The development and decline of phytoplankton blooms in the southern Benguela upwelling system. 1. Drogue movements, hydrography and bloom development

P. C. Brown & L. Hutchings

THE DEVELOPMENT AND DECLINE OF PHYTOPLANKTON BLOOMS IN THE SOUTHERN BENGUELA UPWELLING SYSTEM. 1. DROGUE MOVEMENTS, HYDROGRAPHY AND BLOOM DEVELOPMENT

P. C. BROWN† AND L. HUTCHINGS**

A drogue was placed in a patch of newly upwelled water on five different occasions between 1979 and 1981 in order to follow the temporal sequence of events after upwelling. The drogue moved over distances of 67–200 km within 4–7 days at mean speeds of 18–39 cm·s⁻¹. Drogue movement was variable and generally in the direction of the prevailing wind. However, significant "up wind" movement occurred when the drogue was entrained in counter-currents. Variations in hydrographic parameters at the start of each sequence, and in the bottom mixed layer along the drogue tracks, indicate that upwelling source waters are not always uniform. However, nutrient concentrations in source water were high (mean concentrations for nitrate, silicate and phosphate were 20,8, 16,6 and 1,88 mmol·m⁻³ respectively), whereas oxygen (4,0 dm³·m⁻³) and chlorophyll *a* (0,6 mg·m⁻³) concentrations were low. Once conditions stabilized, phytoplankton blooms developed rapidly in the upper layers, the cycle of bloom development and decline being completed in about 6–8 days. Nutrients decreased rapidly (and oxygen and chlorophyll *a* increased) with nitrates sometimes reaching concentrations of < 1 mmol·m⁻³, and oxygen and chlorophyll *a* peaking at concentrations of up to 9,8 dm³·m⁻³ and 21,2 mg·m⁻³ respectively. Only once did light-limitation (due to deep mixing) influence bloom development. In this case, only moderately high chlorophyll *a* concentrations (~ 10 mg·m⁻³) were attained. Bloom decline was usually associated with low nutrient concentrations and can be attributed mainly to sinking and dispersion of the phytoplankton, because zooplankton grazing appeared to have had an insignificant impact on the phytoplankton blooms.

'n Dryfanker is op vyf geleenthede tussen 1979 en 1981 in 'n kol nuut opgewelde water geplaas ten einde die opeenvolging van gebeure ná opwelling te volg. Die dryfanker het oor afstande van 67–200 km beweeg binne 4–7 dae teen 'n gemiddelde snelheid van 18–39 cm·s⁻¹. Die beweging van die dryfanker was veranderlik en gewoonlik in die rigting van die heersende wind, maar daar was beduidende "windop"-beweging wanneer die dryfanker in teenstrome vasgevang is. Wisselings in hidrologiese parameters aan die begin van elke tydreeks en in die onderste menglaag langs die dryfankerbaan toon dat opwelbronwaters nie altyd eenders was nie. Nogtans was die konsentrasies van voedingsoute in bronwater hoog (gemiddeld onderskeidelik 20,8, 16,6 en 1,88 mmol·m⁻³ vir nitraat, silikaat en fosfaat) en dié van suurstof (4,0 dm³·m⁻³) en chlorofil *a* (0,6 mg·m⁻³) laag. Toe toestande gestabiliseer het, het fitoplanktonopbloeiings gou in die boonste lae ontwikkel en die siklus van opbloei en vergaan is in sowat 6–8 dae voltooi. Voedingsoute het vinnig afgeneem (en suurstof en chlorofil *a* toegeneem); nitraat het soms tot konsentrasies van < 1 mmol·m⁻³ gedaal en suurstof en chlorofil *a* gestyg tot onderskeidelik 9,8 dm³·m⁻³ en 21,2 mg·m⁻³. Net een maal het ligbeperking (weens diep vermenging) die ontwikkeling van 'n opbloeiing geaffekteer. Toe is nie meer as hoërige konsentrasies chlorofil *a* (~ 10 mg·m⁻³) behaal nie. Die verval van opbloeiings is gewoonlik vergesel van lae voedingsoutkonsentrasies en kan hoofsaaklik toegeskryf word aan die sink en verstrooiing van fitoplankton, want beweiding deur soöplankton het blykbaar maar 'n onbeduidende uitwerking op die fitoplanktonopbloeiings gehad.

Upwelling areas are renowned for high organic production (Ryther 1969, Cushing 1971). In the southern Benguela upwelling region (32–34°S), high rates of plankton and fish production have been documented (see reviews by Brown and Hutchings 1985, Shelton *et al.* 1985 and Shannon and Pillar 1986) and attributed directly or indirectly to rich inorganic nutrient concentrations in upwelling water. The main upwelling season is from September to April (Andrews and Hutchings 1980). However, the pulsing tongue-like nature of upwelling in the southern part of the region (Nelson and Hutchings 1983), i.e. from Cape Columbine (~ 33°S) to the Cape Peninsula (~ 34°S), coupled with the paucity of phytoplankton and rich nutrient concentrations in the source water (Andrews and Hutchings op. cit., Brown 1984), results in highly variable concentrations of phytoplankton in the coastal zone. Consequently, the availability of phytoplankton to consumers is not uniform in time or space and may limit the occurrence and productivity of organisms at higher levels in the food web in this area (Borchers and Hutchings 1986). It follows that insight into both the feeding ecology of consumers and the development of phytoplankton populations, together with the dynamics of water after upwelling, is necessary to evaluate trophic interactions in the ecosystem. The physical oceanography of the region has been re-

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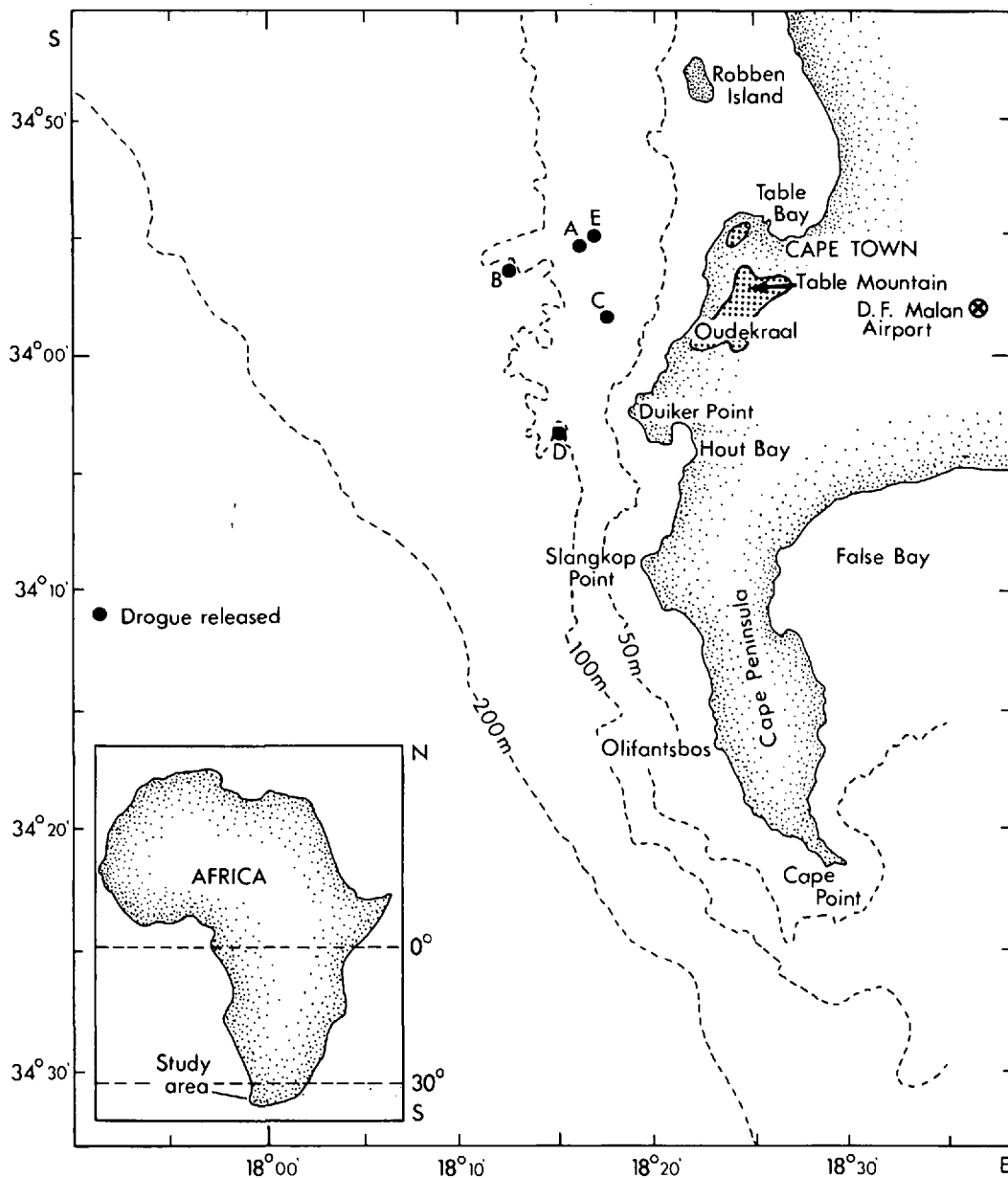
Fig. 1: The Cape Peninsula showing the deployment positions of the drogue during Cruises A, B, C, D and E

viewed by Nelson and Hutchings (1983), Nelson (1985) and Shannon (1985 a, b).

The major aim of the present study was to examine the manner in which phytoplankton populations develop in upwelled water, with emphasis on the time-scale of such events. The intention was to complement a previous transect study off the Cape Peninsula (Andrews and Hutchings 1980), which emphasized spatial and seasonal variations across the shelf zone. In addition, the physical destination of upwelled water (and its developing communities) was of interest in terms of how the primary biological products of upwelling (food for herbivores) may be distributed over the shelf.

The approach of the study involved "marking" a patch of newly upwelled water with a drogue and monitoring the phytoplankton community (and associated environmental parameters) to establish the sequence of events after upwelling (the powerful, intermittent nature of upwelling off the Cape Peninsula made this area an ideal study site). The exercise was repeated five times (Plankton Dynamics Cruises A–E) during the upwelling season, in order to examine variations in the destination of upwelled water and in the patterns of development of phytoplankton communities in this region. Similar approaches have been employed in a number of biological studies, particularly in upwelling areas (e.g. Andrews and Cram 1969, Ryther *et al.* 1971, Herbland *et al.* 1973, Herbland and Voituriez 1974, Nelson and Goering 1978, MacIsaac *et al.* 1985), where rough conditions usually preclude the use of large enclosures suspended in the sea.

The main shortcoming of this approach is the uncertainty as to whether a "patch" of water maintains its physical integrity with time (Beers *et al.* 1971). Mixing of the upwelled body of water may be caused by horizontal shear, diffusion, turbulence, and intrusions of other water bodies. Moreover, the scales of motion important to microscopic phytoplankton are different from those which influence a drogue. Also, drogues are positively buoyant and do not detect vertical motions in the water column. Slippage of water past the drogue may further complicate the situation. We presumed, as a first approximation, that the patches into which the drogues were deployed were large and sufficiently uniform so that horizontal variations would be minimal and events could be followed in the upper mixed layer. In the interpretation of results, attention is directed towards possible artefacts resulting from this assumption. At its worst, such an investigation may not permit calculation of absolute rates of nutrient uptake and phytoplankton growth from state changes in the water column, but it does allow better insight into the time-scale of plankton blooms after upwelling than the earlier transect studies.

This paper deals primarily with physical and chemical aspects of the study: first with drogue movement and factors affecting it, and second with the physical and chemical features of the water column along each drogue track and their influence on phytoplankton bloom development. Another paper (Brown and Hutchings 1987) deals with the nutrient relationships along the drogue tracks and another (Brown *et al.* in prep.) with primary production aspects of the study. Detail on biochemical measurements is described by Barlow (1982, 1984a, b), and Coulter counter particle spectra and production, phytoplankton species analyses and zooplankton biomass and grazing pressures are

described by Olivieri and her associates (Olivieri 1983, Olivieri *et al.* 1985, Olivieri and Hutchings 1985a, b). Current measurements and estimates of shear and dispersion in the vicinity of the drogue during Cruise E are reported by Holden (1981) and Boyd (1982) respectively.

