Vol. 100: 35–53, 1993 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published October 5

Dynamics of bacterioplankton, phytoplankton and mesozooplankton communities during the development of an upwelling plume in the southern Benguela

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ABSTRACT: Temporal changes in the biomass relationships and community structure of the planktonic food web during the development of a plume of upwelled water in the southern Benguela were investigated during 2 consecutive drogue studies. Three distinct water masses of increasing age were encountered. Primary production was highest (1 g C m^{-2} h^{-1}) at the start of the study and decreased as the plume moved offshore. The planktonic community was initially characterised by a high biomass of bacteria (40 to 60 mg C m^{-3}), a diatom-dominated phytoplankton community (>5 mg chl m^{-3}), and a mesozooplankton community (30 to 86 mg C m^{-3}) dominated by the copepod *Calanoides carinatus*. At the start of the second drogue, phytoplankton production and biomass were lower (ca 0.5 g C m^{-2} h^{-1}, 2 to 5 mg chl m^{-3}), and the phytoplankton community was dominated numerically by nanoplanktonic flagellates (2 to 20 µm). Bacterial biomass estimates (190 mg C m^{-3}) were the highest recorded thus far *in situ* in the southern Benguela. Further offshore, primary production rates were < 0.2 g C m^{-2} h^{-1} and the biomass of phytoplankton and bacteria decreased to < 2 mg chl m^{-3} and ca 20 mg bacterial C m^{-3}. *C. carinatus* dominated the copepod biomass throughout the study period, and showed a general inverse relationship with phytoplankton biomass. Grazing impact may have contributed significantly to the decline of the bloom, with copepods ingesting 5 to 10 % of phytoplankton biomass in maturing upwelled water, and up to 38 % towards the end of the bloom. Results suggest that herbivorous copepods become food-limited during the quiescent phase of the upwelling cycle or when the phytoplankton community is dominated by small nano- and picoplanktonic cells. Microheterotrophic pathways appear to be an important component of the pelagic food web in the southern Benguela. The relative dominance of the classical diatom-mesozooplankton food chains versus longer microbial food webs may have important implications for the population dynamics of pelagic fish.

INTRODUCTION

The southern Benguela upwelling region supports commercially important demersal and pelagic fisheries. Anchovy and pilchard stocks, in particular, have shown significant fluctuations in recent years, and appear to be sensitive to changes in environmental conditions (Shannon et al. 1992, Butterworth et al. in press). Considerable research effort is being directed towards quantifying the abundance of key species in the southern Benguela, and an increased understanding of the physical and biological processes which control the population dynamics of these species. A primary goal of process-orientated studies is to determine the structure and trophic dynamics of the pelagic food web in the region.

The planktonic food web in the southern Benguela is

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strongly influenced by the spatial and seasonal variability in the physical environment, and its control of the supply of nitrogen to surface waters (for reviews see Chapman & Shannon 1985, Shannon 1985, Shannon & Pillar 1986, Probyn 1992). Upwelling of cold (8 to 10 °C) nutrient-rich water (> 20 mg-at. NO_3-N m^{-3}) occurs frequently at localised centres in response to southeasterly wind stress during the austral summer. Under the influence of prevailing southeasterly winds, tongues of newly upwelled water move off-shore and northwards to mix with aged upwelled or oceanic water (Andrews & Hutchings 1980).

The discrete plumes of water which develop downstream of upwelling centres are ideal for studying temporal changes in plankton dynamics. Drogues have frequently been used to follow these water masses to investigate the development of phytoplankton communities in the southern Benguela (Barlow 1982a, b, c, Olivieri 1983, Brown & Hutchings 1987a, b) and in other upwelling systems (Beers et al. 1971, Ryther et al. 1971, Herbland et al. 1973, Nelson & Goering 1978, Sorokin & Kogelschatz 1979, Fuhrman et al. 1985).

Intensive studies of the dynamics of phytoplankton growth in upwelling plumes in the southern Benguela (Barlow 1982a, b, Brown 1984, Brown & Hutchings 1985, 1987a, Brown & Field 1986) have shown that phytoplankton biomass and production are usually low in newly upwelled water (<1 mg chl *a* m^{-3}, <5 mg C m^{-3} h^{-1}). After stabilisation of the water column due to sun-warming of water in the euphotic zone phytoplankton primary production is high (100 to 200 mg C m^{-3} h^{-1}), elevating phytoplankton biomass to > 10 mg chl *a* m^{-3}. In the absence of renewed upwelling bloom senescence typically occurs within 6 to 8 d due to nitrate limitation (Barlow 1982a, b, Brown & Hutchings 1987a). Further primary production is sustained largely by regenerated nitrogen (Probyn 1985, 1987, 1988), which has important implications for planktonic food web structure (Probyn et al. 1990, Moloney et al. 1991, Probyn 1992).

A central problem which characterises the southern Benguela upwelling system is that this region exhibits a lower pelagic fish yield than some other eastern boundary upwelling regions (Nixon et al. 1986, Probyn 1992). One explanation for this may be that frequent upwelling results in a temporal and spatial mismatch between production of phytoplankton and the zooplankton prey of many pelagic species (Hutchings 1992). However, in years of much-reduced upwelling frequency and intensity, the southern Benguela may

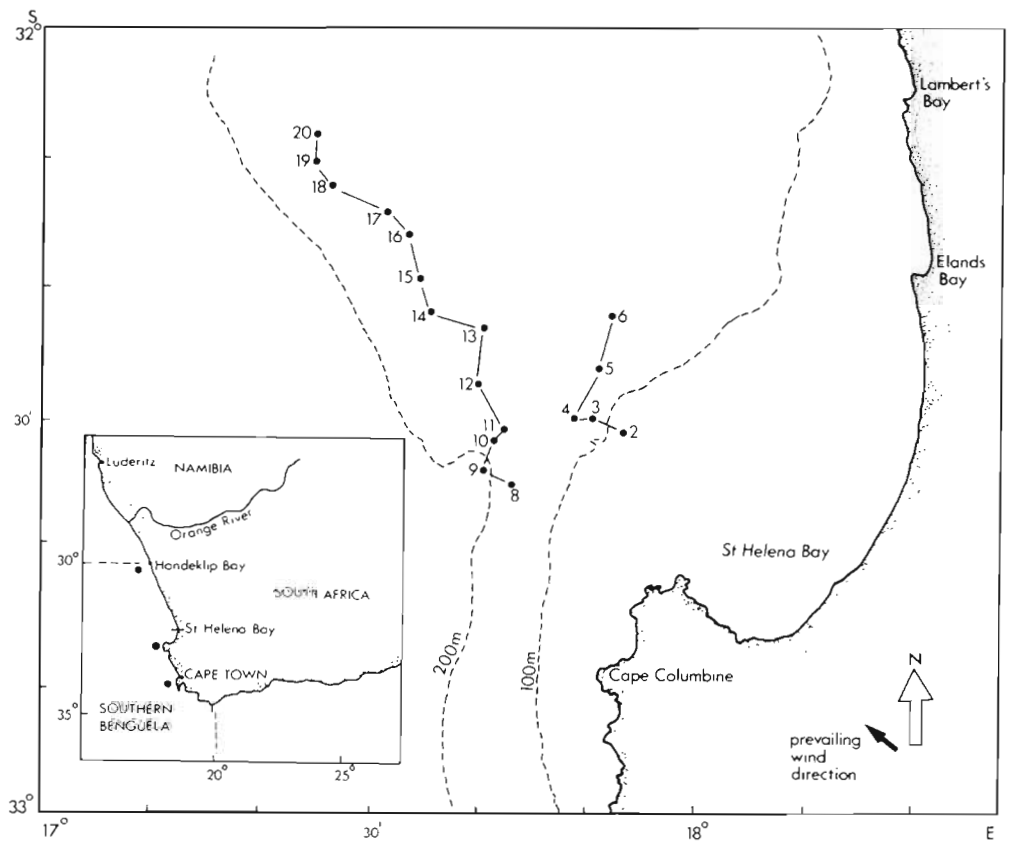

Fig. 1. Cape Columbine region, showing drogue tracks and station positions. All stations were sampled between sunrise (06:45 h) and sunset (19:00 h). Insert shows major upwelling centres (●) in the southern Benguela (from Nelson & Hutchings 1983)

be dominated by smaller phytoplankton cells (< 10 µm) than is generally accepted for an upwelling region (Probyn 1992), leading to longer and less efficient food chains (Moloney et al. 1991). Certainly, the relative roles of nutrient depletion, grazing, senescence and sinking in controlling bloom dynamics remains controversial.

This study forms part of the effort to resolve planktonic food web structure and so better understand the processes regulating pelagic fish population dynamics. A drogue was released downstream of an upwelling centre and followed for 8 d. Our objective was to quantify and study the dynamics of heterotrophic bacterioplankton and mesozooplankton communities in response to phytoplankton growth and decay in a plume of upwelled water. Recent important studies on microzooplankton communities within this region are incorporated into our findings so that a complete description of planktonic community structure can be presented.

SAMPLING AND ANALYTICAL METHODS

Cruise description. During the summer of 1983 a drogue was deployed from the RS 'Africana' into upwelled water on the continental shelf north of Cape Columbine, one of the principal upwelling centres in the southern Benguela (Fig. 1). The 3 m biplanar tetrahedral drogue (see Brown & Hutchings 1987a) was deployed with its midpoint at 10 m depth, and followed for 8 d (13 to 20 March). The water column at the drogue was sampled on 19 occasions to determine the temporal changes in the hydrography, phytoplankton production, and the abundance and distribution of phytoplankton, zooplankton and bacterioplankton.

