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SEASONAL AND INTERANNUAL VARIABILITY IN PHYTOPLANKTON BIOMASS ON THE SOUTHERN AFRICAN CONTINENTAL SHELF: EVIDENCE FROM SATELLITE-DERIVED PIGMENT CONCENTRATIONS

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Surface ocean phytoplankton biomass variability on the southern African continental shelf area is investigated using coastal zone colour scanner data for the period 1979–1986. Coherent interannual trends in surface ocean chlorophyll for both the west coast Benguela and the south coast Agulhas Bank areas correspond with sea surface temperature records, rather than with local records of upwelling-favourable winds. This finding implies that interannual variability in phytoplankton biomass, in contrast to the well-established seasonal cycle, is associated with large-scale oceanic circulation features and forcing mechanisms, rather than with localized upwelling events. The most probable causative mechanism is suggested to be anomalous advective fluxes of warm surface water into areas typically of high biomass deriving from the Agulhas Current retroflection in the south. Studying variability in phytoplankton biomass on the continental shelf in the context of large-scale oceanic circulation features is important to understanding long-term trends in productivity and fisheries resources.

Phytoplankton productivity in the surface ocean forms the basis of the marine food chain and the oceanic carbon cycle. Knowledge of the factors controlling phytoplankton biomass, on various spatial and temporal scales, is essential to understanding the processes determining the size of fish stocks (Parsons *et al.* 1984) and to predicting the removal of anthropogenic carbon dioxide from the atmosphere (Anderson *et al.* 1991). In the ocean areas surrounding southern Africa, high values of surface ocean chlorophyll associated with high phytoplankton biomass are predominantly associated with well defined centres of upwelling on the continental shelf (Shannon 1985). These include the productive Benguela upwelling area and some minor upwelling cells on the Agulhas Bank.

The nature of seasonal variability in coastal upwelling and productivity on the southern African continental shelf has been studied in some detail (Brown *et al.* 1991, Brown and Cochrane 1991, Probyn *et al.* 1994). In the southern Benguela, high biomass of phytoplankton is associated with wind-induced upwelling, upwelling-favourable southerly winds being more pronounced from spring to autumn (Brown and Cochrane 1991). On the eastern Agulhas Bank, upwelling can be described as typical of a temperate continental shelf area (Brown 1992), with coastal upwelling induced by easterly wind confined to areas off prominent capes in summer and autumn (Probyn *et al.* 1994). Establishment of interannual trends in surface ocean chlorophyll, and their relationship to productivity on the southern African continental shelf, has been attempted using ship-based data (Brown and Cochrane 1991), but "time-series from the south and west coasts are too incomplete to be of statistical use". This limitation represents a significance obstacle to elucidating possible relationships between long-term trends in fisheries resources, primary production and environmental forcing factors.

Satellite remote sensing of ocean colour represents an unique means of establishing large-scale temporal and spatial variability in surface ocean chlorophyll, and it can be used as a proxy of phytoplankton biomass and productivity (Platt and Sathyendranath 1988, Balch *et al.* 1992). The potential of remote sensing to studying variability in ocean productivity has been illustrated in several studies utilizing data from the Coastal Zone Colour Scanner (CZCS, Strub *et al.* 1990, Comiso *et al.* 1993, Fiedler 1994, Weeks and Shillington 1994). In a similar approach, the CZCS database is herein used to evaluate phytoplankton biomass variability, which is assumed to be approximated by chlorophyll values (Platt and Sathyendranath 1988), at five distinct areas of relatively higher productivity along the South African coast (Fig. 1). These areas were chosen because of their importance during various life stages of several fish species. Understanding the variability inherent in phytoplankton biomass in these areas, and its relation to large-scale physical forcing mechanisms, is crucial to assessing the future viability of the fisheries resource, and the potential impacts of climate change scenarios.

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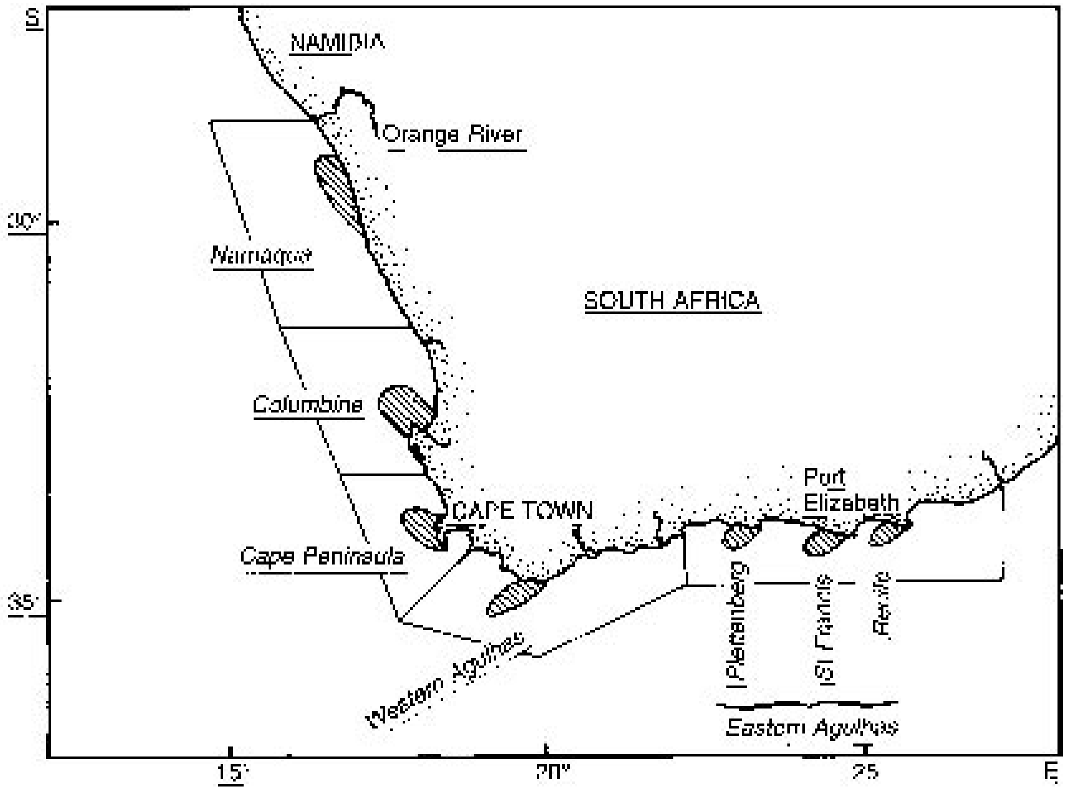

