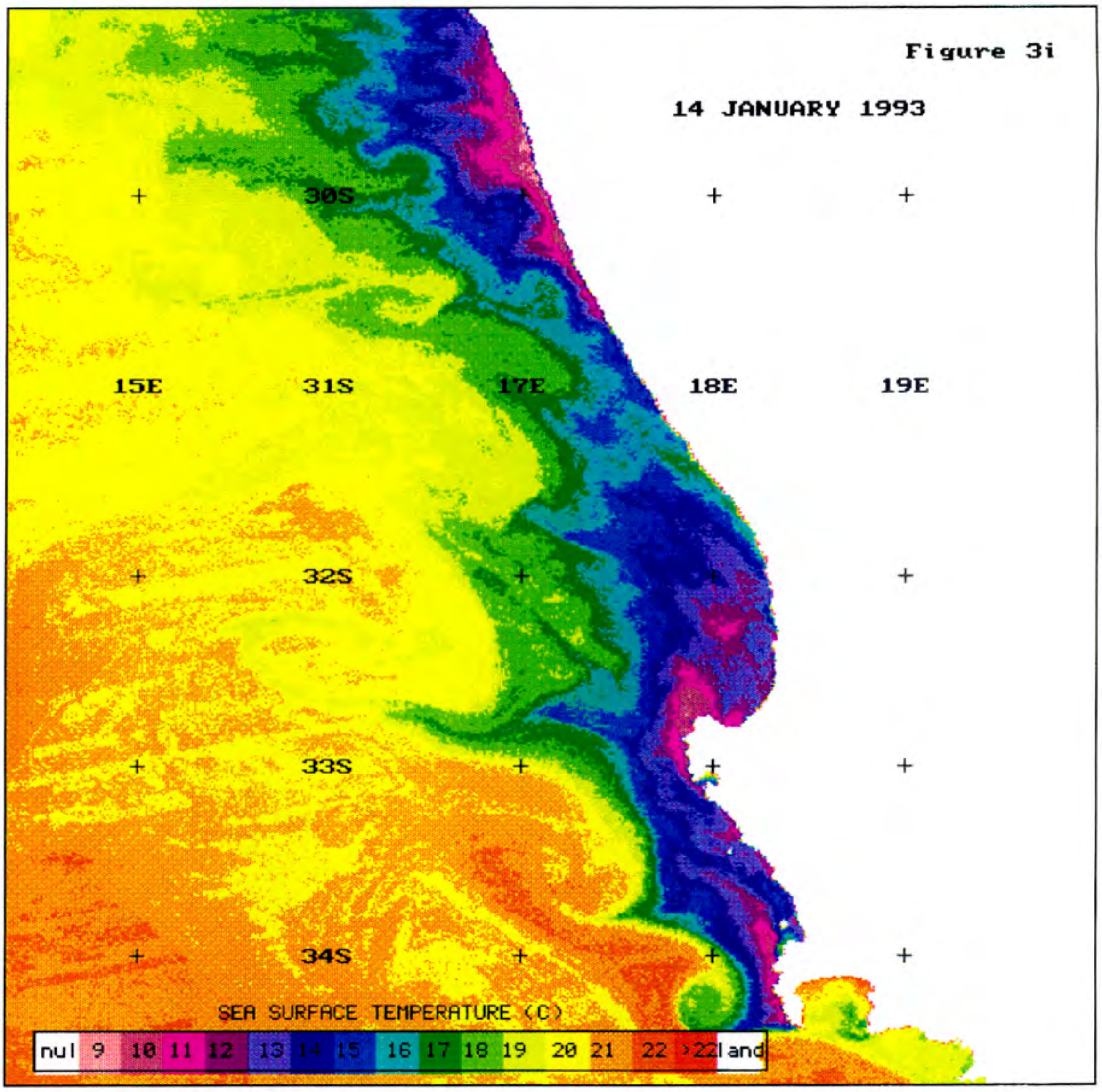
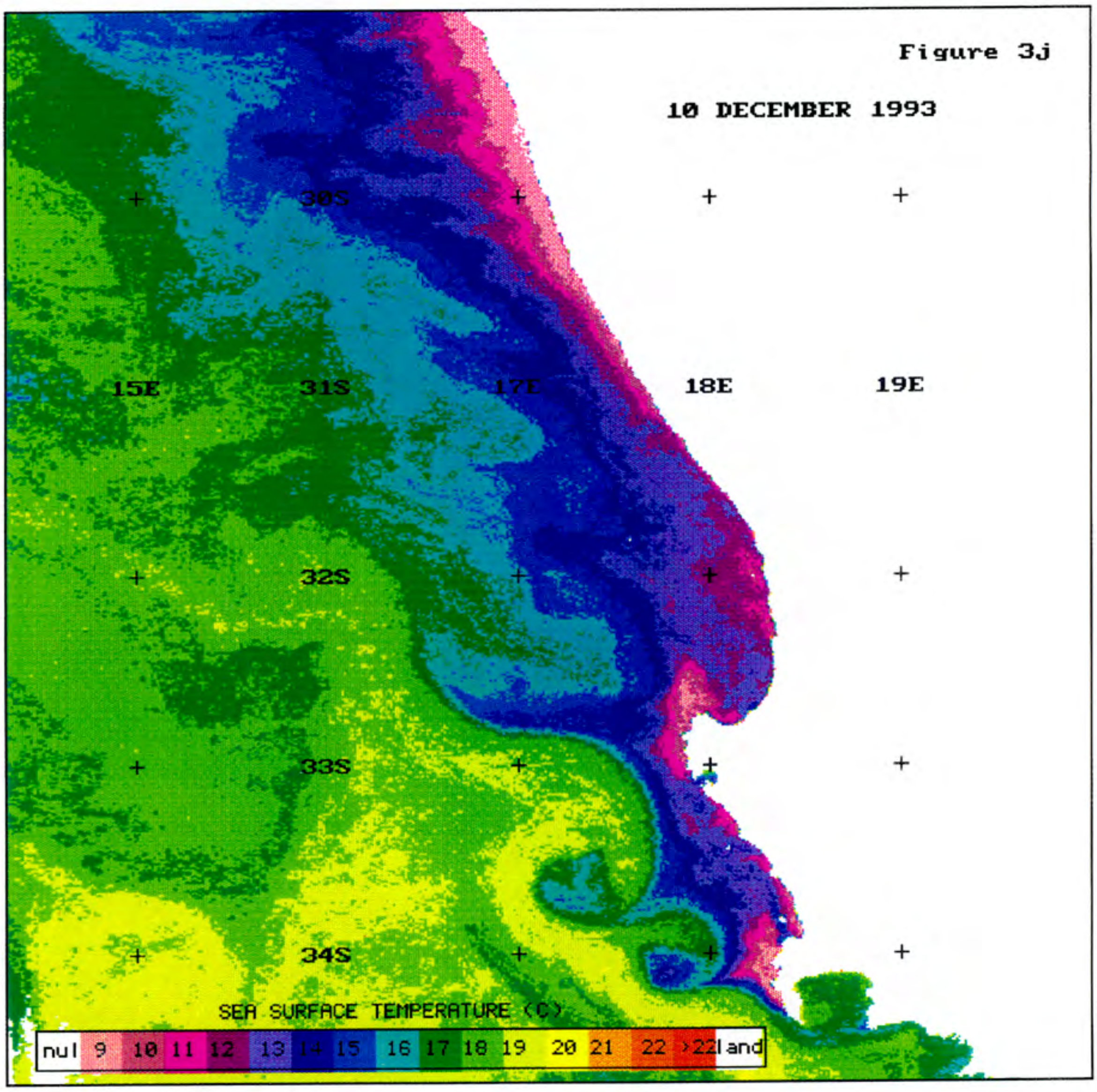


Figure 3i

14 JANUARY 1993



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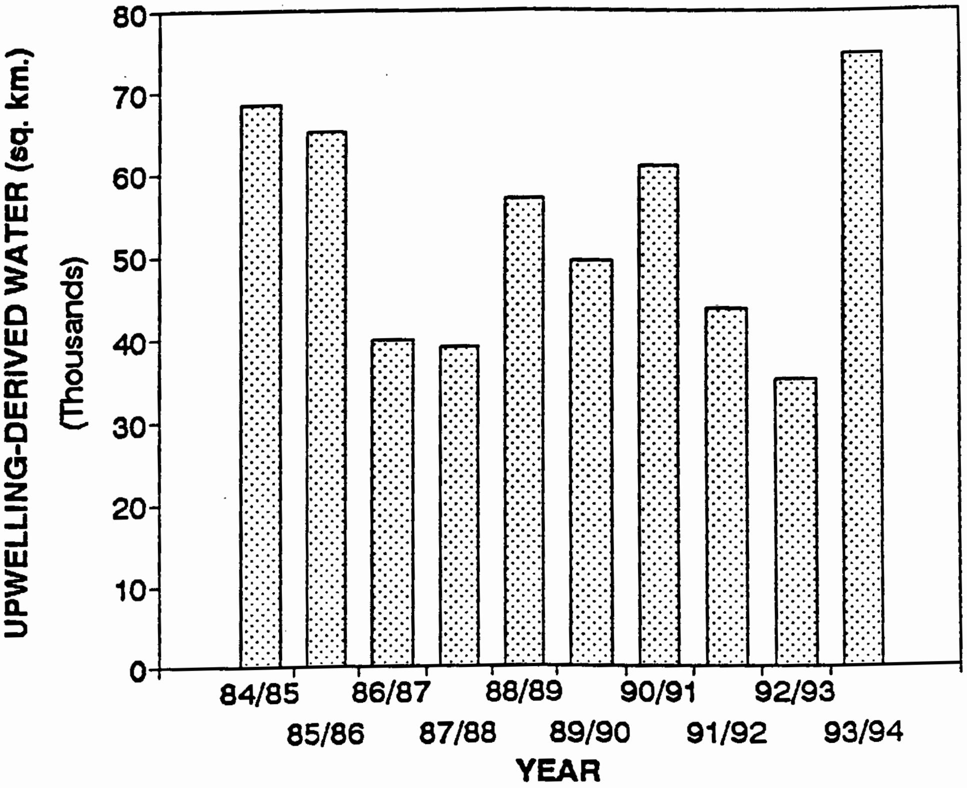
10 DECEMBER 1993