Upwelled water was distinguished from other water types on the basis of physical and chemical characteristics described by Andrews & Hutchings (1980), Waldron (1985) and Brundrit (1986) (see Table 1). The age of the upwelled water was determined from temperature and nitrate data (Barlow 1982a): newly upwelled water typically has the same characteristics as South Atlantic Central Water (SACW), mature upwelled water is warmer (10 to 15 °C) with lower nitrate concentrations (2 to 15 mg-at. NO_3-N m^{-3}), and aged upwelled water (12 to 16 °C) is virtually nutrient-depleted (0 to 2 mg-at. NO_3-N m^{-3}).

A 36 h preliminary survey of surface temperatures, salinity and nutrients showed newly upwelled water to be absent in the study area. The drogue was consequently deployed into maturing upwelled water (MUW) about 10 nautical miles from the upwelling centre on 13 March (20:00 h), and the water column sampled (Stn 2, Fig. 1). The drogue was followed for 37 h, until it was apparent from marked hydrological changes that the drogue had moved into a different body of water. The drogue was retrieved (after Stn 6), mature upwelled water was relocated (1.5 d later), and the drogue was reset. The second drogue was followed for 94 h (Stns 8 to 20, Fig. 1).

Hydrography. Continuous depth-profiles of salinity and temperature were obtained using a Neil-Brown (Mark III) submersible conductivity, temperature and depth (CTD) recorder. Light penetration depths were estimated *in situ* with a LICOR quantum sensor. Water samples were collected from the 100, 50, 10, 1 and 0.1 % light depths, and then at 10 or 20 m intervals to 100 m using a rosette of ten 5 l Niskin sampling bottles. Water from each depth was analysed immediately for nutrient concentrations (nitrate, silicate, phosphate) on a Technicon Autoanalyzer (AAII) according to standard methods modified by Mostert (1983).

Phytoplankton biomass and production. Niskin bottles were used to collect live plankton samples from the sampling depths described above. Chlorophyll *a*, used as an index of phytoplankton biomass, was concentrated from 1 l seawater from each depth onto Whatman GF/C filters (mean pore size 1 µm) and analysed spectrophotometrically by the procedure of the SCOR/UNESCO Working Group 17 (1966). Chlorophyll *a* values were corrected for phaeopigments. Carbon values for phytoplankton were calculated using a C : chl *a* ratio of 60, the approximate mean value for maturing upwelled water in the southern Benguela. Surface samples (100 ml) for microscopic examination were preserved with 5 % neutral formalin and identified and counted using inverted microscopy (Utermöhl 1936, as described by Hasle 1978). For total

Table 1. Characterisation of water types in the southern Benguela upwelling region on the basis of physical, chemical and biological characteristics (from Andrews & Hutchings 1980, Barlow 1982a, Waldron 1985). Upwelling water originates from South Atlantic Central Water (SACW)

Water type	Temperature (°C)	Salinity (‰)	Nitrate (µg-at. N l^{-1})	Chlorophyll (mg m^{-3})
Offshore	>18	> 35.00	< 1	< 1
Shelf	< 8	< 34.70	12–30	< 1
Upwelling/SACW	8–11	34.70–34.90	12–30	< 1
Maturing upwelled	10–18	34.78–34.90	1–10	2–13
Inshore bottom mixed	9.8	34.75	12–28	1–4

particulate carbon and nitrogen analysis, subsamples (100 ml) were screened (180 µm) to remove mesozooplankton and filtered onto pre-ashed (6 h at 400 °C) Whatman GF/F filters (mean pore size 0.7 µm). Filters were stored frozen until they were oven-dried (60 °C) and analysed by high temperature oxidation on a Hereaus (CHN Rapid) Analyser, with cyclohexanone (20.14 % N : 51.79 % C) as a standard.

Measurements of phytoplankton production were made daily at selected light depths in the euphotic zone, at stations sampled before mid-day. Primary production rates were estimated from ^{14}C uptake (10 µCi $NaH^{14}CO_3$) during 4 h *in situ* incubations (Brown 1982, 1984). Samples were concentrated onto GC-50 filters (mean pore size 0.7 µm), and stored in Pico-fluor scintillation cocktail until counted ashore.

Bacterial numbers and biomass. Water samples (20 ml) were preserved with 25 % Analar glutaraldehyde (1.3 % v/v) and stored at 4 °C until they were returned to shore, where they were analysed within a few weeks. Bacteria were counted in 4 different size-classes by the Acridine Orange Direct Counting (AODC) technique (Hobbie et al. 1977, Linley 1983, Painting et al. 1985). At least 20 random fields or 300 bacteria were counted, to obtain a normal distribution of cells (Linley et al. 1981, Scavia & Laird 1987). Bacterial biomass (µg C l^{-1}) was calculated from cell numbers, the total cell volume (μm^3) in all size-classes, and the conservative conversion factor of 0.121 pg C μm^{-3} (Watson et al. 1977, but see also Lee & Fuhrman 1987, Simon & Azam 1989).

Zooplankton abundance and biomass. Mesozooplankton was collected with a Bongo net (57 cm diameter, 200 µm mesh; McGowan & Brown 1966) hauled vertically through the water column from 10 m above the seabed (100 to 200 m) to the surface. Samples were preserved in 5 % buffered formalin. At selected stations, zooplankton samples were collected from discrete depths with the rosette sampler and 5 l Niskin bottles. Zooplankton in 4 l subsamples were concentrated onto a 37 µm Nitex screen, rinsed into sample bottles and preserved with 5 % formalin.

In the laboratory, two 3.9 ml subsamples were taken from each Bongo net sample with a piston pipette and all the animals enumerated (Peterson et al. 1979). Copepods were counted by species and developmental stage; most other zooplankton taxa were identified to genus. The Niskin bottle samples were analysed without subsampling.

To calculate copepod biomass, the numbers of individuals of each species and developmental stage were

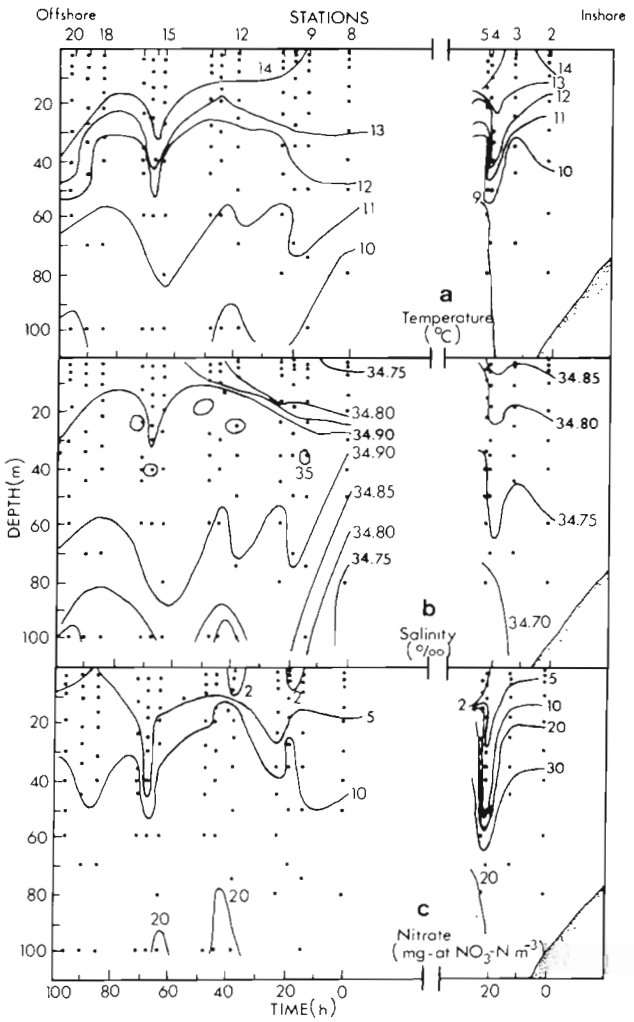

Fig. 2. Vertical sections of (a) temperature, (b) salinity and (c) nitrate

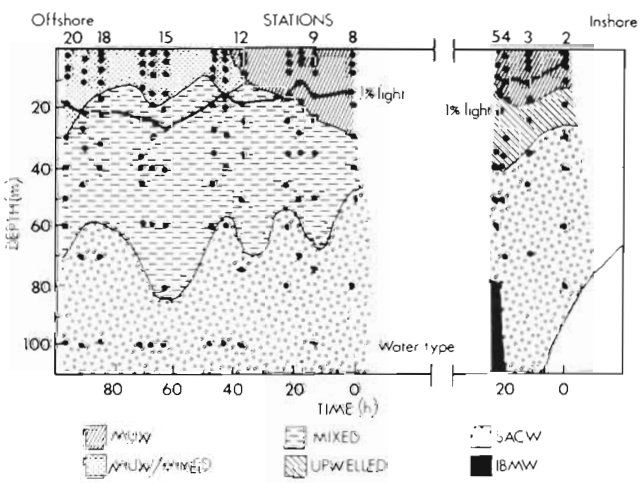

Fig. 3. Water types identified from water column temperature and salinity data. The 1 % light depth is indicated. MUW: maturing upwelled water; UPWELLED: recently upwelled water; MUW/MIXED: maturing upwelled water mixing with older, mature upwelled water; MIXED: mixing of different masses of aged upwelled water; SACW: South Atlantic Central Water; IBMW: Inshore Bottom Mixed Water. Large dots (●) indicate depths sampled

multiplied by their respective dry weights, obtained from living material that had been oven-dried at 60 °C overnight and weighed on a Cahn Model 25 Electrobalance (Peterson et al. 1990). Total biomass was calculated by summing the biomass (B, mg dry wt m^{-3}) of each species:

$$B = \sum_{i=1}^{6} (n_i w_i) \times 10^{-3} \quad (1)$$

where i = developmental stage (C1 to C6); n_i = total no. of the i^{th} stage (m^{-3}); and w_i = individual weight of the i^{th} stage (µg dry wt $animal^{-1}$). Copepod carbon biomass was estimated to be 40 % of the dry weight (Andrews & Hutchings 1980, Parsons et al. 1984).