Fig. 1: Location of the five areas investigated for their satellite-based surface ocean chlorophyll content. Within each area, cut-off chlorophyll values used to determine the PBI (phytoplankton biomass index) were chosen so as to define best the centres of upwelling encompassed by each area

METHODOLOGY

The CZCS was flown aboard the *Nimbus 7* platform and collected ocean colour data from November 1978 to June 1986. Values of surface ocean chlorophyll were obtained from 3-monthly (JFM, AMJ, JAS, OND) composite Level-3 data products available from Goddard Space Flight Center's Distributed Active Archive Centre. These Level-3 products result from Level-1 radiance data processed through a pigment-concentration algorithm and diffuse attenuation coefficient algorithm, with flagged scenes containing unreliable data excluded. Assumptions in the atmospheric correction of the data processing resulted in an accuracy of 35% in ocean colour measurements in open ocean water (Case 1), and within a factor of 2 generally. The 3-monthly composites are arithmetic averages of pigments for all pixels containing valid data from daily composite images. Values are therefore not true means and are biased against conditions associated with cloud cover. Each pixel represents 0.776° latitude or longitude, or an area approximately 17 × 19.5 km in size.

Problems associated with (non-gradual) decreasing sensor sensitivity, and the implications for data applications, have been discussed in detail elsewhere (Strub *et al.* 1990, Balch *et al.* 1992, Comiso *et al.* 1993, Fiedler 1994). In short, correction for long-term changes is believed to be good, whereas short-term changes may not be accounted for. Temporal averaging "may help reduce the size of abrupt changes" and "the effects of random clouds" (Strub *et al.* 1990).

On the Agulhas Bank, remote sensing of surface chlorophyll is complicated by non-uniform pigment profiles. In general, the eastern Bank is characterized by shallower thermoclines and subsurface chlorophyll maxima than the western sector (Probyn *et al.* 1994). A subsurface chlorophyll maximum implies that the surface expression of phytoplankton biomass will be