METHODS

Five cruises were conducted off the Cape Peninsula (Fig. 1) during the periods 7–11 December 1979 (Cruise A), 3–9 December 1980 (Cruise B), 4–11 February 1981 (Cruise C), 6–13 March 1981 (Cruise D) and 20–26 October 1981 (Cruise E) on board R.S. *Africana II*. Underway mapping of sea surface temperature and salinity, together with periodic bathythermograph (BT) profiles (e.g. Olivieri 1983 for Cruise A) and observations of sea colour and clarity permitted demarcation of the largest patch of clear, cool, relatively newly upwelled water apparent off the Cape Peninsula at the time. Some flexibility in the starting time of each cruise allowed the research vessel to sail after a few days of strong south-east winds.

Once a suitable patch of upwelled water had been detected, a 3-m biplanar, tetrahedral canvas drogue, set with the midpoint at 10 m, was deployed and tracked for 4–8 days. Drogue design, shown in Figure 2, was based on that of Boyd (1983), but the drogue was enlarged to allow a radio transmitter and flashing light to be attached to the float to facilitate tracking. During Cruises A and B a similar, but smaller (approximately 2 X 3 m), drogue was used without the radio transmitter unit. The superstructure was as compact as possible to minimize windage and drag. Windage and drogue slippage were calculated according to the method of Holden (1985). Drogue slippage, estimated by balancing the drag force of the drogue against the combined forces of the float, was about 20 per cent of the mean current speed (25 $cm \cdot s^{-1}$) during the five cruises. As slippage speeds are typically 10–20 per cent of the true water speed (Holden op. cit.), estimated slippage of the drogue in the present study was considered to be normal.

Drogue position and wind speed and direction were recorded each hour on board ship. Navigation fixes were made by means of Decca or radar to an accuracy of approximately 0,25–0,6 km, depending on time of day and location (G. Nelson, Sea Fisheries Research Institute, pers. comm.). Wind speed was measured from the ship with a cup anemometer 10 m above the sea, with direction estimated by the deck officer. Hourly wind data prior to and during each study were also obtained from the Cape Point and Cape Columbine lighthouses. Incident photosynthe-
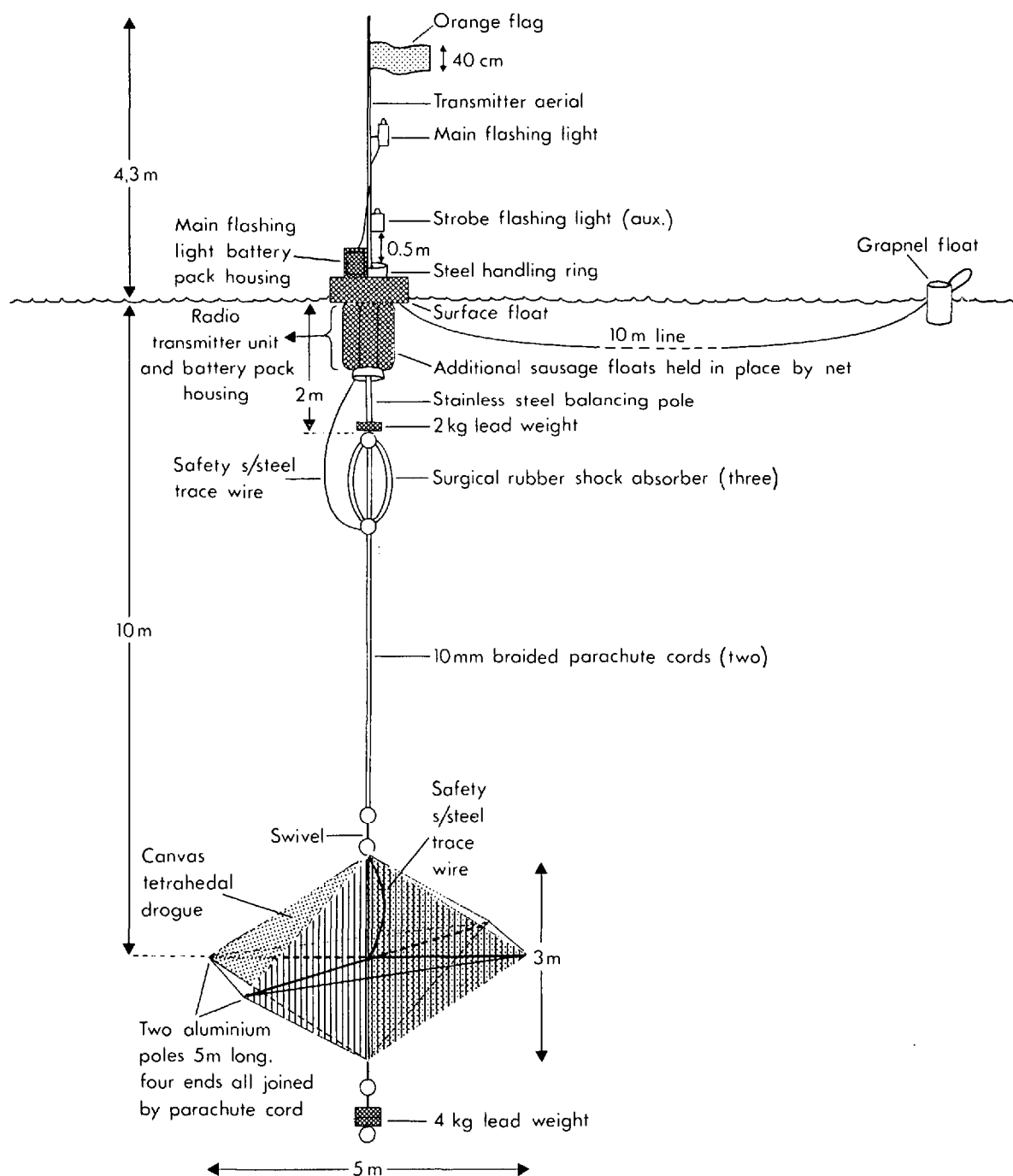
Orange flag

40 cm

Transmitter aerial

Main flashing light

4,3 m

Main flashing
light battery
pack housing

Strobe flashing light (aux.)

0.5 m

Steel handling ring

Radio
transmitter unit
and battery pack
housing

Surface float

Grapnel float

10 m line

Additional sausage floats held in place by net

2 m

Stainless steel balancing pole

2 kg lead weight

Safety s/steel
trace wire

Surgical rubber shock absorber (three)

10 m

10 mm braided parachute cords (two)

Safety
s/steel
trace
wire

Swivel

Canvas
tetrahedal
drogue

3 m

Two aluminium
poles 5m long.
four ends all joined
by parachute cord

4 kg lead weight

5 m

Fig. 2: Design of the drogue used during this survey

Table I: Summary of drogue and wind dynamics during the five drogue studies (A-E)

Cruise	Tracking period		Drogue movements							Wind (as measured on board ship)			
			Displacement		Distance covered (km)	Speed				Mean direction* (°)	Run (km)	Speed (m·s⁻¹)	
	Hours	Days	Distance (km)	Direction* (°)		Hourly (cm·s⁻¹)		Daily (km·d⁻¹)					
						Mean	Range	Range				Mean	Range
A (Dec. 79)	102	4,25	32	023 (NNE)	67	18	0–64	12,0–20,1		196 (SSW)	3 252	7,5	1–16
B (Dec. 80)	144	6	151	341 (NNW)	200	39	0–155	23,6–51,6		190 (SSW)	4 902	9,5	2–16
C (Feb. 81)	168	7	43	263 (WSW)	155	26	0–128	13,8–31,8		186 (S)	5 334	8,8	0–20
D (Mar. 81)	167	7	45	318 (NW)	123	20	0–52	13,5–21,6		166 (SSE)	6 359	10,5	0–20
E (Oct. 81)	160	6,7	13	036 (NNE)	115	20	0–73	13,1–22,5		225 (SSE)	4 062	7,0	0–18

*Note that, according to normal convention, "drogue direction" is expressed as that towards which the drogue moves, whereas "wind direction" is that from which the wind blows

tically active radiation (PAR) was monitored on board ship with a Lambda LI-190S atmospheric sensor coupled to an LI-500 integrator. Because of instrument failure during December 1980 (Cruise B) and March 1981 (Cruise D, Days 5-6), total hourly radiation measurements (daW·h·m⁻²) made by the South African Weather Bureau at the D.F. Malan Airport (see Fig. 1) were used. Total radiation was converted to PAR (μE·m⁻²·s⁻¹), the missing PAR measurements in Cruises B and D being determined by means of predictive regression equations obtained for concurrent data sets from Cruise A in December 1979 (PAR = 20,6 daW + 19,4, r = 0,96, n = 94) and from Cruise D (Days 1-4) in March 1981 (PAR = 18,8 daW + 58,0, r = 0,93, n = 77) respectively.

Sampling was conducted at approximately 08h30, 12h30 and 18h00 local time each day. During Cruise A, a fourth station was conducted at 22h00 to obtain a night-time sample of zooplankton and a temperature profile. Submarine light penetration was established during daylight stations with an underwater quantum sensor (Lambda LI-192S), and a bathy-thermograph (BT) temperature profile was made. Ten water samples were drawn (with 18- or 5-ℓ NIO bottles), from the upper 100 m or shallower, covering the euphotic zone (100-, 50-, 25-, 10- and 1-per-cent light depths), the thermocline zone and deeper. Subsamples were taken for analyses of oxygen, nutrients, chlorophyll a, biochemical composition, particle spectra and phytoplankton species, and for primary productivity and zooplankton grazing

experiments. Discrete temperature measurements and water samples for salinity measurements were obtained at the same depths by means of Nansen-Pettersson bottles. These data were used for sigma-t density analyses.

Salinity was measured ashore on an inductively coupled salinometer, and concentrations of dissolved oxygen were determined on board by Winkler titration. Water samples for nutrient analysis were stored at -20°C until analysed ashore for phosphate, nitrate (including nitrite) and silicate concentrations, according to the auto-analyser methods described by Mostert (1983). For analysis of chlorophyll a, 1ℓ of water from each depth was filtered through a 47-mm Toyo GC-50 glassfibre filter (0,7 μm mean pore size) at a vacuum of 30 kPa, stored frozen, and analysed spectrophotometrically in 90-per-cent acetone using a modification of the SCOR-UNESCO method (Strickland and Parsons 1972). A calibration curve was prepared with pure chlorophyll a standards and used for calculating concentrations of chlorophyll a (Swart and Barlow 1981). No correction was made for phaeopigments.

RESULTS

Drogue movement, wind and currents
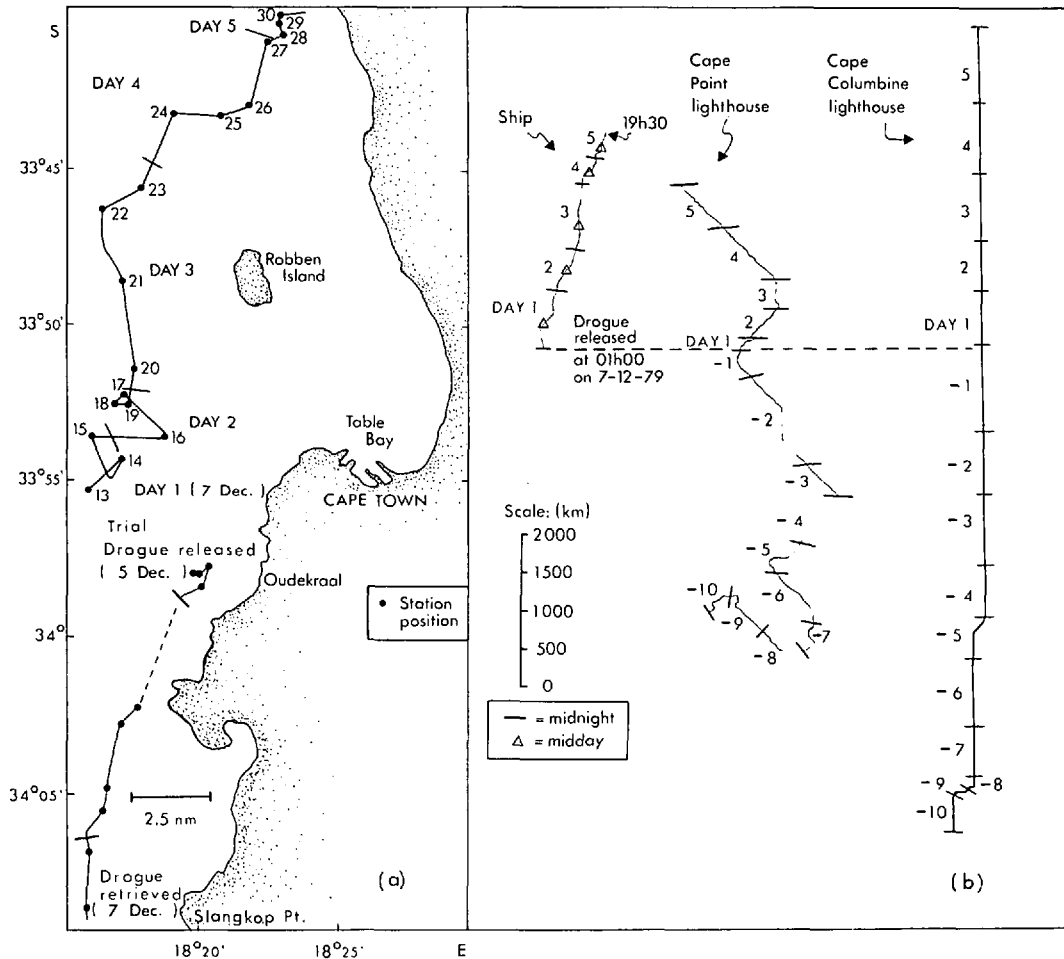
On each cruise, the drogue was deployed in