Zooplankton grazing. Copepod ingestion rates (I, mg C m^{-3} d^{-1}) were calculated from copepod abundances (m^{-3}), body weights (W, µg C $ind.^{-1}$) and phytoplankton biomass (P, mg C m^{-3}) using the Mullin & Brooks (1976) algorithm.

$$I = 0.00073 PW^{0.35} \quad \text{if } P \leq 57 W^{0.35} \quad (2)$$

$$I = 0.0416 W^{0.7} \quad \text{if } P > 57 W^{0.35} \quad (3)$$

RESULTS

Hydrography

A section of water column temperatures (Fig. 2a) to 100 m shows a vertically stratified water column with warm surface water. From salinity data it was clear that water in the upper 30 m at all stations was of

Table 2. Estimates of phytoplankton production at selected light depths in the euphotic zone at stations sampled before mid-day. Integrated data were used to calculate P^B values (mg C mg^{-1} chl h^{-1}). Bacterial biomass (mg C m^{-3}) and the functional linear regression describing the relationship between bacterial biomass and phytoplankton production are also shown. –: no measurements were made

Stn	Drogue	Depth (m)	Light level (%)	Bacteria (mg C m^{-3})	Chl *a* (mg m^{-3})	Primary production (mg C m^{-3} h^{-1})	*P/B* (h^{-1})	Integrated chl (mg m^{-2})	Integrated production (mg C m^{-2} h^{-1})	P^B
Maturing upwelled water										
3	1	0	100	49.2	9.0	108.85	0.18	105.9	1114.2	10.5
		3	50	49.4	9.6	186.67				
		4	25	45.3	8.5	124.61				
		6	10	57.8	10.4	97.47				
		11	1	49.2	9.6	19.82				
6	1	0	100	31.9	3.0	14.15	0.13	65.9	522.2	7.9
		2	50	23.5	4.8	35.93				
		4	25	28.9	5.4	50.81				
		7	10	61.3	6.9	64.32				
		11	1	42.4	8.3	42.03				
9	2	0	100	63.4	4.4	38.24	0.10	77.3	465.3	6.0
		3	50	144.9	5.0	42.72				
		5	25	66.6	4.2	35.66				
		8	10	175.1	4.6	34.75				
		16	1	72.8	5.6	5.21				
12	2	0	100	49.6	4.9	42.78	0.11	86.5	559.2	6.5
		2	50	–	4.8	56.50				
		4	25	44.6	6.1	50.29				
		8	10	44.0	6.2	32.02				
		19	1	–	1.3	2.26				
MUW/mixed water										
15	2	0	100	25.7	–	1.12	–	–	66.1	–
		4	50	18.9	–	2.12				
		8	25	18.5	–	5.08				
		14	10	22.7	–	2.97				
		27	1	4.4	–	0.27				
18	2	0	100	13.0	0.7	7.56	0.32	11.5	223.0	19.4
		3	50	19.4	0.7	13.22				
		7	25	–	0.5	14.06				
		11	10	28.3	0.8	13.92				
		22	1	15.1	0	0.86				

Phytoplankton production (X) vs bacterial biomass (Y): $\ln Y = \ln 2.74 + 0.46 \ln X$, n = 27, r = 0.694, $p < 0.001$

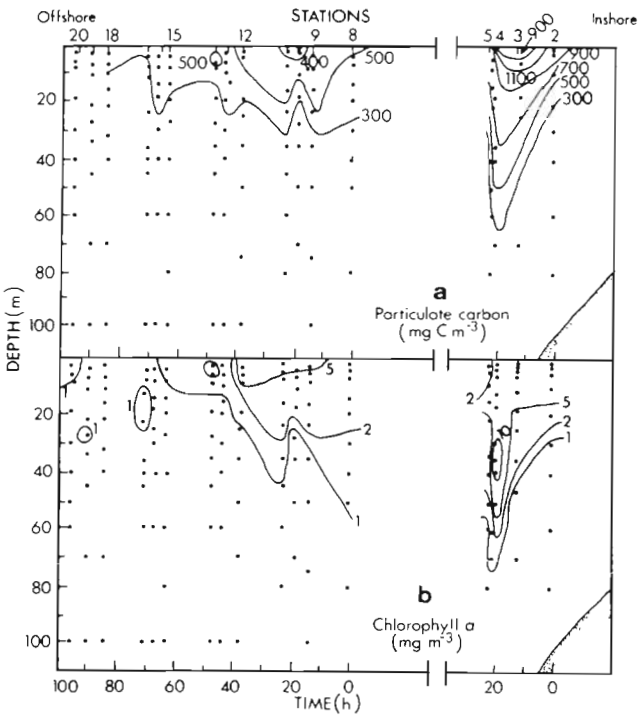

Fig. 4. Vertical sections of (a) particulate carbon and (b) chlorophyll *a* concentrations

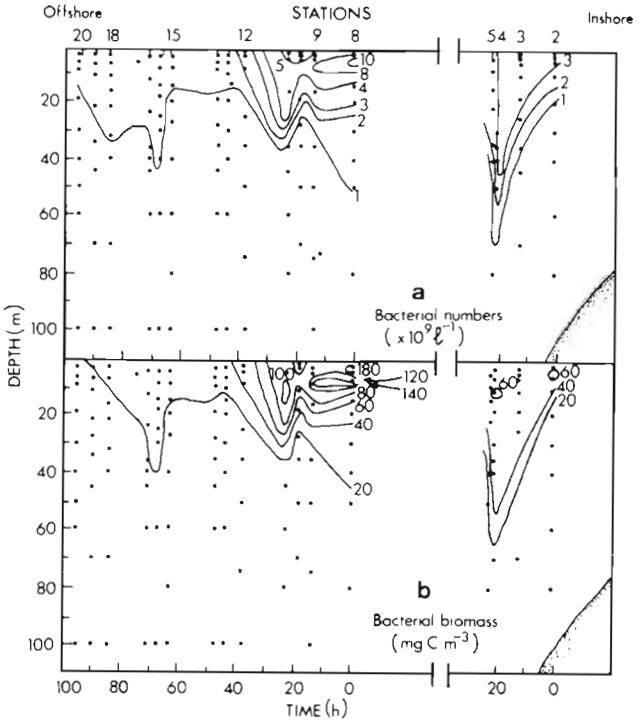

Fig. 5. Distribution of bacterial (a) numbers and (b) biomass

upwelling origin (< 34.9‰; Fig. 2b, Table 1), indicating upwelling and sun-warming of the surface layers prior to the study period. Furthermore, nitrate concentrations (1 to 10 µg-at. NO^3-N l^{-1}; Fig. 2c) in the warm surface waters (> 13 °C) were typical of MUW (Barlow 1982a, Waldron 1985). Variations in density (sigma-t) followed temperature variations and have not been shown here.

SACW (< 11 °C, < 34.9‰, 15 to 20 µg-at. NO_3-N l^{-1}) was present below 60 m along most of the drogue track. Silicate and phosphate data (not presented) showed similar patterns of distribution to those of nitrate, being low in warm surface water (silicate: 2 to 10 µg-at. l^{-1}; phosphate: 0 to 1.2 µg-at. l^{-1}) and higher in SACW (20 to 30 µg-at. Si l^{-1} and 0.5 to 2.4 µg-at. PO_4 l^{-1}).

The principal hydrographic features in the study area, identified from water column structure (Table 1), are shown schematically in Fig. 3. The general feature is that, as the drogue moved offshore, a layer of MUW in the upper 20 to 30 m was separated from a bottom SACW layer by a mixed boundary layer of aged upwelled water (Waldron 1985). Of note is the salinity front present between Stns 12 and 13, suggesting surface mixing of MUW with older water offshore. The 1% light depth was typically between 15 and 25 m in depth, except at the beginning of the first drogue study (4 m at Stn 2). From hydrographic data it appears that the drogue moved out of the upwelling plume just prior to Stn 4, where localised deep mixing was observed.

Phytoplankton production

High rates of primary production were observed in MUW, where maximum rates were generally found at 3 to 8 m depth, corresponding to 25 to 50% light penetration depths (Table 2). Highest values were measured inshore at Stn 3 (186.67 mg C m^{-3} h^{-1}) where integrated primary production was also highest (1114.2 mg C m^{-2} h^{-1}). Phytoplankton production rates declined further offshore, with lowest values (< 15 mg C m^{-3} h^{-1}, 66 to 223 mg C m^{-2} h^{-1}) being associated with the stations furthest offshore in MUW/mixed water.

Specific production rates (P^B) of phytoplankton were calculated using integrated data (see Table 2). In MUW, P^B values were initially relatively high (10.5 mg C mg^{-1} chl h^{-1}) and generally decreased (to 6.2 mg C mg^{-1} chl h^{-1}) as the bloom declined further offshore.

Particulate carbon, phytoplankton and bacterial biomass

Vertical sections show a stratified distribution of particulate carbon, chlorophyll *a* and bacterial numbers

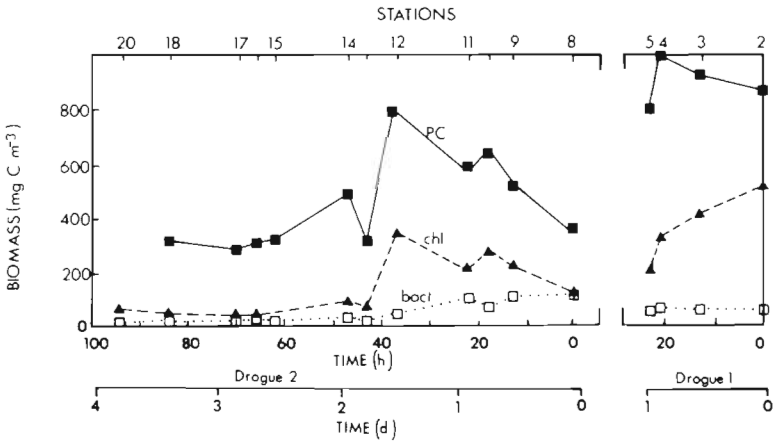

Fig. 6. Changes in the average biomass of particulate carbon (PC), chlorophyll *a* (chl) and bacteria (bact) in the upper 20 to 40 m of the water column

and biomass (Figs. 4a, b & 5a, b). For each variable, largest concentrations were found in the upper 30 m in the inshore region. When data were analysed relative to the water types largest values were found in MUW. Discrete measurements of bacterial biomass at Stn 8 (up to 190 mg C m^{-3}; Fig. 5) were the highest recorded thus far *in situ* in the southern Benguela. In older MUW/mixed water, mixed water and SACW, concentrations of PC, chl *a* and bacteria were low.