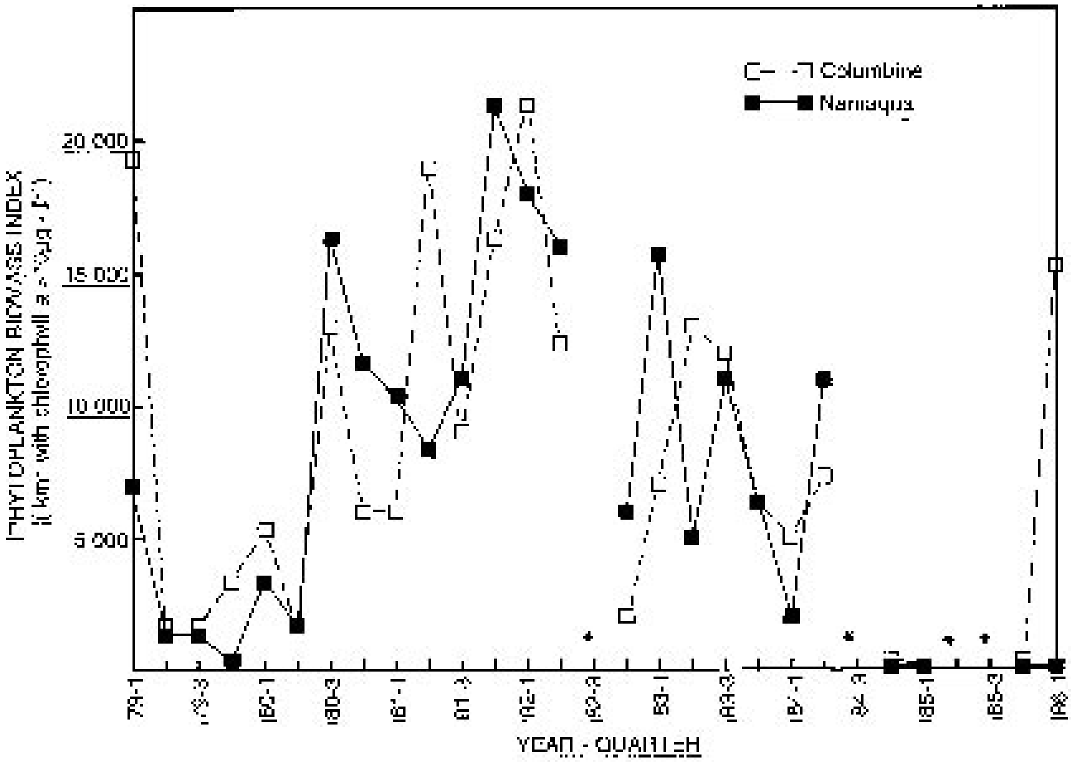

Fig. 2: Comparative quarterly values for the PBI (area represented by chlorophyll values exceeding 10 $\mu g \cdot \ell^{-1}$) at the Columbine ad Namaqua upwelling cells in the southern Benguela, 1979–1986. Asterisks indicate periods with insufficient data coverage owing to cloud-cover

more limited, and remote sensing techniques may underestimate the true value. As, however, the deep chlorophyll maximum is typically associated with lower rates of primary productivity (Brown 1992), the implications for remotely sensed data may be somewhat diminished. With this in mind, the data presented here are evaluated qualitatively only.

RESULTS AND DISCUSSION

Interannual variability in phytoplankton biomass along the South African coast

The five areas investigated in this study encompass the Namaqua upwelling cell (off Hondeklip Bay), the Columbine cell (off Cape Columbine and St Helena Bay), the Cape Peninsula cell, and the western (in the vicinity of Cape Agulhas) and eastern Agulhas Bank (combination of Plettenberg, St Francis and Recife upwelling cells). Their locations are shown in Figure 1. The Columbine and Namaqua cells in the southern Benguela represent the areas of most intense upwelling along the South African coast (Brown and Cochrane 1991) and are characterized by both the highest values of nearshore surface chlorophyll and the most extensive offshore extension of enhanced chlorophyll. Phytoplankton biomass at those two sites are compared on the basis of the areal extent of surface water chlorophyll values exceeding 10 $mg \cdot m^{-3}$, which typifies conditions in the vicinity of active upwelling centres. Cut-off values at lower chlorophyll values found on the continental shelf produce the same result; results are presented based on the higher value, which constrains the areas of interest to specific upwelling cells. Although the other three study areas have relatively lower phytoplankton biomass, they are in close proximity to fish spawning areas (Hutchings 1994) and may therefore serve as important feeding areas during critical stages of the life cycle of pelagic fish. As phytoplankton biomass at these

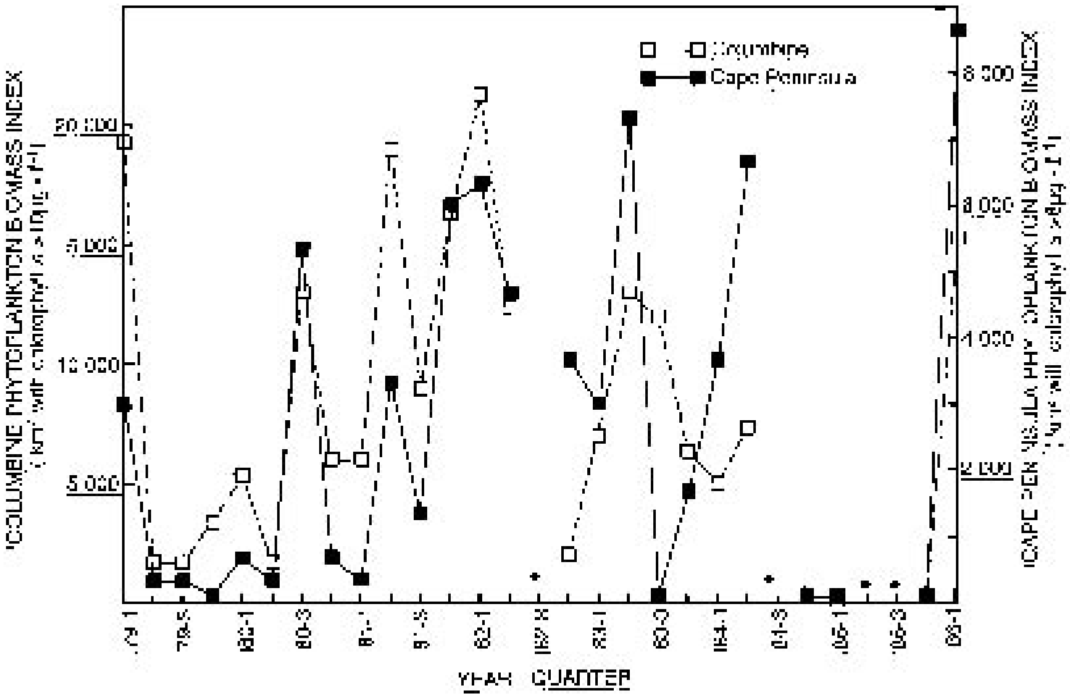

Fig. 3: Comparative quarterly values for the PBI established at the Columbine and Cape Peninsula upwelling cells, measured as the area represented by chlorophyll values exceeding 10 and 6 μg·ℓ$^{-1}$ respectively, 1979–1986. Asterisks indicate periods with insufficient data coverage owing to cloud-cover

sites is generally lower than in the southern Benguela, a lower value of surface chlorophyll (6 mg·m^{-3}) is used to best represent variability inshore of the shelf edge.