Fig. 3: (a) Drogue track A (7-11 December 1979) showing station positions, (b) progressive vector diagrams for hourly wind measurements on board ship and at the Cape Point and Cape Columbine lighthouses. The track of the trial drogue (5-7 December) is also illustrated in (a)

recently upwelled water off the Cape Peninsula within the 50- and 100-m depth contours in the vicinity of the Oudekraal-Duiker Point upwelling centre (see Fig. 1), an area which is the base of the Cape Peninsula upwelling tongue (Nelson and Hutchings 1983) and the primary upwelling site in the southern Benguela itself (Taunton-Clark (1985)). Basic drogue movement and wind statistics are presented in Table 1. Overall northward displacement varied between 13 km NNE in October 1981 (Cruise E) and 151 km NNW in December 1980 (Cruise B), while in February 1981 (Cruise C) the drogue ended up 43 km west of its position of release. Mean speed and direction were calculated as they are

important in terms of potential net movement of surface waters over a particular period.

Individual drogue tracks and progressive vector diagrams (PVD) for hourly wind measurements on board ship and at the Cape Point and Cape Columbine lighthouses are illustrated in Figures 3-7. Southerly to south-easterly winds predominated strongly prior to each study period and, except in October 1981, during the first few days after launching the drogue. Near-surface currents, as depicted by drogue movement, were generally in a direction similar to the wind. However, in a number of instances, current and wind directions were not the same (discussed later). This finding supports the
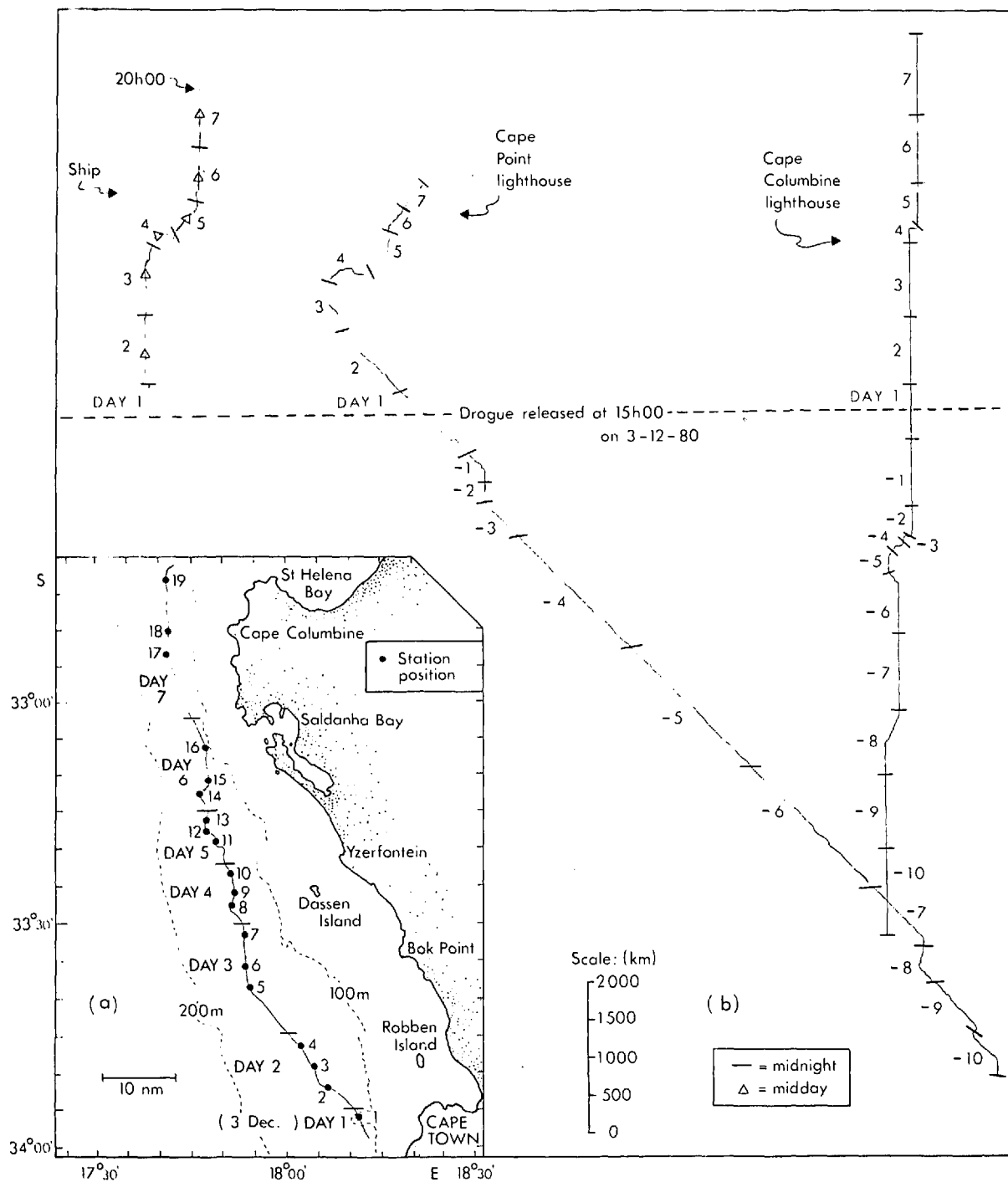
Fig. 4: (a) Drogue track B (3-9 December 1980) showing station positions, (b) progressive vector diagrams for hourly wind measurements on board ship and at the Cape Point and Cape Columbine lighthouses
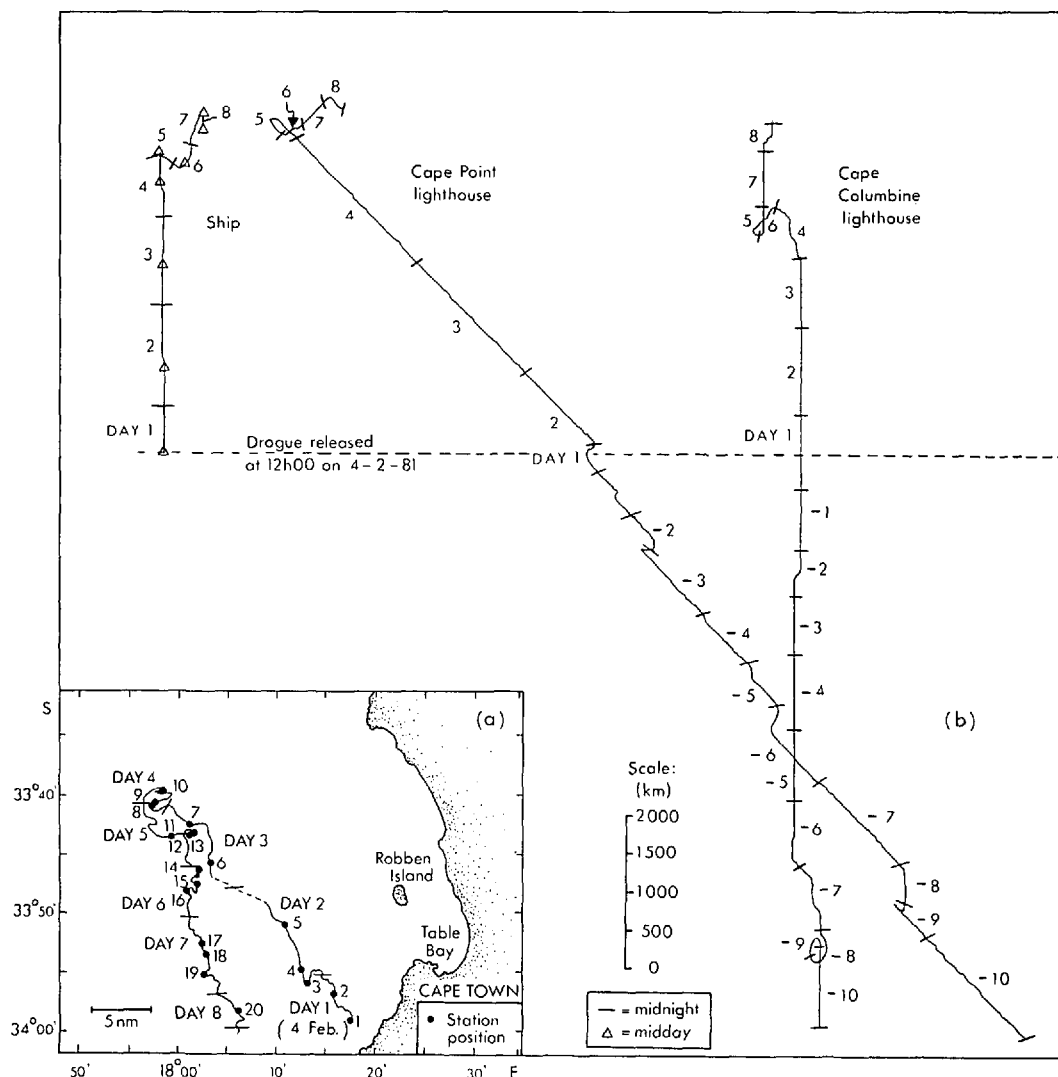
Fig. 5: (a) Drogue track C (4–11 February 1981) showing station positions, (b) progressive vector diagrams for hourly wind measurements on board ship and at the Cape Point and Cape Columbine lighthouses

assumption that windage due to the drogue super-structure was minimal. The main points of interest regarding drogue movements are summarized in the following subsections.

Cruise A (Fig. 3) — Prior to the release of the main drogue, a trial drogue (see Fig. 3) moved steadily southwards close to the coast, opposing southerly winds of 5–10 m·s⁻¹. It appeared to be entrained in a coastal counter-current similar to that described by Nelson (1985). However, after the main drogue was

released farther offshore the drogue meandered northwards for three days, briefly reversing on each of Days 1 and 2 (for detail on wind variation refer to Figure 16). Thereafter the drogue moved north-eastwards. The shape of the drogue track was roughly similar to that of the PVD of wind measured from the ship.

Cruise B (Fig. 4) — The fastest mean drogue speed and greatest northward displacement was measured during this cruise (see Table I), the drogue travelling

from the Cape Peninsula to Cape Columbine be-
tween the 100- and 200-m isobaths in six days. The
wind reversal on Day 4 did not markedly alter its
course and it appeared to be in a jet current moving at
speeds of up to 155 cm·s⁻¹ (Table I). Nelson and
Hutchings (1983) and Nelson (1985) have discussed
the jet-like formation of topographically steered
currents in this region.

Cruise C (Fig. 5) — In February 1981 the drogue
moved offshore with strong southerly winds (mean
12,0 m·s⁻¹), but it changed direction on Day 4 just
prior to the wind reversal on Day 5. Thereafter, it
moved southwards against gentler winds in what
appeared to be a barotropic adjustment to a change
in sea level after the strong winds subsided (G.
Nelson, pers. comm.).

Cruise D (Fig. 6) — The drogue moved southwards
against moderate to light winds in a manner similar
to that of the December 1979 trial drogue (see Fig. 3).
On Day 2, the drogue reversed direction off Slangkop
and moved offshore at a time of strong (> 13 m·s⁻¹)
southerly winds. The drogue reversal occurred in an
area where Nelson (1985) has described a retroflec-
tion of the inshore counter-current. He postulated
that entrainment of the counter-current into a north-
flowing current farther offshore is compensation for
the acceleration of the shelf-edge jet off the Cape
Peninsula.