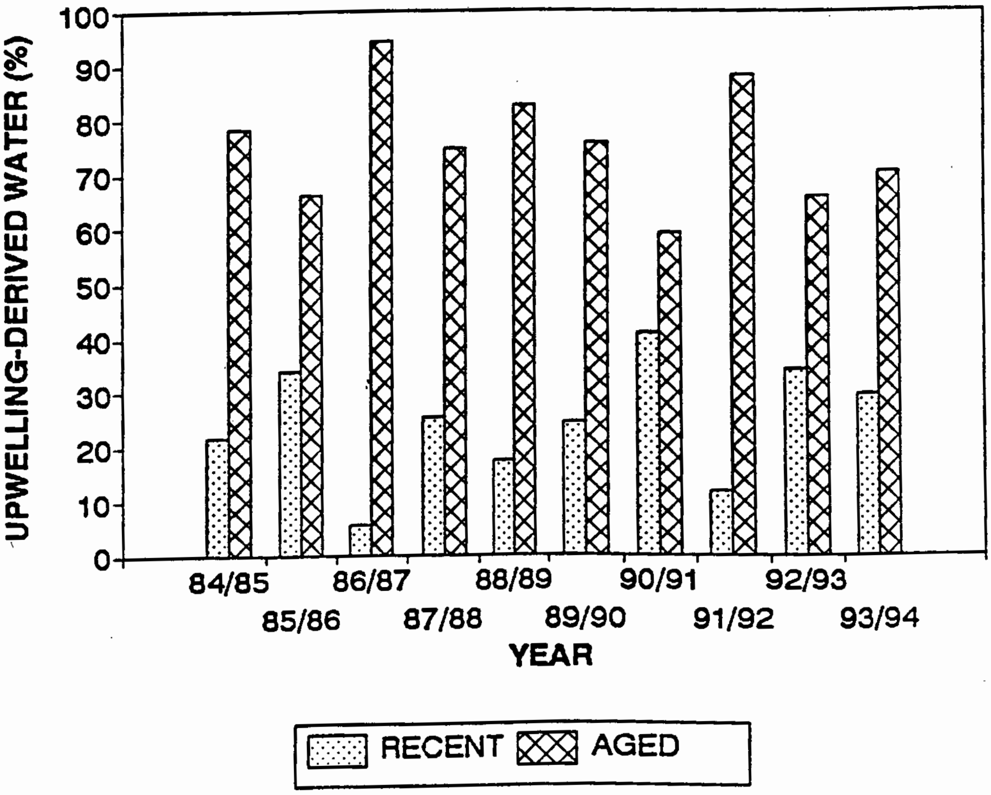
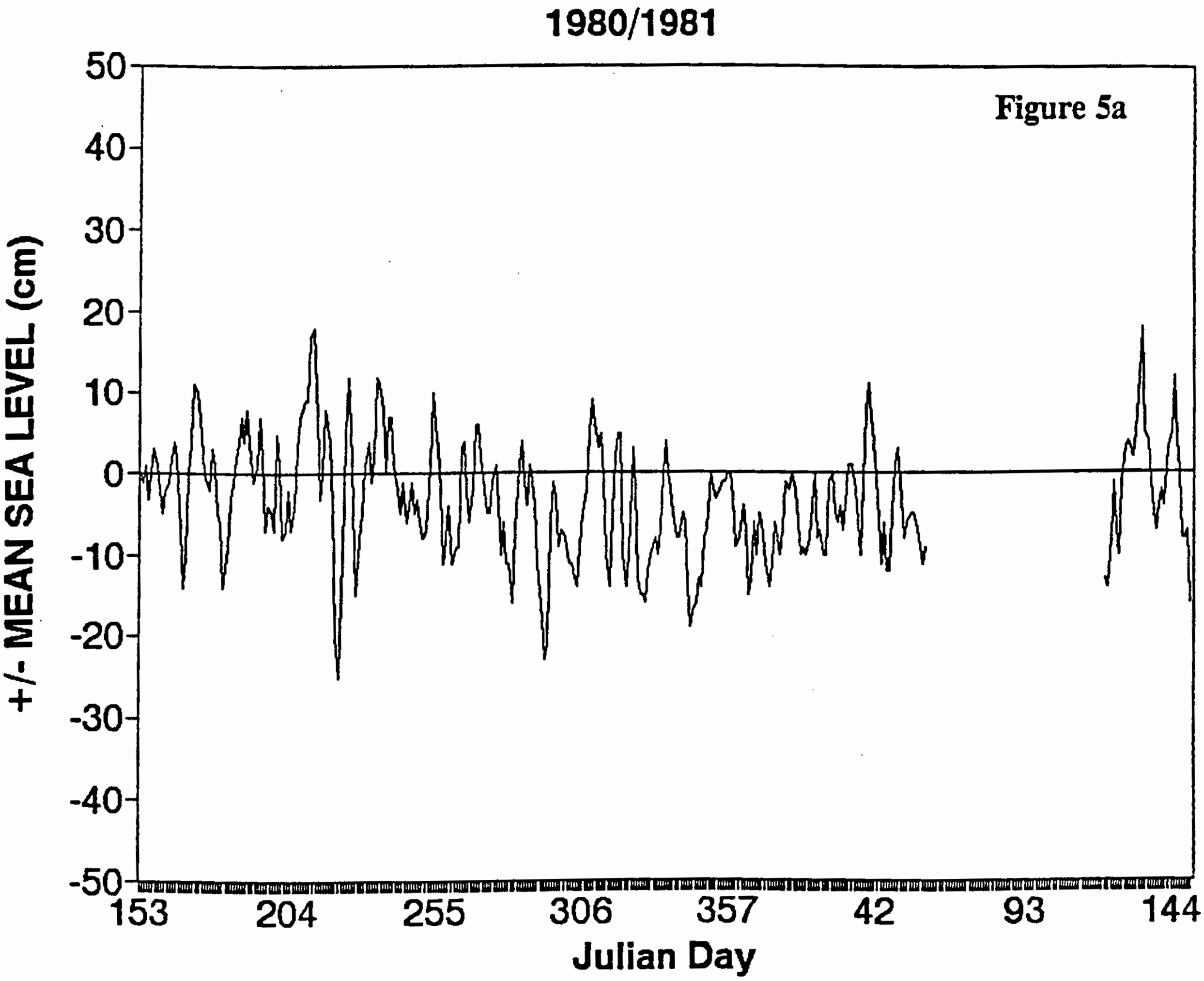


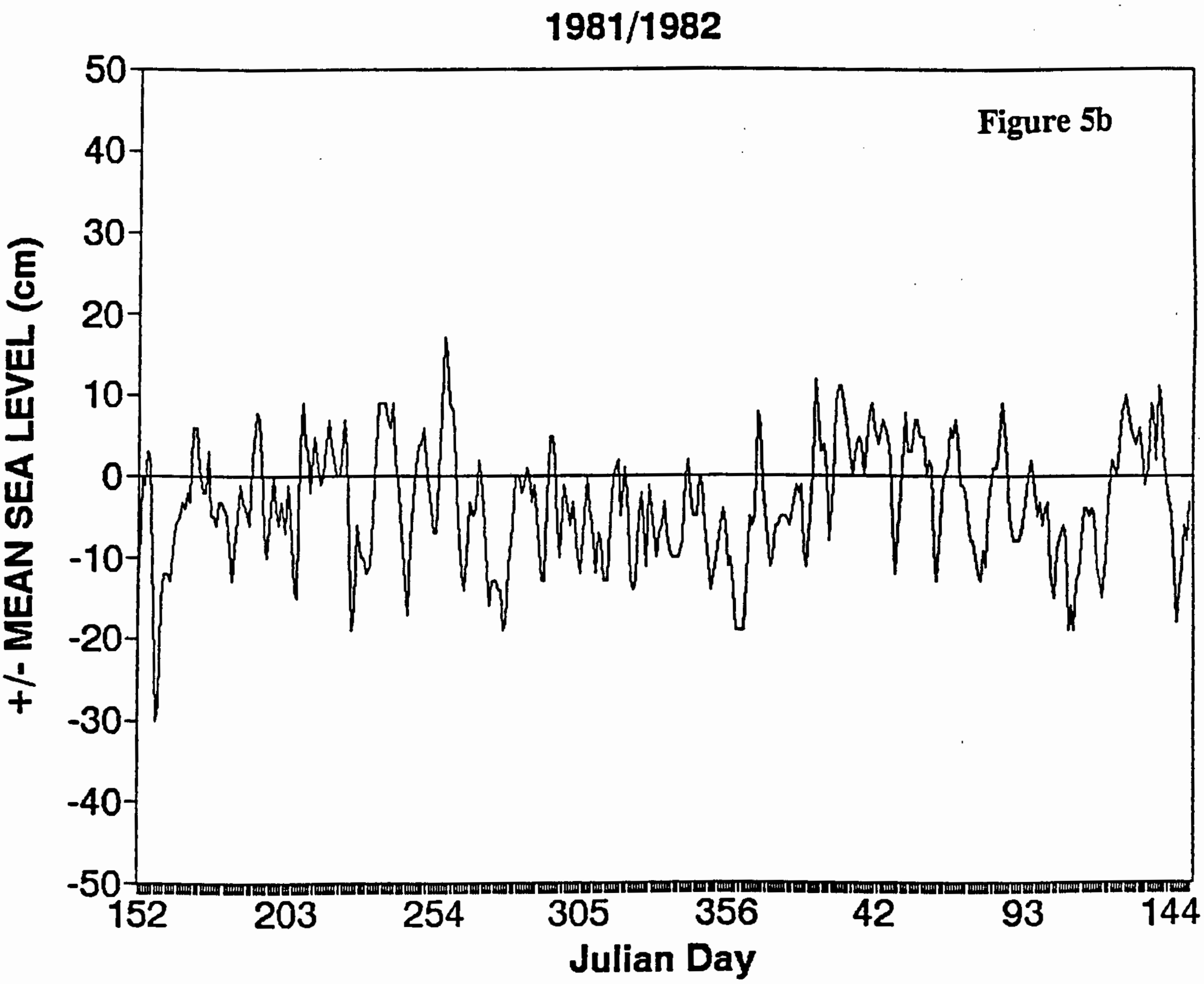
Figure 4.

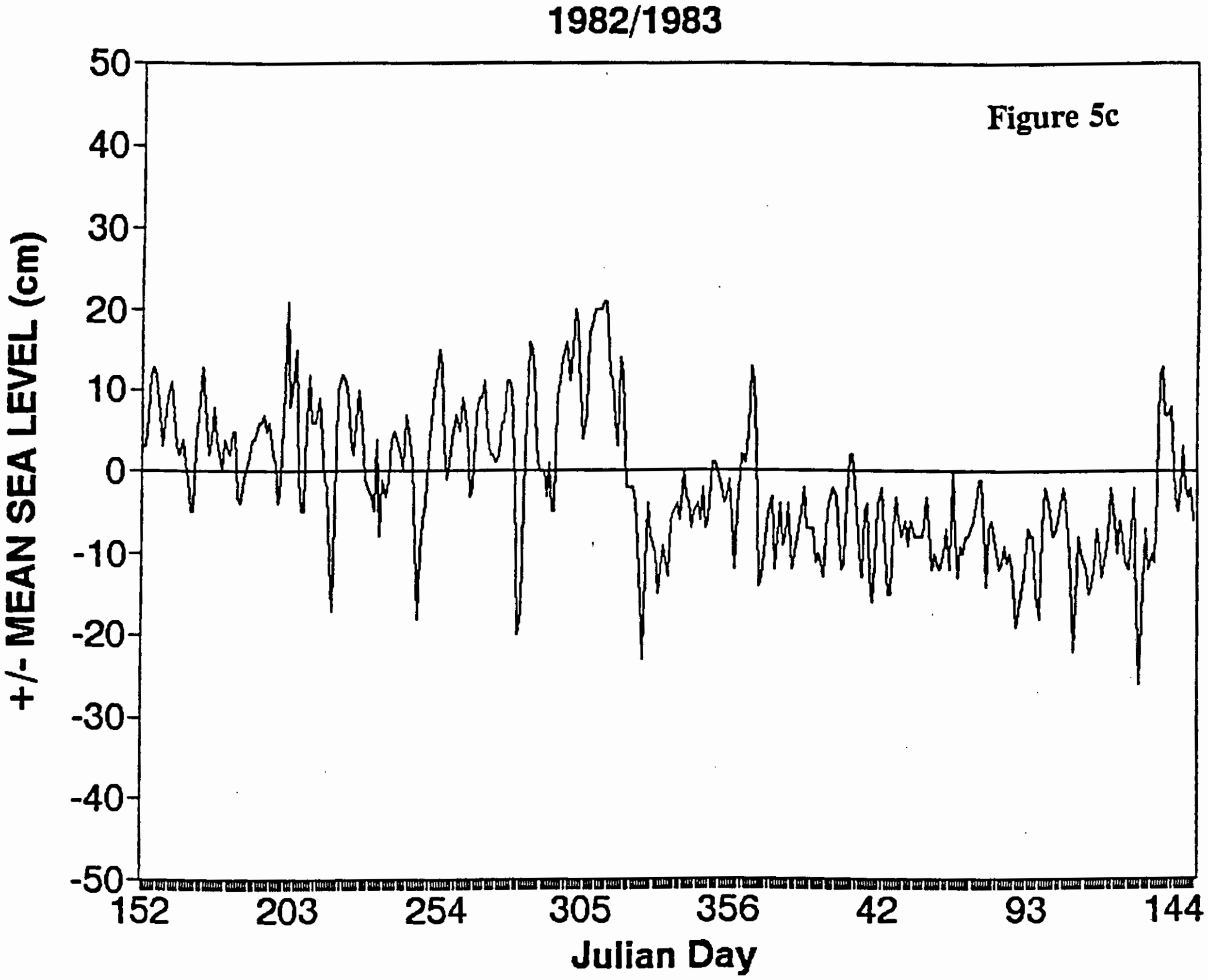
Upper: area of upwelling-derived water (10-16°C) obtained from satellite imagery for the ten upwelling events occurring between 1984/85 and 1993/94.

Lower: relative percentages of recent (10-13°C) and aged (14-16°C) components of upwelling-derived water for the same ten upwelling events.



Figures 5a - 5j inclusive. Sea level time series at Saldanha Bay showing positive and negative residuals about the long-term mean sea level for each year between 1980/81 and 1989/90.