COLUMBINE

The most pronounced feature of interannual variability in phytoplankton biomass at Columbine, also evident at the other areas studied, is a marked decrease in biomass during 1979/80, followed by a gradual increase, which peaked in 1981/82 (Fig. 2). Although relatively sparse data coverage for the period mid-1984 to mid-1985 precludes establishing the extent of seasonal variability in phytoplankton biomass, the data are suggestive of reduced biomass, similar to that observed in 1979/80. High phytoplankton biomass during the annual peak varies in areal extent by as much as a factor of 4 during the period 1979–1986.

NAMAQUA

The marked interannual variability in biomass observed at Columbine, i.e. reduced biomass during 1979/80 followed by a gradual increase, is also evident at the Namaqua cell (Fig. 2). There are, however, notable differences between these two adjacent cells. The seasonal peak in phytoplankton biomass during 1981 and 1985/86 is present at Columbine, but absent at Namaqua. Another interesting difference is the offset in the timing of peak phytoplankton biomass in 1981/82 and early 1983, with the initiation of enhanced productivity at Namaqua preceding that at Columbine in both cases (Fig. 2).

CAPE PENINSULA

Interannual variability in phytoplankton biomass at the Cape Peninsula cell exhibits the best co-variation with Columbine of all the areas studied (Fig. 3). The only difference between the two appears to have been in 1983/84, when peak phytoplankton biomass at the Cape Peninsula cell equivalent to that of the preceding years contrasted with the conditions at Columbine. Also interesting is the fact that the biomass

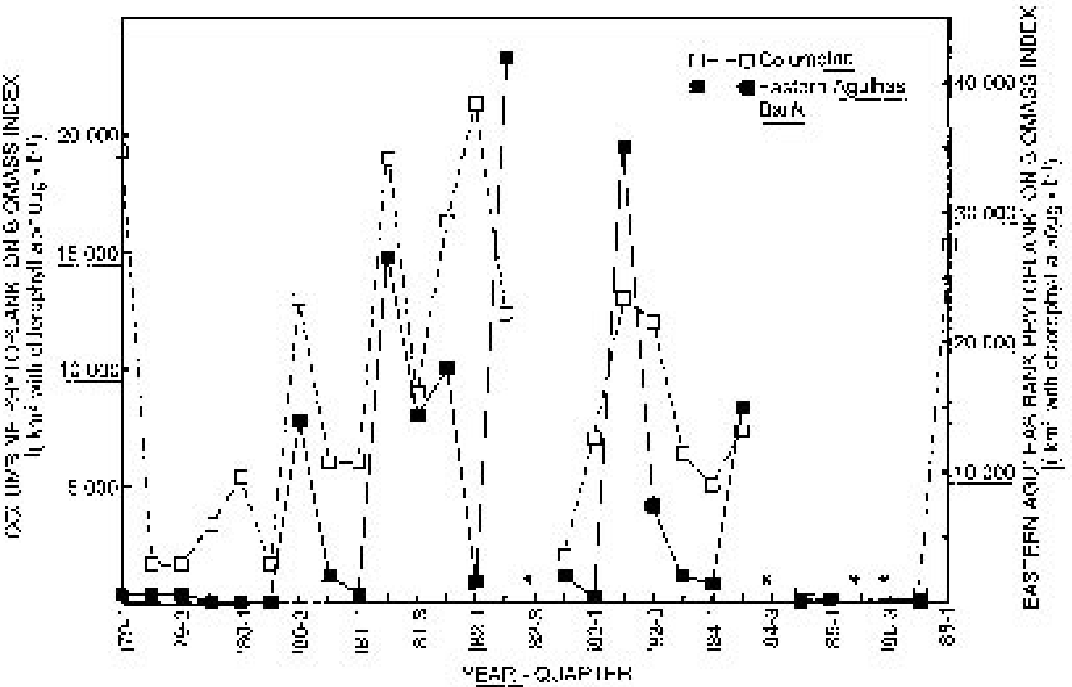

Fig. 4: Comparative quarterly values for the PBI established at the Columbine and eastern Agulhas Bank upwelling cells, measured as the area represented by chlorophyll values exceeding 10 and 6 μg·ℓ$^{-1}$ respectively, 1979–1986. Asterisks indicate periods with insufficient data coverage owing to cloud-cover

peak in early 1981, absent at Namaqua as mentioned above, is present at both the Columbine and Cape Peninsula cells.