Fig. 6 shows temporal changes in the average biomass of phytoplankton, bacteria and particulate carbon in the upper 30 m of the water column. Chlorophyll and particulate carbon concentrations were highest in MUW at inshore stations, and lowest in MUW/mixed water further offshore (see also Fig. 4). A slight increase in primary production in MUW from Stns 9 to 12 (Table 2) was accompanied by a relative increase in the mean concentration of phytoplankton and particulate carbon at these stations. Mean bacterial biomass values (Fig. 6) were highest in MUW at Stns 8 to 12, and lowest in MUW/mixed water (see also Fig. 5).

The phytoplankton community in surface water was dominated throughout this study, in terms of numbers, by nanoplankton-sized cells (2 to 20 µm) which showed a temporal succession in the dominant taxa. Inshore during Drogue 1, when primary production levels were highest, small chain-forming diatoms were abundant (> 5000 cells ml^{-1}; Table 3). In MUW sampled during Drogue 2 diatom abundances were reduced and the phytoplankton community was dominated by nanoflagellates (3000 to 5000 cells ml^{-1}; Table 3). Nanoplankton diatom abundances were further reduced in MUW/mixed water; nanoflagellates remained numerically dominant although their numbers declined to < 2000 cells ml^{-1}. Netplankton-sized (> 20 µm) diatoms and flagellates were also present in surface waters during the study (Table 3) and showed a gradual decline in abundance. In MUW, netplankton diatoms were generally an order of magnitude more abundant than netplanktonic flagellates.

Microscopic examination of preserved water samples showed that bacteria were chiefly free-living, probably due to the absence of large detrital aggregates. Small particles of detrital material (ca 5 µm diameter) were common, often bounded by mucilaginous material, but were generally not characterised by high densities of attached bacteria.

Table 3. Numerically dominant phytoplankton and protozoans (ind. ml^{-1}) in surface waters. Ciliates include oligotrichs and tintinnids. Flagellates include both autotrophs and heterotrophs

Stn	Flagellates		Diatoms		Ciliates	*Noctiluca*	Numerically dominant diatom	Mean volume (μm^3)
	2–20 µm	> 20 µm	2–20 µm	> 20 µm				
2	956	107	5240	386	64	0	*Skeletonema* sp.	353
4	568	35	5212	342	48	0	"	
8	4105	32	209	78	3	0.9	*Chaetoceros* spp.	1000
9	4092	20	312	225	6	1.6	and	
10	3049	34	285	256	23	4.7	*Cerataulina*	9060
11	4824	12	388	109	16	1.6	"	
12	2566	33	972	178	20	0.6	"	
13	1190	15	67	38	14	0.4	"	
14	1659	9	311	45	10	0.3	"	
15	1439	8	39	10	1	0	*Nitzschia* spp.	200
16	1825	4	11	8	2	0	"	

Table 4. Regression equations describing the biomass relationships between bacteria (mg C m^{-3}) and the concentrations of chlorophyll (mg m^{-3}) and particulate carbon (mg C m^{-3}) in coastal water during this study. Power curves ($Y = aX^b$) provided the best fit. Data from all depths were used, and were grouped according to the age of surface water. Maturing upwelled water (MUW) was observed at Stns 2 to 5 and 8 to 12; mature upwelled water of different ages was mixing at Stns 13 to 20 (MUW/mixed)

Stations	Drogue	Regression equation	n	r^2	p
Bacteria (Y) vs Chlorophyll (X):					
2–5	1	$\ln Y = \ln 1.69 + 0.60 \ln X$	43	0.655	0.001
8–12	2	$\ln Y = \ln 3.41 + 0.55 \ln X$	43	0.766	0.001
13–20	2	$\ln Y = \ln 2.98 + 0.33 \ln X$	52	0.450	0.001
Bacteria (Y) vs Particulate carbon (X):					
2–5	1	$\ln Y = 1.14 \ln X - \ln 3.81$	34	0.816	0.001
8–12	2	$\ln Y = 1.45 \ln X - \ln 4.89$	36	0.799	0.001
13–18	2	$\ln Y = 1.66 \ln X - \ln 6.51$	35	0.704	0.001

The relative contribution of different bacterial morphotypes to the total population differed with water type. Small cocci (0.25 µm equivalent spherical diameter, ESD) comprised a relatively small percentage (< 18 %) of the total numbers in MUW and mixed water, but were more abundant (25 %) in SACW. Large cocci (0.65 µm ESD) were numerically dominant (48 to 58 %) in each water type. Small rods (0.72 µm ESD) accounted for a relatively large proportion (20 to 30 %) of the populations. Large rods (1.09 µm ESD) were present in all water types, but numbers were low (< 2 %).

In terms of total bacterial biomass, the contribution by small cocci was negligible in each of the different water types, while large cocci (50 %) and small rods (35 to 42 %) were clearly dominant. Due to their volume, large rods contributed about 10 % to the population biomass in mixed and SACW. The weighted mean cell biomass, calculated from the total bacterial biomass and total cell numbers, was highest in MUW (18.33 fg C $cell^{-1}$), decreasing to 17.66 fg C $cell^{-1}$ in mixed water, and 15.69 fg C $cell^{-1}$ in SACW. These values assume a constant carbon content per unit volume, and primarily reflect the increased average cell size in productive upwelled water.

The relationships between bacteria and chl *a* and PC during this study were examined in relation to the age of the surface water. All relationships were found to be significant (Table 4), and best described by power functions.

Zooplankton

Zooplankton numbers and biomass were dominated by copepods, with *Calanoides carinatus* as the dominant species. From counts of Niskin bottle samples it was evident that virtually all of the copepods were found in the upper 40 to 60 m of the water column at our sampling times (Fig. 7). In calculating average numbers it was therefore assumed that Bongo samples, although collected over the whole water column, actually represented the upper 50 m of the water column.

From the Bongo samples it was evident that the total abundance of copepods during this study was high (2000

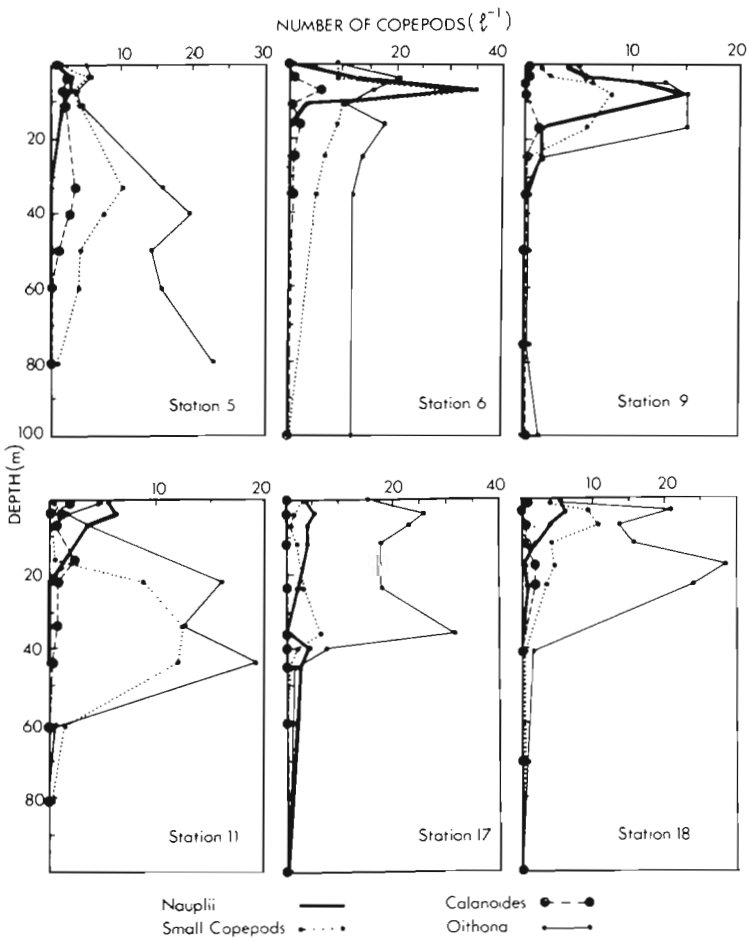

Fig. 7 Vertical distribution of copepods at 6 stations, determined from Niskin bottle samples. Small copepods include *Paracalanus parvus, P. scottii, Ctenocalanus vanus, Centropages brachiatus* and *Calanoides carinatus* copepodites (C1 to C3)

