S. Afr. J. mar. Sci. 21: 217–233
1999

SEASONAL CHANGES IN PHYTOPLANKTON BIOMASS ON THE WESTERN AGULHAS BANK, SOUTH AFRICA

*B. A. MITCHELL-INNES**, *A. J. RICHARDSON*† *and S. J. PAINTING**

Data on temporal and spatial changes in phytoplankton biomass and distribution on the western Agulhas Bank during the main spawning season of pelagic fish were obtained from monthly cruises conducted between August and March in 1993/94 and September and March in 1994/95. The period was divided into three oceanographic seasons based on different levels of upwelling activity: late winter (August and September), spring (October–December) and summer (January–March). Cross-shelf and vertical distribution patterns of chlorophyll changed markedly during these seasonal periods, reflecting changes in hydrographic structure and in nutrient availability. During late winter, chlorophyll was evenly distributed in the deep, upper-mixed layer (>40 m) across the shelf. A clump-forming *Thalassiosira* sp. contributed to the moderately high mean chlorophyll concentration (1.9 mg·m^{-3}) in the upper 30 m. In October and/or September, warming of surface waters inshore gave rise to a modest (2–5 mg chl·m^{-3}) spring bloom, typical of the temperate zone. This was terminated in November by an influx across the shelf of warm, nutrient-impoverished water. Upwelling was sporadic and weak in spring. Summer was characterized by intense, episodic upwelling inshore, with pronounced cross-shelf thermal gradients, intensified by the presence of water of Agulhas origin along the shelf-edge. During an upwelling cycle, rapid hydrographic and biological changes occur over four phases: onset of upwelling, sustained upwelling, quiescence and downwelling. The upwelling productive zone, bounded by the 20°C isotherm, varied from <12 to 50 miles across the shelf. Chlorophyll was low in newly upwelled water (<0.5 mg·m^{-3}) and attained peak concentrations in mature upwelled water (5–25 mg·m^{-3}). Outside the productive zone, mean chlorophyll levels were low (<0.5 mg·m^{-3}). Enhanced phytoplankton growth during the spring bloom in September and/or October may be an important factor contributing to spawning success of pelagic fish in the southern Benguela.

The South African Sardine and Anchovy Recruitment Programme (SARP) was conducted during a two-year period from August 1993 to March 1995 in the southern Benguela (Painting *et al.* in press a, b). The sampling programme covered three regions of importance in the life cycle of the commercially important anchovy *Engraulis capensis*: the western Agulhas Bank, a major spawning ground between August and March; the Cape Peninsula region, important during the larval transport phase; and the West Coast, a nursery for juvenile fish (Hutchings 1992). One of the primary objectives of SARP was to study within-season variability of the spawning of anchovy in response to such environmental conditions as hydrography and food availability for larval and adult anchovy (Painting *et al.* in press a, b).

The western Agulhas Bank is situated between Cape Point and Cape Agulhas off the south of the African continent (Fig. 1). The coastline is irregular, with several capes and bays, and the shelf is broad and evenly sloping. The outer shelf is strongly influenced by oceanic flow originating from the western boundary Agulhas system, whereas the inner shelf is characterized by upwelling typical of the eastern boundary system of the Benguela (Boyd *et al.* 1985, Largier and Swart 1987, Largier *et al.* 1992, Boyd and Shillington 1994). These contrasting influences are most pronounced in summer, when upwelling is well established and when quasi-steady north-westward flow of Agulhas Current water along the shelf-edge is greatest (Largier *et al.* 1992). Warm Agulhas Current water (>21°C) pushes shorewards against the cold, productive coastal water, creating strong thermal gradients, a feature of the region in summer. Under those conditions, the shelf-edge jet current embedded within the frontal region and intensified by convergence as the shelf narrows towards Cape Point, funnels coastal water from the western Agulhas Bank northwards (Hutchings 1992). In that way, eggs and larvae of pelagic fish are transported away from the western Agulhas Bank to their nursery grounds on the West Coast (Hutchings 1992).

The physical processes operating on the western Agulhas Bank strongly affect the temporal and spatial distribution of phytoplankton, resulting in a combination of temperate zone and upwelling seasonal patterns

* Marine & Coastal Management (formerly Sea Fisheries), Private Bag X2, Rogge Bay 8012, Cape Town, South Africa.
E-mail: bminnes@sfri2.wcape.gov.za
† Oceanographt Department, University of Cape Town, Private Bag, Rondebosch 7701, Cape Town, South Africa.
E-mail: arichard@physci.uct.ac.za

Manuscript received: June 1998

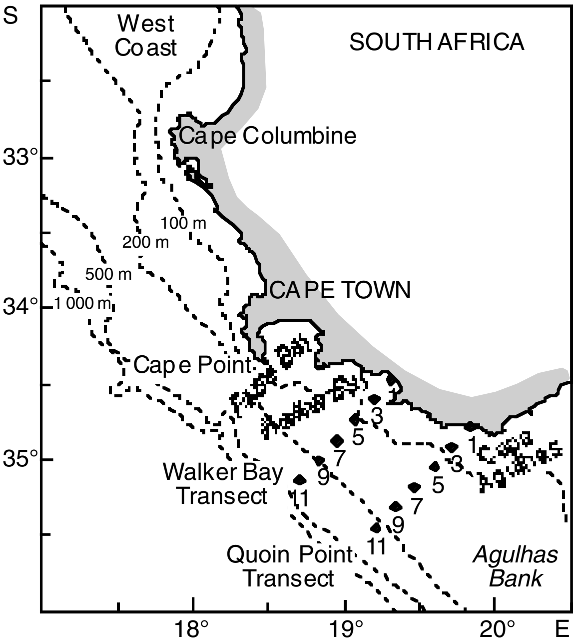

Fig. 1: Map of the South-Western Cape showing the Walker Bay and Quoin Point transects sampled during the SARP study

(Tromp *et al.* 1975, Shannon *et al.* 1984, Boyd *et al.* 1985, Probyn *et al.* 1994). In winter, strong turbulent mixing results in evenly distributed chlorophyll within a deep (60 m), upper-mixed layer across the shelf (Boyd *et al.* 1985, Largier *et al.* 1992). Increasing stratification in early spring gives rise to inshore blooms typical of the temperate zone (Shannon *et al.* 1984). In summer, upwelling processes dominate and high chlorophyll concentrations develop inshore, particularly in Walker and False bays (Tromp *et al.* 1975, Shannon *et al.* 1984, Brown 1992). Oceanic forcing results in intrusions of warm water of Agulhas origin along the shelf-edge. These intrusions intensify stratification over the midshelf in summer, forming a continuation of the trough in the thermal structure which extends south of Cape Agulhas and eastwards to the central Agulhas Bank (Largier *et al.* 1992, Probyn *et al.* 1994). Deep, subsurface chlorophyll maxima are characteristic of mid- and outershelf waters on the Agulhas Bank in summer (Carter *et al.* 1987, Probyn *et al.* 1994).

Successful spawning by anchovy on the Agulhas Bank and the subsequent growth and development of early larval stages are dependent on a stable food supply, consisting primarily of zooplankton (James 1987, Hutchings 1992). The copepod biomass needed to sustain serial spawning by adult anchovy (Peterson *et al.* 1992, Richardson *et al.* 1998, Painting *et al.* in press b) and the copepod nauplii, ciliates and dinoflagellates required for larval survival (Lasker 1975, Hutchings 1992) must in turn be supported by adequate primary production. To understand the population dynamics of anchovy and other pelagic fish, it is therefore important to understand the dynamics of different components of the pelagic foodweb during the anchovy spawning season (see Fowler 1998, Painting *et al.* in press b, Richardson *et al.* in prep.). This study describes the temporal and spatial distribution of chlorophyll biomass in relation to the physical and chemical environment between August and March on the western Agulhas Bank. It also assesses the possible impact of seasonal changes of phytoplankton biomass on spawning success of anchovy, and of sardine *Sardinops sagax*, which also spawn on the Bank.

MATERIAL AND METHODS

SARP was conducted from August 1993 to March 1994 and from September 1994 to March 1995 (Painting *et al.* in press a). Two transects were sampled monthly off Quoin Point and Walker Bay on the western Agulhas Bank (Fig. 1). Transects, consisting of six stations 10 miles (18.5 km) apart and extending from two miles off the coast to beyond the 200-m isobath, were traversed within a 12-h period. The Quoin Point transect was sampled before the Walker Bay transect, except in March 1994. Data from additional stations sampled during most cruises are included in Table I. NOAA AVHRR satellite images were obtained on a daily basis during each cruise from the Satellite Acquisitions Centre. Hourly data on wind speed and direction were obtained from the Cape Point lighthouse for the study period.

At each station, continuous temperature and fluorescence profiles to 100 m, or to within 10 m of the seabed, were measured using a thermistor and profiling fluorometer (Chelsea Instruments AquaTracka MkIII). Discrete samples for extracted chlorophyll *a*, nutrient and phytoplankton analyses were collected at the surface and at the depth of the maximum fluorescence using Niskin bottles. Chlorophyll *a* was measured fluorometrically using a Turner Designs Model 10-000R fluorometer (Parsons *et al.* 1984). Water samples were concentrated onto Whatman GF/F filters, which were extracted in 90% acetone for 24 h at –20°C.