Cruise E (Fig. 7) — Prior to the drogue deployment
in October 1981, the wind was generally lighter and
more variable than before the other cruises (Figs
3–6). Drogue movement was erratic, limited to a
relatively small area and not always in sympathy with
changes in wind speed or direction. Daily transects of
six Neil-Brown acoustic current-meter profiles across
the drogue track provided seven sections of currents
during the cruise (Holden 1981). The north-south
and east-west components of the currents (Fig. 8)
reveal a complex current structure with persistent
northward flow above the 70- and 180-m isobaths
(Holden op. cit.). Southward currents and reduced
northward flow on Days 2 and 3 were associated with
the wind reversal during this period, because the
resumption of southerly winds on Day 4 resulted in
the re-establishment of strong northerly flow. The
erratic drogue movements during Cruise E may be
explained by the drogue's location in a shear zone
between northerly and southerly currents, as depicted
in Figure 8.

A fundamental problem relates to the extent to
which the same body of water was being followed by
the drogue and the typical scales involved in the

dispersive processes operative around the drogue. In
an attempt to ascertain these parameters, Boyd
(1982) deployed six 1-m drogues at 2, 10 and 20 m in
the vicinity of the main drogue on a number of
occasions during Cruise E. He found that consider-
able dispersion of the drogues at different depths
may be caused by shear, and he estimated that
particles at 9 and 11 m would have, on average,
separation speeds of 2,1 cm·s⁻¹. On the other hand,
horizontal separation of drogues at the same depth
was an order of magnitude less (± 0,19 cm·s⁻¹ at
10 m). However, it should be noted that Boyd's rates
of "horizontal separation" supply only a lower limit
to the actual diffusion of particles in the water. The
drogues, being several orders of magnitude larger
than the phytoplankton cells which they were at-
tempting to track, cancelled out the effects of
diffusion on the population of particulate matter in
the water body, and, therefore, could not simulate
the effects of diffusion. Nonetheless, Boyd (op. cit.)
concluded that the combined effects of pair-separ-
ation and shear would rapidly destroy any horizontal
patchiness that might otherwise occur on a scale of
less than a few hundred metres. The dynamics of
larger scale (5–10 km) plankton patches could not be
determined in this study.

For the purposes of the hydrobiological study, the
effects of both dispersion and slippage have been
ignored. It is assumed that the patches into which the
drogue was released were sufficiently large and
uniform to compensate for these effects. Patches of
high chlorophyll *a* observed by CZCS imagery (Shan-
non *et al.* 1985) would lend support to this assump-
tion, being of the order of 20–100 km in extent.

ART maps

As part of the more extensive CUEX surveys
(Shannon 1985b), airborne radiation thermometry
(ART) flights (Taunton-Clark 1982, 1985, Jury 1985)
were undertaken prior to and/or during Cruises A,
B, C and E. These flights provide some perspective of
the larger oceanographic features prevailing around
the drogue. Surface temperature distributions rele-
vant to the drogue studies are presented in Figure 9.
The most complete ART coverage was for Cruise A.
The trial drogue moved southwards upstream of the
main axis of the tongue of upwelled water (see Fig. 9,
Days −1 and −2), whereas the main drogue moved
northwards along the tongue axis until Day 5, when
it moved inshore into cooler water. Strong thermal
fronts persisted offshore along the edge of the
upwelling cell.

Only one ART flight was made during Cruise B,
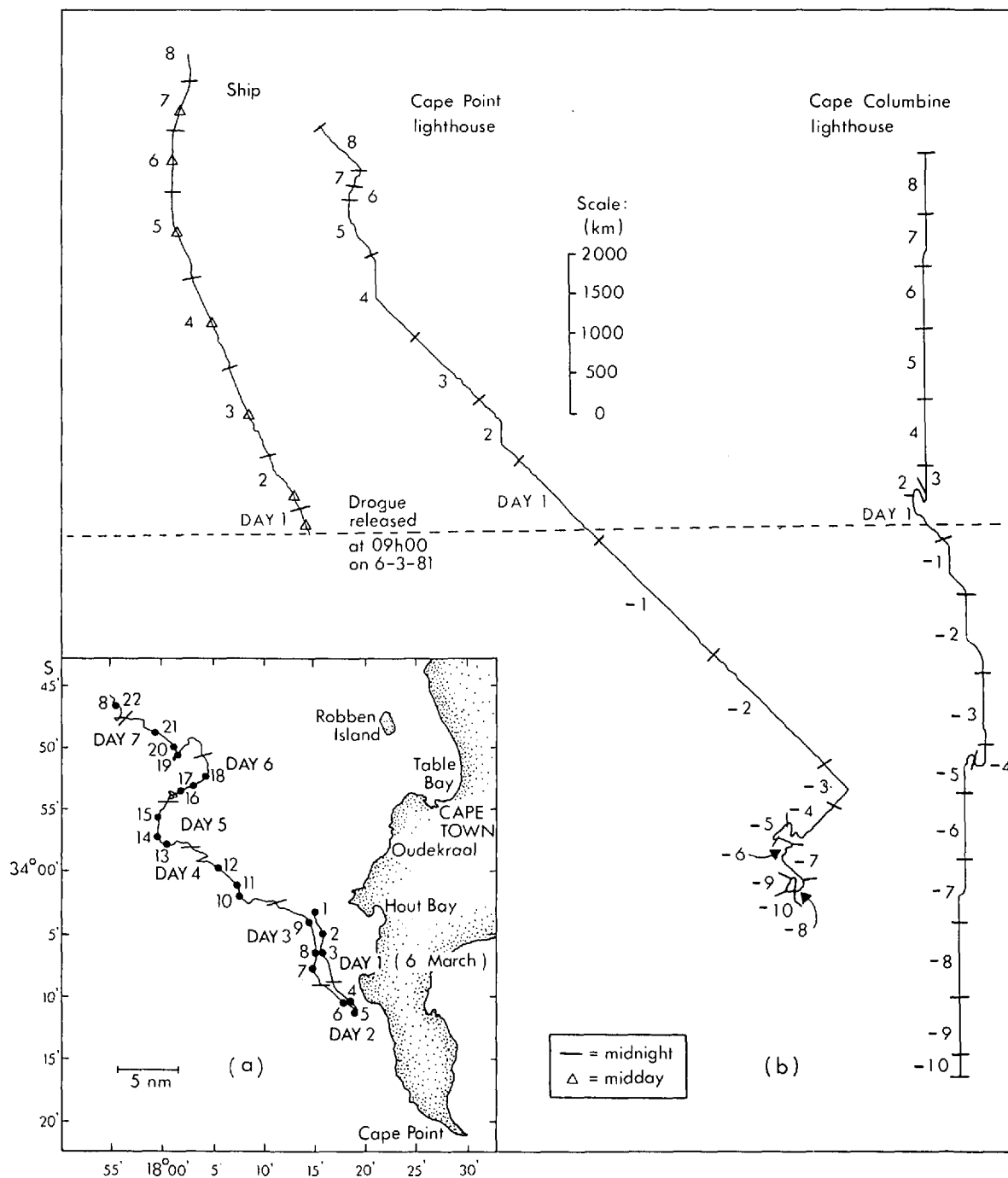i.e. one day prior to launching the drogue. Upwelling