1981/1982
Figure 5b
+/- MEAN SEA LEVEL (cm)
50
40
30
20
10
0
-10
-20
-30
-40
-50
152
203
254
305
356
42
93
144
Julian Day


1982/1983
Figure 5c
50
40
30
20
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0
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-40
-50
+/- MEAN SEA LEVEL (cm)
152
203
254
305
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42
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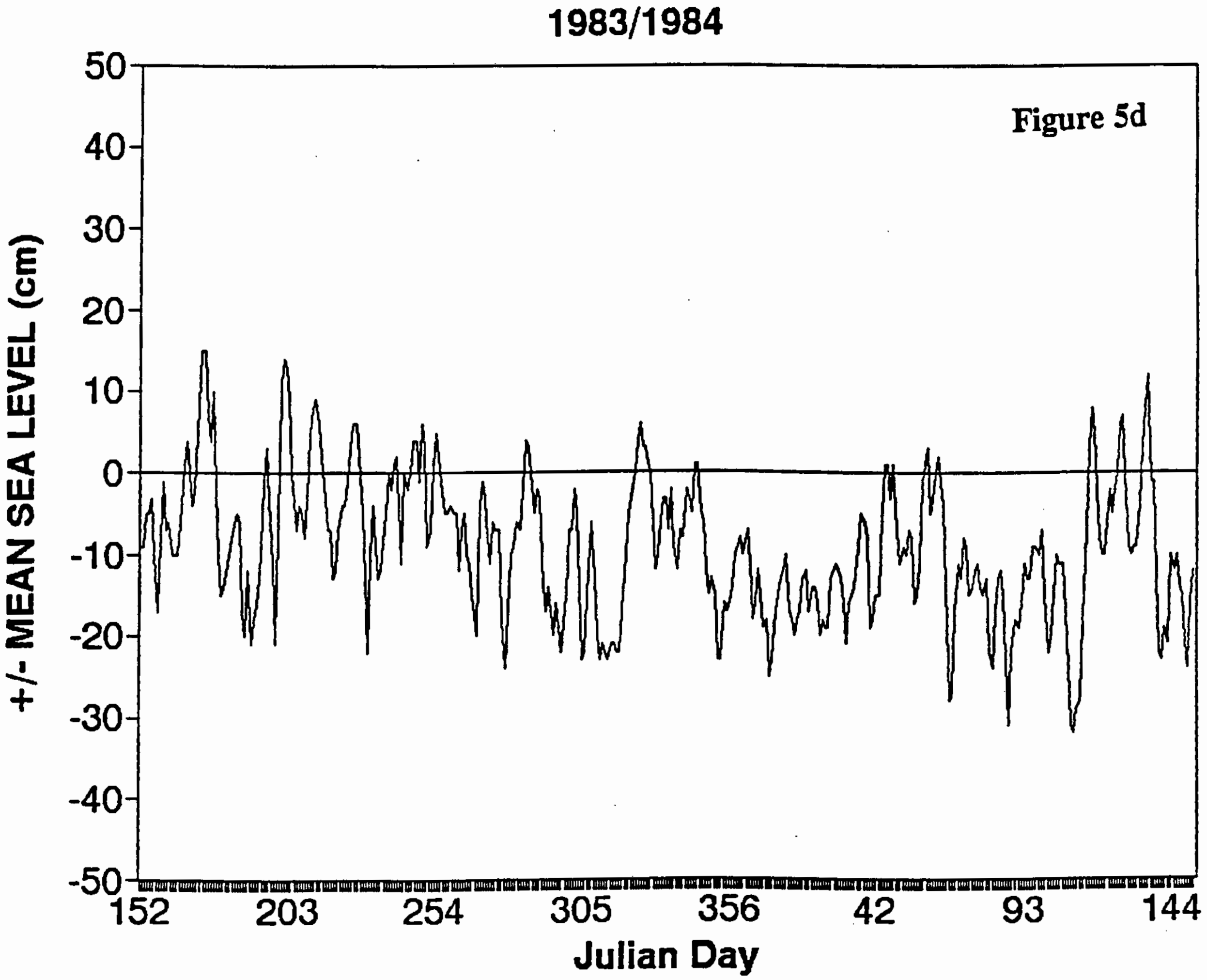
144
Julian Day


1983/1984
Figure 5d
+/- MEAN SEA LEVEL (cm)
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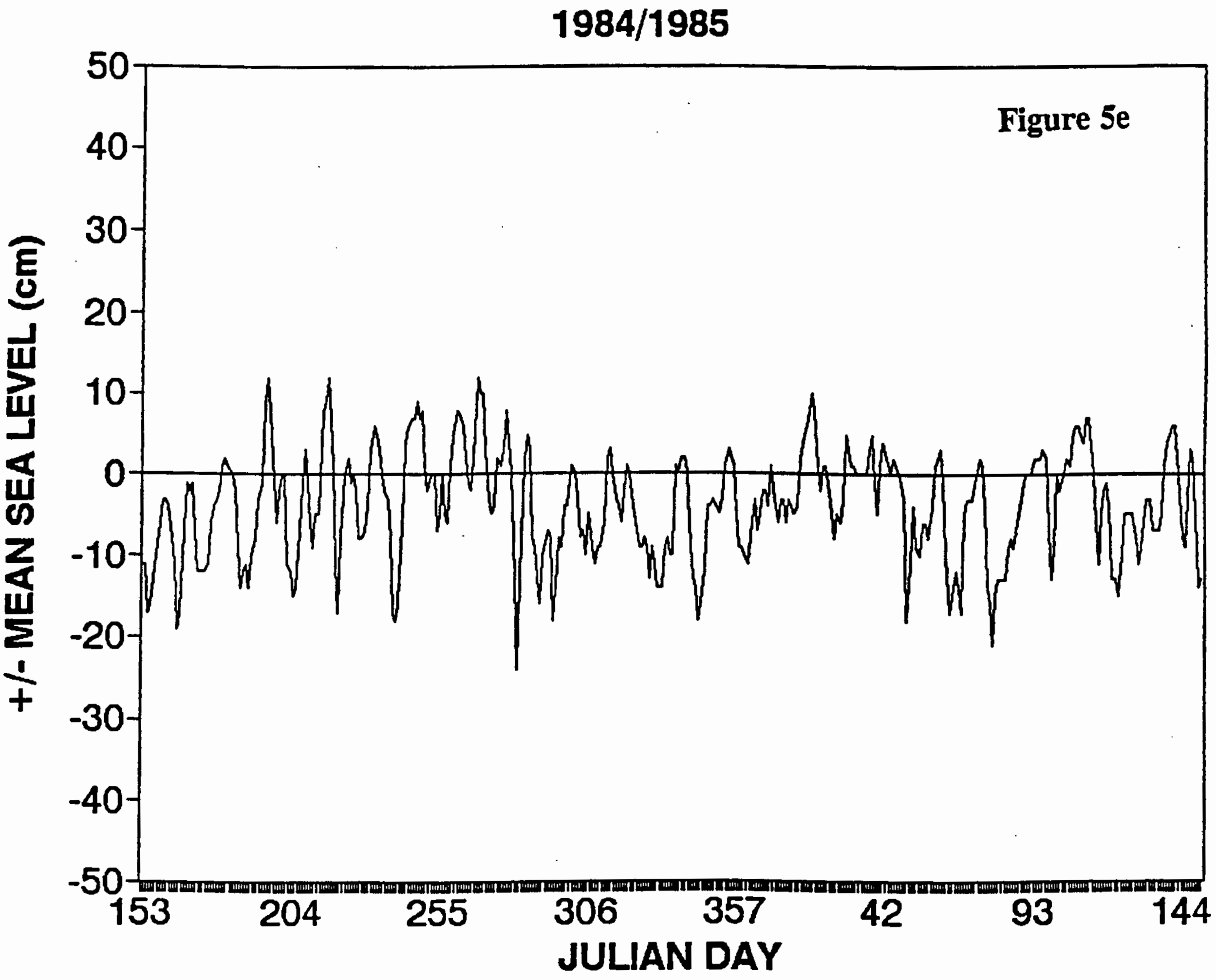
Julian Day


1984/1985
Figure 5e
+/- MEAN SEA LEVEL (cm)
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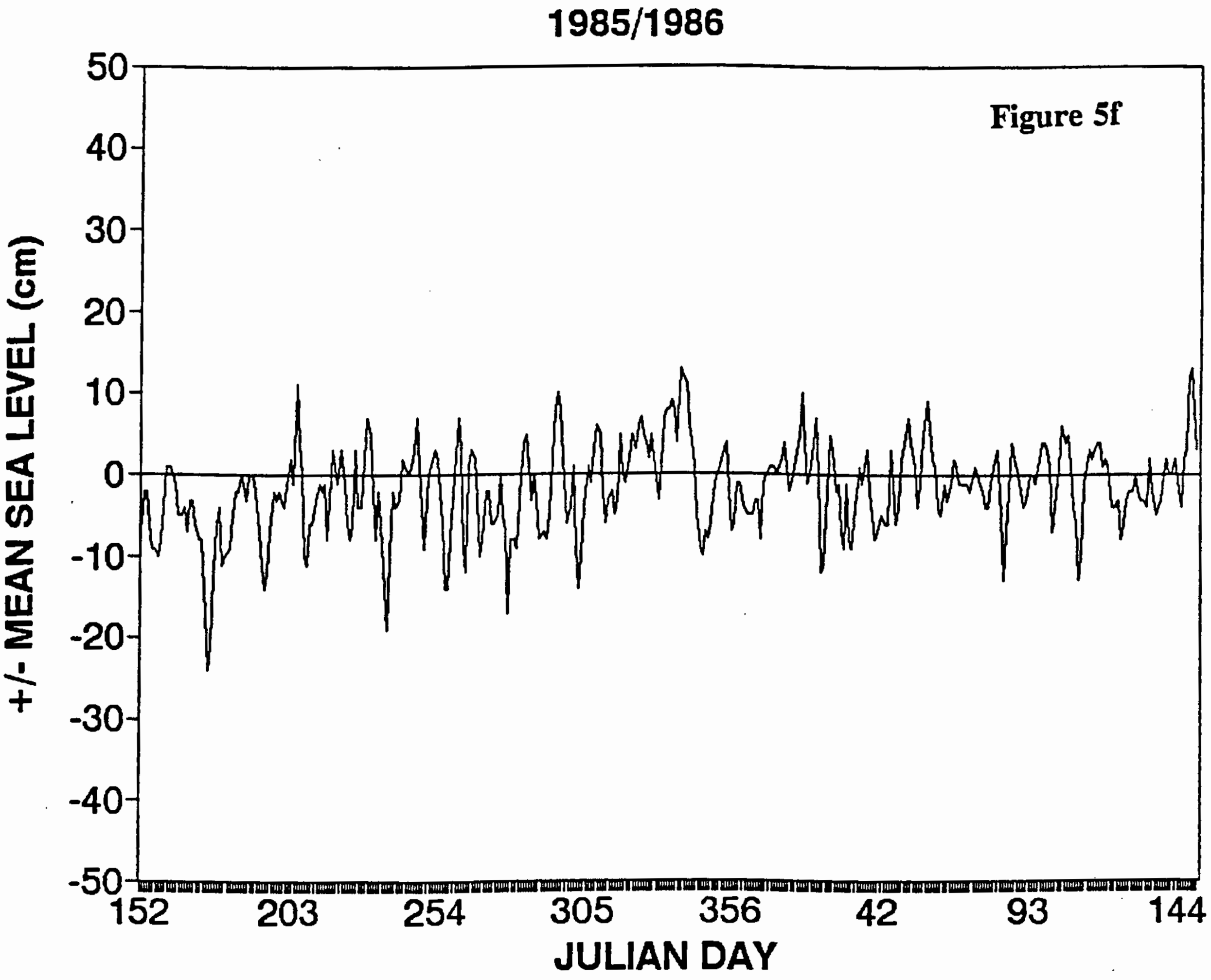
JULIAN DAY


1985/1986
Figure 5f
+/- MEAN SEA LEVEL (cm)
50
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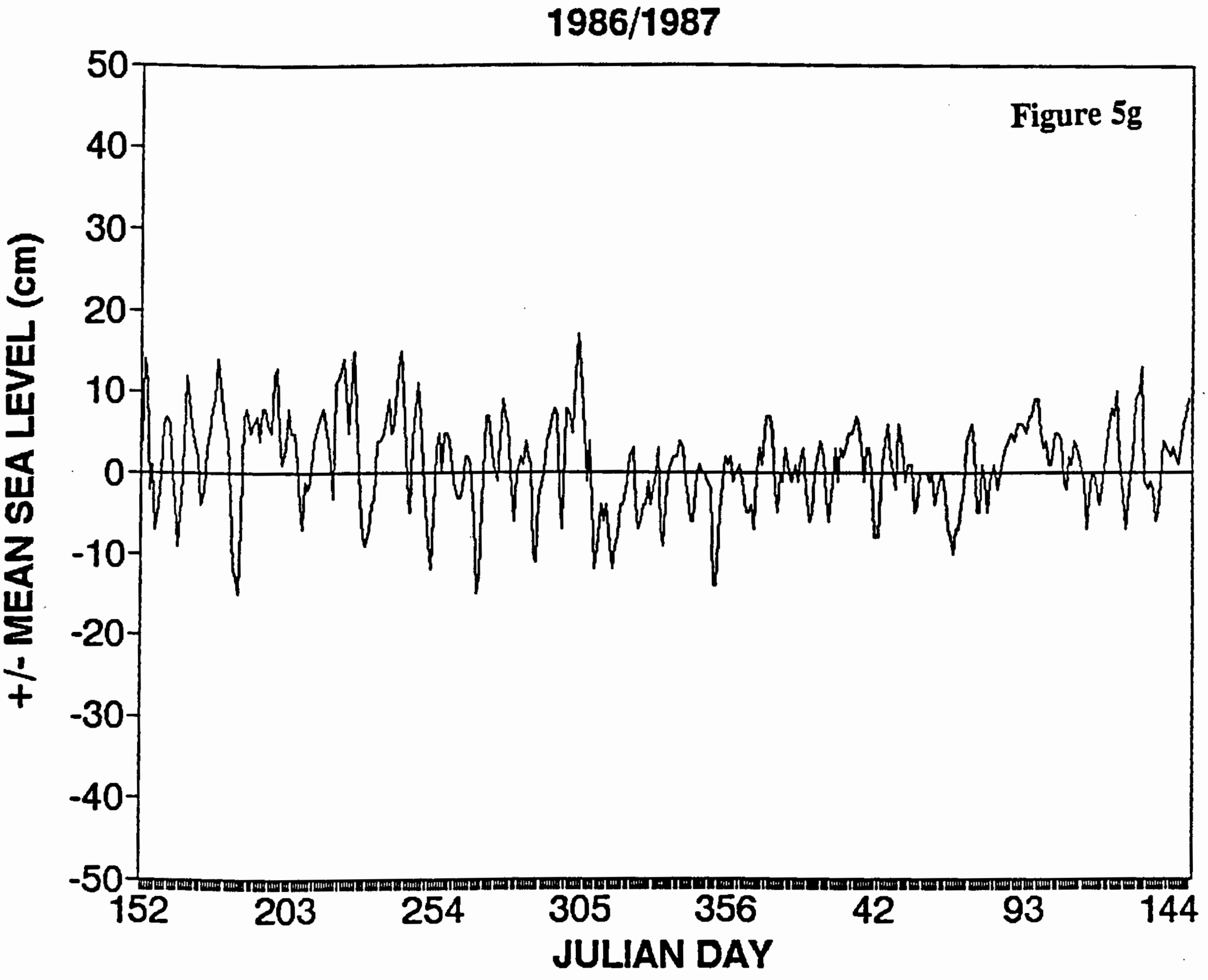
JULIAN DAY