Table I: Descriptive statistics of oceanographic and biological parameters for each seasonal period. Data from the Quoin Point and Walker Bay transects as well as additional stations sampled were used

Parameter	*n*	Mean	Range	*SD*
Late winter (August/September)				
SST (°C)*	48	15.2	13.3 – 16.2	0.6
Upper-mixed layer (m)	42	62.1	16.6 – 101	27
Nitrate (mmol·m^{-3})	34	3.5	0.4 – 10.6	2.2
Phosphate (mmol·m^{-3})	33	0.7	0.2 – 1.3	0.3
Silicate (mmol·m^{-3})	34	4.2	1.8 – 8	1.6
Mean chlorophyll in upper 30 m (mg·m^{-3})†	48	1.9	0.4 – 5.7	1.2
Mean chlorophyll in upper 50 m (mg·m^{-3})†	48	1.7	0.4 – 5.5	1
Spring (October/December)				
SST (°C)*	128	17.9	13.8 – 20.7	1.4
Upper-mixed layer (m)	126	34.7	3.6 – 75.4	15.5
Nitrate (mmol·m^{-3})	98	0.9	0.0 – 10.9	1.3
Phosphate (mmol·M^{-3})	99	0.5	0.1 – 3.2	0.4
Silicate (mmol·m^{-3})	99	3.3	1.0 – 14.3	1.6
Mean chlorophyll in upper 30 m (mg·m^{-3})†	128	1.2	0.2 – 6.3	1.1
Mean chlorophyll in upper 50 m (mg·m^{-3})†	127	1.1	0.2 – 5.0	0.8
Summer (January/March)				
SST (°C)*	94	17.8	9.9 – 22.4	3.3
Upper-mixed Layer (m)	94	19.3	1.8 – 48.5	11.7
Nitrate (mmol·m^{-3})	67	3.3	0.0 – 21.2	5.5
Phosphate (mmol·m^{-3})	67	0.7	0.1 – 2.6	0.7
Silicate (mmol·m^{-3})	67	5.4	1.0 – 28.3	5.5
Mean chlorophyll in upper 30 m (mg·m^{-3})†	94	2.1	0.1 – 6.8	1.8
Mean chlorophyll in upper 50 m (mg·m^{-3})†	94	1.5	0.1 – 4.3	1

n = Number of cases
* Sea surface temperatures were within 2 m of the surface
† Phytoplankton biomass is shown as the mean chlorophyll concentration in the upper 30 or 50 m at each station; the overall mean is based on these mean values

Fluorescence was measured before and after acidification to correct for phaeopigments. For each cruise, *in situ* fluorescence readings at the point of sampling were related to extracted chlorophyll concentrations in order to calibrate the fluorescence profiles in terms of chlorophyll equivalents. Nutrient samples were frozen for later analysis using standard methods (Mostert 1983, 1988). Phytoplankton samples were fixed in buffered formalin; occasional samples were examined using an inverted microscope.

RESULTS

Three oceanographic seasons were defined on the basis of observed hydrographic conditions and upwelling activity (Richardson *et al.* 1998): late-winter (August/September), spring (October–December) and summer (January–March). These oceanographic seasons lag behind conventional calendar seasons by at least a month.

Late winter

HYDROGRAPHIC CONDITIONS

Three cruises were conducted in late winter: in August and September of 1993 and September 1994. Vertical sections show temporal and spatial changes in temperature and chlorophyll distribution along selected transects (Fig. 2). Late winter was characterized by deep mixing, with isothermal water often extending below 80 m at mid- and outer-shelf stations. There was little change in hydrographic structure between monthly surveys (Figs 2a, b). Sea surface temperatures (SST) were clustered within a narrow range of 13–16°C (mean = 15.2°C, Table I), with cooler temperatures inshore and warmer temperatures offshore. The upper-mixed layer (UML), defined here as the depth where the difference in temperature from the surface is 0.5°C, ranged in depth from 17 m inshore to 101 m offshore (mean = 62.1 m, Table I). In surface waters, nitrate (mean = 3.5 mmol·m^{-3}), silicate (mean = 4.2 mmol·m^{-3}) and phosphate (mean

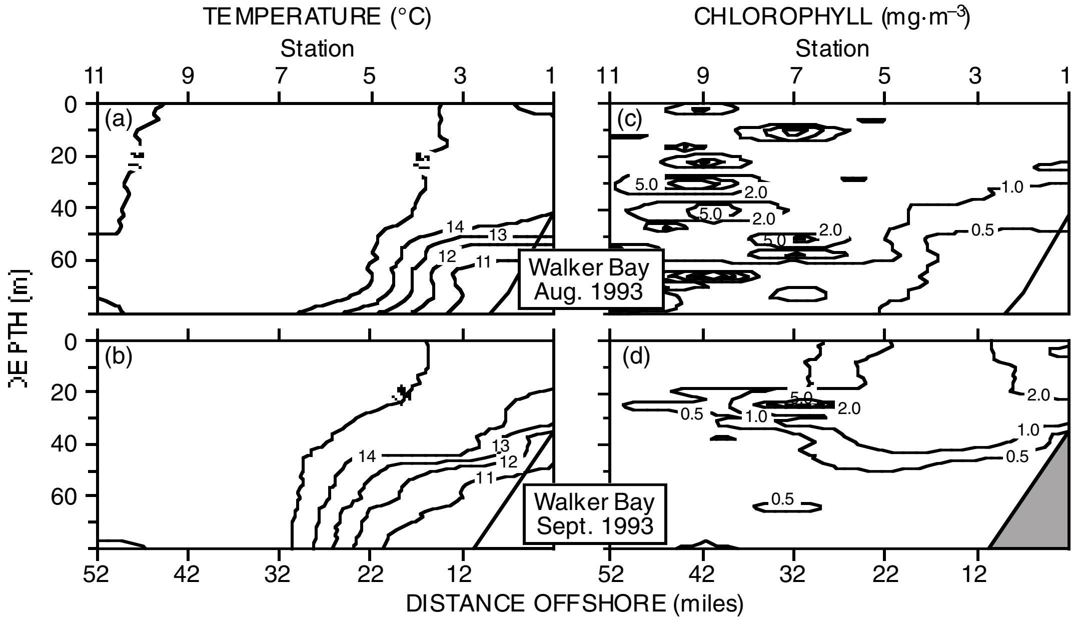

Fig. 2: Vertical cross-shelf sections of (a, b) temperature and (c, d) chlorophyll along the Walker Bay transect during late winter

= 0.7 mmol·m^{-3}) concentrations were moderate (Table I).

CHLOROPHYLL DISTRIBUTION

Chlorophyll profiles were characterized by multiple sharp peaks caused by gelatinous masses of the diatom *Thallasiosira* sp. These peaks were predominately above the thermocline, apparently randomly distributed, and were small and sparse over the inner shelf, but larger (3–15 mg·m^{-3}) and more numerous on the mid and outer shelf. The most numerous and highest peaks were found in August 1993 (Fig. 2c). Background chlorophyll (<2 mg·m^{-3}) was evenly distributed within the UML. In September, inshore chlorophyll concentrations increased to >2 mg·m^{-3} (Fig. 2d).

Spring

HYDROGRAPHIC CONDITIONS

Six cruises were conducted during spring. Vertical sections show temporal and spatial changes in temperature and chlorophyll distribution along selected transects (Fig. 3). Surface temperatures ranged from 14 to 21°C (mean = 17.9°C, Table I). During that period, intrusion of cold (10°C) water onto the shelf raised and intensified the thermocline. Concurrently, there was warming of surface waters over the inner shelf. However, the hydrographic structure in early October 1994 was more typical of late winter, with a deep UML over the outer shelf (Fig. 3b). In November of both 1993 and 1994, warm (17–18°C) water covered the shelf to a depth of about 40 m (Figs 3c, d). Very warm (≥20°C) water appeared over the outer shelf in December (Fig. 3e).

Coastal upwelling, indicated by steeply rising isotherms inshore, was mainly subsurface in October and November 1993 (Figs 3a, c), with surface upwelling apparent in December 1994 (Fig. 3e). Cool surface temperatures resulting from upwelling were confined to the inner shelf; surface temperatures were never <14°C, indicating that upwelled water had not reached the surface.

The depth of the UML was on average 34.7 m, ranging from 4.5 m inshore (under upwelling conditions in December 1994) to 51.1 m offshore in October 1994 (Table I). Nutrient concentrations in surface waters were lower than during other seasons, with mean nitrate, phosphate and silicate values of 0.9, 0.5 and 3.3 mmol·m^{-3} respectively (Table I).