WESTERN AND EASTERN AGULHAS BANK

The general trend in interannual variability in phytoplankton biomass on the Agulhas Bank mirrors that in the southern Benguela (Fig. 4), suggesting that large-scale forcing mechanisms may be at work. However, small differences do exist, e.g. the apparent absence of enhanced biomass on the Agulhas Bank in early 1979, when the other sites had elevated biomasses. Although the western and eastern Agulhas Bank are characterized by different hydrographic conditions, the surface expression of phytoplankton biomass in these two areas shows remarkable agreement, especially in terms of temporal coherence of the peak biomass period (Fig. 5). The most notable difference between the western and eastern Agulhas Bank appears to be variability in the relative magnitude of peak productivity.

Seasonality of peak phytoplankton biomass

Although there is a remarkable degree of correspondence in interannual variability in the phytoplankton biomass over the five upwelling areas (Figs 2–5), the period in which the areal extent of high biomass is most pronounced differs (Fig. 6). At the northernmost West Coast site, the Namaqua upwelling cell, biomass is greatest during summer (JFM), a result supported by Brown (1992) in her study of *in situ* chlorophyll data. Farther south there is a progressive decrease in the frequency of peak summer biomass, and a trend towards predominantly autumn (AMJ) enhanced phytoplankton abundance on the western and eastern Agulhas Bank. Lower chlorophyll values on the Agulhas Bank during summer has been recorded elsewhere and attributed to nutrient-limitation caused by a more stratified water column (Brown 1992). Another observation borne out by the study of Brown (1992), i.e. seasonal biomass variability in the southern Benguela, is not very pronounced, at least for the period 1979–1986 (Fig. 6).

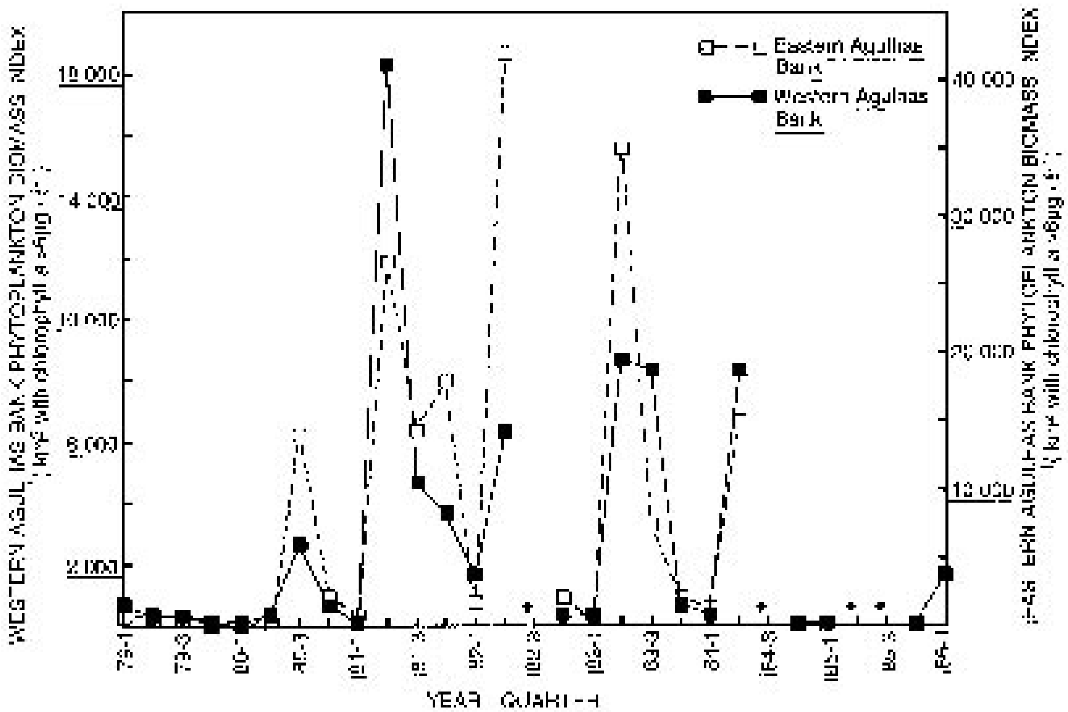

Fig. 5: Comparative quarterly values for the PBI established at the western and eastern Agulhas Bank upwelling cells, measured as the area represented by chlorophyll values exceeding 6 μg·ℓ$^{-1}$, 1979–1986. Asterisks indicate periods with insufficient data coverage owing to cloud-cove

The importance of the timing of the peak phytoplankton biomass abundance can be evaluated in the context of its phasing relative to specific stages in the life cycle of pelagic fish. Anchovy *Engraulis capensis*, for example, spawn on the western Agulhas Bank from October to February. The eggs and larvae are then transported to the West Coast to inshore nursery areas, with recruitment beginning in April/May (Hutchings 1992). The young fish then move south to the Agulhas Bank, where they spawn at an age of about one year. The critical larval stage therefore coincides with periods of enhanced phytoplankton biomass.

Offshore extent of high phytoplankton biomass at Cape Columbine

The offshore extent of high phytoplankton biomass was determined on an east-west transect across the Columbine cell (Fig. 7). The most striking aspect of phytoplankton biomass along the Columbine transect is the considerable amount of variability involved. The 5 mg·m^{-3} isoline is located anywhere from the coast to 140 km offshore, whereas the 10 mg·m^{-3} isoline occasionally reaches distances of 100 km offshore. The dataset also highlights one of the inherent limitations of coastal monitoring sites: the gradual increase in biomass during the period 1979–1982 is best expressed offshore, with relatively less interannual variability expressed closer to the coast. This is an important point to consider when attempting to relate time-series data obtained from coastal monitoring sites to large-scale features, and in choosing locations for palaeoceanographic studies of ocean productivity.