1986/1987
Figure 5g
+/- MEAN SEA LEVEL (cm)
50
40
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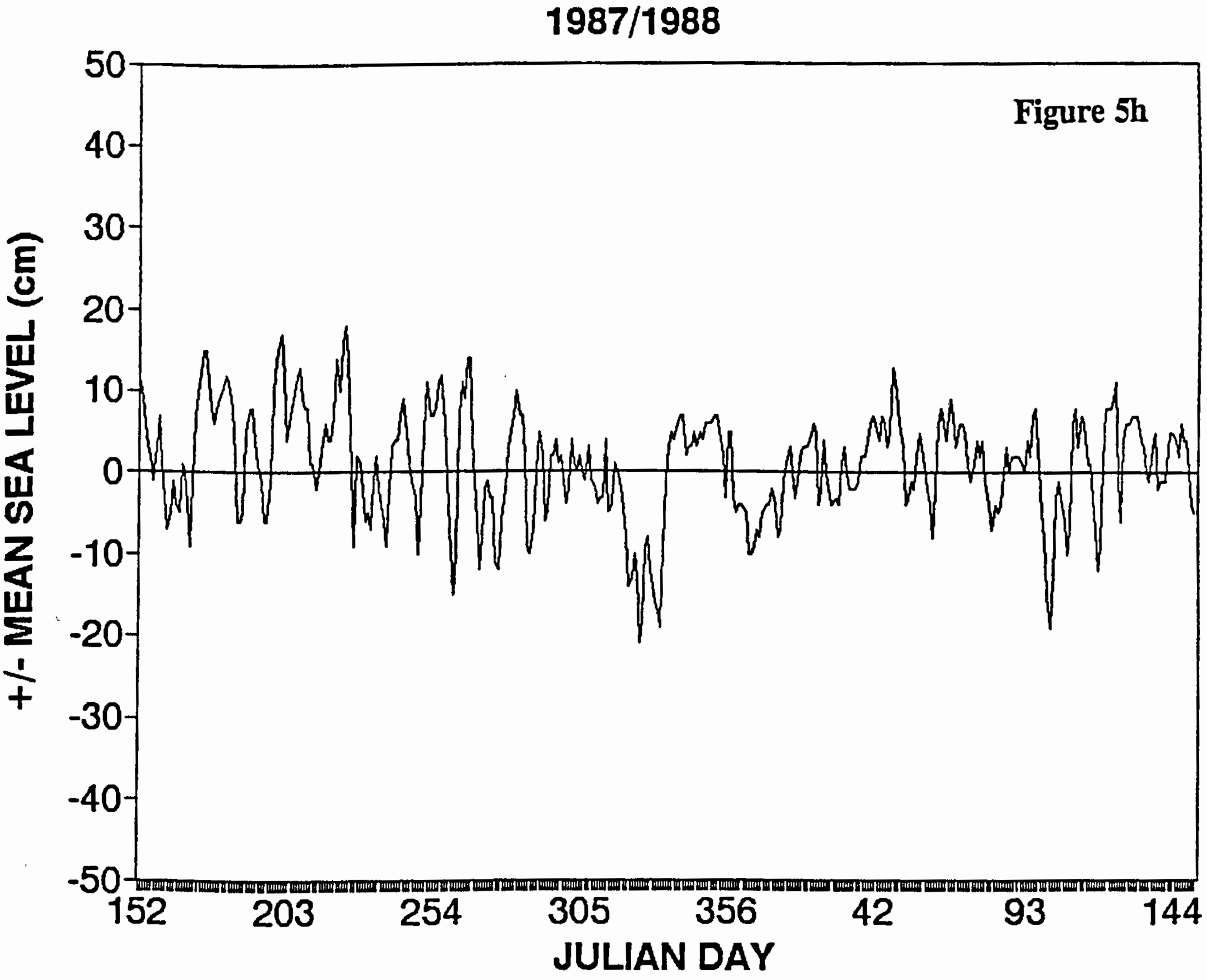
JULIAN DAY


1987/1988
Figure 5h
+/- MEAN SEA LEVEL (cm)
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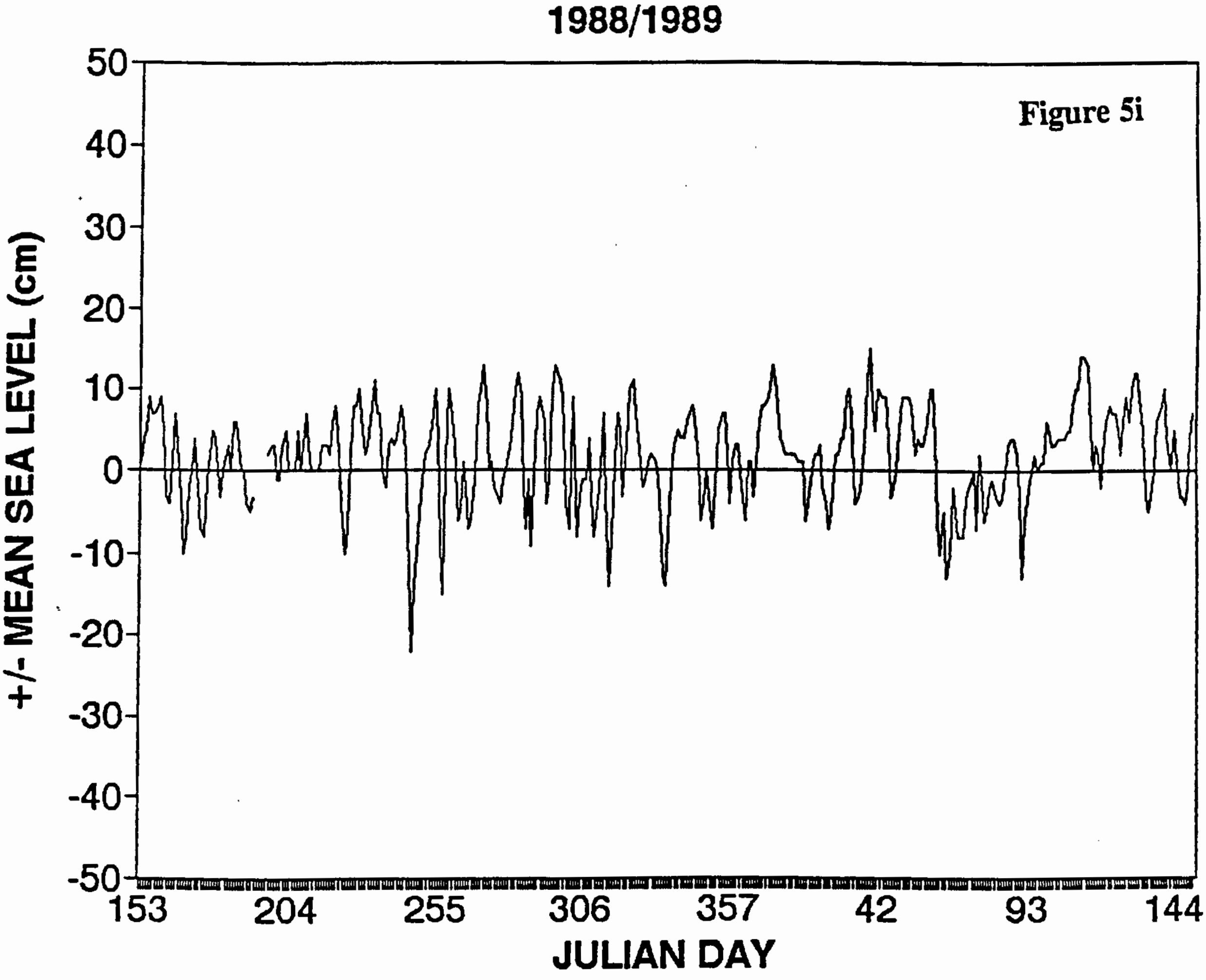
JULIAN DAY


1988/1989
Figure 5i
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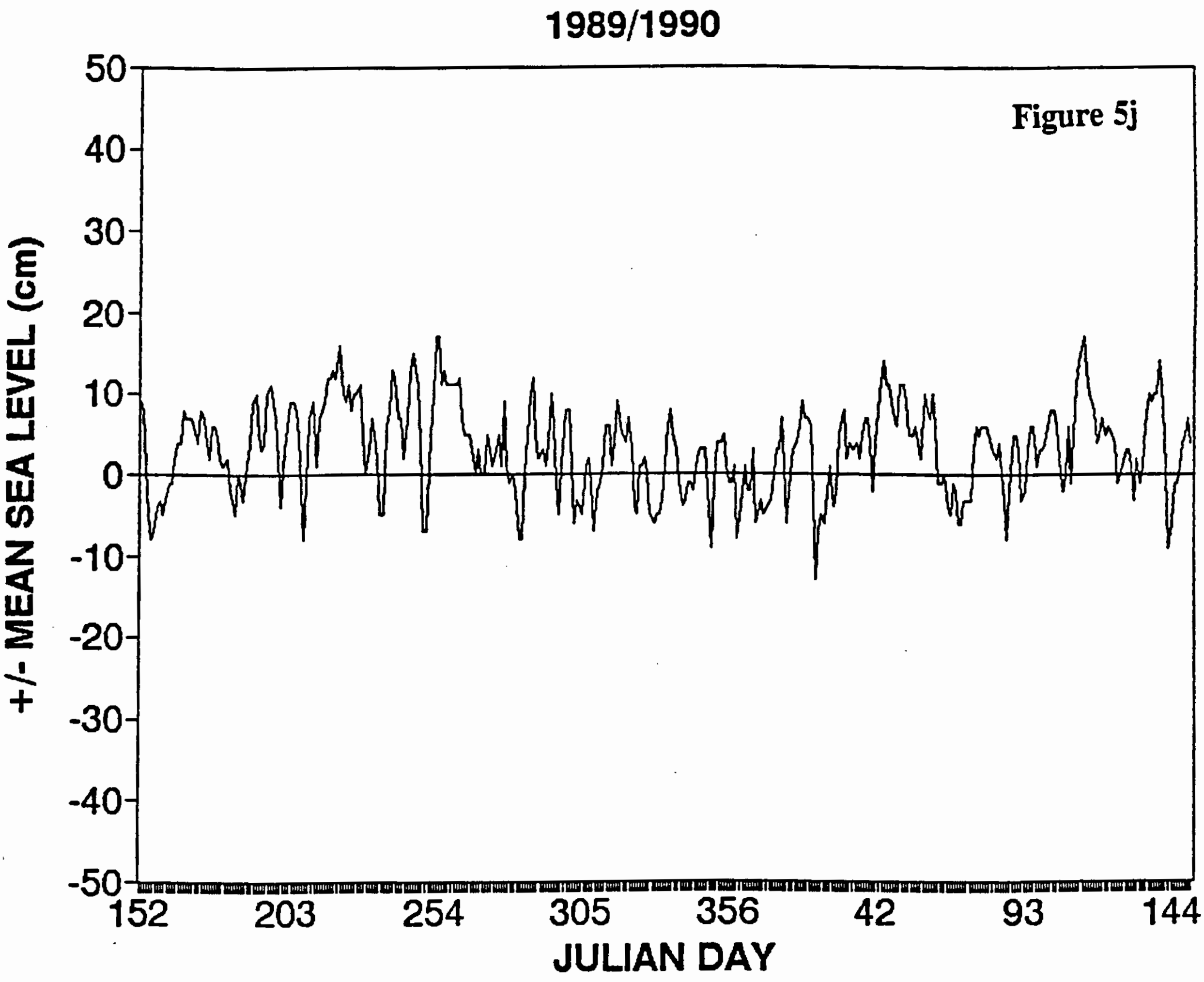
-40
-50
+/- MEAN SEA LEVEL (cm)
153
204
255
306
357
42
93
144
JULIAN DAY