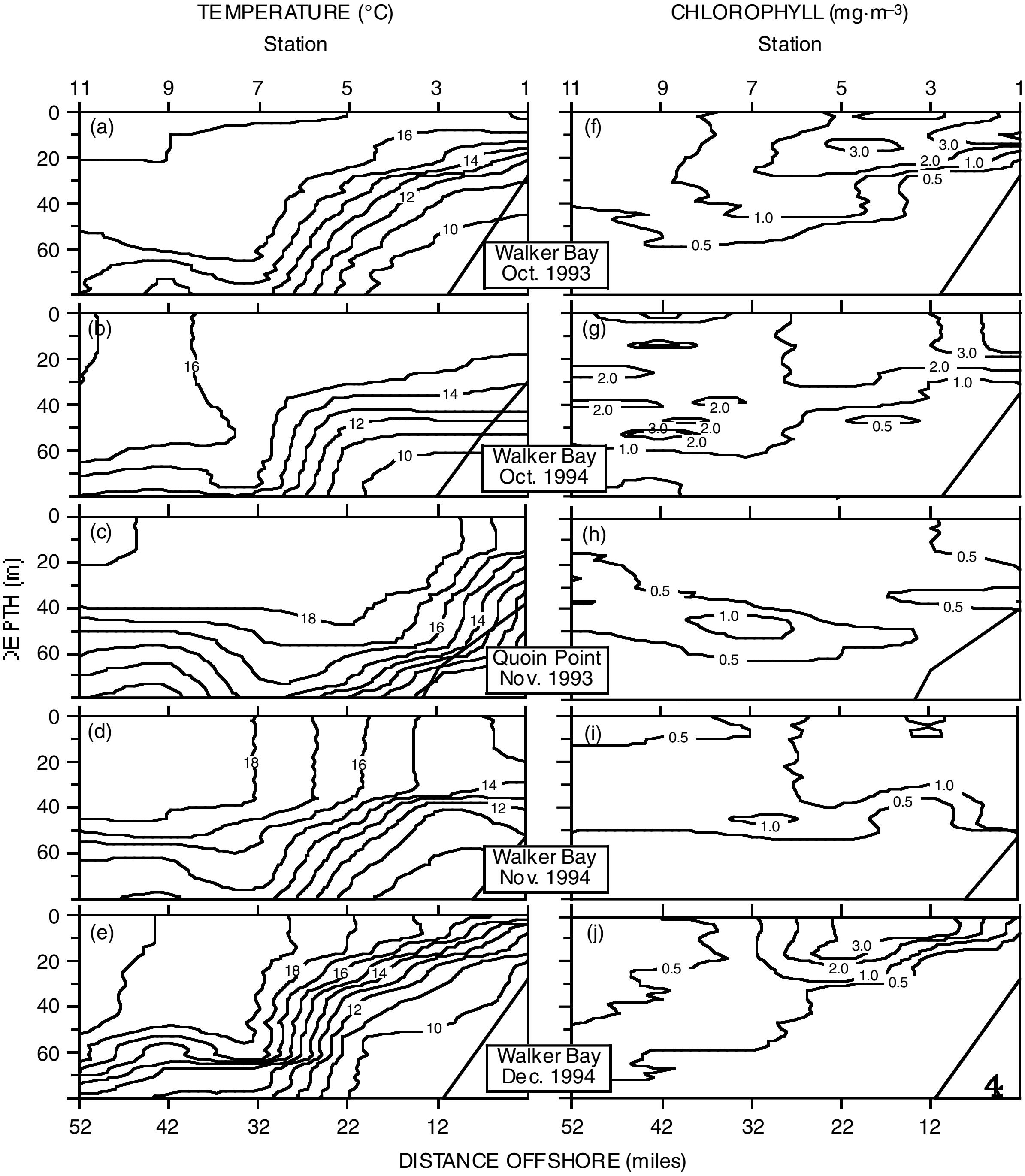

Fig. 3: Vertical cross-shelf sections of (a–e) temperature and (f–j) chlorophyll along the Quoin Point and Walker Bay transects during spring

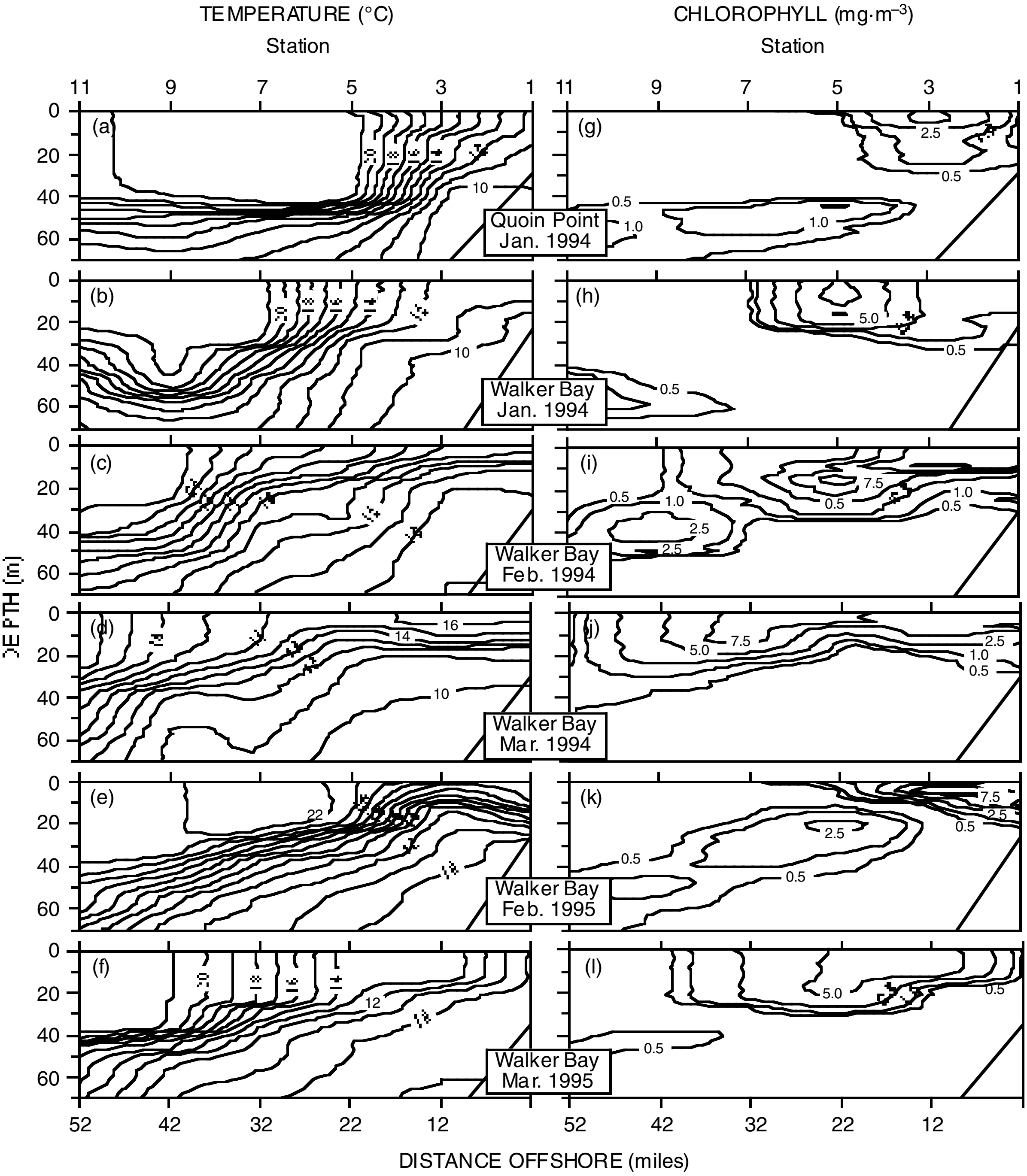

Fig. 4: Vertical cross-shelf sections of (a–f) temperature and (g–l) chlorophyll along the Quoin Point and Walker Bay transects during summer

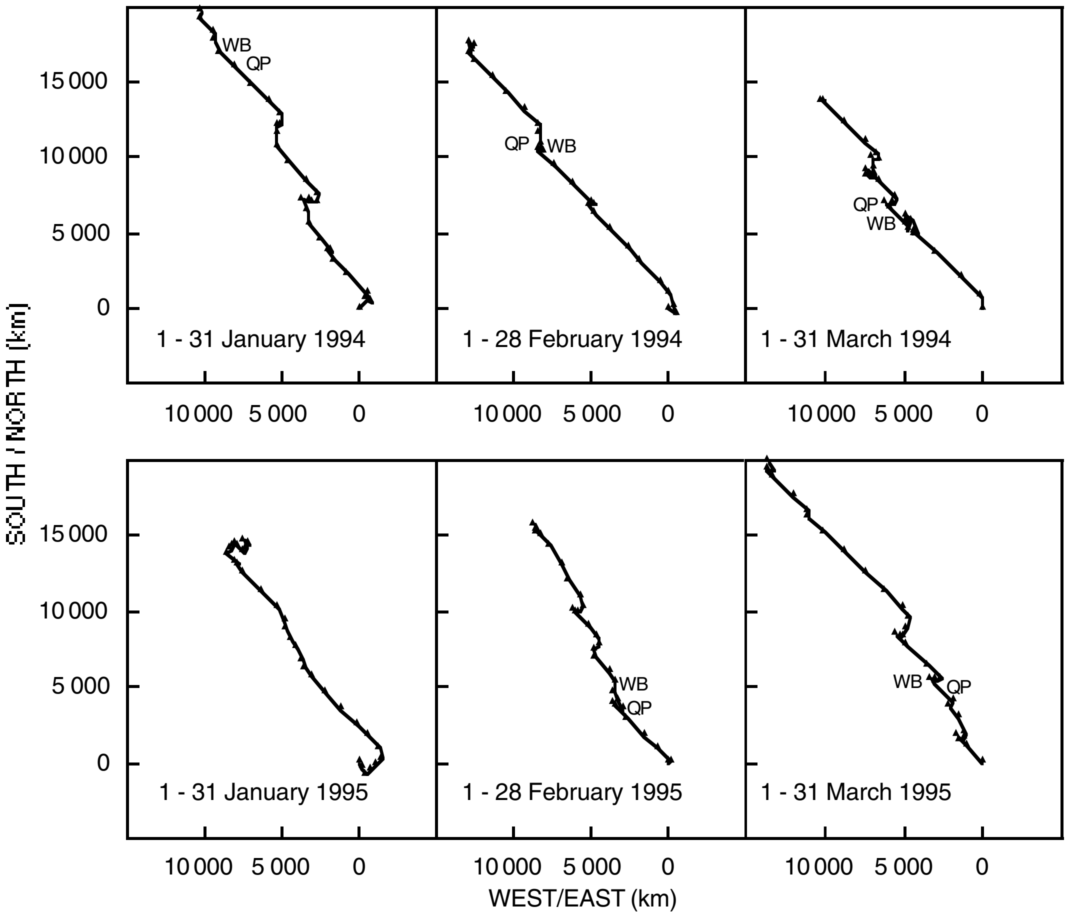

Fig. 5: Progressive vectors of winds measured at the Cape Point lighthouse in January, February and March 1994 and 1995. Dates when the two transects, Quoin Point (QP) and Walker Bay (WB) were traversed each month are shown. There was no survey in January 1995