A knowledge of the position of the phytoplankton biomass "front" in relation to the cross-shelf faunal boundaries is important to understanding the effect of hydrodynamics on the distribution of biological populations. It has been suggested that chlorophyll concentrations can be used to distinguish between phytoplankton taxa and size (Brown and Cochrane 1991, Mitchell-Innes and Pitcher 1992), concentrations

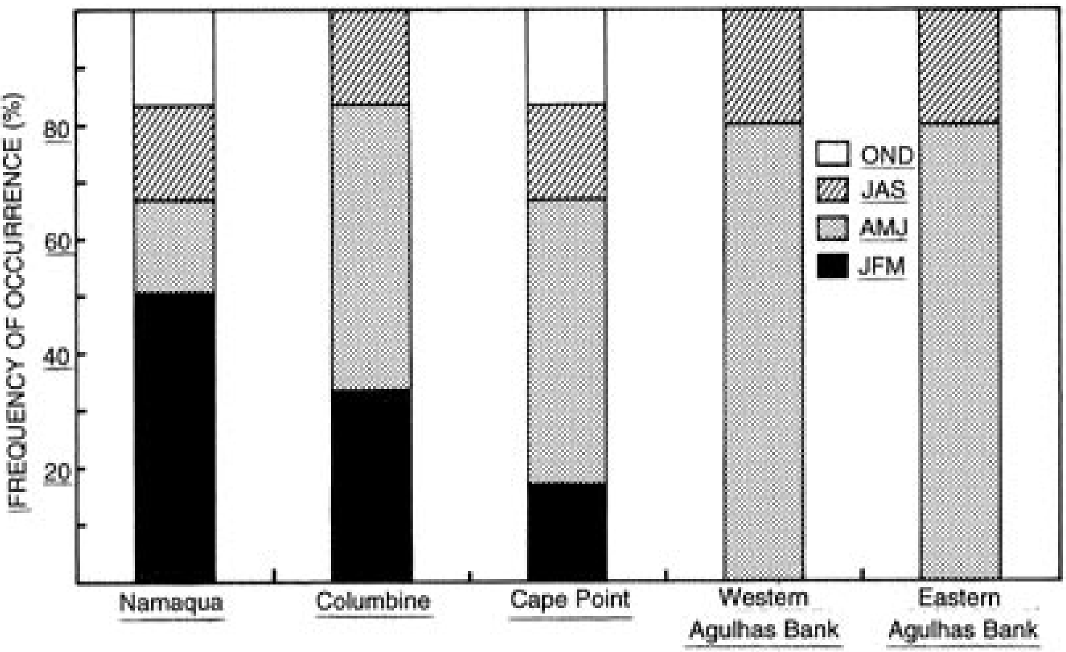

Fig. 6: Frequency of the seasonal (JFM, AMJ, JAS, OND) occurrence of the peak phytoplankton biomass period for the period 1979–1986 for the five areas studied, based on the CZCS-based PBI index

<3 mg·m^{-3} being roughly equated with small cells such as microflagellates, and concentrations >3 mg·m^{-3} with large-celled diatom-dominated communities. In addition, euphausiids, a major component of the zooplankton diet of many fish species in the Benguela, display distinctive cross-shelf distribution patterns (Barange and Boyd 1992), which may in turn relate to their own preferred prey. Establishing offshore trends in chlorophyll values may therefore provide insight into the location of faunal boundaries and have important implications for the trophic structure of different parts of the Benguela upwelling system.

An increase in the offshore extent of high phytoplankton biomass does not necessarily imply better fish recruitment associated with an enhanced food supply. If the increased offshore extent of phytoplankton biomass accompanies increased longshore winds of sufficient magnitude, the associated increased offshore advection and turbulence may be detrimental to the year-class strength of some fish species (Crawford *et al.* 1990), rather than advantageous. Limited offshore upwelling, on the other hand, may result in the shoreward migration of species such as hake (Shannon *et al.* 1988), and possibly even increased catches. Also important to consider is the duration of upwelling events. As mentioned before, phasing between phytoplankton productivity cycles and that in zooplankton is critical to the efficiency of the marine foodweb (Hutchings 1992). The 3-monthly averaged data presented here cannot be used to address these processes, and future studies employing remote sensing techniques will have to concentrate on events happening on time-scales of days to weeks.