1989/1990
Figure 5j
+/- MEAN SEA LEVEL (cm)
50
40
30
20
10
0
-10
-20
-30
-40
-50
152
203
254
305
356
42
93
144
JULIAN DAY

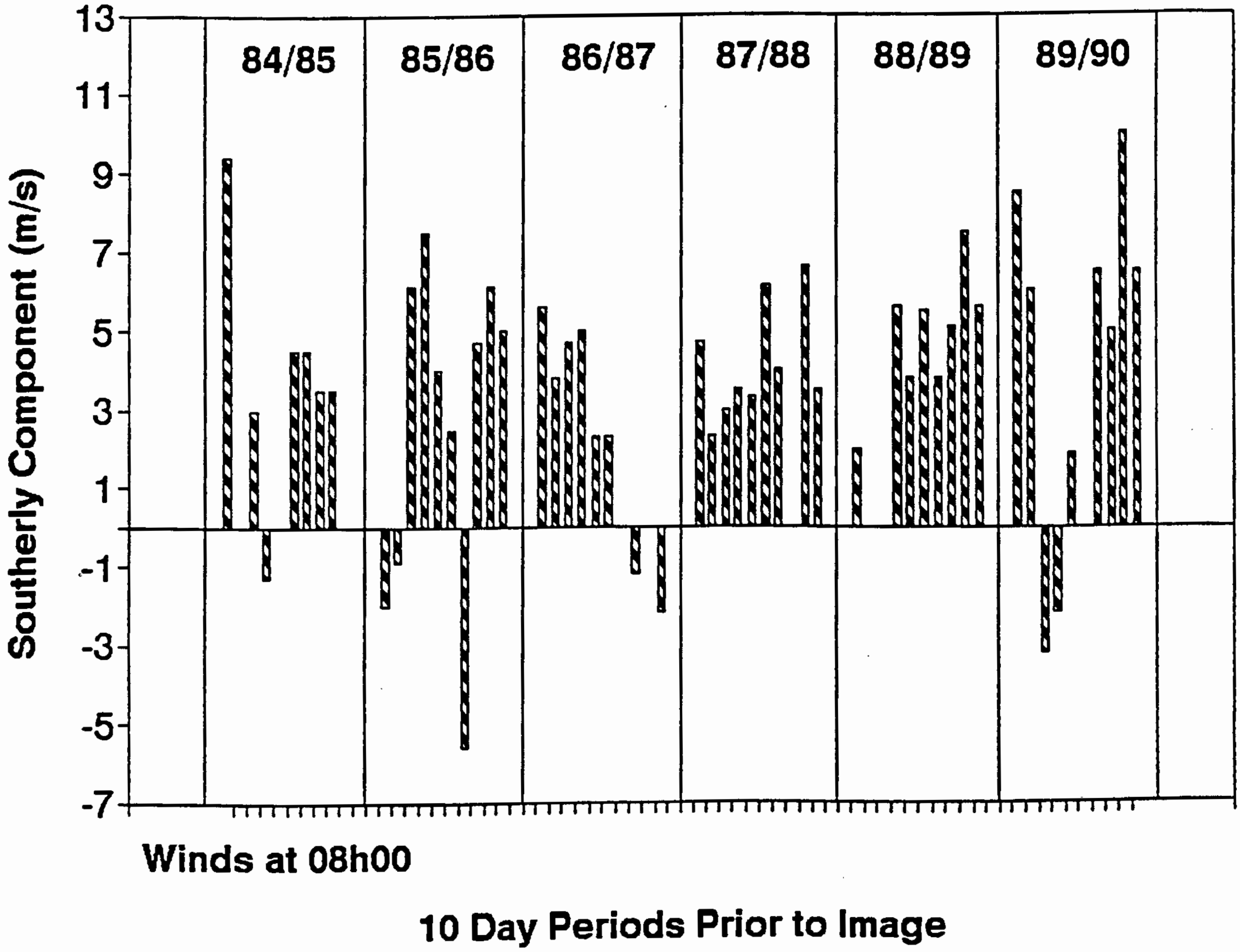


Figure 6. Southerly components of wind in the ten day periods preceding sea surface temperature satellite images of upwelling events in the period 1984/85 to 1989/90. Winds were measured at Cape Columbine.

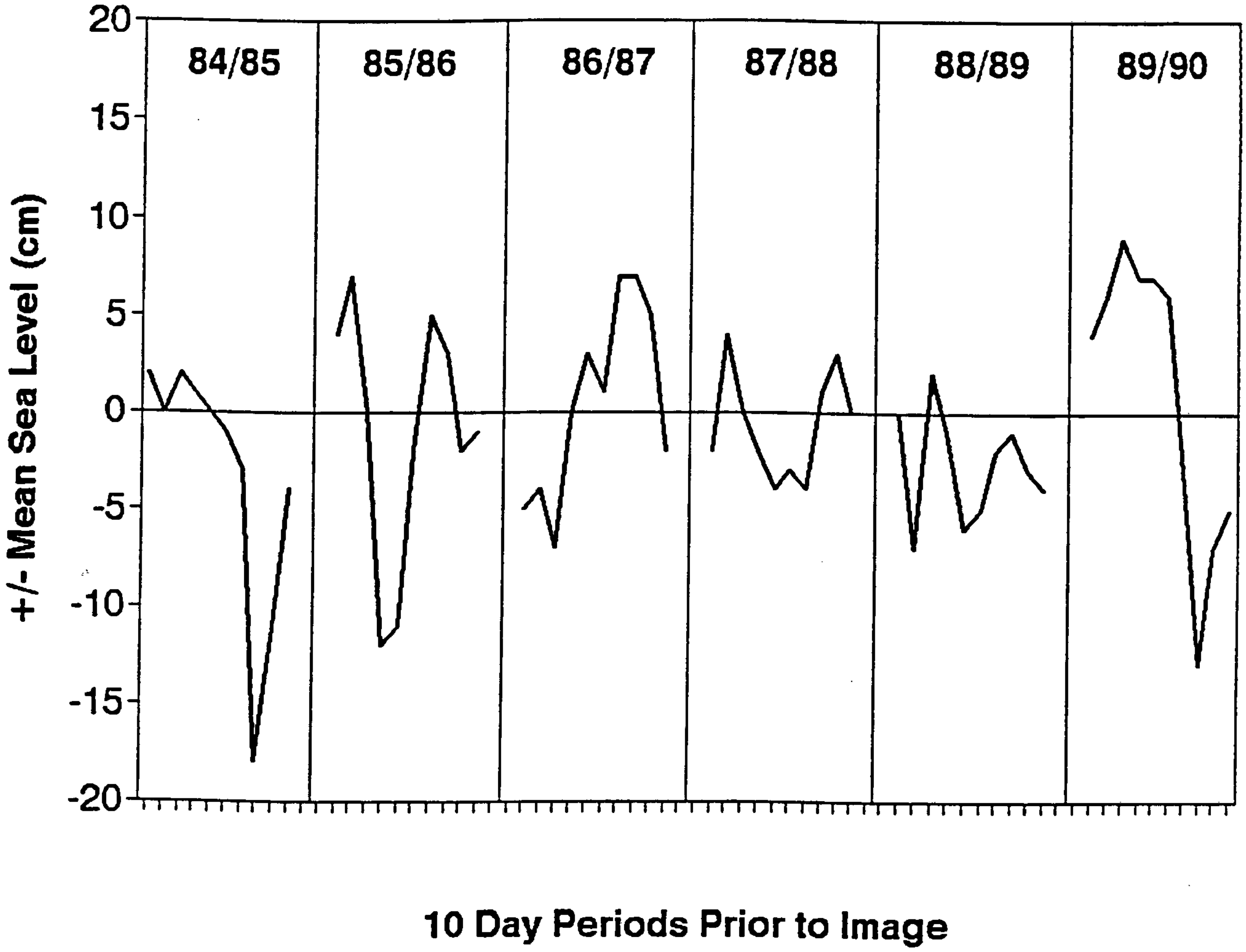


Figure 7. Sea level fluctuation at the coast in the ten day periods preceding sea surface temperature satellite images of upwelling events in the period 1984/85 to 1989/90. Sea level was measured at Saldanha Bay.

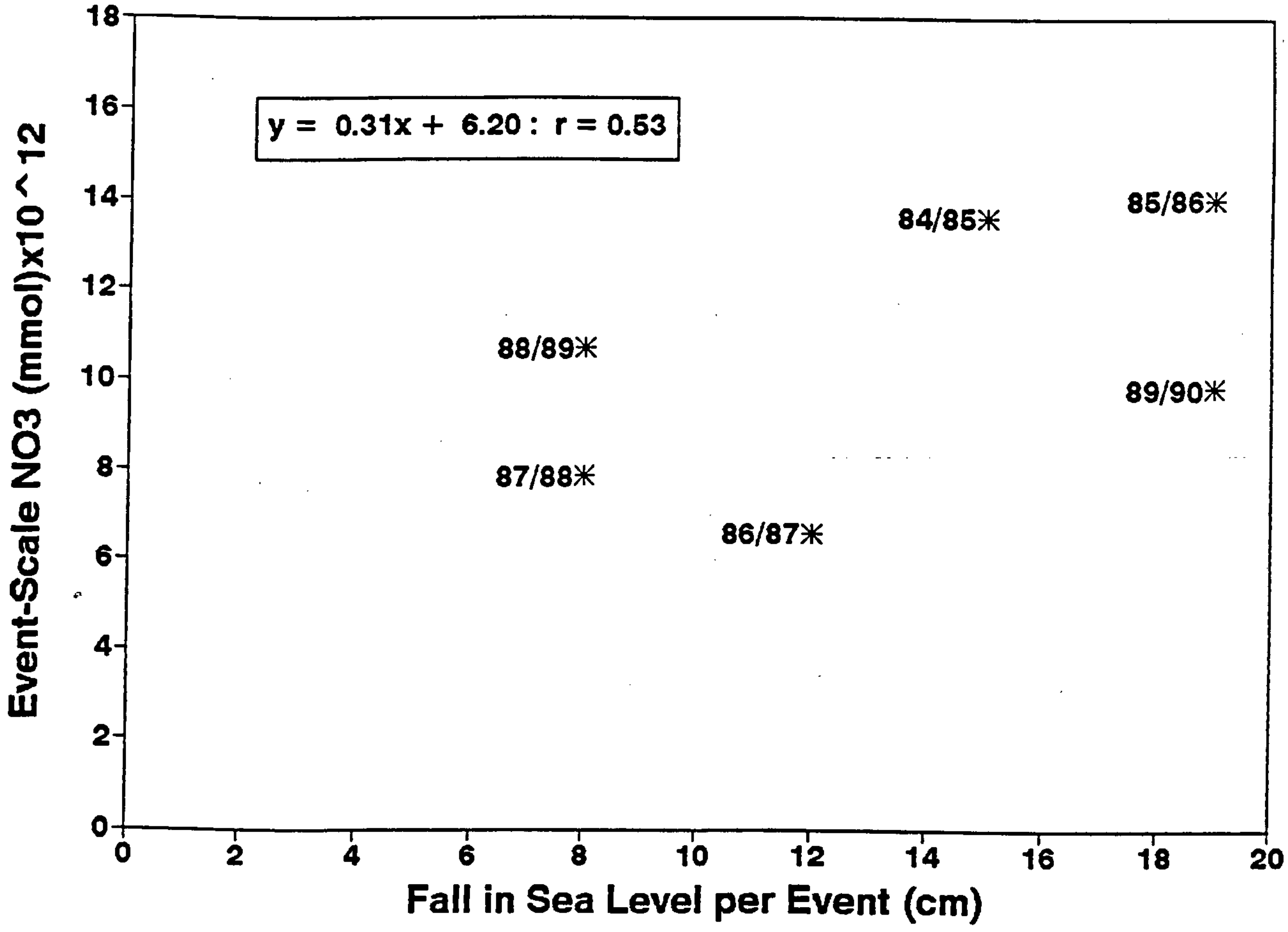


Figure 8. Fall in sea level at Saldanha Bay preceding upwelling events in the period 1984/85 to 1989/90 plotted against the amount of NO_3-N associated with each event.