CHLOROPHYLL DISTRIBUTION

The sharp peaks characteristic of late-winter chlorophyll profiles were absent, except in mid- and outer-shelf waters during the early October 1994 cruise (Fig. 3g). Chlorophyll concentrations were higher over the inner shelf, initially as a spring bloom and later as an upwelling bloom, and declined offshore. The spring bloom (2–5 mg·m^{-3}) extended to midshelf in October (Figs 3f, g). The continuing presence of gelatinous masses of *Thalassiosira* sp. contributed to higher mean chlorophyll concentrations (>2 mg·m^{-3}) offshore in October 1994 (Fig. 3g). In November, chlorophyll concentrations declined to low levels across the shelf within a deep, warm UML. In December 1994, after upwelling, there were high concentrations of chlorophyll (3–5 mg·m^{-3}) in surface waters of Walker Bay (Fig. 3j).

Summer

HYDROGRAPHIC CONDITIONS

Five cruises were conducted during summer. Vertical sections show temporal and spatial changes in temperature and chlorophyll distribution along selected transects (Fig. 4). There was often strong upwelling

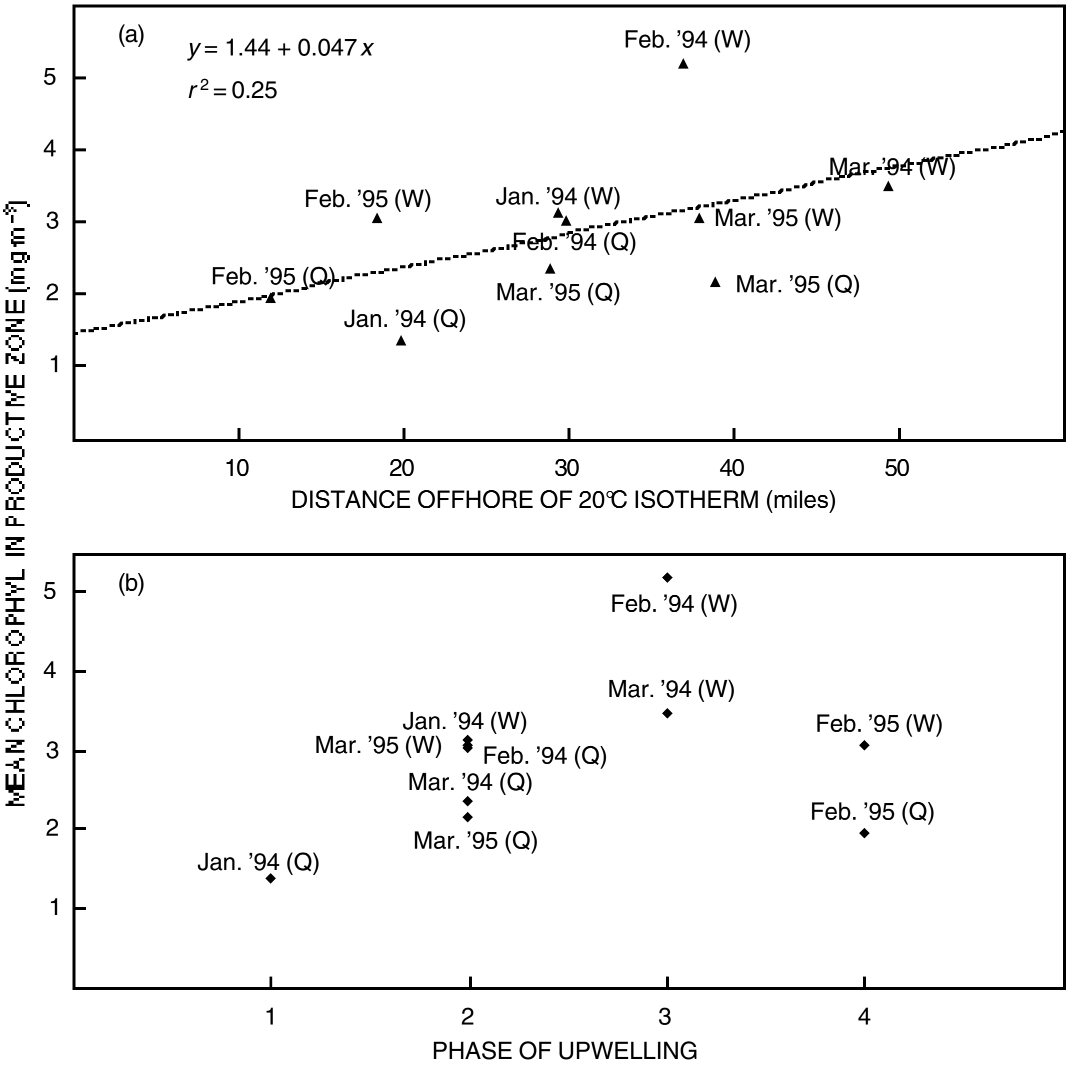

Fig. 6: Relationship between mean chlorophyll (in upper 30 m) within the productive zone and (a) distance offshore of the 20°C isotherm bounding the productive zone and (b) the phase of the upwelling cycle (1 = onset of upwelling, 2 = sustained upwelling, 3 = quiescence, 4 = downwelling). Data points are labelled with date and transect (Q = Quoin Point, W = Walker Bay)

inshore, indicated by water of 11–12°C (Figs 4a, f), which accentuated inshore-offshore temperature gradients (Figs 4a, b). The further intrusion of cold (10°C) water onto the shelf raised and intensified the thermocline (Fig. 4d). The depth of the UML (mean = 19 m, Table I) declined steadily during the season and ranged from 2 m inshore to 49 m offshore. UML depths are often greater over the shelf than at the shelf-break (Fig. 4b).

Various stages of upwelling may be distinguished from the monthly sections (Fig. 4), from the onset of upwelling, sustained upwelling, quiescent conditions and downwelling. These and intermediate stages can be related to the wind regime a few days prior to the cruises (Fig. 5). The Quoin Point transect in January 1994 (Fig. 4a), sampled after several days of strong