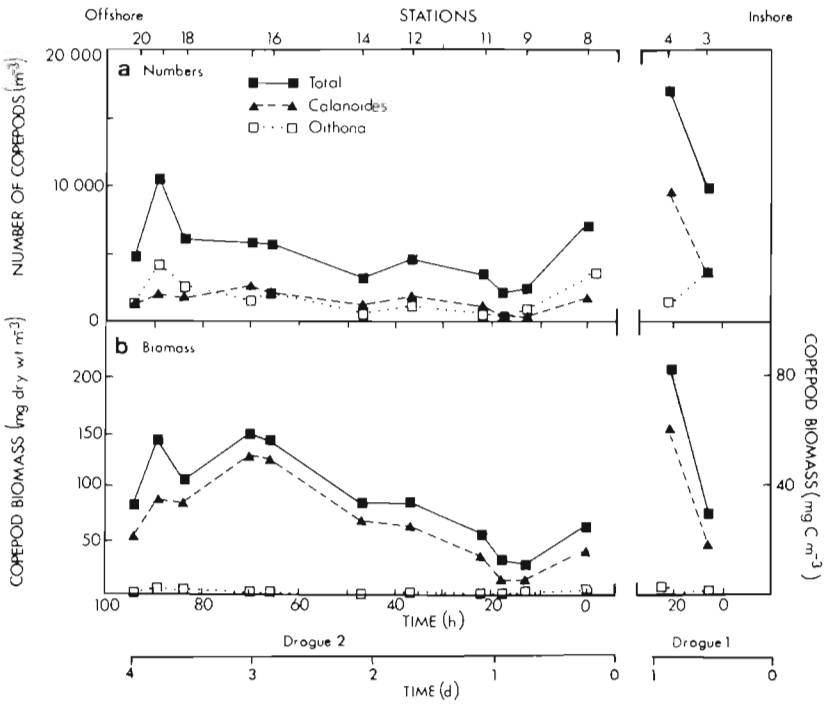

Fig. 8. (a) Number and (b) biomass of copepods in the upper 50 m of the water column, calculated from Bongo samples

to 17200 ind. m^{-3}, mean = 6400 m^{-3}), with *Calanoides carinatus* accounting for an average of 30 % of total numbers (see Fig. 8a). Other important copepods in rank order of abundance were *Oithona* spp., *Centropages brachiatus*, and various small copepods (body weight < 10 µg dry wt) including *Ctenocalanus vanus*, *Paracalanus parvus* and *P. scottii*. Copepods which occurred in 5 or more samples included *Rhincalanus nasutus*, *Metridia lucens*, *Calanus agulhensis* and *Oncaea* spp.

A comparison of total numbers (m^{-3}) estimated from Niskin bottle samples and Bongo net samples (Table 5) showed that counts were comparable for *Calanoides* copepodite stages (C1 to C5), except at Stn 17. *Calanoides* nauplii and small copepods (*Centropages*, *Oithona*, *Ctenocalanus* and *Paracalanus*) were more abundant in the Niskin water than in the Bongo net samples. Numbers of *Calanoides* males and females collected by the 2 samplers showed no clear trends.

Fig. 8 shows variations in copepod numbers and biomass with time. For *Calanoides carinatus* maximum abundances were found during the first drogue, associated with the highest chlorophyll *a* concentrations. Abundances were low at the start of the second drogue, but increased with time. For other copepods, the trends were similar but markedly reduced.

Mean copepod biomass over the study period was 37 mg C m^{-3} or 2 g C m^{-2}, with *Calanoides carinatus* accounting on average for 67 % of this total (Fig. 8b). These copepods showed a temporal increase in their total biomass during the second drogue, increasing from ca 20 mg C m^{-3} at the beginning of the drogue to 58 mg C m^{-3} by Day 3, and subsequently declining to 33 mg C m^{-3} by Day 4. In general, an inverse relationship between copepod biomass and chlorophyll *a* concentration was observed (Figs. 6 & 8b). The biomass data are compared in Table 6. Ratios of copepod : chlorophyll carbon calculated from the average concentrations in surface waters showed that copepod biomass averaged 11 % of the phytoplankton biomass in MUW, and 96 % in older MUW/mixed water. If data are integrated over all sampling depths (50 m for copepods, 100 m for phytoplankton), the ratio of copepod carbon to phytoplankton carbon averages 18 % in MUW, and 128 % in MUW/mixed water. The latter ratios are likely to be more realistic considering the migratory behaviour of copepods and their subsequent ability to integrate their food environment over the entire water column.

Noctiluca miliaris were abundant during this study, showing a wide range in organism size. Numbers observed in the Niskin bottle samples (Fig. 9) and from inverted microscope counts (Table 3) were 2 orders of magnitude larger than the Bongo samples due to inclusion of cells in the smaller size-classes, with highest numbers observed in MUW during Drogue 2.

DISCUSSION

Hydrography

Hydrographic features identified off Cape Columbine during this study are similar to those described by Waldron (1985). Quantitative data on concentrations of nitrate and chlorophyll within the different water types are consistent with previous records for the southern Benguela (see reviews by Chapman & Shannon 1985, Shannon 1985, Shannon & Pillar 1986). From temperature, salinity and nitrate sections it was clear that upwelling was not active. The water column was vertically stratified, with 3 distinct water masses being observed in the upper 30 m. Although all were identified as maturing upwelled water (MUW), each was at a different stage of hydrological and biological development. Phytoplankton

Table 5. Comparison of copepod counts (ind. m^{-3}) obtained from Niskin bottle and Bongo net samples. Total value excludes nauplii (Naup.). Counts from discrete Niskin samples collected in the upper 50 m were integrated over this depth (ind. m^{-2}) and divided by 50 (ind. m^{-3}). Total counts per Bongo sample were divided by the volume of seawater filtered (m^3). *Calanoides carinatus* copepodites were grouped according to their developmental stages: C1 to C5, female (♀) and male (♂). All copepodite stages were combined for *Centropages brachiatus* (Cent.), *Oithona* spp. (Oith.), and *Ctenocalanus vanus/Paracalanus parvus* and *P. scotti* (Cteno./Para.) counts. NC: not counted. Total counts estimated from Niskin samples (*N*) are compared with totals from Bongo samples (*B*)

Sample type	*Calanoides carinatus*					Cent.	Oith.	Cteno./Para.	Total	*N/B*
	Naup.	C1–C3	C4–C5	♀	♂					
Stn 5										
Bongo	290	1105	2290	0	8	NC	NC	NC	–	
Niskin	830	1105	2288	0	8	615	11383	4458	19857	–
Stn 6										
Bongo	439	1197	909	96	0	840	1350	1780	6172	
Niskin	3615	1690	910	0	83	1790	10028	5005	19506	3.2
Stn 9										
Bongo	215	184	129	62	12	450	905	690	2432	
Niskin	3133	180	170	5	115	918	5615	1380	8383	3.5
Stn 11										
Bongo	102	597	350	135	10	920	640	790	3442	
Niskin	780	555	565	240	0	3198	8165	1955	14678	4.3
Stn 17										
Bongo	333	448	1130	707	323	530	1660	960	5758	
Niskin	2058	270	425	83	120	683	17238	1730	20549	3.6
Stn 18										
Bongo	466	423	509	574	218	400	2540	1350	6014	
Niskin	1205	383	428	160	143	1443	13110	1463	17130	2.9

growth was at its peak during Drogue 1, which was closest to the upwelling centre and therefore marked by the youngest water. Drogue 2, further offshore from the upwelling centre, was characterised by older water. Salinity and biological fronts between Stns 12 and 13 suggested that MUW was mixing with water which was even older, although still of upwelling origin. As the Benguela current in this region generally flows northwards, older water is also likely to have originated to the south of Cape Columbine. Mixing of MUW masses of different ages effectively accelerated the biological development of the plume being studied. Major water masses in the aphotic zone were identified as mixed water, and South Atlantic Central Water which is lifted onto the shelf during upwelling.

Table 6. A comparison of phytoplankton (*P*) and total copepod (*K*) biomass, using average concentrations in maturing upwelled water and MUW/mixed water, and biomass data integrated over the water column (50 m for copepods, 100 m for phytoplankton). Chlorophyll *a* was used as an index of phytoplankton biomass. –: no data collected. Means ± standard deviations are also shown

Stn	Drogue	Concentration (mg C m^{-3})			Integrated (mg C m^{-2})		
		P	*K*	*K* · *P*	*P*	*K*	*K* · *P*
Maturing upwelled water							
3	1	394	30	0.08	9576	1490	0.16
4	1	307	86	0.28	26070	4310	0.17
6	1	–	33	–	8676	1630	0.19
8	2	116	26	0.22	5864	1290	0.22
9	2	223	11	0.05	5774	540	0.09
11	2	237	22	0.09	8282	1100	0.13
12	2	358	33	0.09	5269	1660	0.32
				0.11 ± 0.06			0.18 ± 0.07
MUW/mixed							
14	2	93	33	0.35	1772	1660	0.94
16	2	40	56	1.40	3789	2800	0.74
17	2	38	58	1.53	1209	2920	2.42
18	2	41	42	1.02	–	2080	–
19	2	–	56	–	–	2820	–
20	2	66	33	0.50	1637	1650	1.01
				0.96 ± 0.47			1.28 ± 0.67

The planktonic community

Phytoplankton

Our initial measurements of phytoplankton biomass and production in surface waters were high. Nitrate concentrations were between 2 and 5 mg-at. m^{-3}, and the phytoplankton community was dominated by diatoms. These observations are characteristic