Fig. 6: (a) Drogue track D (6-13 March 1981) showing station positions, (b) progressive vector diagrams for hourly wind measurements on board ship and at the Cape Point and Cape Columbine lighthouses
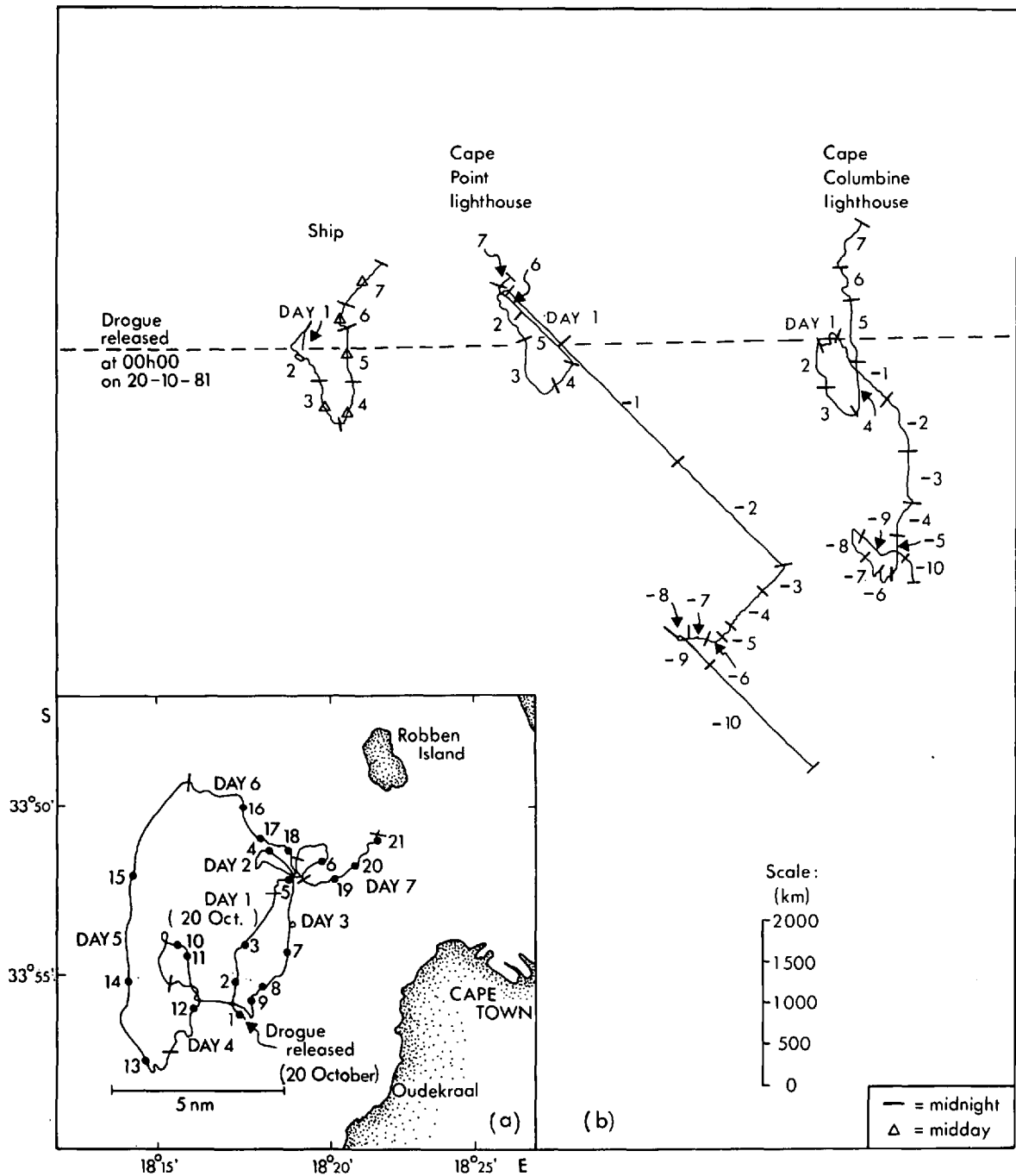
Fig. 7: (a) Drogue track E (20–26 October 1981) showing station positions, (b) progressive vector diagrams for hourly wind measurements on board ship and at the Cape Point and Cape Columbine lighthouses
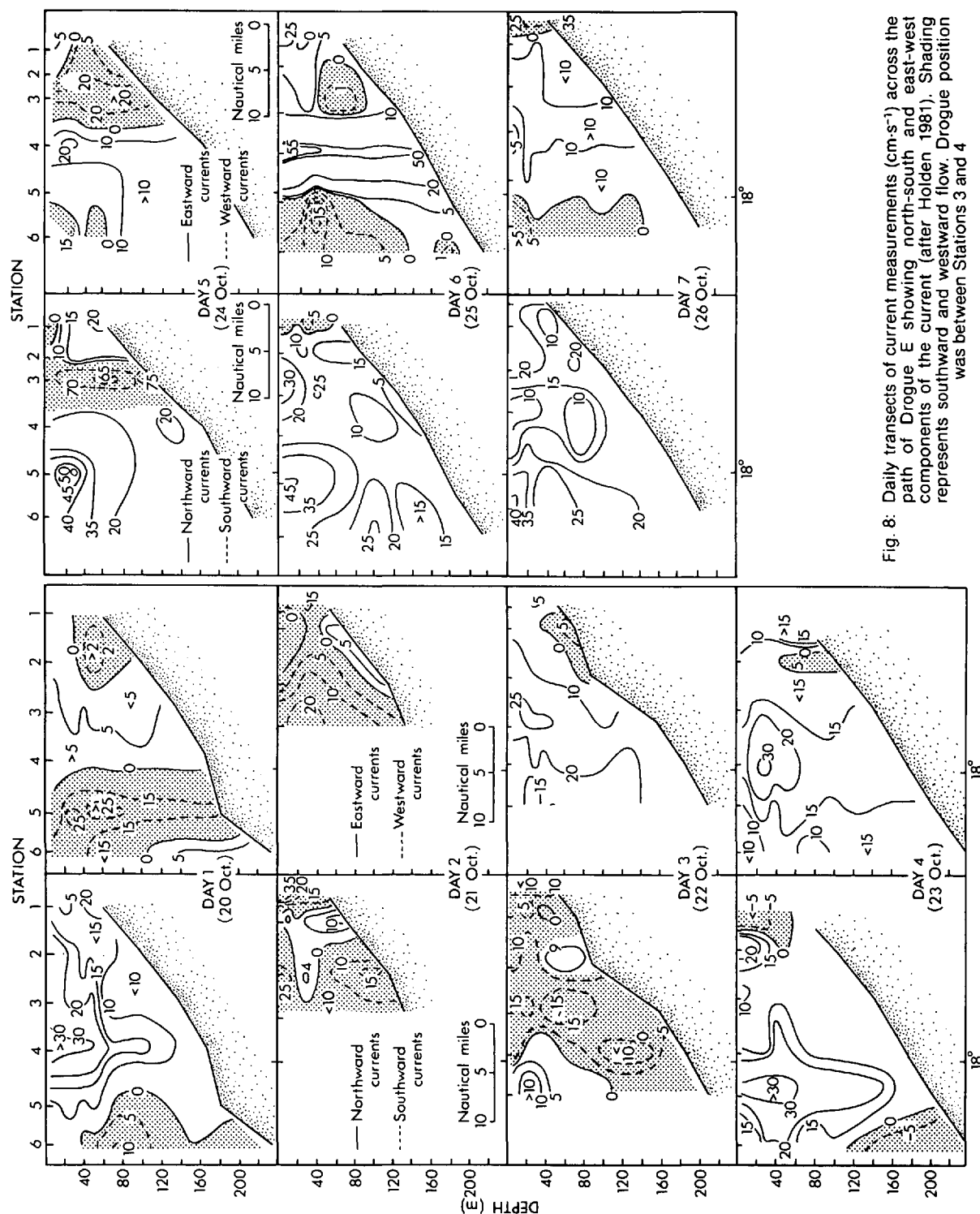
Fig. 8: Daily transects of current measurements (cm·s⁻¹) across the path of Drogue E showing north-south and east-west components of the current (after Holden 1981). Shading represents southward and westward flow. Drogue position was between Stations 3 and 4
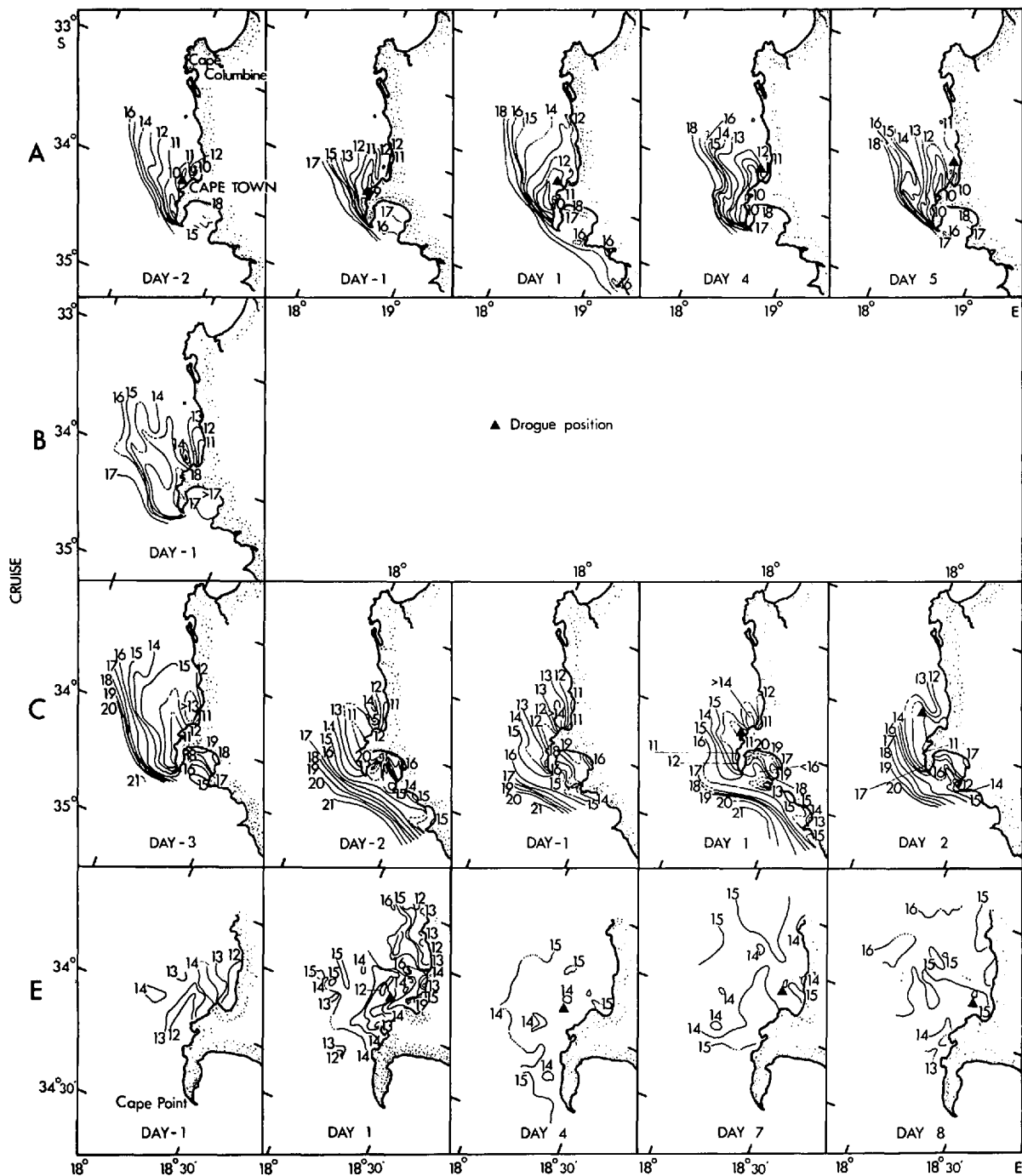
Fig. 9: Sea-surface temperature (°C) distribution in the Cape Peninsula region of the southern Benguela from ART data (after Taunton-Clark 1982) collected before and during Cruises A, B, C and E, with drogue positions indicated where appropriate. Note the scale change for Cruise E
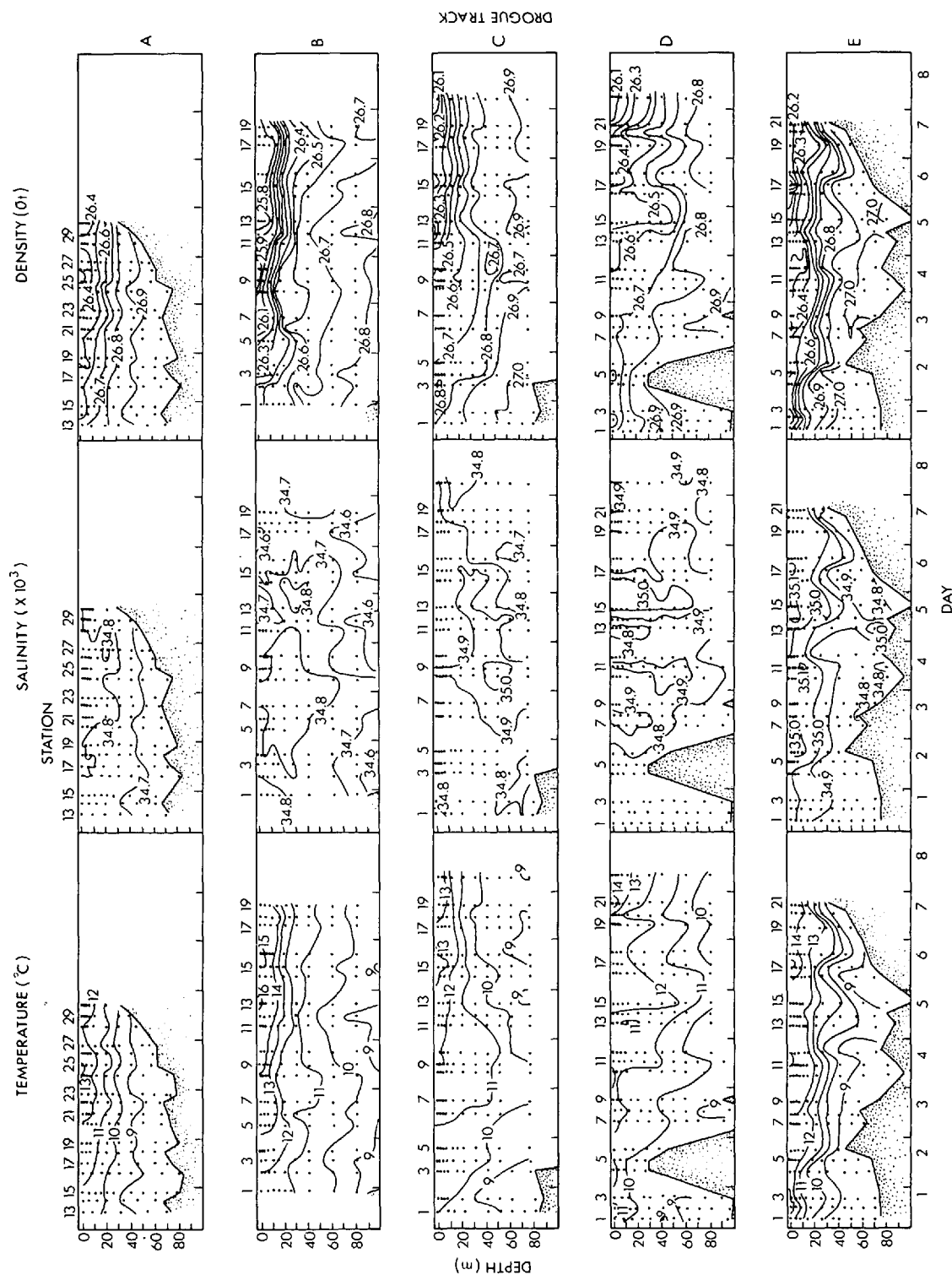
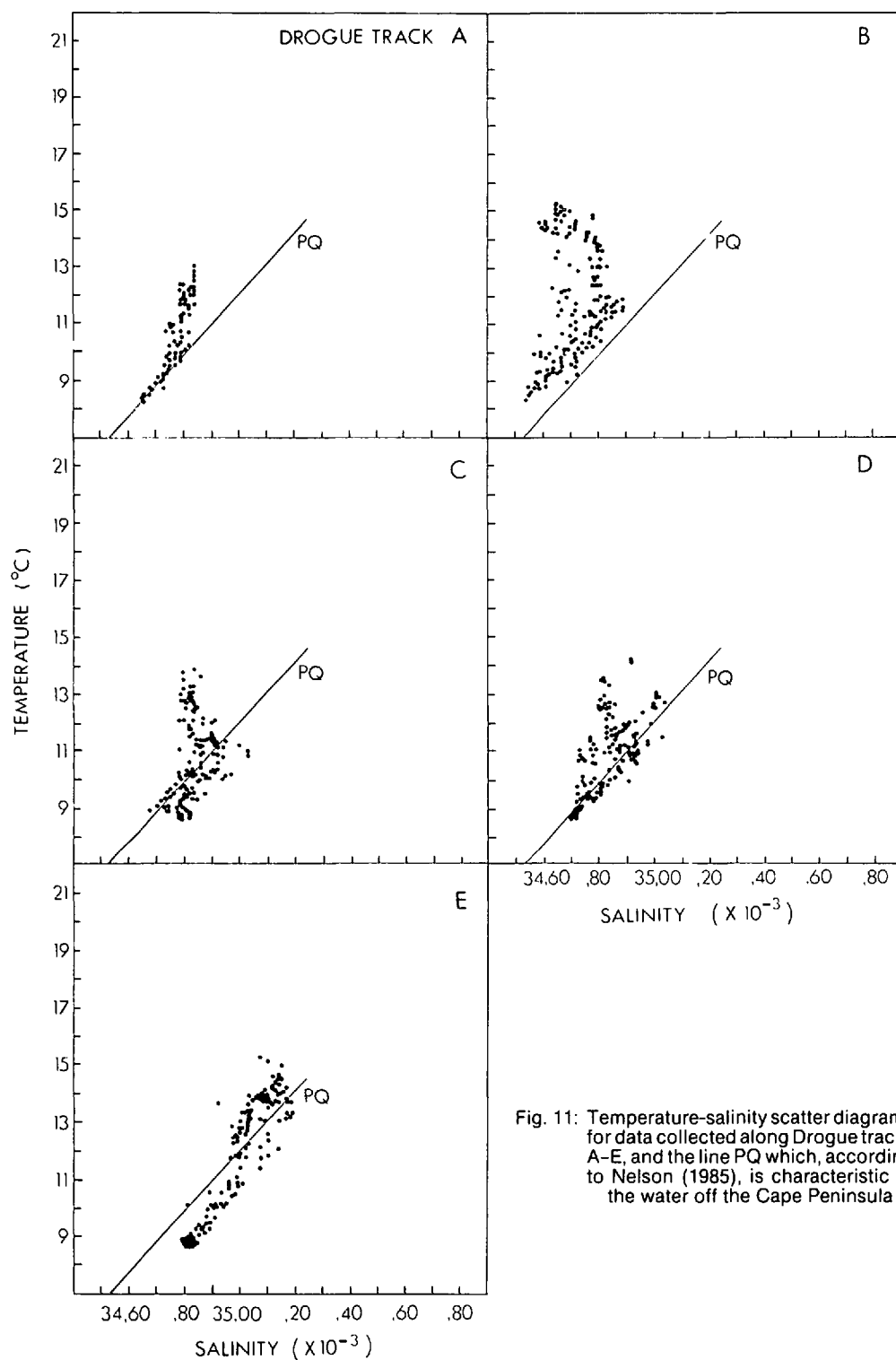Fig. 10: Vertical sections of temperature, salinity and density (sigma t) along Drogue tracks A–E