Interannual variability in phytoplankton biomass in relation to environmental indices

On the inner continental shelf, phytoplankton biomass generally increases following injection of nutrients into the surface ocean associated with upwelling events initiated by favourable longshore winds. Several studies concerned with the effect of environmental variability on fisheries resources have therefore attempted to relate variability in coastal upwelling in the southern Benguela with coastal wind records (Nelson and Hutchings 1983, Walker 1986, Hutchings and Taunton-Clark 1990, Shannon *et al.* 1990a). In the case of Cape Columbine, as illustrated in Figure 8, it is clear that the relationship between

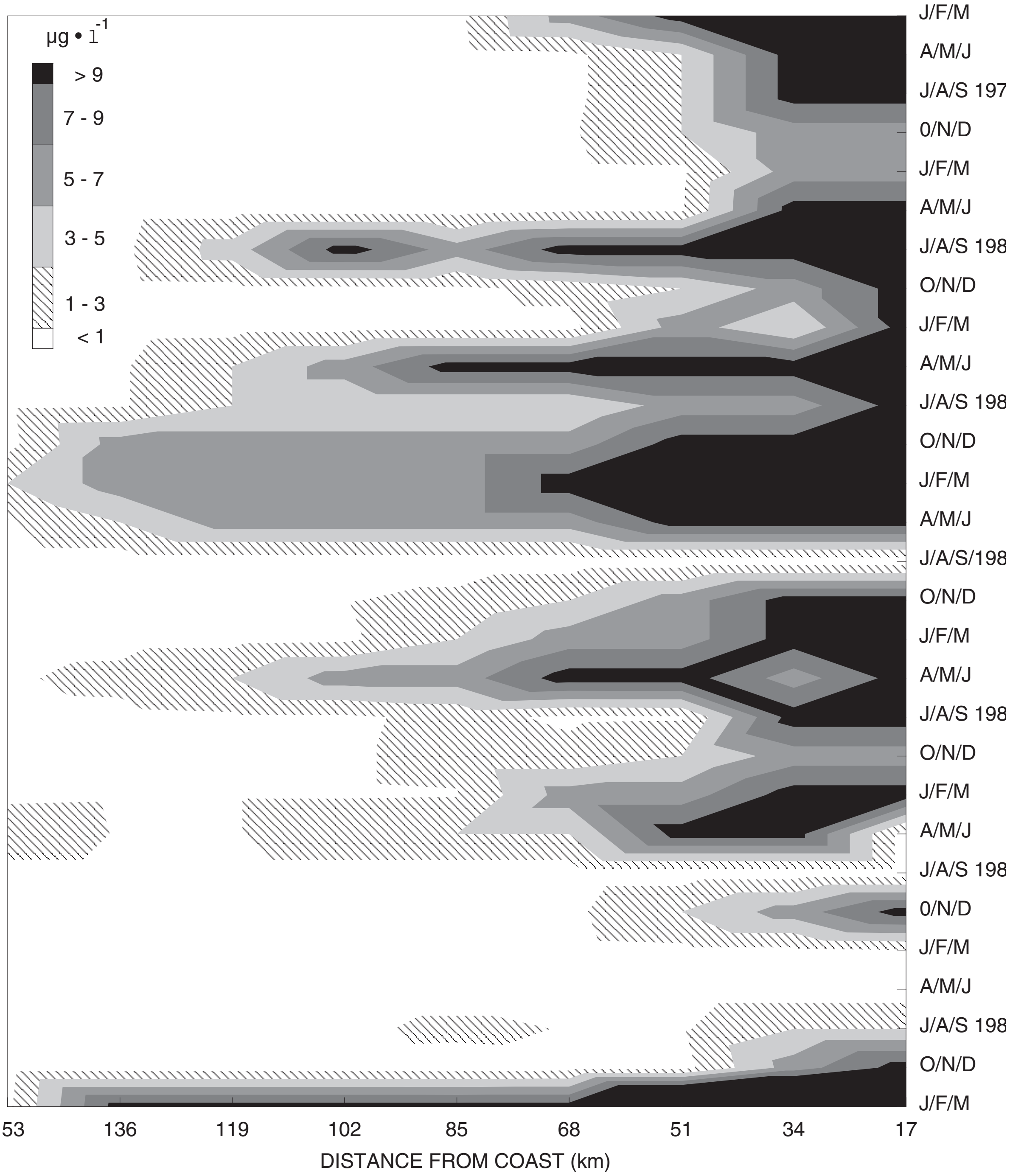

Fig. 7: The offshore extent of upwelling at Columbine, as deduced from CZCS-based chlorophyll values for pixels along the line indicated in Figure 1

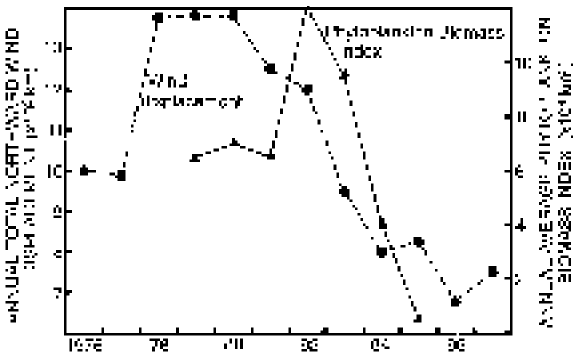

Fig. 8: Interannual variability in the PBI at the Columbine upwelling area, compared to the long-term trend in northward, upwelling-favourable, wind displacement, as obtained from Hutchings and Taunton-Clark (1990)