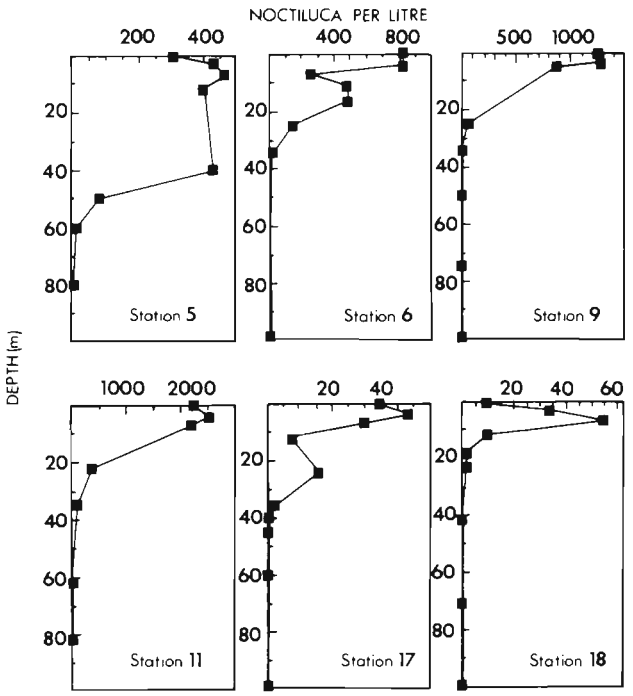

Fig. 9. Abundance of *Noctiluca miliaris* through the water column, as determined from Niskin bottle samples

of near maximal phytoplankton bloom conditions which follow favourable upwelling conditions when nitrate concentrations (up to 25 mg-at. m^{-3}) and the light environment are optimal. They are comparable also with previously recorded observations at the height of the bloom in the southern Benguela (Barlow 1982a, Brown 1984, Brown & Hutchings 1987a, b, Brown & Field 1986). Further offshore, in older water, phytoplankton biomass and production values indicated that the bloom was in the declining growth phase. The numerically dominant phytoplankton here were the nanoplanktonic flagellates. A temporal succession in the numerically dominant phytoplankton groups has been clearly demonstrated in many studies on the dynamics of phytoplankton after upwelling. The initial phytoplankton community is generally dominated by chain-forming diatoms, such as *Chaetoceros* spp. and *Skeletonema costatum* (Olivieri 1983, Hutchings et al. 1984, Shannon & Pillar 1986) or *Thalassiosira*. During stratification, conditions are not optimal for diatom growth and they are succeeded by flagellates (< 20 µm diameter) and picophytoplankton (< 2 µm) (see Hutchings et al. 1984, Probyn 1987, Mitchell-Innes & Winter 1987, Pitcher et al. 1991), although large diatoms still dominate the biomass. Despite their small numbers, netphytoplankton-sized diatoms (> 20 µm) contributed ca 50 % of the total biomass during Drogue 2 (Painting et al. 1993).

The P^B values (6 to 10 mg C mg^{-1} chl h^{-1}) observed in Table 2 are moderately high and indicative of the high photosynthetic activity per unit chlorophyll that has frequently been observed for the productive waters of the southern Benguela region (see Carter et al. 1987, Walker & Peterson 1992). Community turnover times (P/B) of 1 to 3 d^{-1} (for a 10 h day) are fast but comparable to rates of 0.7 to 4.0 exhibited by nanophytoplankton and netphytoplankton (*Thalassiosira* sp.) communities observed in the southern Benguela by Lucas & Probyn (unpubl.) and in culture (Furnas 1982, 1990). Nevertheless, a cautionary note needs to be introduced here regarding our estimates of chlorophyll biomass.

There has been considerable argument that trapping of phytoplankton cells on glass-fibre filters (GF/F and GF/C) leads to an underestimate of picoplanktonic chlorophyll *a* from oligotrophic waters (Yentsch 1983, Taguchi & Laws 1989). In the more productive southern Benguela region Lucas & Probyn (unpubl.) found that picoplankton (< 2 µm) contributed < 5 % of phytoplankton chlorophyll *a* in inshore regions, but up to about 30 % at mid- and shelf-edge stations. On the basis of their results we would estimate that < 10 % of picoplankton chlorophyll could have been lost in this study due to the filters used, which would not seriously alter P^B or P/B estimates in this study. Yet recent studies by Walker & Peterson (1992) have shown that picoplankton (< 2 µm) may account for up to 90 % of phytoplankton biomass and 48 % of primary production when the community is dominated by flagellates. In diatom-dominated communities picophytoplankton contribute < 20 % of the total carbon biomass and < 15 % of the total production. Their findings suggest that total phytoplankton biomass and production may have been underestimated during this study, particularly towards the end of the bloom. In general, however, the estimates of biomass and production obtained are comparable with those from previous studies, possibly due to the relatively large volumes (1 l) of water filtered. The differential use of GF/C and GF/F filters for biomass and production respectively is likely to result in an overestimate of the specific production rates (P^B) in the flagellate-dominated communities. The P^B value of 19.4 recorded in the older MUW/mixed water (Stn 18), for example, is unrealistically high and probably largely due to the discrepancy in the average pore sizes of the different filters.

The principal factors responsible for the decline of the phytoplankton bloom in this study are unclear. Nitrate concentrations exceeded 2 mg-at. NO_3-N m^{-3} in older offshore surface waters (Fig. 2), yet chlorophyll *a* concentrations and primary production rates were low (Fig. 4, Table 2). Light limitation seems unlikely since the hydrographic data show that the upper mixed layer was well within the euphotic zone (1 %

light depth). Grazing pressure by the mesozooplankton and microzooplankton communities could account for low biomass and low production while the P^B ratio was high, consistent with non-limiting conditions. Mesozooplankton grazing rates in this study (see below) removed between 5 and 10 % of phytoplankton biomass in MUW and up to 38 % of algal biomass towards the end of the bloom when copepod biomass exceeded phytoplankton biomass. A similar situation has been recorded for the western English Channel where an inverted trophic pyramid indicated a grazer-controlled phytoplankton population (Holligan et al. 1984). Further, microzooplankton may readily remove up to 100 % of the algal biomass daily in the small size-classes (Matthews & Probyn unpubl.).

Bacterioplankton

Spatial variability in the number and biomass of bacteria was observed in relation to the dominant water types, with highest values recorded in MUW and lowest values in SACW. Similar abundances were reported by McManus & Peterson (1988) for the upwelling region off central Chile. Bacterial community structure, in terms of dominant morphotypes, was also observed to vary in relation to the water types identified. These changes are indicative of different levels of bacterial activity and productivity. Small cocci, for example, which comprised ca 25 % of the bacterial community in SACW, probably represented the starved mini-cells characteristic of organically depauperate environments (Morita 1984, Davis & Robb 1985, Verheye-Dua & Lucas 1988). Spatial variability in bacterial abundance and activity may be comparable with those changes occurring with time after each upwelling event. In a microcosm simulation, Painting et al. (1989) followed the development and interactions of natural phytoplankton and microbial communities during the growth and decay of a phytoplankton bloom in MUW. Bacterial numbers were low in recently upwelled water and increased during phytoplankton growth. The community was dominated (numbers and biomass) by large cocci and small rods during phytoplankton growth, and by small cocci (numbers) and large rods (biomass) during phytoplankton decay. Characterisation of the plateable bacterial populations showed a succession in the dominant strains (*Vibrionaceae* → *Pseudomonadaceae* → *Neissereaceae/Flavobacteriacea*). Plateable isolates showed variability in their diversity, and catabolic and hydrolytic properties during the development and decay phases of the phytoplankton bloom. Bacteria showed rapid uptake of dissolved substrates during phytoplankton growth, but exhibited much slower uptake rates during the decline of the bloom, when it was surmised that the bacteria were utilising more refractory substrates.

Some comment needs to be made here on our estimate of bacterial biomass in view of recent claims that the carbon : biovolume conversion factor for marine bacterioplankton should be in the range of 0.2 to 0.35 pg C μm^{-3} (Lee & Fuhrman 1987, Simon & Azam 1989) rather than the 0.121 pg C μm^{-3} value (Watson et al. 1977) we have used. Had we used the higher conversion factors, our bacterial biomass estimate would have doubled or trebled. Such values would require a dramatic reconsideration of carbon mass-balance fluxes to accommodate elevated bacterial carbon consumption requirements with respect to carbon flows to higher trophic orders (see Lucas 1986). As it is, simulations of carbon flow (Moloney et al. 1991) estimate that less than 13 % of total photosynthetic carbon fixation is available for pelagic fish consumption. This amount would be completely accounted for if the bacterial biomass and associated carbon requirements were elevated by 2 to 3 times. Alternatively, we would have to reconsider the proportion of bacteria that is regarded

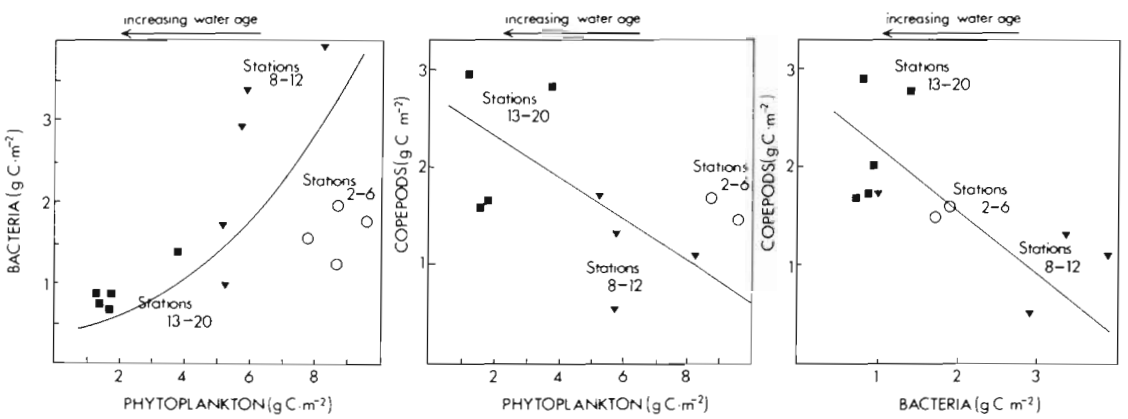

Fig. 10. General biomass relationships between phytoplankton, bacteria and copepods in the water column during the drogue study in the southern Benguela

as metabolically inactive (Morita 1984) or invoke perhaps 4-fold increased DOC concentrations (Kirchman et al. 1991) as a carbon resource for the bacteria. However, we have no evidence to support either of these alternatives and so have adhered to our estimates of bacterial carbon based on a more conservative carbon : biovolume estimate.