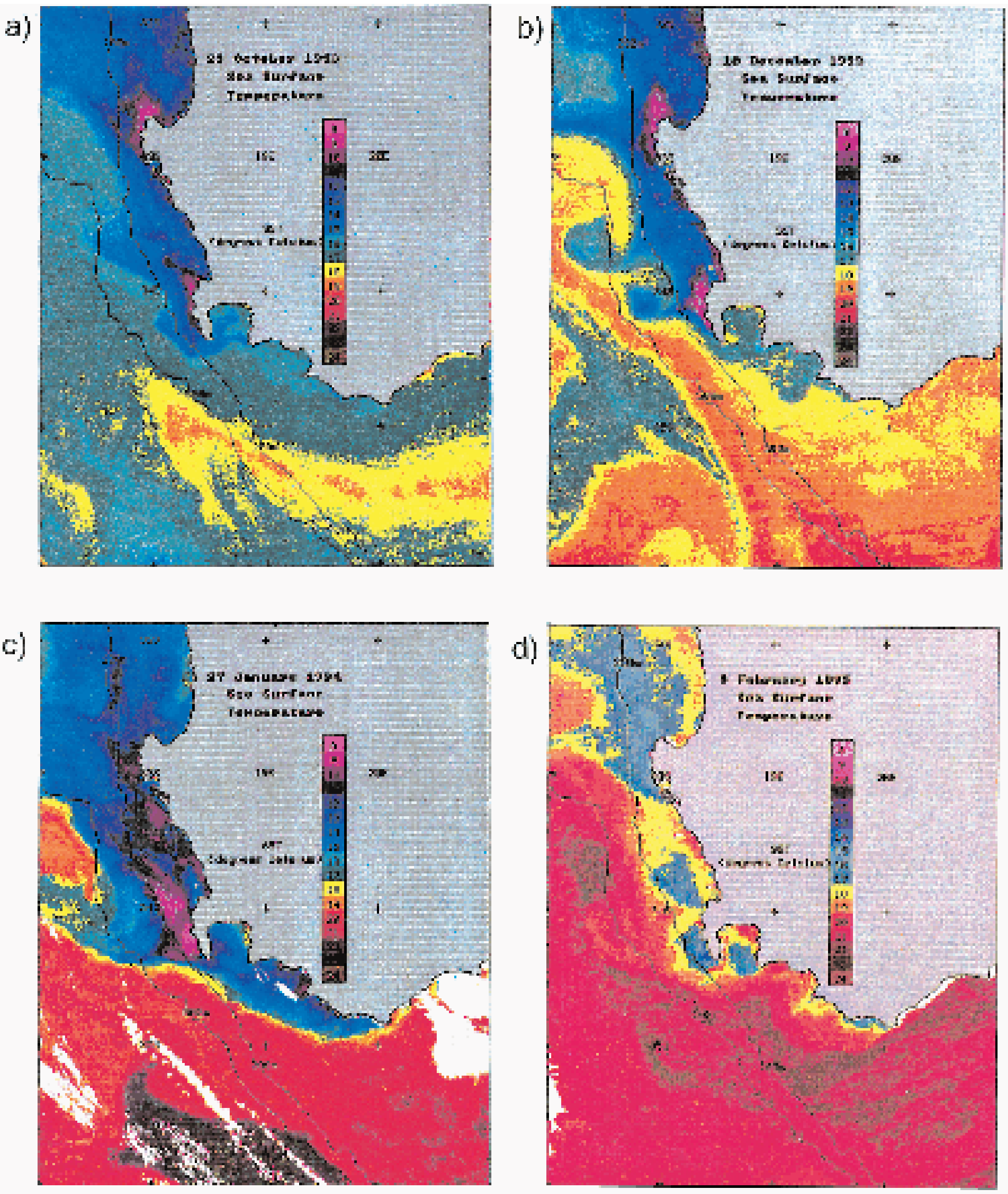

Fig. 7: Satellite images of the southern Benguela showing SST distribution on the western Agulhas Bank in (a) October 1993, (b) December 1993, (c) January 1994 and (d) February 1995

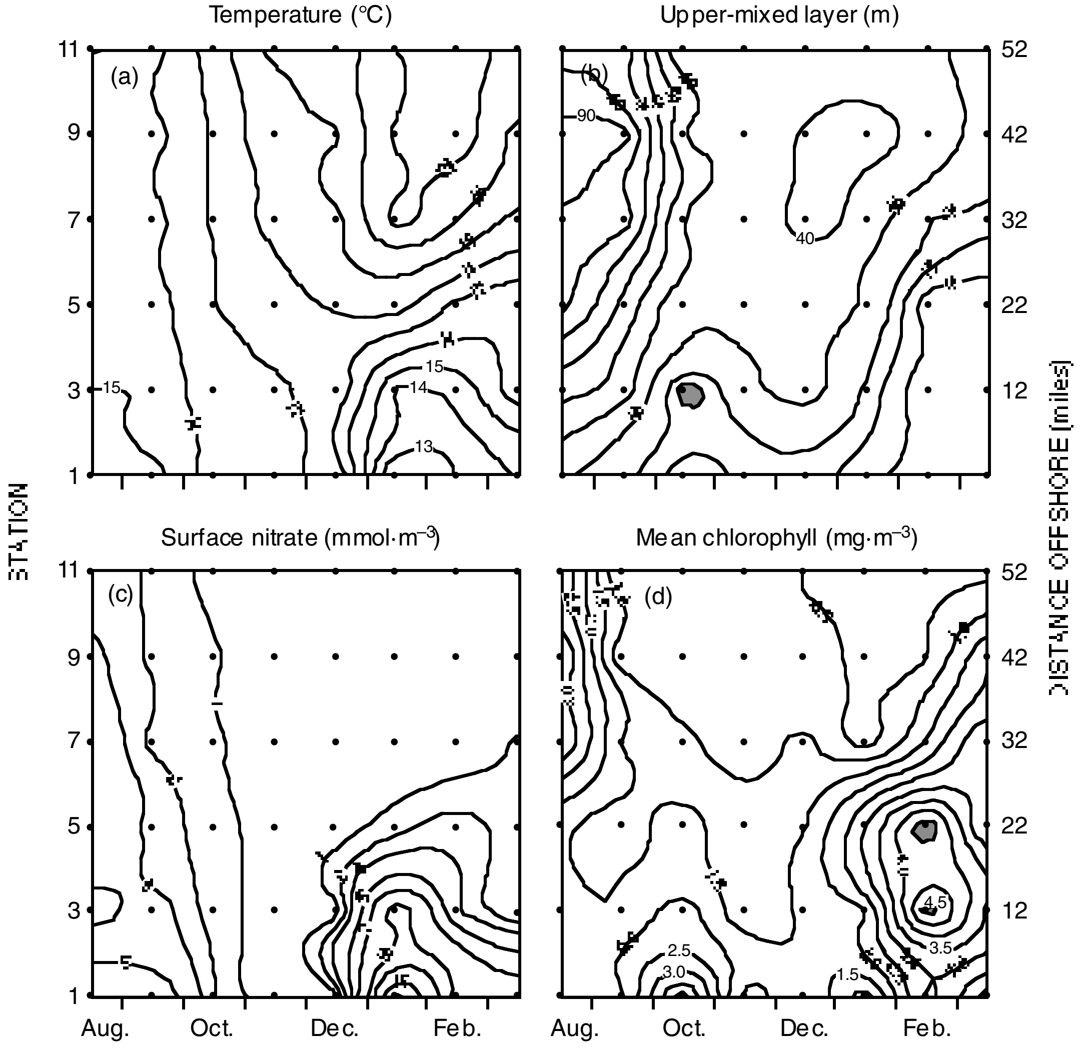

Fig. 8: Monthly changes across the shelf in (a) SST, (b) depth of the upper mixed layer, (c) surface nitrate and (d) mean chlorophyll in the upper 30 m during the 1993/94 surveys. Data are averages from both transects offshore

south-easterly winds (Fig. 5a), showed the onset of upwelling, characterized by steeply sloping isotherms rising to the surface, with cold water (<12°C) inshore. With continuing south-easterly winds during the Walker Bay transect, the upwelling front had advanced across the shelf while there was warming of surface waters (Fig. 4b). The transect in February 1994 (Fig. 4c) was sampled during a quiescent period after cessation of upwelling winds (Fig. 5b), and showed a levelling of isotherms as the water column warmed. In March 1994, the transect was sampled after weak and variable winds (Fig. 5c); it showed a stratified water column with a shoreward return of near-surface water (Fig. 4d). The transect in February 1995 (Fig. 4e), sampled after steady north-westerly winds (Fig. 5e), showed a strong onshore movement of surface water, resulting in downwelling, indicated by downward-sloping isotherms inshore. In March

1995 (Fig. 4f), two fronts were apparent after upwelling winds resumed after a brief quiescent period (Fig. 5f).

There were pronounced differences in nutrients between the upwelling-derived coastal water and warm, offshore water. Nitrates ranged from 16–21 mmol·m^{-3} in the coldest, newly upwelled water inshore to <2 mmol·m^{-3} in mature upwelled water of ≥16°C. In warm offshore water, surface nitrates were <1 mmol·m^{-3} throughout the summer.

CHLOROPHYLL DISTRIBUTION

As upwelling intensified from January onwards, chlorophyll concentrations in surface waters increased, but were more variable than in other seasons (Fig. 4). Concentrations were initially low (<0.5 mg·m^{-3}) in cold (11–12°C), newly upwelled water near the coast (Figs 4g, l), but increased as the upwelled water warmed and stratified (Figs 4i, j). In the quiescent phase, peak chlorophyll concentrations (>10 mg·m^{-3}) developed in subsurface layers (Figs 4i, j). An upwelling productive zone, encompassing chlorophyll concentrations >0.5 mg·m^{-3} within the upper 20–30 m, extended from the coast to the front, separating coastal from offshore waters. From inspection of Figure 4, the 20°C isotherm was chosen as the offshore boundary of the productive zone. This isotherm varied in position during different phases of upwelling, from close inshore at the onset of upwelling (Fig. 4a) to 50 miles from the coast after strong upwelling (Fig. 4d). After steady north-westerly winds, the productive zone contracted shorewards (Fig. 4k). Mean chlorophyll (within the upper 30 m) within the productive zone (bounded by the 20°C isotherm) varied from 1.34 to 5.17 mg·m^{-3}. Mean concentrations increased with an increase in the offshore extent of the productive zone (Fig. 6a) and were maximum during quiescent conditions (Fig. 6b). Chlorophyll concentrations in the warm, upper-mixed layer, outside of the productive zone and offshore of the oceanic front, were very low (0.1 mg·m^{-3}). There, higher concentrations (1 mg·m^{-3}) were found within a deep (30–50 m) subsurface chlorophyll maximum layer, coincident with the thermocline (Figs 4i, k).

Monthly and seasonal comparisons

Satellite images of SST (Fig. 7) show seasonal changes in major surface hydrographic features in the southern section of the southern Benguela and the contrasting influences of both eastern and western boundary systems on the western Agulhas Bank. In late October 1993, there was strong upwelling off the Cape Peninsula and Cape Columbine, while much of the western Agulhas Bank was covered by oceanic water. Along the shelf-edge, warm water of Agulhas origin penetrated from the eastern Agulhas Bank. By December, warm (18°C) water covered much of the southern sector of the shelf as Agulhas Current water penetrated farther northwards along the shelf edge; again, despite intense upwelling farther north there was little evidence of surface upwelling on the western Agulhas Bank. By January 1994, upwelling was established on the western Agulhas Bank and an intense thermal gradient separated inshore from offshore water. The February 1994 image showed a quiescent period when much of the shelf was covered in warm (>19°C) water.