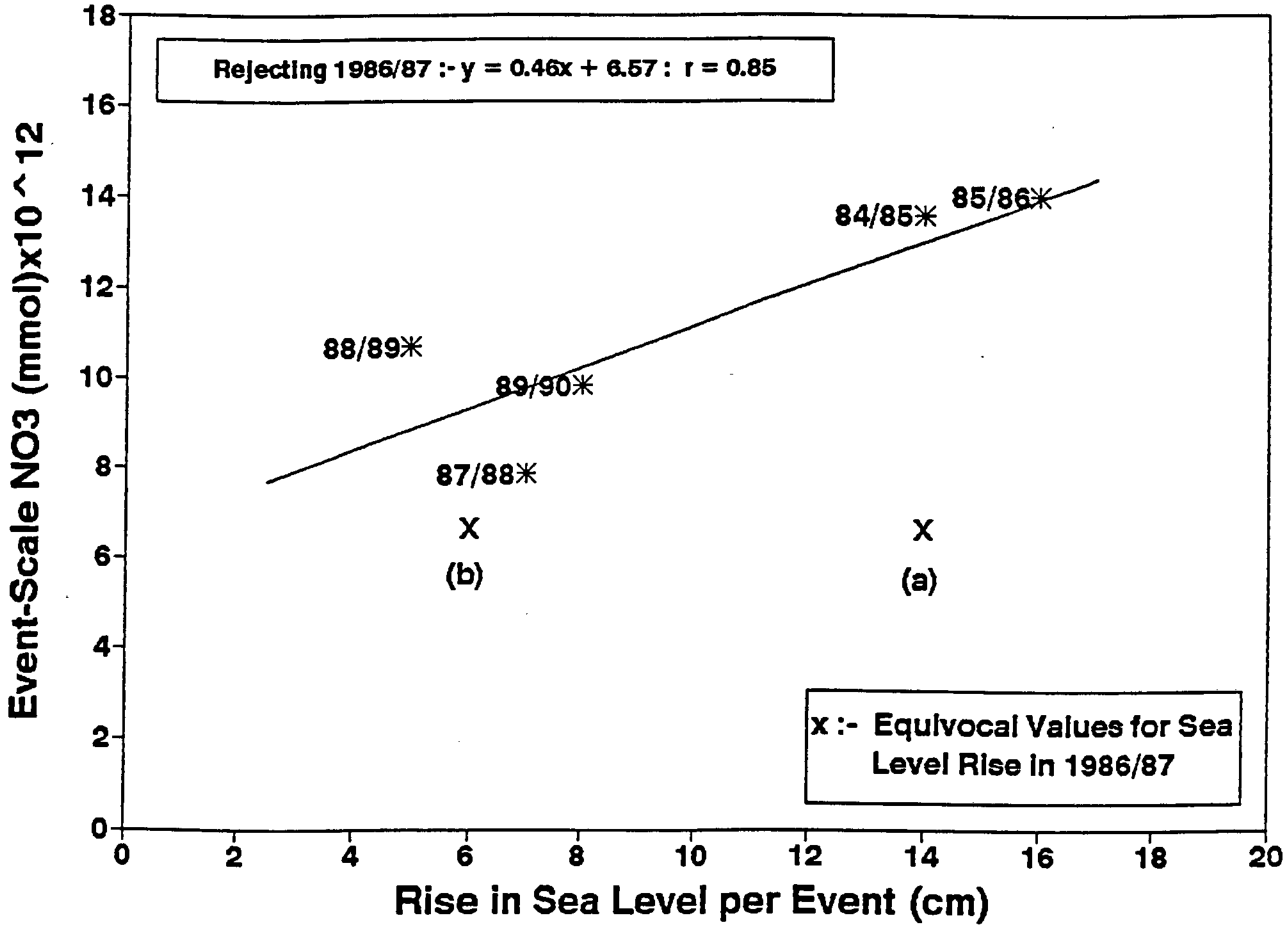


Figure 9. Rise in sea level at Saldanha Bay preceding upwelling events in the period 1984/85 to 1989/90 plotted against the amount of NO_3-N associated with each event.

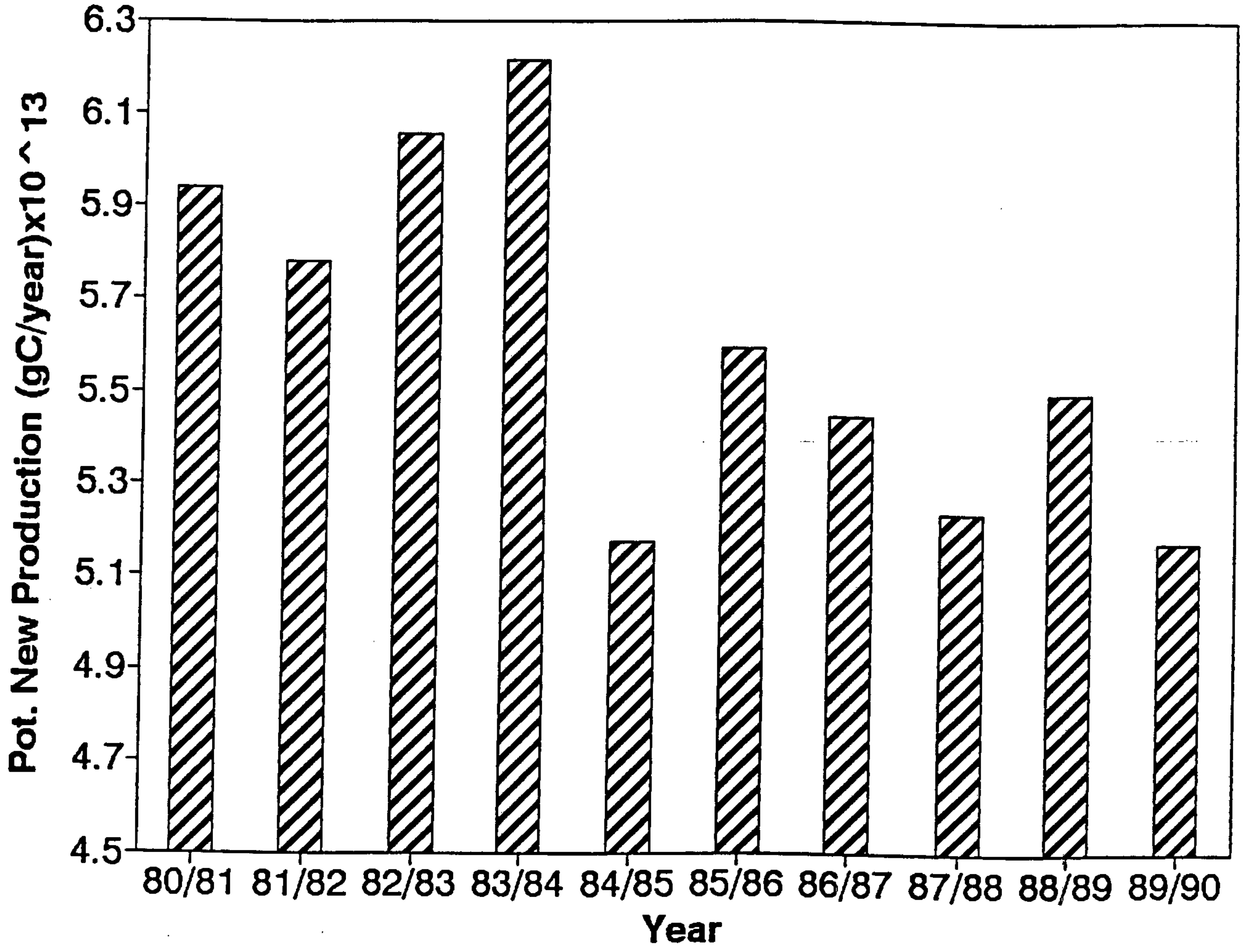


Figure 10. Annual estimates of potential new production ($gC.y^{-1}$ $x10^{13}$) for the decade of the 1980s.

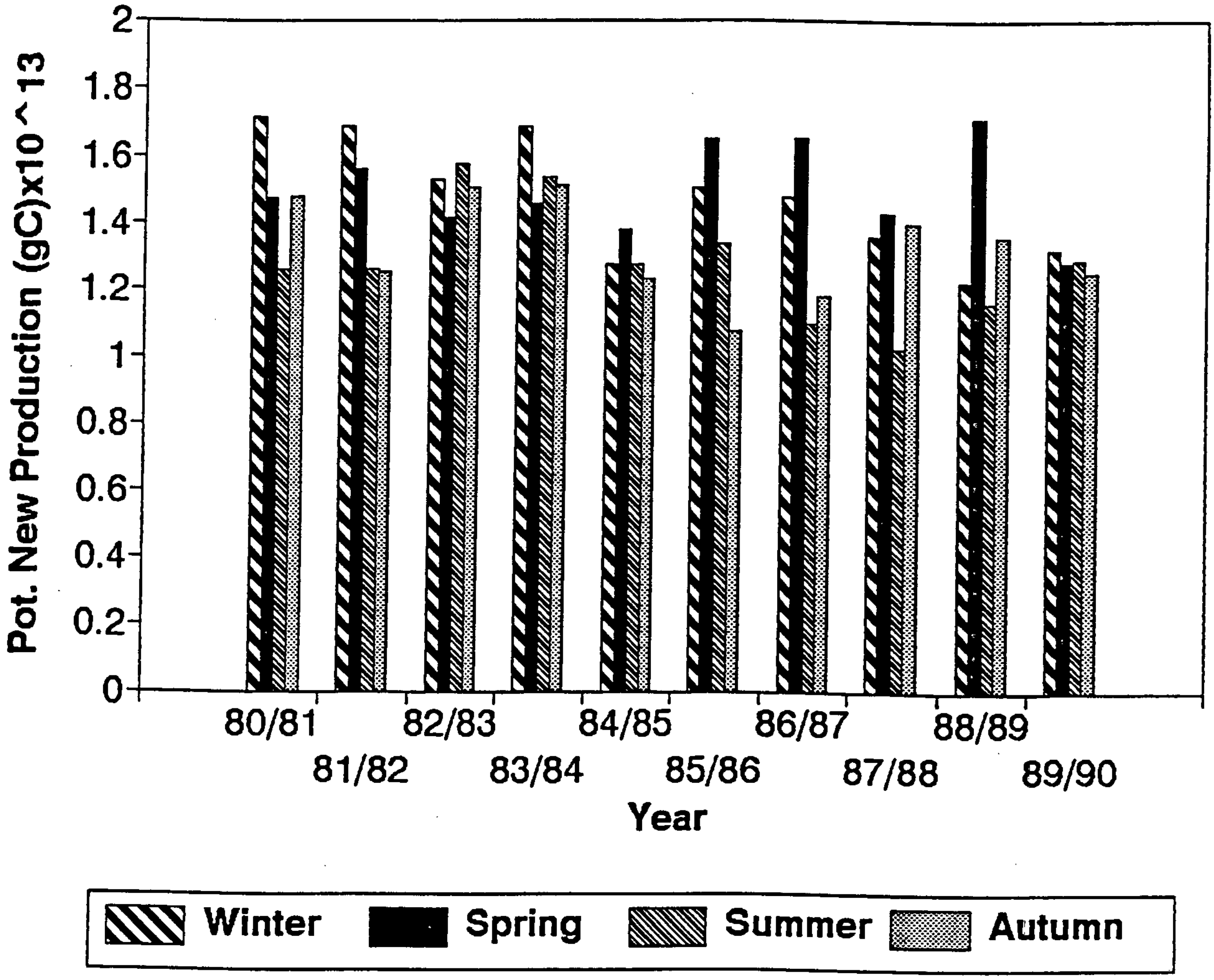


Figure 11. Seasonal components of annual potential new production estimates for the decade of the 1980s.