Bacterial biomass was correlated with phytoplankton biomass, production and particulate carbon (Tables 2 & 4) during this study. Plots of bacterial biomass vs phytoplankton biomass (Fig 10a) and phytoplankton production (not shown) show 3 distinct clusters of data. Association of each cluster with a different water type suggests that the dynamics of the planktonic communities within each water type were different. Initially, during high levels of phytoplankton production and biomass (Stns 2 to 6) bacterial biomass was only 17 % of phytoplankton biomass. Later, as primary production and phytoplankton biomass decreased, relative bacterial biomass increased to 50 % (Stns 13 to 20). In a similar study in the southern Benguela, Verheye-Dua & Lucas (1988) observed that the ratio of bacterial biomass : chlorophyll *a* increased with increased aging of upwelled water. They proposed, as did Barlow (1982a), that older water may be dominated by bacteria and detritus, while younger water will be dominated by active phytoplankton with high chlorophyll concentrations.

Relationships between discrete measurements of bacterial biomass and phytoplankton biomass and production, and between bacteria and PC were generally best described by power curves. This relationship suggests that bacteria initially respond positively to available carbon resources (e.g. chl *a*) but that their biomass is reduced when substrate availability (either readily utilisable PDOC or more refractory substrates) is high and prolonged, probably due to predation by a developing community of bacterivores (Verheye-Dua & Lucas 1988). Simulations of changing biomass relationships in a planktonic community after upwelling (e.g. Moloney et al. 1991) demonstrate the sensitive links between phytoplankton growth, bacterial growth and their subsequent control by bacterivorous protozoa. Certainly, numerous experimental studies have shown that flagellates and ciliates can control bacterial biomass (Andersen & Fenchel 1985, Sherr et al. 1986a, b, Lucas et al. 1987) and that there is a well-ordered succession of phytoplankton → bacteria → protozoa (Laake et al. 1983, Hagström & Larsson 1984, Lucas et al. 1987, Painting et al. 1989). As predation is density-dependent, it is to be expected that at higher bacterial densities, predation will have a greater impact, so accounting for the non-linear relationship between bacteria and chlorophyll *a* or PC.

Microzooplankton

Until recently, the role of microzooplankton (< 200 µm) in the southern Benguela upwelling region had not been addressed. However, microzooplankton abundances, their grazing impact and their role in nitrogen recycling have now received some attention (see Lucas et al. 1987, Matthews 1991, Moloney et al. 1991, Matthews & Probyn unpubl.).

An early study of microflagellate bacterivory using a simulated *in situ* microcosm of an upwelling event demonstrated that the heterotrophic microflagellate *Pseudobodo* sp. could consume approximately 19 bacteria flagellate^{-1} h^{-1} (Lucas et al. 1987). For typical field densities of heterotrophic flagellates (1 to 3 × 10^3 cells ml^{-1}), where on average about 50 % are < 5 µm in diameter, it was calculated that the flagellates could clear 5 to 30 % of the water column daily. An important finding by Lucas et al. (1987) was that the calculated nitrogen regeneration rate based on C : N stoichiometry could not account for observed N regeneration rates based on ^{15}N studies in this region. This implied that the microbial food chain was longer and more complex than a simple 2-step model. Recently, Probyn (1992) noted that the average annual *f*-ratio for the southern Benguela is 0.2 to 0.3 associated with the overall dominance of small phytoplankton cells (< 10 µm) utilising regenerated nitrogen. This is indicative of an active microbial food web in which microzooplankton activity is closely coupled to phytoplankton and bacterioplankton production.

This conclusion is supported by direct estimates of microzooplankton abundance and grazing rates for 2 regions of the southern Benguela (Matthews 1991, Lucas & Probyn unpubl.). Matthews (1991) found that microzooplankton (< 300 µm) numbers ranged from 7.8 to 21.0 × 10^3 cells l^{-1}, averaging 11.9 × 10^3 cells l^{-1}. Individuals were dominated primarily by oligotrich aloricate ciliates (*Strombidium* and *Strombilidium* spp.). However, at some locations the heterotrophic dinoflagellate *Gyrodinium* sp. was important. Tintinnids were always observed, as were the autotrophic ciliates *Myrionecta rubra* and *Laboea strobila*. This mixed species assemblage exhibited an average filtration rate of 8.71 µl cell^{-1} l^{-1} and consumed about 91 to 157 % of the < 2 µm autotroph standing stock, but only about 8 to 29 % of the potential < 2 µm autotrophic production over a 12 h period. This represents a 5 % removal of the total phytoplankton biomass under diatom bloom conditions and an average of 46 % (sometimes > 100 %) removal under post-bloom conditions over a 12 h period.

In a similar study, Lucas & Probyn (unpubl.) examined microzooplankton grazing at inshore, mid-shelf and shelf-edge sites in the southern Benguela upwell-

ing region. In their study, netplanktonic diatoms > 10 µm (*Thalassiosira* sp.) dominated (73 %) algal biomass (28.5 µg chl *a* l^{-1}) at the inshore station while at the mid-shelf and shelf-edge stations nano- and picoplankton dominated (86 %) phytoplankton biomass (2.1 and 0.35 µg chl *a* l^{-1} respectively). Microzooplankton grazing was confined almost entirely to the < 10 µm nano- and picoplanktonic size-classes. Grazing removed 5 % of the total algal biomass per 24 h at the inshore station and ca 90 % per 24 h at the mid-shelf and shelf-edge stations. Values for the removal of algal production over the same locations for the same period were 3 and 50 % respectively.

The conclusion to be drawn from these findings, which compare favourably with similar studies by Landry & Hassett (1982), Gifford (1988) and Rassoulzadegan et al. (1988), is that microzooplankton grazing can at times exert a considerable impact on primary production, removing from as little as 5 % of daily production to as much as 100 %. In the southern Benguela region it would appear that initial diatom-dominated blooms are characterised by little microzooplankton grazing but that later nano- and picoplankton dominated assemblages are heavily grazed by microzooplankton. Similar plankton successions have been reported from other temperate regions. In the Japan Sea, for example, the spring phytoplankton bloom is followed by a community dominated by heterotrophic microplankton which cycle the organic material fixed during the bloom (Sorokin 1977).

Although no quantitative studies have been done on the dinoflagellate *Noctiluca miliaris*, in the southern Benguela, abundances observed in this study appear to be high. They are, for example, an order of magnitude higher than estimates reported from the North Sea (Uhlig & Sahling 1982). It is likely that this dinoflagellate had a significant impact on the structure of the planktonic community. Apart from reports of *N. miliaris* predation on copepod eggs (Daan 1987), relatively little is known about the trophic ecology of *N. miliaris*. Unpublished data by H. Verheye (pers. comm.) show that *N. miliaris* are able to ingest large phytoplankton cells, such as *Coscinodiscus gigas*, as well as eggs of *Calanoides carinatus*. Considering the range in sizes of *N. miliaris* individuals noted, it is likely that this dinoflagellate could consume a wide range of planktonic size-classes, including microzooplankton. High predation on bacterivores by *N. miliaris* in MUW during Drogue 2 may account for the high associated bacterial biomass.

Table 7. Estimates of the grazing impact of the copepod community at Stn 8, calculated from the Mullin & Brooks (1976) algorithm (see 'Methods'). Grazing rates were calculated for each copepodite stage (C1 to C5) and females of *Calanoides carinatus*. All developmental stages were combined for the smaller copepod species (Small = *Oithona* spp., *Ctenocalanus vanus, Paracalanus parvus, P. scottii*) and *Centropages brachiatus* (Centro.). A purely herbivorous diet and a feeding period of 10 h d^{-1} were assumed for each species. *I/i*: ingestion per individual (µg C $ind.^{-1}$ h^{-1}); *I*: ingestion rate (mg C m^{-3} d^{-1}); *P* = phytoplankton biomass (115.5 mg C m^{-3} at Stn 8)

Copepod	Body wt (µg C)	$57\,W^{0.35}$	*I/i*	Abundance (ind. m^{-3})	*I*	*I/P* (%)
C1	2	72.6	0.1	186	0.1	0.11
C2	3	83.7	0.1	372	0.3	0.29
C3	6	106.7	0.1	581	0.8	0.73
C4	12	136.0	0.2	277	0.6	0.48
C5	24	173.4	0.3	304	0.8	0.67
Females	48	221.0	0.3	65	0.2	0.18
Centro.	10	127.6	0.2	430	0.8	0.70
Small	4	92.6	0.1	5020	5.5	4.77
Total			1.4	7235	9.1	7.93

Mesozooplankton

Copepods observed were typical of an upwelling community. *Calanoides carinatus* is common in the Benguela upwelling region, and is a dominant member of all upwelling systems on the African coast (Smith 1982, Peterson & Painting 1990, Verheye 1991). Estimates of copepod abundance and biomass in this study are higher than previously published estimates for the southern Benguela (see review by Shannon & Pillar 1986). The mean value of 2 g C m^{-2} for copepod biomass is double the average value reported by these authors, Borchers & Hutchings (1986) and Verheye & Hutchings (1988). However, biomass values calculated here are not easily compared with earlier data sets due to differences in sampling equipment and processing methods. Size-fractionated wet weights were used routinely, whereas copepod biomass in more recent studies has been calculated from numerical abundances (see 'Methods'). Using this latter approach, copepod biomass estimates of 0.5 to 5 g C m^{-2} have been obtained at different locations in the southern Benguela upwelling region (Painting & Huggett 1989, Peterson & Hutchings 1989, Verheye et al. 1992).