The close correspondence in monthly changes in SST, UML depth, surface nitrates and mean chlorophyll (in the upper 30 m) across the shelf for 1993/94 and 1994/95 is shown in Figures 8 and 9. During the study, SST was constant across the shelf in late winter, increased inshore in spring and exhibited a pronounced inshore-offshore gradient once upwelling was established in summer. The UML was initially very deep across the shelf, becoming shallower inshore as surface waters warmed in spring. Nitrate concentrations were inversely related to temperatures; concentrations were moderate across the shelf in winter, low in spring and increased inshore once upwelling was established in summer. Elevated chlorophyll concentrations generally corresponded with high nitrate concentrations, except in spring when chlorophyll concentrations increased inshore as the depth of the UML declined. The highest chlorophyll concentrations were in maturing upwelled water at midshelf in summer, whereas the lowest concentrations were in warm, oligotrophic water of Agulhas Current origin over the shelf-edge in late spring and summer. Mean chlorophyll across the shelf (Stations 1–9) varied widely from month to month, particularly during spring and summer (Fig. 10a). The spring bloom in September and/or October is clearly evident, followed by a minimum in November, with peak concentrations during the upwelling season. Cross-shelf differences in chlorophyll were most pronounced in summer and showed little variation in winter (Fig. 10b).

Phytoplankton distribution in relation to SST fell within an ever-broadening, dome-shaped envelope, reflecting increasing thermal variability from winter to summer (Fig. 11). In each season, the range in mean chlorophyll concentrations (in the upper 30 m) was similar (Table I). The overall mean was 1.9 mg·m^{-3} in winter, 1.2 mg·m^{-3} in spring and 2.1 mg·m^{-3} in summer. Peak concentrations (> 4 mg·m^{-3})

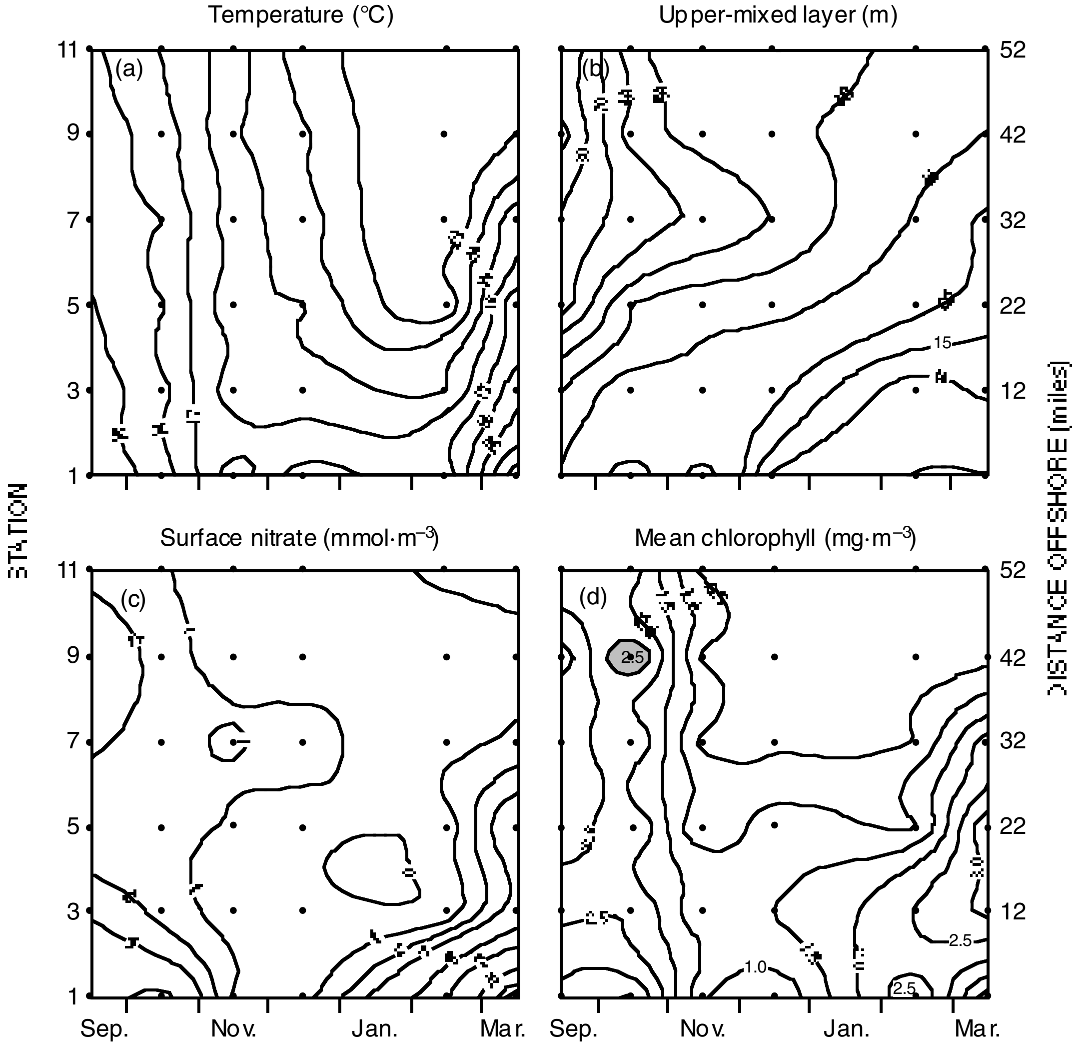

Fig. 9: Monthly changes across the shelf in (a) SST, (b) depth of upper mixed layer, (c) surface nitrate and (d) mean chlorophyll in the upper 30 m during the 1994/95 surveys. Data are averages from both transects offshore

were within water of 13–17°C in winter, 14–17°C in spring and 13–18°C in summer (Fig. 11).

DISCUSSION

Seasonal cross-shelf changes in chlorophyll distribution

The SARP study showed well-defined differences in phytoplankton distribution patterns, which reflected changes in hydrographic structure and nutrient availability during the three seasonal periods of study. In late winter, when strong westerly winds are common, the combination of wind mixing and tidal stirring over the continental shelf resulted in a well-mixed water column (Largier and Swart 1987), with chlorophyll evenly distributed through the deep, upper-mixed layer across the shelf. A *Thallasiosira* sp. embedded in gelatinous masses was present in oceanic water. This species contributed to the moderately high biomass

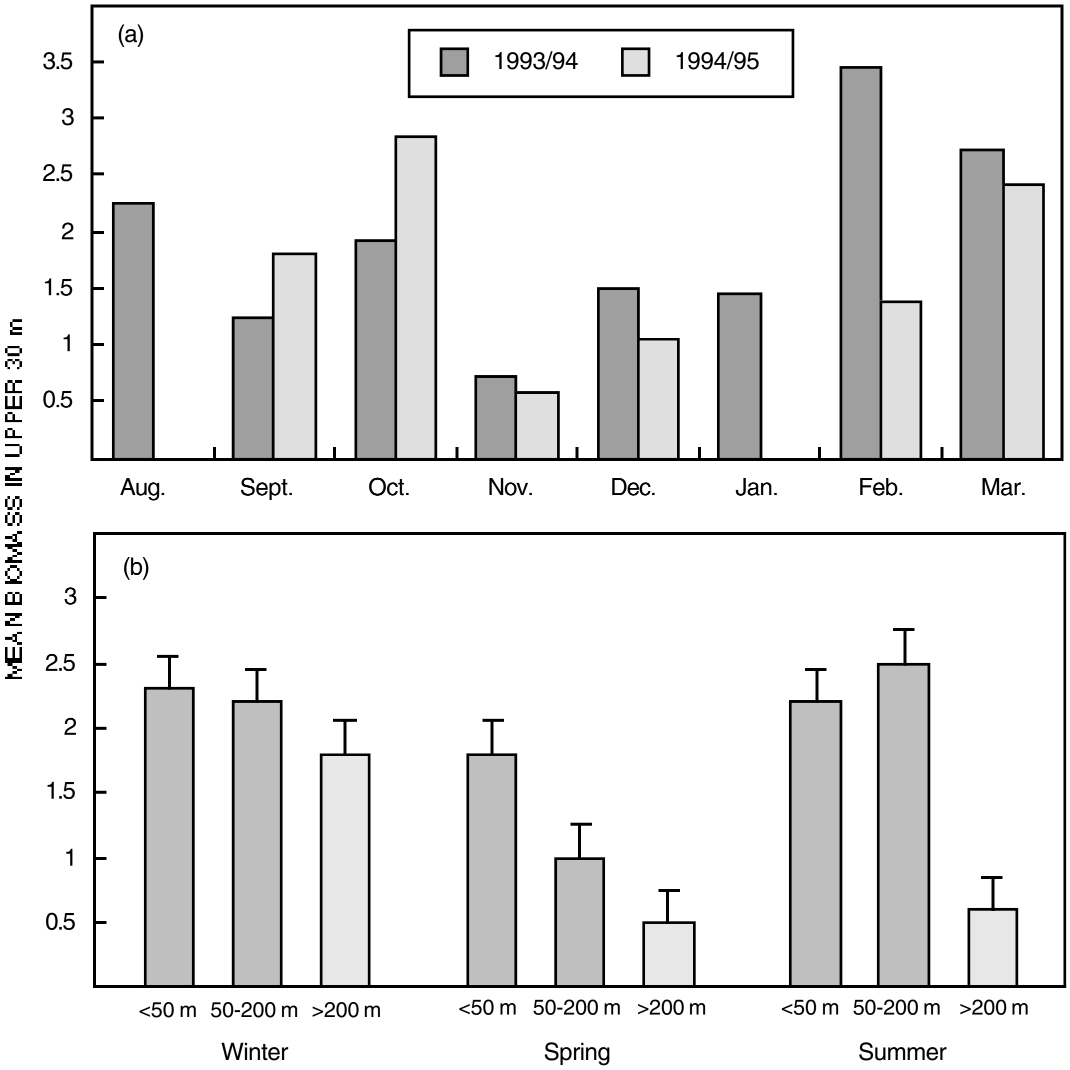

Fig. 10: Changes in mean chlorophyll in the upper 30 m, (a) monthly, during the 1993/94 and 1994/95 surveys (over the shelf region), and (b) seasonally, at inshore (<50 m), shelf (50–200 m) and offshore (>200 m) stations. Data from the shelf stations (Stations 1–9) from both transects were used to calculate monthly means in (a); all available data were used in (b). Error bars denote 1*SE*

found in late winter, particularly on the mid and outer shelf (Figs 8, 9).