Fig. 11: Temperature-salinity scatter diagrams for data collected along Drogue tracks A-E, and the line PQ which, according to Nelson (1985), is characteristic of the water off the Cape Peninsula

Table II: Variation in the mean salinity of the 0-10 m layer along each drogue track

Cruise	Mean	sd	Range.	Difference	Difference (%)
A	34,80	0,03	34,75–34,84	0,09	0,26
B	34,74	0,07	34,60–34,80	0,23	0,66
C	34,84	0,03	34,80–34,90	0,10	0,28
D	34,84	0,08	34,73–35,01	0,28	0,80
E	35,06	0,06	34,97–35,16	0,10	0,54

was less vigorous than during Cruise A, the coolest water (11–12°C) being close inshore on the mid to southern part of the Cape Peninsula. A warm patch lay to the north of the Peninsula in the lee of Table Mountain (see Fig. 1). In February 1981 (Cruise C) strong upwelling was evident for three days prior to drogue deployment, with water of < 11°C present off the central Peninsula. The drogue was placed in the middle of a large cool tongue (Day 1), then moved rapidly offshore along the tongue axis on Day 2.

During October 1981 (Cruise E) weak upwelling was apparent one day prior to drogue deployment, cool water (< 12°C) being present in the south. The drogue was launched in what appears to be the remnants of this upwelling, and close to a fairly strong gradient in surface temperature. Isotherms suggest that, inshore, a tongue of warm water was moving southwards, while farther offshore cooler water was moving north. Under the influence of light, variable winds, the surface thermal structure disappeared and weak gradients, more typical of winter conditions (Andrews and Hutchings 1980), prevailed.

Hydrography along drogue tracks

TEMPERATURE, SALINITY AND DENSITY

Vertical sections of temperature, salinity and density (sigma t) along the track of each drogue are presented in Figure 10. Mean temperatures in the upper 10 m increased along the drogue tracks, ranging between 9,9 and 14,9°C. Deep temperatures were less variable, 8–9°C water occurring below 40–50 m when the sounding was less than 100 m (Drogue tracks A and E). At soundings greater than 100 m (Drogue tracks B, C and D), this uniformly cool water was deeper, usually below 80 m.

Temperature and density sections show similar structure; mixing and solar warming increased sur-face temperatures, thereby decreasing densities. Salinity did not contribute much to changes in density as it usually decreased slightly with depth. Occasionally, a weak subsurface salinity maximum occurred between about 20 and 50 m (e.g. on Cruises B, C and D), indicating that low salinity water had upwelled and moved over more saline water. More recent CTD casts in southern Benguela coastal waters (e.g. Brundrit 1985, Waldron 1985) indicate that this is a common occurrence.

Temperature-salinity (t/s) scatter diagrams are presented for each cruise in Figure 11 and contrasted with the t/s line PQ of Nelson (1985), which is characteristic of the t/s relationship for most of the water (shelf and oceanic) off the Cape Peninsula. Although t/s analyses in shallow coastal waters do not allow precise identification of water types, the scatter diagrams illustrate some interesting points. For Cruises A, C and D, the lower temperatures and salinities coincide with line PQ. Equivalent data for Cruises B and E lie roughly parallel to line PQ, but above and below it respectively, suggesting that the salinity of the upwelled water was lower than normal for Cruise B and higher for Cruise E. This finding suggests that the water which upwells is not necessarily uniform and perhaps not of the same origin. The more saline water encountered along Drogue track E (October 1981) may reflect the seasonal transition from winter to spring, because salinities throughout the water column in winter are higher than during the upwelling season (see Fig. 27 of Andrews and Hutchings 1980). At higher temperatures, deviation above the original t/s slope of each cruise was clearly due to solar warming of surface water. The point of inflection (which initiates deviation from the line characteristic of the cooler, deeper water in each study), is at about 9,5, 10, 11, 9 and 11,5°C for Cruises A–E respectively. These differences suggest that the temperature of the source water is not constant, but that it may vary at least between 9 and 11,5°C. It follows that the use of a specific temperature limit to define active upwelling (e.g. Andrews and Hutchings 1980 used temperatures of less than 10°C) may be misleading.

As salinity is a conservative parameter, it may be used to investigate the physical consistency of the water along each drogue track (Waldron 1985). There was little variation (< 1 per cent) in the mean salinity of the upper 10 m layer along each drogue track (Table II), and individual salinity values at 0 and 10 m (Fig. 12) also suggest that the water masses along Drogue tracks A, B (until Station 11) and C were fairly consistent. The decrease in salinity north of Station 11 (Drogue track B) may be due to the
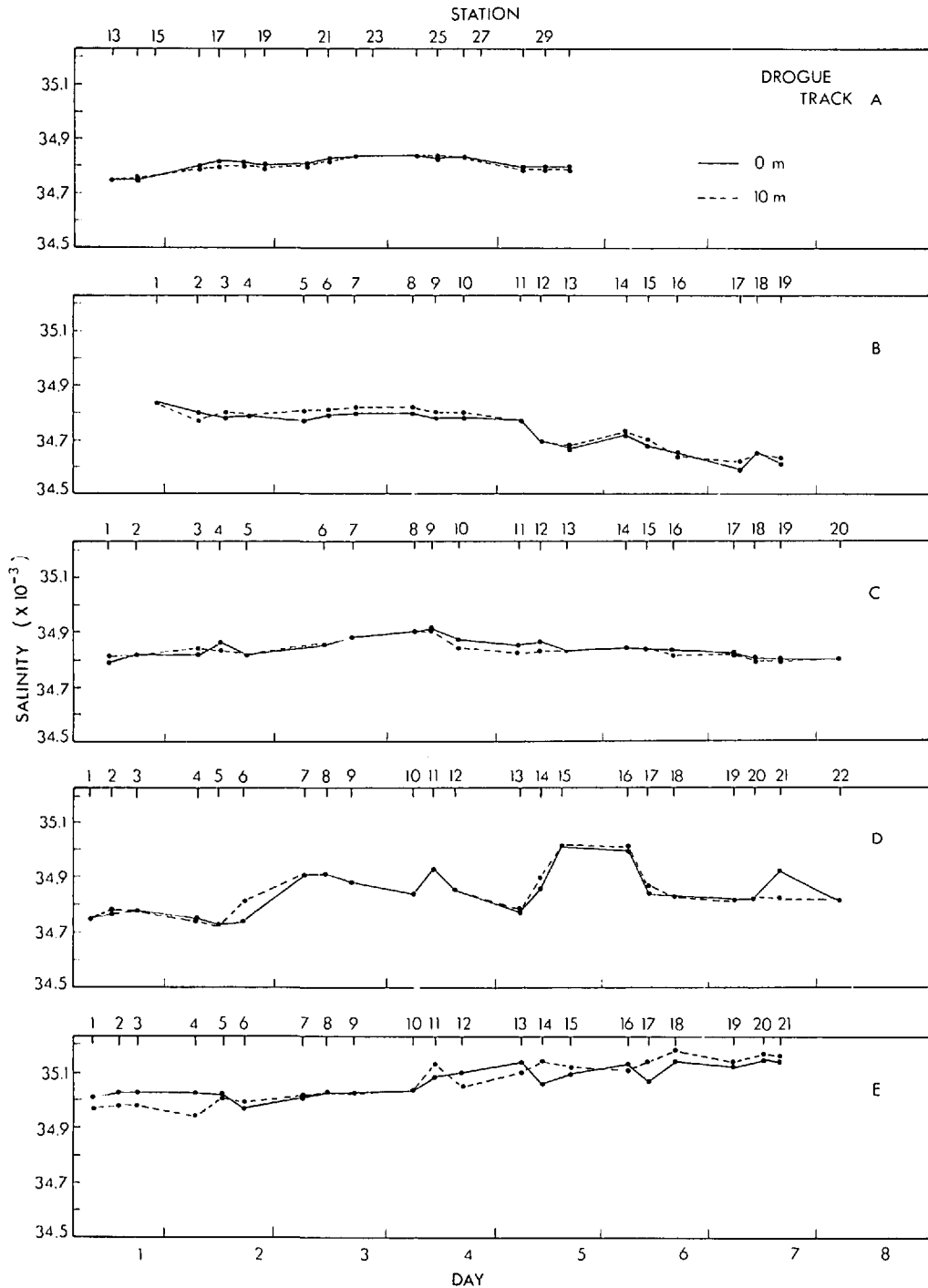
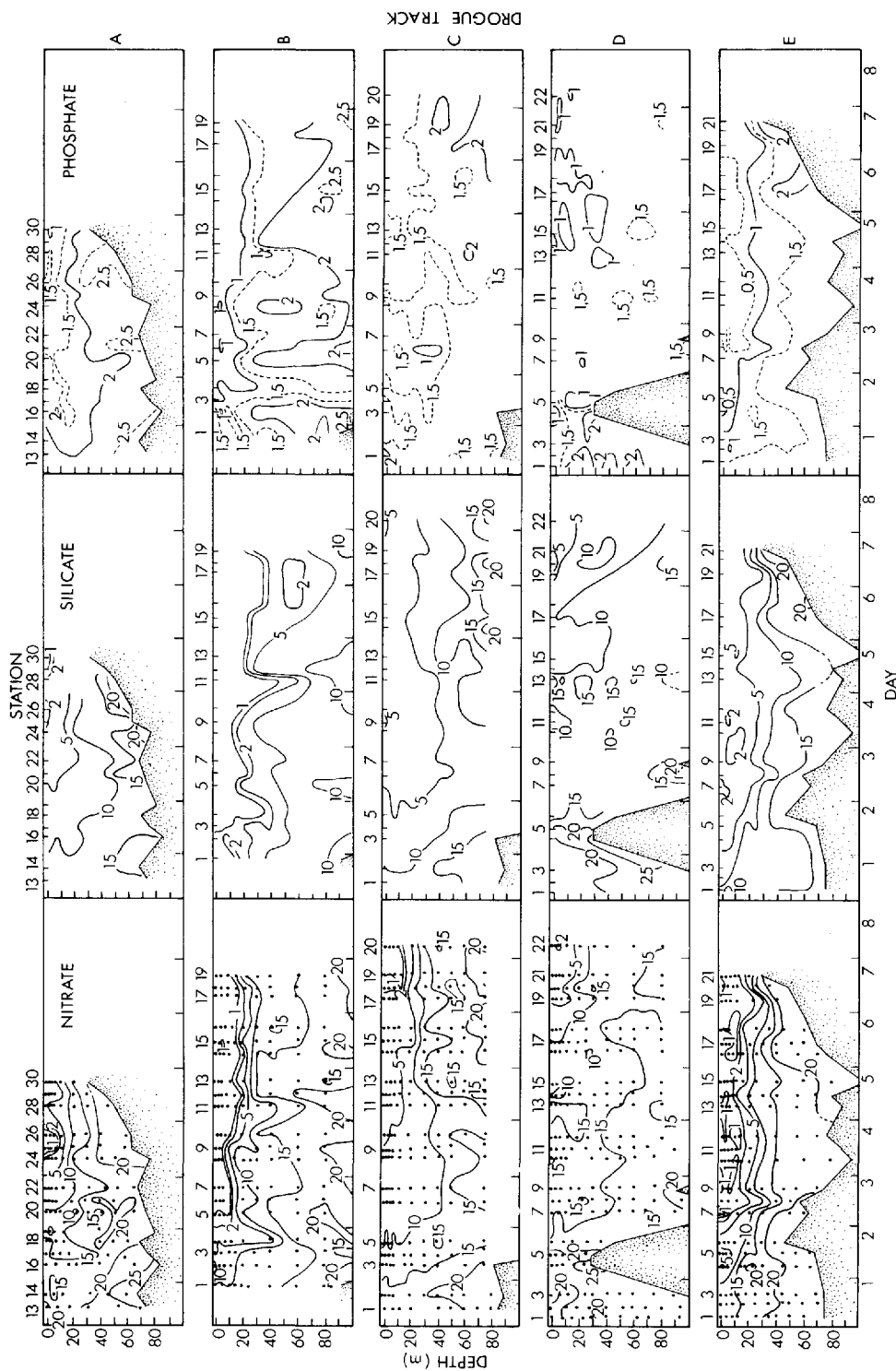Fig. 12: Salinity at the surface and 10 m along Drogue tracks A-E