Verheye (1991) and Verheye & Field (1992) observed that the vertical distribution of *Calanoides carinatus* was characterised by ontogenetic layering, with older stages occupying progressively greater depths in the water column. Copepodite stages 1 to 3 generally occupied the upper 20 m, while older juveniles (C4 and C5) and adults

were typically found between 15 and 40 m. During quiescent upwelling conditions, vertical migrations appeared to occur within these depth ranges for all developmental stages. The only notable exception was for adult females, which appeared to migrate more extensively. Higher abundances of female *Calanoides carinatus* in the Bongo net samples (Table 5) may have been largely attributable to migration of females to depths between 50 m and the maximum sampling depth of the Bongo net (see 'Methods'). Furthermore, it is unlikely that Niskin bottles are quantitative samplers for larger copepods, which probably avoid such sampling apparatus, or for groups which are patchily distributed (see Omori & Ikeda 1984, Pillar 1984). Higher abundances of *C. carinatus* nauplii and the smaller copepod species (*Centropages brachiatus, Oithona* spp., *Ctenocalanus vanus*, etc.) in Niskin samples than in Bongo samples suggest that the Bongo net (mesh size 200 µm) is non-quantitative for animals of this size. These results have considerable implications for our studies of ecosystem dynamics in the southern Benguela, as the abundances and trophic significance of the smaller copepods are likely to be underestimated, possibly by as much as 4 times (Table 5).

In terms of the general biomass relationships copepod biomass was relatively low at the height of the phytoplankton bloom, and increased during the decline of the bloom (Fig. 10b). In phytoplankton-rich MUW, copepod biomass was equivalent to 16 to 32 % of phytoplankton biomass (Table 6). Assuming a simple diatom-copepod food chain, a daily food requirement of 30 % of their total biomass, and a purely herbivorous diet, these copepods were calculated to consume 5 to 10 % of phytoplankton biomass. In older MUW/mixed water copepod biomass exceeded phytoplankton biomass (average K/P = 128 %; Table 6) and copepods were calculated to consume on average 38 % of phytoplankton biomass to meet their daily requirements. Although there appeared to be sufficient phytoplankton to meet the copepod grazing requirements, these estimates are complicated by evidence suggesting that not all phytoplankton biomass is available to these grazers. Bartram (1980) showed that many copepods feed inefficiently on particles < 10 µm diameter. More recent studies have shown that larger copepod species prefer to feed on particles > 10 µm (Harris 1982, Price et al. 1983). In this study, the phytoplankton community in surface waters was numerically dominated by organisms in the 2 to 20 µm size range. It is therefore unlikely that all of the phytoplankton biomass and production was available to herbivorous mesozooplankton, particularly in older MUW/mixed water where diatom abundances were low. Furthermore, copepod ingestion rates may be influenced by the total biomass of available food. Estimates of the grazing impact of the copepod community calculated from the Mullin & Brooks (1976) equations showed that the total copepod community consumed 1 to 8 % of phytoplankton biomass in MUW (see Tables 7 & 8) and 5 to 9 % of phytoplankton biomass in older MUW/mixed water, where phytoplankton biomass was lower. These estimates concur with previous measurements in the southern Benguela, which have consistently shown that < 10 % of the total phytoplankton biomass is grazed by copepods (Peterson et al. 1990, Olivieri & Hutchings unpubl.). Copepods in older water thus appear to become increasingly food-limited and are likely to face starvation and a reduction in their growth, fecundity and secondary production rates (Borchers & Hutchings 1986, Attwood & Peterson 1989). Copepods may, however, be able to supplement their herbivorous dietary requirements. In the southern Benguela, Probyn et al. (1990) showed that microzooplankton contributed 14 % to the nitrogen requirements of mesozooplankton in aged upwelled water.

Table 8. Total copepod ingestion rates (I, mg C $m^{-3} d^{-1}$) at each station. P: phytoplankton biomass (mg C m^{-3}). –: species were not counted

Stn	Drogue	P	*Calanoides* I	Centro. I	Small I	Total I	I/P (%)
Maturing upwelled water (MUW)							
3	1	394.0	4.4	2.3	5.7	12.4	3.2
4	1	307.0	14.2	3.8	6.3	24.3	7.9
5	1	197.0	7.3	–	–	–	–
6	1	220.0	4.4	1.8	3.4	9.6	4.4
8	2	115.5	2.8	0.8	5.5	9.1	7.9
9	2	222.8	0.9	0.9	1.8	3.6	1.6
10	2	243.3	0.9	1.2	1.2	3.3	1.4
11	2	236.6	2.6	1.9	1.6	6.1	2.6
12	2	357.8	4.7	1.3	2.4	8.4	2.3
MUW/mixed							
14	2	93.0	2.2	0.6	1.8	4.6	4.9
16	2	40.3	1.7	0.2	1.6	3.5	8.6
17	2	37.8	1.8	0.3	1.2	3.3	8.8
18	2	41.0	1.3	0.3	1.9	3.4	8.4
20	2	65.7	1.5	0.8	2.2	4.5	6.8

Food web dynamics

A central rationale for the study of food web dynamics in the southern Benguela upwelling region is that of estimating the potential of the envi-

ronment to support the economically important pelagic and demersal fisheries of the region. Furthermore, food web trophodynamics and carbon positioning pathways may significantly alter ocean-atmosphere CO_2 fluxes (see Longhurst 1991).

Recent studies by James (1987) and James & Findlay (1989) demonstrate that the Cape anchovy *Engraulis capensis* acquires the bulk of its daily energy requirements (ca 10 % body wt d^{-1}; Shannon & Field 1985) by size-selective particulate feeding on items > 720 µm in diameter, particularly calanoid copepods and euphausiids. In the absence of large prey items, anchovy resort to filter-feeding on the larger phytoplankton cells (e.g. *Chaetoceros* spp., 10 to 100 µm) although direct grazing on primary producers is only of minor trophic importance. Although average phytoplankton production in upwelling areas ought to be sufficient to sustain a higher mesozooplankton biomass, the patchy nature of the environment and the pulsed nature of upwelling causes intermittent starvation and a decrease in zooplankton fecundity (see also Hutchings 1981, Borchers & Hutchings 1986, Attwood & Peterson 1989, Hutchings 1992).

On the basis of James' (1987) study, one might therefore expect the pelagic fish biomass to be limited by mesozooplankton abundance. A review of fishery yields in different productive regions by Hutchings (1992) confirms that the southern Benguela system is amongst the least productive of upwelling systems. The maximum fisheries yield in the Humboldt system (14×10^6 t) is an order of magnitude higher than that in the southern Benguela (3×10^6 t), California (1×10^6 t) or Canary (2×10^6 t) upwelling regions. Nixon et al. (1986) proposed that in upwelling systems where the frequency of upwelling is reduced or more sustained (e.g. Peru), the fisheries yield improves, presumably because the herbivorous community is better established in a more stable environment.

What then is the fate of primary production in the southern Benguela upwelling region? This study indicates that < 10 % of the primary production is consumed by mesozooplankton, a value supported by Moloney et al. (1991) in which < 13 % of total photosynthetically fixed carbon is estimated to be available to pelagic fish. In their simulation study, 75 % of the fixed carbon was lost through respiration and sinking. In the southern Benguela upwelling region, Pitcher et al. (1989) showed that chlorophyll *a* sinking rates ranged from 0 to 0.91 m d^{-1} and were related to taxonomic and size-related properties. Maximum vertical flux from the euphotic zone amounted to 13.8 % of daily primary production although in general carbon flux did not exceed 6.1 % of primary production. Netphytoplankton (< 200 µm) diatoms typically dominate developing blooms and exhibit the fastest sinking rates (Pitcher et al. 1989). They have a strong requirement for NO_3 assimilation, as indicated by their high (ca 0.7) *f*-ratio values (Probyn 1985). However, regional and annual averages of the *f*-ratio in the southern Benguela yield a value of 0.2 to 0.3 associated with the overall dominance by small phytoplankton cells (< 10 µm) utilising regenerated nitrogen (Probyn 1992). This observation implies an active microbial food web in which microzooplankton activity and nitrogen regeneration are closely coupled to autotrophic and bacterioplanktonic production (Lucas et al. 1987, Matthews 1991, Lucas & Probyn unpubl.).

It is this conclusion which ties together the observations in this study. Although primary production is high, it is dominated by small cells and together with the episodic nature of upwelling pulses in this region, suppresses mesozooplankton biomass and production. Furthermore, microzooplankton grazing rates are high, explaining the low *f*-ratio but also the observation that there is little sedimentation and inefficient trophic transfer to higher consumers because of small cell sizes. A final consideration, however, is whether there is a link between small cells, microzooplankton consumers and the mesozooplankton-fish food chain. This problem was addressed by Matthews (1991) who concluded that in maturing upwelled water only 3 % of the nitrogen ingested by protozoa was transferred to mesozooplankton, suggesting that this pathway was not an important trophic link. In aged upwelled water, however, microzooplankton potentially contribute 14 % to mesozooplankton production (Probyn et al. 1990). In trophodynamic terms, it would seem that the dominance of microzooplanktonic and microbial food webs conflicts with the interests of pelagic fish.

Acknowledgements. We thank the Captain, navigation officers and crew of the RS 'Africana', and technical assistants from the Sea Fisheries Research Institute, for their cooperation and assistance during the sampling procedures. Our thanks are extended to Geoff Bailey and Sybrand Mostert for nutrient analyses, to Frieda Verheye-Dua for assistance with bacterial counts, to John Roberts and Marius Coetzee for computer assistance, and to Tony Van Dalsen for the final figures. CHN analysis was done by the Chemistry Department of the University of Cape Town. Constructive criticism by Jenny Huggett and Drs Coleen Moloney, Hans Verheye, Mark Gibbons and anonymous reviewers greatly improved this manuscript. We are indebted to the Benguela Ecology Programme (BEP) of the South African National Committee for Oceanographic Research (SANCOR), and to the Sea Fisheries Research Institute, for financial contributions to this study.

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This article was presented by J. G. Field, Rondebosch, South Africa

Manuscript first received: August 30, 1991
Revised version accepted: April 26, 1993