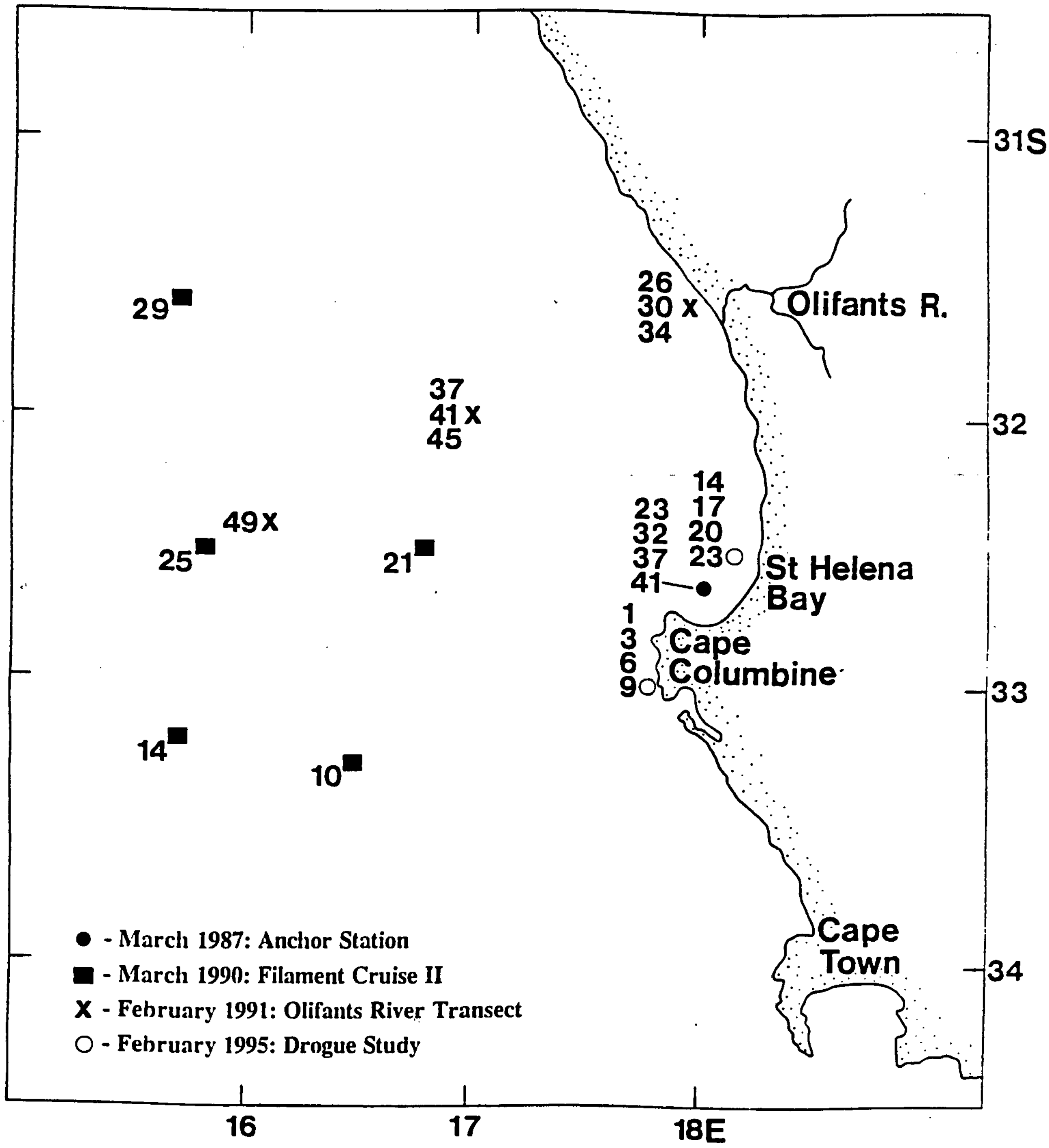


Figure 12. Location of stations in the southern Benguela where $^{15}NO_3$-N experiments were conducted on the phytoplankton to determine their NO_3-N uptake.

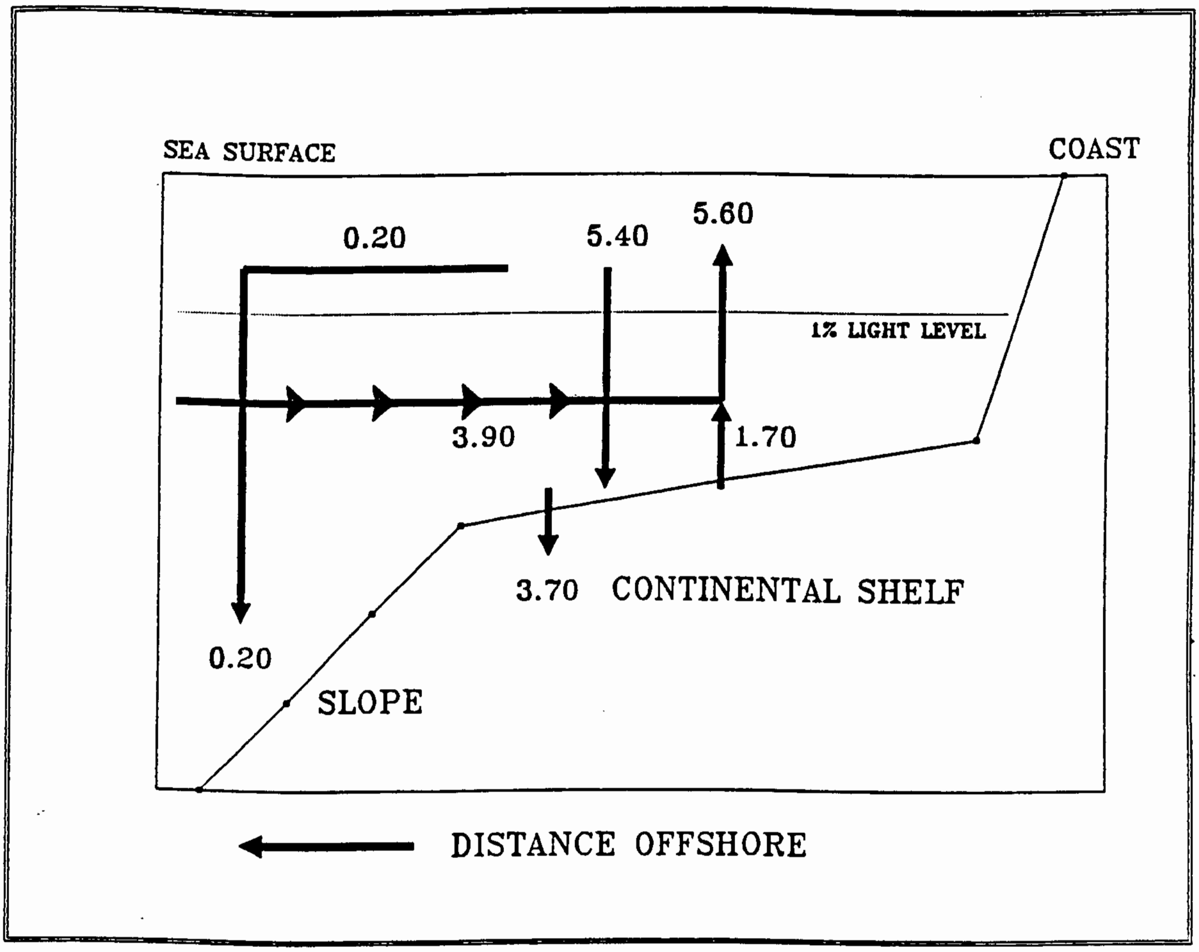


Figure 13. Two dimensional network of carbon pathways between ocean, shelf and sediment. Annual estimates of carbon flux (gC x10^{13}) have been assigned to each pathway.

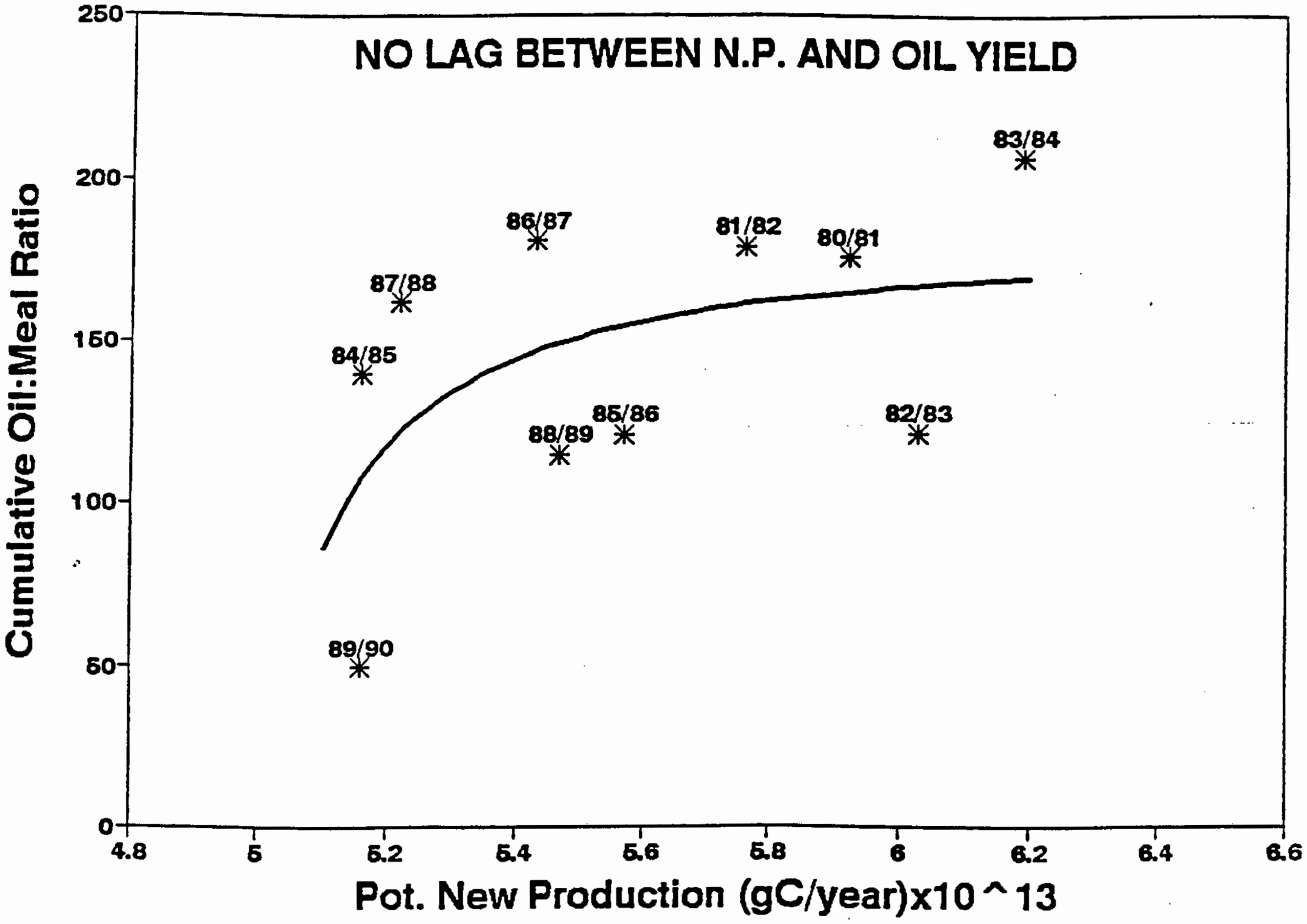


Figure 14. Annual potential new production *vs* cumulative oil:meal ratio (annual) with no time lag between the variables. The spread of data was indicative only, of a rectangular hyperbola fit.

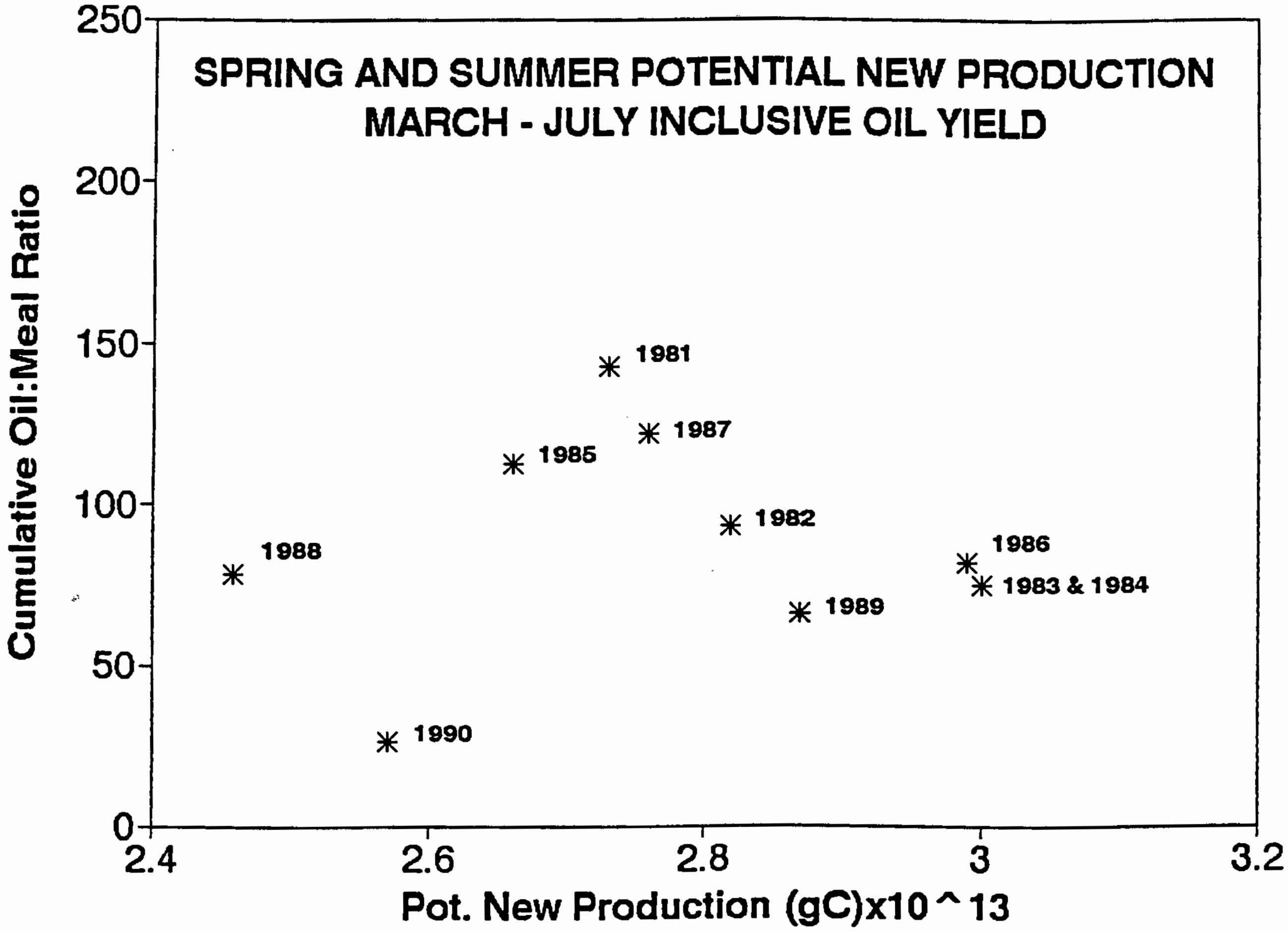


Figure 15. Potential new production for the combined Spring and Summer period (September - February inclusive) *vs* cumulative oil:meal ratio for the following March - July inclusive period.