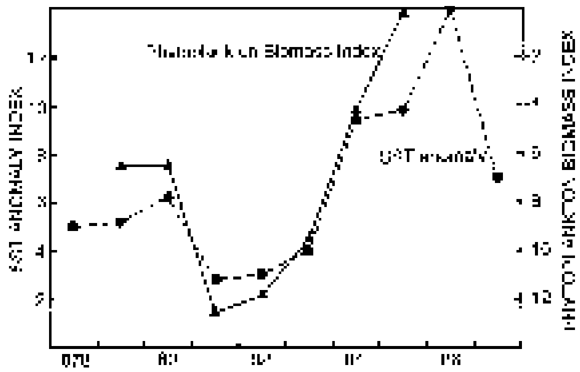

Fig. 9: Annual sea surface temperature anomalies obtained from and described in Crawford *et al.* (1990), compared to relative annually averaged PBI values for the Columbine upwelling cell

upwelling-favourable winds and phytoplankton biomass is not straightforward. Although the period of least favourable upwelling winds, 1984–1985, coincides with the period of lowest phytoplankton biomass, the opposite is not true. The period of most pronounced upwelling-favourable winds (1978–1980) coincides with intermediate phytoplankton biomass, whereas the highest phytoplankton biomass occurs in the years 1982–1983, a period of intermediate wind displacement (Fig. 8). This "decoupling" between phytoplankton biomass and local winds is, however, consistent with the proposed concept of an "optimal environmental window" (Parsons *et al.* 1984). According to that theory, increased turbulence associated with periods of high wind displacement may impede productivity rather than enhance it. It also highlights the problems associated with applying wind data obtained at fixed coastal stations to establish the extent of upwelling, and from that phytoplankton productivity, over the extensive areas inhabited by pelagic and mesopelagic fish during various stages in their life history.

Another aspect of the "decoupling" between coastal wind records and surface ocean productivity to consider is the possible role of larger-scale forcing mechanisms, such as the advective influx of warm surface water. The interannual trend in variability of phytoplankton biomass observed in the study area, i.e. increased biomass during the period 1981–1983 and relatively lower biomass during the periods preceding (1979–1980) and following (1984–1985), exhibits a remarkable agreement with records of sea surface temperature within the Benguela system (Fig. 9). High values for the SST anomaly index of Crawford *et al.* (1990), i.e. warmer conditions, agree with periods of reduced biomass, and *vice versa*. Walker (1987) also observed a "sustained cool event from 1981 to 1983" and described 1984 as "the most marked warm event" during the period 1971–1984. It has been suggested that warm anomalies in the southern Benguela are attributable to "variable penetration of the Agulhas Current into the Atlantic" (Mann 1992). Although little is known about interannual variability in the Agulhas Current retroflection, an anomalous westward penetration in early 1984 has been documented by Walker (1986); it was similar to the better known event in 1986 (Shannon *et al.* 1990b). The anomalous westward penetration of warm Agulhas Current water as a causative mechanism for interannual variability in phytoplankton biomass in the southern Benguela provides a possible explanation for the remarkable correspondence between West Coast and Agulhas Bank sites.

Nevertheless, the overall picture may be more complex than simply variability in the longitudinal extent of Agulhas Current retroflection, as suggested by the following observations:

(i) reduced biomass during 1984 also coincides with the occurrence of a recognized Benguela *Niño*, and a positive SST anomaly in the equatorial Atlantic similar to a small positive SST anomaly in the equatorial Atlantic in 1979/80 (Carton and Huang 1994);

(ii) 1980 and the period 1984–1985 are characterized by reduced zonal wind stress in the equatorial Atlantic relative to the period 1981–1983 (Carton and Huang 1994);

(iii) the Subtropical Convergence in the South Atlantic reached its southernmost extreme (for the period 1976–1983), during the summer of 1979/80 (Walker *et al*. 1984), i.e. coinciding with the period of minimum phytoplankton abundance established in this study.

During October to March 1979/80 and 1982/83, the 20°C sea surface temperature isotherm in both the South-West Indian Ocean and south-eastern Atlantic showed a distinctive warming trend in a southerly direction (Gillooly and Walker 1984, Walker 1987). Periods of reduced productivity in the northern Benguela have been linked to Benguela *Niños* (Crawford *et al*. 1990), which are characterized by periods of reduced zonal wind stress in the western equatorial Atlantic, followed by increased advection of warm water towards the south (Shannon *et al*. 1990a). Although the southern Benguela is believed to be beyond the range of the southward migration of the Angola/Benguela front, the existing data do not rule out its possible influence farther south. The results presented here suggest that, in order to understand long-term trends in productivity on the southern African continental shelf, environmental processes need to be scrutinized not only on a local scale, but in the context of the larger-scale processes that determine, for example, Agulhas Current flow into the Atlantic, and possibly also Benguela *Niños*.

CONCLUSIONS

It is suggested that interannual variability in upwelling intensity on the South African continental shelf is associated with the increased advection of warm surface water, rather than anomalies in the local windfield. The most probable source of this warm water is the westward penetration of the Agulhas Current retroflection, although a possible link to Benguela *Niños* cannot be ruled out. Benguela *Niños* are linked to processes in the equatorial Atlantic, and variable westward penetration of the Agulhas Current presumably to processes in the Indian Ocean. Although the timing of such events does not coincide with the well-known ENSO event, it is possible that a connection between these processes is hidden within a lag period, induced by the nature of the teleconnection. To understand processes such as productivity and its relation to fisheries resources on a local scale, it is therefore necessary to consider physical forcing mechanisms associated with global scale processes.

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