On the western Agulhas Bank, spring started in temperate-zone mode and ended in upwelling mode. With warming of surface water and the decline in the depth of the UML over the inner and mid shelf (Figs 8, 9), higher chlorophyll concentrations developed inshore. In temperate regions, a pronounced bloom occurs in spring, when increasing light levels and stability promote rapid phytoplankton growth in nutrient-rich water (Harris 1986). On the western Agulhas Bank in September and/or October, the spring bloom was modest and confined to the inner shelf, presumably because the UML was still deep over the mid and outershelf (Figs 8, 9). In 1994, moderately high chlorophyll concentrations, augmented by the continuing presence of *Thalassiosira* sp. over the mid and outershelf, extended across the shelf in early October. In

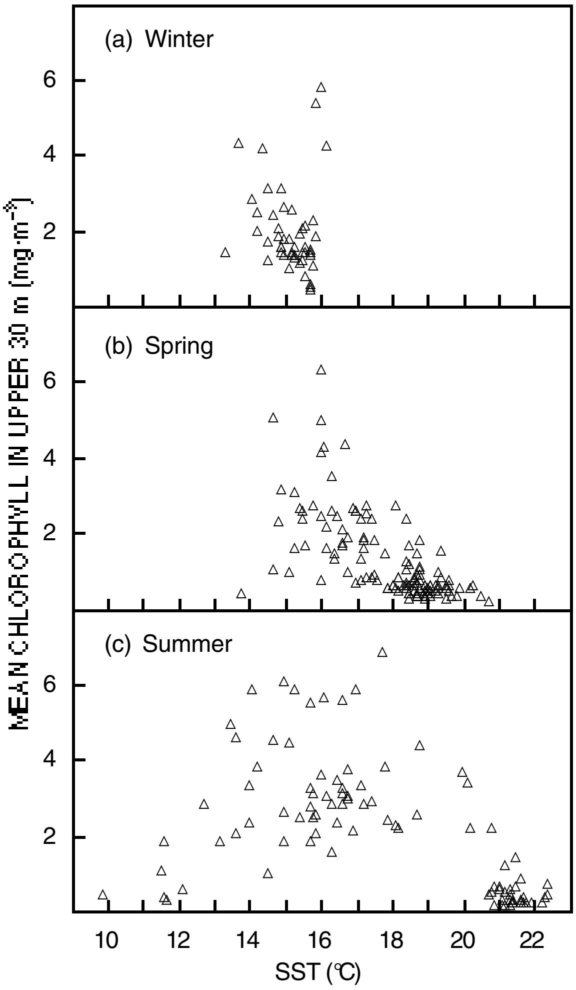

Fig. 11: Seasonal changes in mean chlorophyll in the upper 30 m in relation to SST in (a) late winter, (b) spring and (c) summer

both years, the bloom was cut short by an influx of warm, nutrient-impoverished water over the shelf in November, a common event at that time of year under conditions of reduced south-easterly wind and increased westerly winds (Boyd *et al.* 1985). Moderate nutrient reserves built up in winter and declined to low levels in spring. Once nutrient reserves were depleted, there was little replenishment in surface waters because surface upwelling was intermittent and weak in spring and increasing stability of the water column reduced mixing from the deep nutricline region (Boyd *et al.* 1985).

In the more northerly sectors of the southern Benguela, the upwelling season lasts from September to March (Shannon 1985). However, on the western Agulhas Bank, the upwelling season is shorter as upwelling-favourable winds occur mainly from January to March, largely because of the orientation of the coastline (Boyd *et al.* 1985, Jury 1988). The satellite images (Fig. 7) showed that, while upwelling was intense off the Cape Peninsula, there was no surface evidence of upwelling on the western Agulhas Bank. In this study, subsurface upwelling occurred as early as October, but it was not strong enough to reach the surface until December when, in response to upwelling, a bloom with peak chlorophyll concentrations of 4 mg·m^{-3} developed in Walker Bay (Fig. 3j).

From January onwards, upwelling is episodic but well developed on the western Agulhas Bank, forming a largely two-dimensional response to the longshore wind stress (Largier *et al.* 1992). Strong, upwelling-favourable winds generally persist for 2–4 days (Nelson and Hutchings 1983, Largier *et al.* 1992), although there may occasionally be prolonged upwelling (Largier *et al.* 1992); these southerly winds are followed by a 2–4 day period of quiescence or wind reversals (Pitcher *et al.* 1995). On the western Agulhas Bank, there is a delayed response of about two days to upwelling wind stress (Boyd *et al.* 1985, Jury 1988). Nevertheless, the hydrodynamic structure over the shelf changes rapidly in response to alternating periods of wind forcing and quiescence. The rapidity of change can be assessed by comparing the position of the front on the Quoin Point transect (Fig. 4a) to that on the Walker Bay transect (Fig. 4b), which was traversed 20 h later. Short-term changes follow the same sequence from upwelling to stabilizing, and stratification to relaxation under quiescent conditions (Andrews and Hutchings 1980, Gonzalez-Rodriguez *et al.* 1992, Mitchell-Innes and Pitcher 1992, Pitcher *et al.* 1992). However, the time-course of this sequence is dependent on wind patterns modulated by the passage of low pressure cells south of the continent (Nelson and Hutchings 1983).

Rapid changes in the hydrography of the upper-mixed layer over the shelf were matched by changes in chlorophyll distribution. Phytoplankton biomass ranged from very low (<0.5 mg·m^{-3}) concentrations in newly upwelled water close inshore to high (5–25 mg·m^{-3}) concentrations in the inshore to midshelf regions in maturing upwelled water. Temporal variation in biomass was most marked in midshelf as the productive zone expanded under upwelling conditions or contracted shorewards following onshore winds. Mean chlorophyll concentrations within the productive zone were highest during periods of quiescence, but declined sharply under conditions of downwelling.

The presence of Agulhas Current water along the shelf-edge (Fig. 7c) characterizes this region in summer (Largier *et al*. 1992) and results in warm water intrusions across the shelf during periods of oceanic forcing and onshore winds (Fig. 7d, Boyd *et al*. 1985, Largier *et al*. 1992). In this warm, oligotrophic water, biomass is low and uniformly distributed in the UML, with a deep subsurface maximum in the vicinity of the thermocline (30–50 m), where light and nutrient requirements are finely balanced (Carter *et al*. 1987, Probyn *et al.* 1994).

During periods of strong upwelling, thermal differences between cool upwelled water (<14°C) inshore and warm water (>21°C) offshore create an intense front, which often extends in an arc from Cape Agulhas to the Cape Peninsula (Fig. 7c). The offshore extent of productive waters is effectively limited by this front, leaving a large sector of the shelf west and south of Cape Agulhas covered by warm oligotrophic surface water.

Interannual variability

The monthly surveys during the two years of the SARP study permit examination of interannual differences, with certain caveats. Interannual differences in monthly mean cross-shelf chlorophyll (in the upper 30 m) may be related to differing wind patterns during the two SARP seasons (Painting *et al.* in press a). Southerly winds were stronger in January and February 1994 than in 1995, but whether the observed higher chlorophyll levels (Fig. 10a) resulted from increased upwelling or because of the timing of cruises is not known. Monthly cruises during the dynamic summer period give only a "snapshot" of conditions at the time of the cruise and cannot be used to assess average monthly conditions. However, in less dynamic periods such as winter and spring, monthly cruises may be more representative of average conditions. In spring 1994, prolonged westerly winds and the delayed onset of consistent south-easterly winds extended the presence of oceanic water and moderately high chlorophyll levels across the mid and outer shelf in September and October 1994 (Fig. 9). Changes in timing and in extent of the spring bloom over the inner shelf may have an impact on the productivity and the size structure of the phytoplankton community, with repercussions within the foodweb (Harris 1986, Pitcher *et al.* 1992).

Spring and summer mean values of chlorophyll estimated from this study were somewhat lower, whereas late winter values were higher than those reported for the western Agulhus Bank (Shannon *et al.* 1984, Brown 1992). It is noteworthy that the presence of a *Thalassiosira* sp., which made a large contribution to moderately high chlorophyll levels in late winter in this study, was not reported in previous studies.