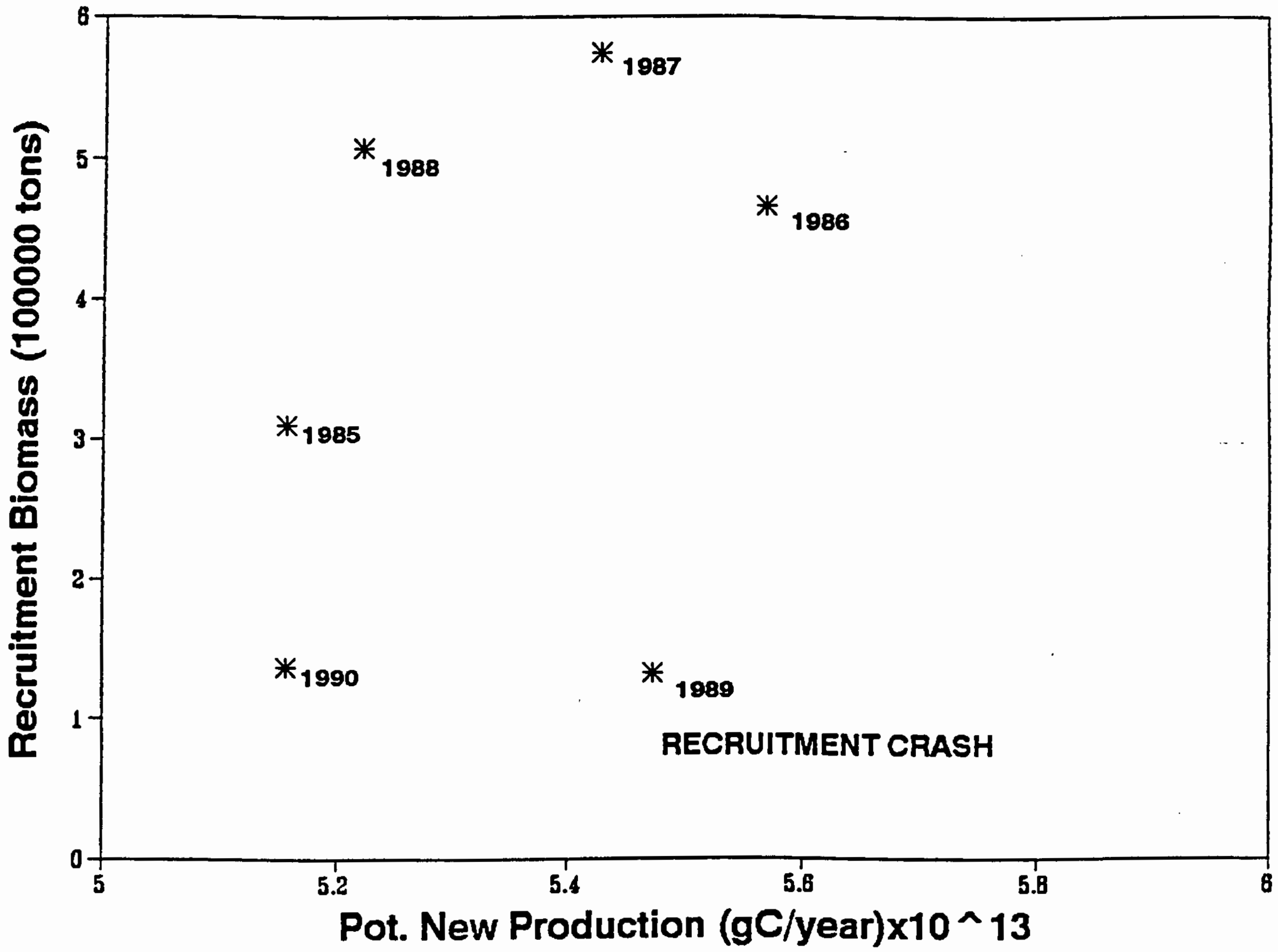


Figure 16. Annual estimates of potential new production *vs* recruitment biomass (measured acoustically at the end of the potential new production period i.e. in May of each year). Recruitment biomass estimates were not available prior to 1985.

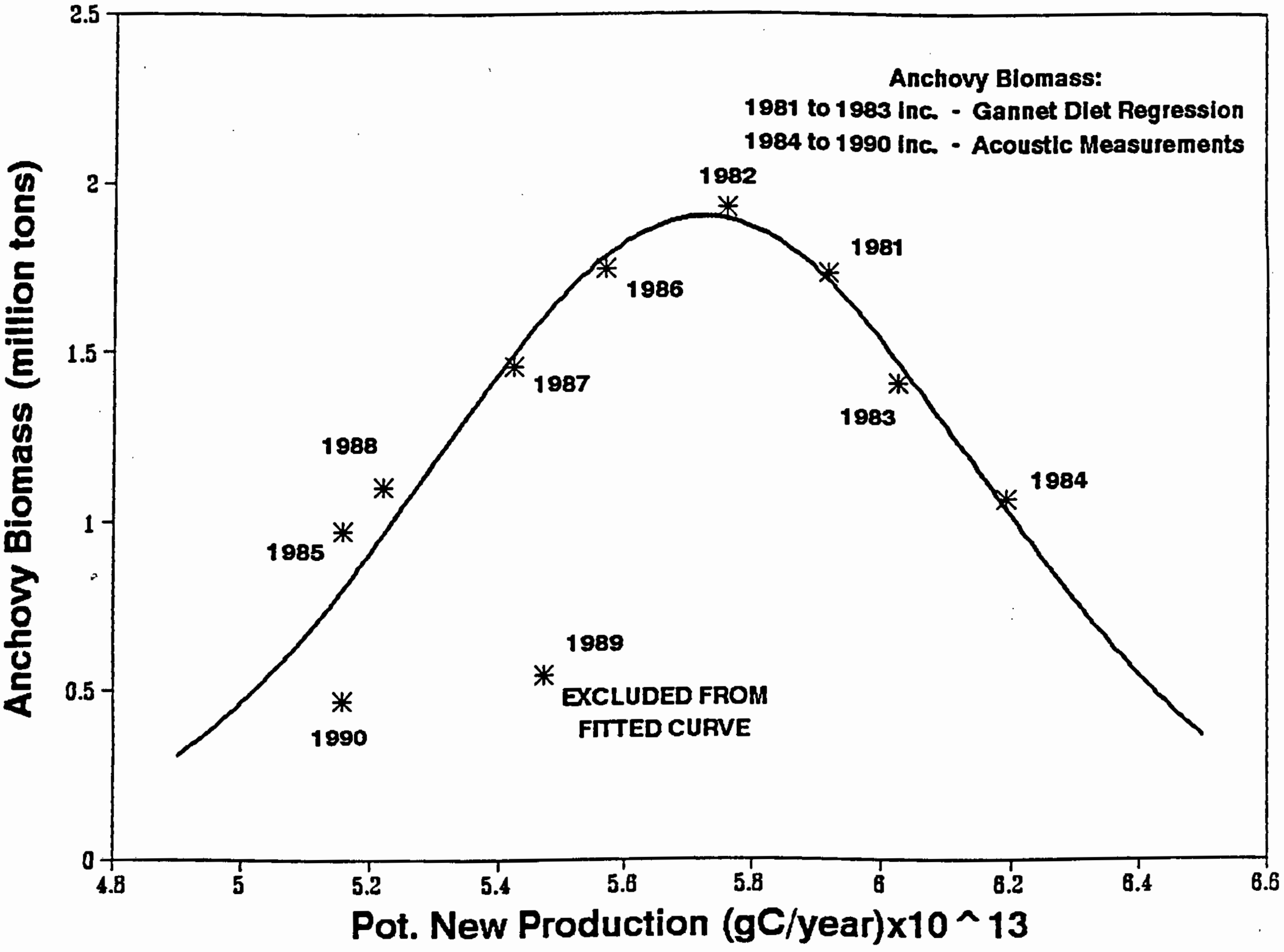


Figure 17. Annual estimates of potential new production *vs* estimates of anchovy spawner biomass. The fitted line is a Gaussian Area curve:

$$y = 1.90e^{[-0.5(x-5.72/0.43)^{\wedge}2]}.$$

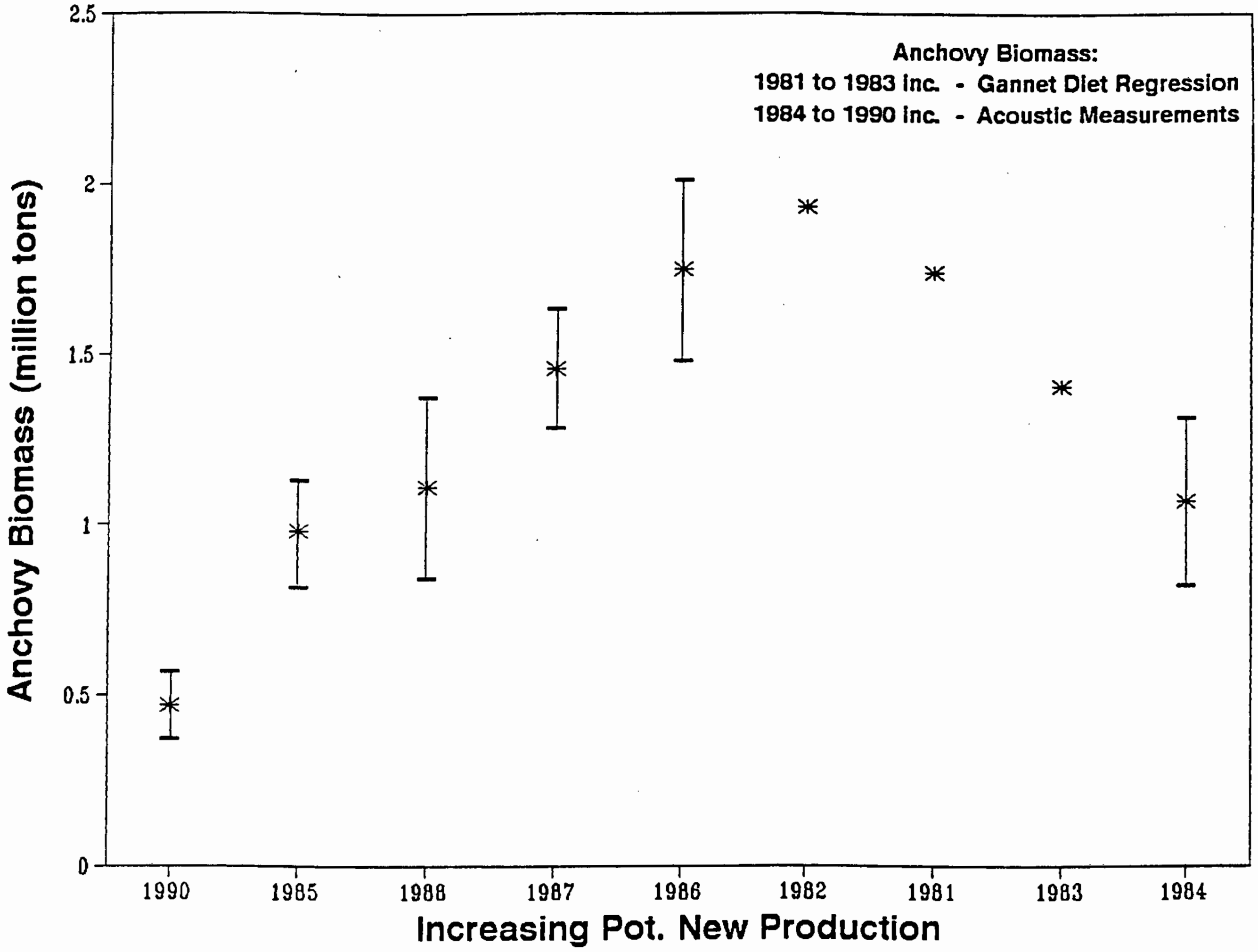


Figure 18. Annual estimates of potential new production (ranked according to year and excluding 1989) *vs* estimates of anchovy spawner biomass. Error bars on the acoustic estimates of biomass represent one standard error. Error bars are not yet available for the regressed values of anchovy biomass (R. Crawford, Pers. Comm.).