Fig. 13: Vertical sections of nitrate, silicate and phosphate concentrations (mmol·m⁻³) along Drogue tracks A-E
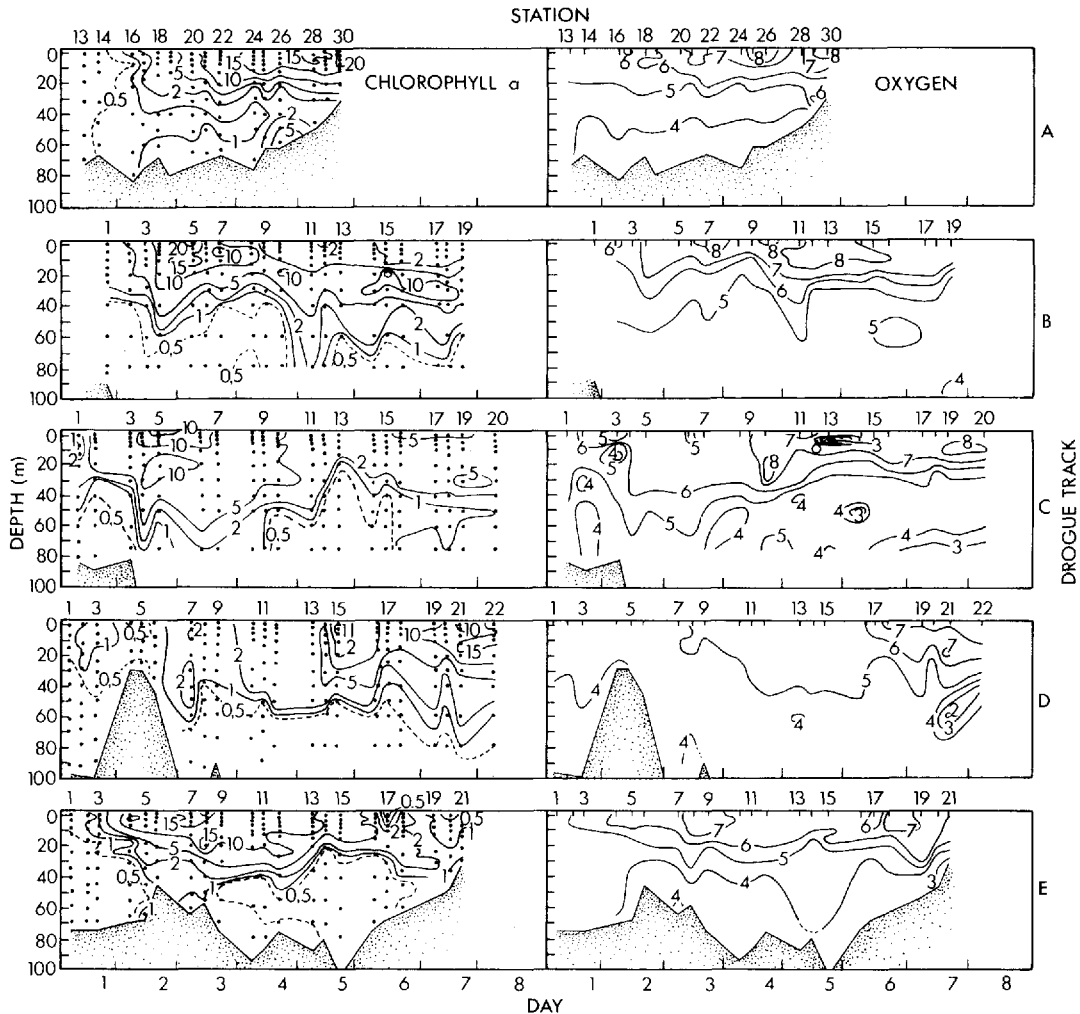
Fig. 14: Vertical sections of chlorophyll a (mg·m⁻³) and dissolved oxygen (dm³·⁻³) concentrations along Drogue tracks A-E

entrainment of low salinity water from upwelling sites off Yzerfontein and Cape Columbine (see Fig. 4). During Cruise D, salinity was particularly variable between Stations 5 and 16 after the drogue turned off Slangkop and meandered towards the north-west (see Fig. 6). These abrupt changes in salinity (Fig. 12) suggest that different water bodies mixed into the original water mass; therefore, attempts to trace biological sequences along Drogue track D should be treated with care. The gradual increase in salinity along Drogue track E, however, may be due to gradual mixing with more saline water and insola-

tion-induced surface evaporation, because the relatively strong thermocline would have minimized the entrainment of deep, low salinity water into the upper layers. Wind reversals (see Fig. 7) and opposing currents (see Fig. 8), maintained the drogue in a small area in which the salinity changed gradually.

NUTRIENT, CHLOROPHYLL a AND OXYGEN DISTRIBUTIONS

Vertical sections of nitrate, silicate and phosphate concentrations along each drogue track are presented
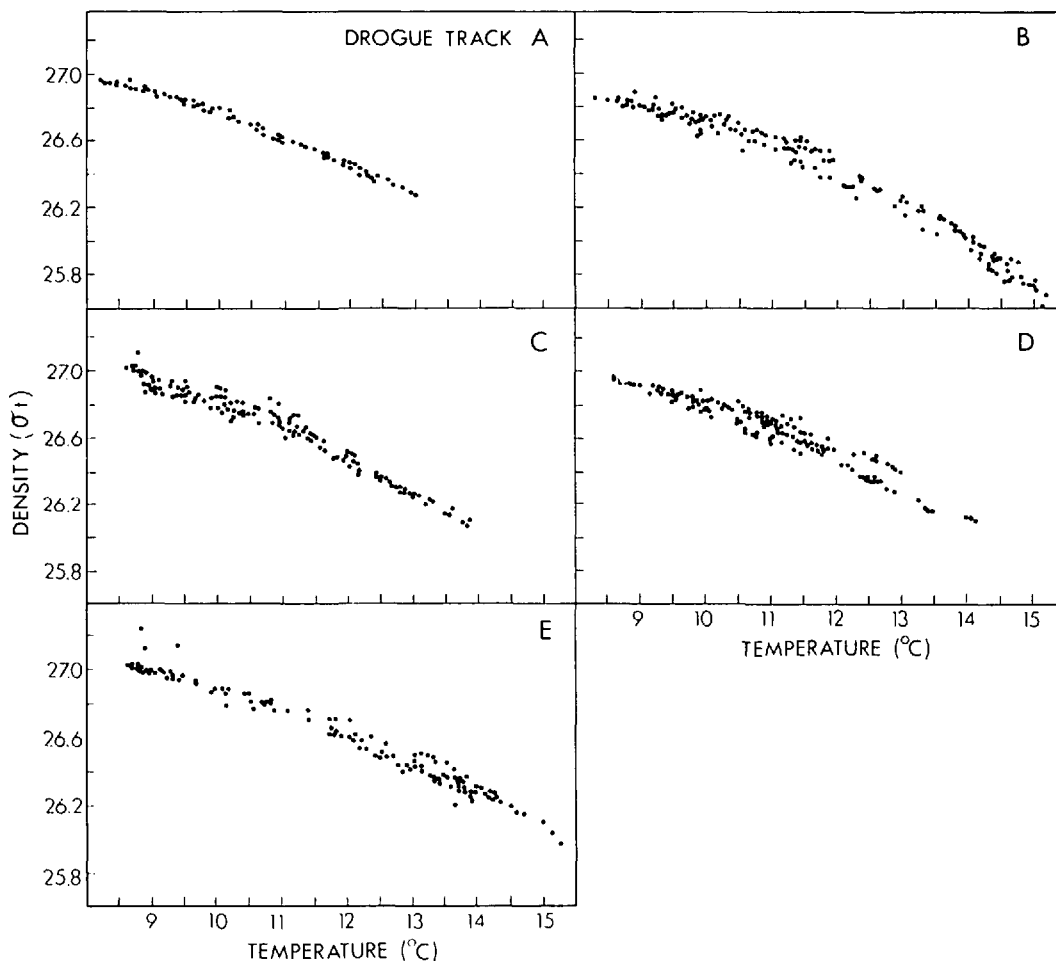
Fig. 15: Relationships between density and temperature for data collected along Drogue tracks A-E

in Figure 13. Nitrate and silicate concentration varied widely (from < 1 to 26,8 and 25,1 mmol·m⁻³ respectively) but generally decreased in the surface waters along the drogue tracks, whereas concentrations were higher at depth. Phosphate concentrations' were less variable (c. 0,3–2,81 mmol·m⁻³), but they showed a similar though weaker tendency to increase with depth and to decrease along the drogue tracks.

Silicate concentrations along Drogue track B were exceptionally low; in fact, virtually all the values were zero above the 1 mmol·m⁻³ isoline (which ranged between about 10 and 30 m after Station 3). Although concentrations of zero have occasionally been recorded off the Cape Peninsula (P. C. Brown, unpublished data), they are unlikely to be common because, in two and a half years of monthly monitoring off the Cape Peninsula, Andrews and Hutchings (1980) did not report any zero values. Moreover,

below 50 m, ratios of nitrate : silicate were consistently higher (mean 2,7) and silicate : phosphate lower (mean 3,6) for Cruise B than for other cruises. In the other cruises, the mean ratios were 1,2–1,5 and 6,3–10,3 respectively (Brown and Hutchings 1987). The abnormal ratios and unusually low silicate concentrations suggest that the silicate analyses may have been faulty, possibly as a result of contaminated blanks. The data are, therefore, interpreted with caution and excluded from "typical" mean values.