Implications for the pelagic ecosystem

This study shows how several factors reduce the overall productivity of the western Agulhas Bank. In late winter and spring, the exceptionally deep UML over the shelf, coupled with strong mixing (Boyd *et al.* 1985, Largier and Swart 1987), delay the onset of a spring bloom typical of the temperate zone and limit its offshore extent. In addition, the comparatively low reservoir of nutrients accumulated during winter in the UML further limits the spring bloom. In summer on the western Agulhas Bank, the shorter upwelling season (Jury 1988) and the slow upwelling response to wind forcing (Boyd *et al.* 1985, Jury 1988) reduce both seasonal upwelling and nutrient input into surface waters, and hence phytoplankton productivity.

Despite the lower overall productivity of the western Agulhas Bank compared to other regions in the southern Benguela (Brown *et al.* 1991, Pitcher *et al.* 1992, Painting *et al.* in press a), it is apparent that the timing of the spring bloom in relation to other environmental factors favourable for spawning (Hutchings 1992, Painting *et al*. in press b) is important. Peak spawning periods of anchovy (October–November) and sardine (August–October, Fowler 1998, Painting *et al.* in press b) both overlap with the spring bloom in September and/or October. This bloom, although modest, provides a more constant food environment for large calanoid copepods, the preferred food of anchovy (James 1987), compared to the highly productive but strongly pulsed upwelling environment in summer (Hutchings 1992, Richardson *et al.* in prep.). For sardine, which are non-selective filter feeders (Van der Lingen 1994), their peak spawning period coincides with a period of enhanced food supply of phytoplankton, microzooplankton (including nauplii) and mesozooplankton (Richardson *et al.* 1998, in prep., Painting *et al.* in press b).

The coincidence of phytoplankton blooms, rapid copepod growth and production rates, and peak spawning of pelagic fish suggests closer linkages between these elements of the pelagic foodweb in September and/or October than was previously thought. For sardine, there appears to be a direct relationship between high concentrations of phytoplankton and enhanced egg production (Fowler 1998). However, for anchovy, the linkages are obscured as a result of declining fish populations (Painting *et al.* in press b). Nevertheless, the apparently overriding requirement by anchovy for constant thermal conditions during the spawning process (Hutchings 1992, Richardson *et al*. 1998, Painting *et al*. in press b) is fulfilled on the western Agulhas Bank during the "temperate phase" in spring, before the main upwelling season begins in January. During this phase, there is enhanced phytoplankton growth over the innershelf during the spring bloom, which stimulates copepod egg production (Richardson *et al*. 1998, in prep.). These two factors, i.e. constant thermal conditions and a stable food supply, can only be attained together during the temperate phase on the western Agulhas Bank, and they may play a role in spawning success. The suggestion that spawning success of sardine and possibly anchovy are related *inter alia* to the extent of the spring bloom on the western Agulhas Bank could be investigated in broader temporal and spatial scale in the future using SeaWiFS satellite imagery.

ACKNOWLEDGEMENTS

We thank the many people from both Marine & Coastal Management (MCM) and the Benguela Ecology Programme for their cooperation and assistance during the SARP study. In particular, we thank Ms E. Wright and Mr M. R. Berryman, (both MCM) for their help in data handling. Drs J. L. Largier of the University of Cape Town (UCT) and A. J. Boyd and G. C. Pitcher (both MCM) are thanked for their constructive comments on an early draft of the manuscript. We are grateful to Ms S. J. Weeks and Mr C. Whittle (both UCT) for processing the satellite images.

LITERATURE CITED

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

BOYD, A. J. and F. A. SHILLINGTON 1994 — Physical forcing and circulation patterns on the Agulhas Bank. *S. Afr. J. Sci.* **90**(3): 114–122.

BOYD, A. J., TROMP, B. B. S. and D. A. HORSTMAN 1985 — The hydrology off the South African south-western coast between Cape Point and Danger Point in 1975. *S. Afr. J. mar. Sci.* **3**: 145–168.

BROWN, P. C. 1992 — Spatial and seasonal variation in chlorophyll distribution in the upper 30 m of the photic zone in the southern Benguela/Agulhas ecosystem. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 515–525.

BROWN, P. C., PAINTING, S. J. and K. L. COCHRANE 1991 — Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. *S. Afr. J. mar. Sci.* **11**: 537–564.

CARTER, R. A., McMURRAY, H. F. and J. L. LARGIER 1987 — Thermocline characteristics and phytoplankton dynamics in Agulhas Bank waters. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 327–336.

FOWLER, J. L. 1998 — Egg and larval ecology of anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) in the southern Benguela ecosystem. M.Sc. thesis, University of Cape Town: iv +153 pp.

GONZALEZ-RODRIGUEZ, E., VALENTIN, J. L., ANDRÉ, D. L. and S. A. JACOB 1992 — Upwelling and downwelling at Cabo Frio (Brazil): comparison of biomass and primary production responses. *J. Plankt. Res.***14** (2): 289–306.

HARRIS, G. P. 1986 — *Phytoplankton Ecology. Structure, Function and Fluctuation*. London; Chapman & Hall: 384 pp.

HUTCHINGS, L. 1992 — Fish harvesting in a variable, productive environment – searching for rules or searching for exceptions? In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 297–318.

JAMES, A. G. 1987 — Feeding ecology, diet and field-based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 673–692.

JURY, M. R. 1988 — A climatological mechanism for wind-driven upwelling near Walker Bay and Danger Point, South Africa. *S. Afr. J. mar. Sci.* **6**: 175–181.

LARGIER, J. L., CHAPMAN, P., PETERSON, W. T. and V. P. SWART 1992 — The western Agulhas Bank: circulation, stratification and ecology. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 319–339.

LARGIER, J. L. and V. P. SWART 1987 — East-west variation in thermocline breakdown on the Agulhas Bank. In *The Benguela and Comparable Ecosystems.* Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 263–272.

LASKER, R. 1975 — Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fishery Bull., Wash.* **73**(3): 453–462.

MITCHELL-INNES, B. A. and G. C. PITCHER 1992 — Hydrographic parameters as indicators of the suitability of phytoplankton populations as food for herbivorous copepods. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 355–365.

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

MOSTERT, S. A. 1988 — Notes on improvements and modifications to the automatic methods for determining dissolved micronutrients in seawater. *S. Afr. J. mar. Sci.* **7**: 295–298.

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

PAINTING, S. J., BOYD, A. J., HUTCHINGS, L., MITCHELL-INNES, B. A., and J. J. AGENBAG (in press a) — Oceanographic processes and linkages between upwelling, phytoplankton and copepods during the South African Sardine and Anchovy Recruitment Programme (SARP). *Fish. Oceanogr.*

PAINTING, S. J., COETZEE, J., FOWLER, J. L. and K. L. COCHRANE (in press b) — Fish distribution and spawning success during the South African Sardine and Anchovy Recruitment Programme (SARP). *Fish. Oceanogr.*

PARSONS, T. R., MAITA, Y. and C. M. LALLI 1984 — *A Manual of Chemical and Biological Methods for Seawater Analysis*. New York; Pergamon: [xiv] + 173 pp.

PETERSON, W. T., HUTCHINGS, L., HUGGETT, J. A. and J. L. LARGIER 1992 — Anchovy spawning in relation to the biomass and the replenishment rate of their copepod prey on the western Agulhas Bank. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 487–500.

PITCHER, G. [C.], AGENBAG, J. [J.], CALDER, D. [A.], HORSTMAN, D. [A.], JURY, M. [R.] and J. TAUNTON-CLARK 1995 — Red tides in relation to the meteorology of the southern Benguela upwelling system. In *Harmful Marine Algal Blooms*. Lassus, P., Arzul, G., Erard, E., Gentien, P. and C. Marcaillou (Eds). Paris; Technique et Documentation – Lavoisier: 657–662.

PITCHER, G. C., BROWN, P. C. and B. A. MITCHELL-INNES 1992 — Spatio-temporal variability of phytoplankton in the southern Benguela upwelling system. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 439–456.

PROBYN, T. A., MITCHELL-INNES, B. A., BROWN, P. C., HUTCHINGS, L. and R. A. CARTER 1994 — A review of primary production and related processes on the Agulhas Bank. *S. Afr. J. Sci.* **90**(3): 166–173.

RICHARDSON, A. J., MITCHELL-INNES, B. A., FOWLER, J. L., BLOOMER, S. F., VERHEYE, H. M., FIELD, J. G., HUTCHINGS, L. and S. J. PAINTING 1998 — The effect of sea temperature and food availability on the spawning success of Cape anchovy *Engraulis capensis* in the southern Benguela. In *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources*. Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *S. Afr. J. mar. Sci*. **19**: 275–290.

RICHARDSON, A. J., VERHEYE, H. M., MITCHELL-INNES, B. A., FOWLER, J. L., and J. G. FIELD (in preparation) — Seasonal and event-scale variation in growth of a dominant copepod in the Benguela upwelling system and implications for the spawning of sardine.

SHANNON, L. V. 1985 — The Benguela ecosystem. 1. Evolution of the Benguela, physical features and processes. In *Oceanography and Marine Biology. An Annual Review* **23**. Barnes, M. (Ed.). Aberdeen; University Press: 105–182.

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

TROMP, B. B. S., LAZARUS, B. I. and D. HORSTMAN 1975 — Gross features of the South Western Cape coastal waters. Unpublished Report, Sea Fisheries Research Institute, South Africa: 43 pp.

VAN DER LINGEN, C. D. 1994 — Effect of particle size and concentration on the feeding behaviour of adult pilchard *Sardinops sagax*. *Mar. Ecol. Prog. Ser*. **109**: 1–13.