Chlorophyll a and dissolved oxygen concentrations also varied widely (0–21,2 mg chll a·m⁻³ and 1,94–9,80 dm³ O_2·m⁻³) — see Fig. 14 — with trends inverse to those of the nutrient concentrations (i.e. concentrations decreased with depth and increased along the drogue track). However, there were exceptions in that chlorophyll a concentrations along Drogue tracks B, C and E reached a maximum and

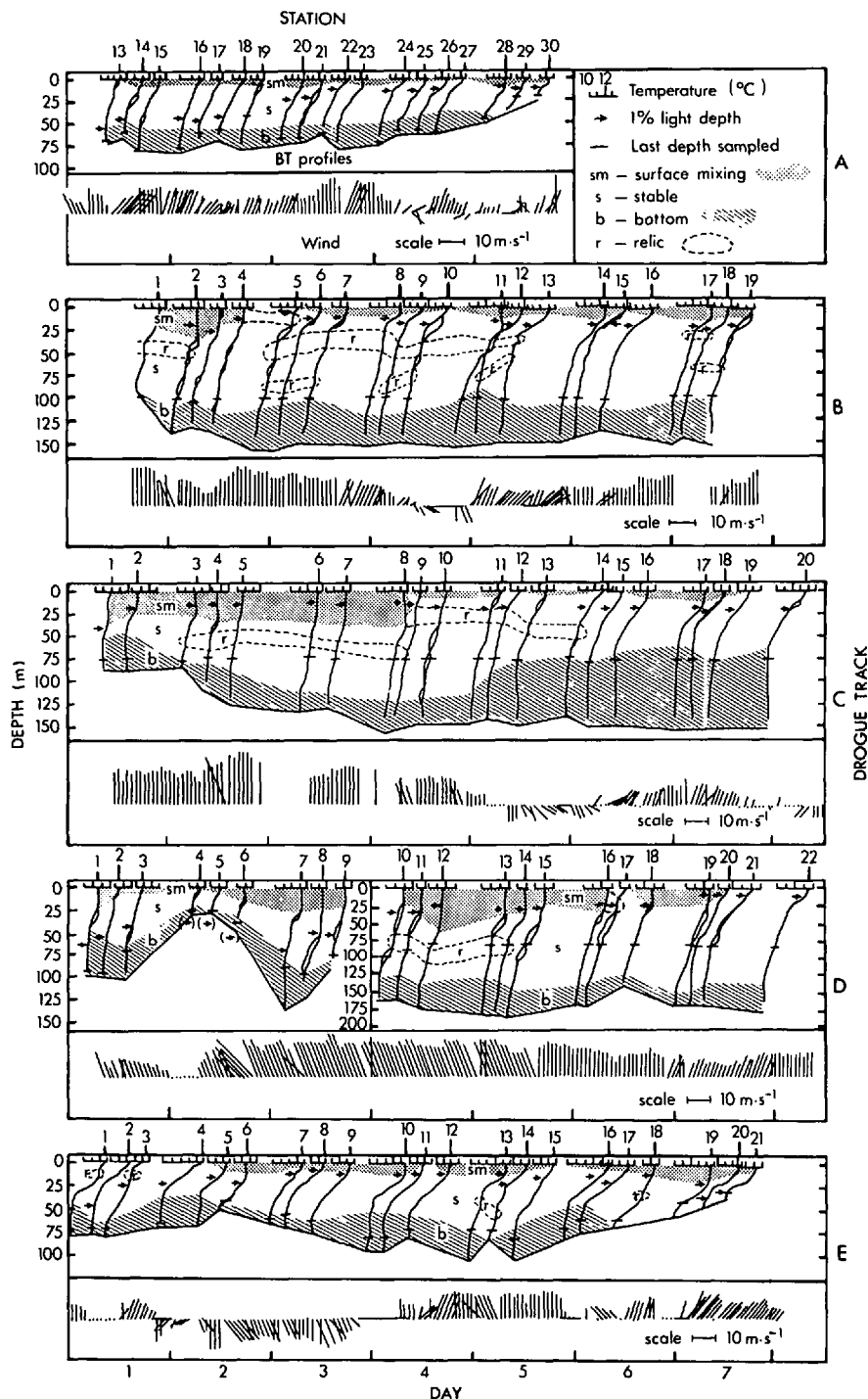Fig. 16: Hourly wind stick-vector diagrams and bathythermograph profiles along Drogue tracks A–E. The water column is partitioned into surface mixing, relic and bottom mixed layers, with a stable layer between the surface mixing and bottom mixed layers. The 1-per-cent light depth and the last depth at which water samples were drawn, are also indicated. Wind vectors show the direction in which the wind is blowing

then started to decrease.

WATER-COLUMN STRUCTURE

Temperature and salinity characteristics of South Atlantic water (Sverdrup *et al.* 1942) reveal that density is largely dependent on temperature in this area. Moreover, strong temperature/density correlations have been drawn for local waters (Fig. 15 and Bang 1973). Therefore, temperature is considered to be a good indicator of density, and bathythermograph (BT) profiles are used to estimate water-column stability. However, it should be noted that this correlation may not extend into the microscale (Bang op. cit., Waldron 1985).

Difficulties are often encountered in attempts to establish the depth of mixing in the ocean. For convenience Parsons *et al.* (1977) suggest the use of the bottom of the main thermocline as the lower limit of the surface mixing layer. However, even a slight density gradient is enough to prevent mixing. Therefore, in this study, the water column is considered to be stable if temperature decreases with depth (see Fig. 16). Vertical distribution of nutrient and chlorophyll *a* concentrations (also partly dependent on water-column structure), helped clarify uncertainties regarding the relative stability of isothermal parts of the water column. For example, where obvious nutrient or chlorophyll *a* gradients exist through an isothermal portion of the water column, it is unlikely that active mixing was taking place, at least not at a rate that would significantly influence phytoplankton distribution or growth.

Series of BT profiles (together with the depth of the 1-per-cent light level and wind stick vector diagrams) are presented in Figure 16 to illustrate the structure of the water column along each drogue track. During Cruise E, a well developed thermocline was maintained throughout the study. However, at the commencement of the other cruises, there was only a weak thermocline, but in each case its intensity increased along the drogue track. At each station, the water column was partitioned into layers based on its relative stability. Although not always present, the "surface mixing" layer, distinguishable by isothermal water at the sea surface (and also uniform depth profiles of nitrate and chlorophyll *a*), varied in thickness to a maximum of 63 m (Cruise D, Station 12). The depth of the 1-per-cent light level (normally taken to be the lower limit of the euphotic zone) varied between about 9 and 60 m (Fig. 16) and was usually deeper than the surface mixing layer. A notable exception to this trend was found along the first half of Drogue track C, where the depth of the

surface mixing layer was sometimes more than twice that of the 1-per-cent light depth. In most instances an isothermal lens of water was also present close to the sea bed. This "bottom mixed" layer was usually 20-50 m thick, but it varied up to a maximum of 90 m (Cruise C, Stations 17-20).

The layer between the surface mixing and bottom mixed layers, the "stable" layer, generally comprised the bulk of the water column. It was characterized by the existence of temperature (decreasing), nutrient (increasing) or chlorophyll *a* (variable) gradients, the strongest gradients usually being close to the surface mixing layer (and to the 1-per-cent light depth) in the main thermocline. However, cells of isothermal water were sometimes contained within the stable layer (see Fig. 16) and were probably relics attributable to previous upwelling and mixing events (Bang 1973).

The depth of the surface mixing layer may be roughly related to wind speed (see Fig. 16); moderate winds (mean speed 7,5 m·s^{-1}) during Cruise A were associated with a relatively shallow surface mixing layer (mean depth 6 m, range 0-15 m), whereas strong winds during Cruise C (mean speed for Days 1-3 was 13,9 m·s^{-1}) accompanied a deeper surface mixing layer (mean depth 32 m, range 25-40 m). However, it should be noted that the effect of the wind may be modified by the structure of the water column, a weak temperature gradient being more susceptible to wind erosion than a highly stratified one. Wind direction may also influence water-column stability. For instance, onshore winds, which generally blow for short periods during the upwelling season, are less liable to cause turbulence than offshore winds, because they tend to bring a shallow film of warm water shorewards (Bang and Andrews 1974), thereby stabilizing the water mass (e.g. Cruise A, Stations 25-26; Cruise B, Stations 9-10; Cruise C, Stations 11-12; Cruise E, Stations 3-4). However, when northwesterly winds persisted for more than a day (e.g. Days 4-7 during Cruise E), significant surface mixing did occur. Opposing wind and current directions may also aid destabilization of the near-surface layer (e.g. Stations 16-18 of Cruise C).

Stabilization of the cold turbulent upwelling water is undoubtedly caused by the heating effect of the sun, either directly at the sea surface or indirectly when warmed "older" upwelled water mixes with newly upwelled water. Mean temperatures along the drogue tracks are presented in Figure 17 together with values of incident photosynthetically active radiation (PAR), which may be considered an index of heat input. Temperatures near the sea surface tend to increase along the drogue tracks; the occasional

Fig. 17: Incident hourly photosynthetically active radiation (PAR) and mean temperatures along Drogue tracks A-E. PAR for Cruise B was calculated from total radiation measurements
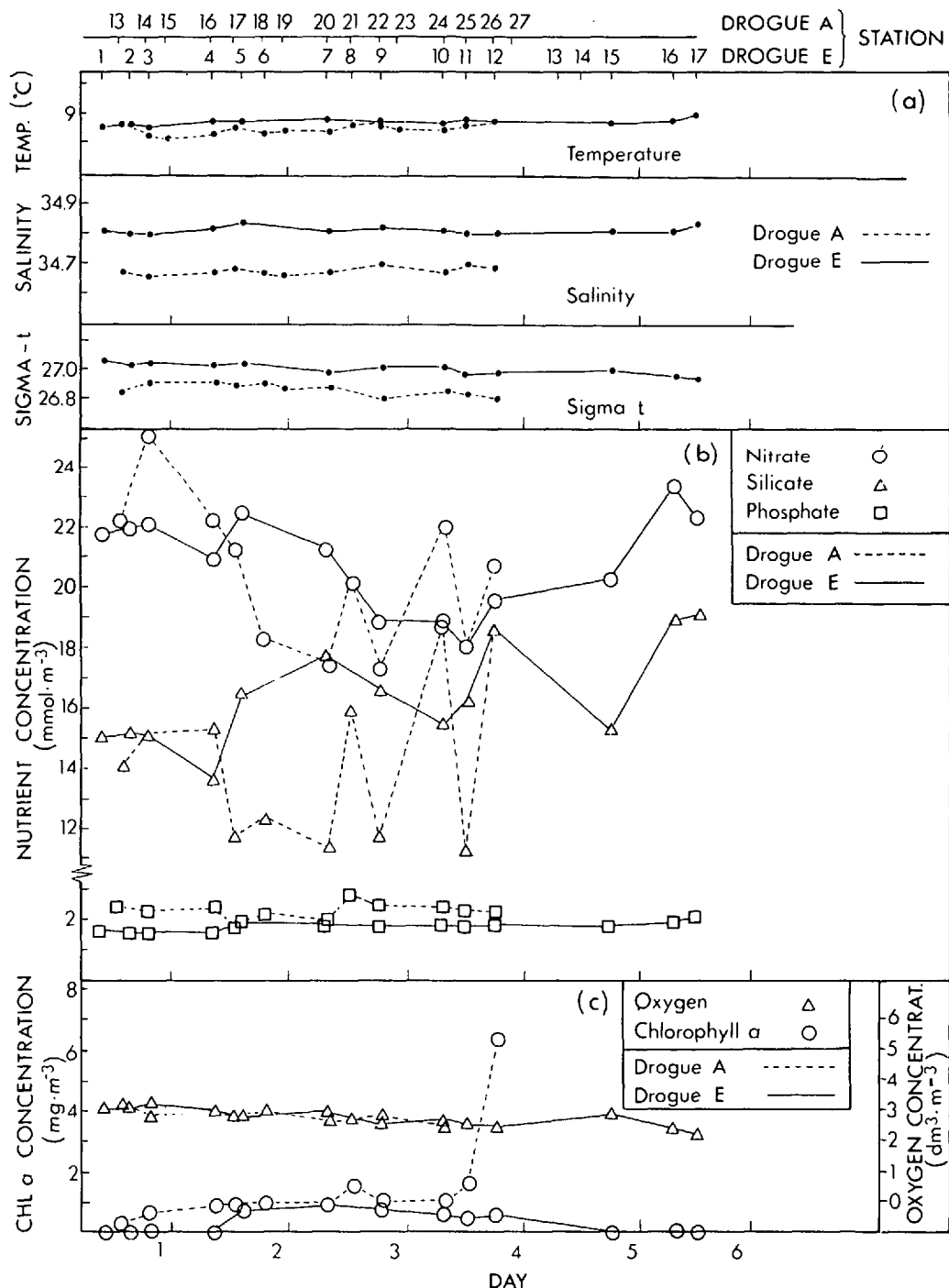
Fig. 18: (a) Temperature, salinity and density, (b) nutrient concentrations and (c) chlorophyll a and oxygen concentrations in the bottom mixed layer along Drogue tracks A and E

decrease may be due to entrainment of deeper colder water into the surface layer, or perhaps, to slippage of water past the drogue, allowing "younger" up-welled water to overtake the sampling position.

"BOTTOM MIXED" WATER

Variations in the hydrography of the "bottom mixed" layer along Drogue tracks A and E are illustrated in Figure 18. Results for all the cruises are summarized in Table III. Temperature and salinity were generally low and hardly varied. Nutrient concentrations near the bottom (mean nitrate and silicate concentrations were 20,8 and 16,6 mmol·m^{-3} respectively) were high relative to those in surface waters (see Fig. 13), and they varied up to two-fold during any one cruise. This variation reflects either differences in the degree of nutrient regeneration during the formation of the source water or, more likely, differences in the nutrient-enrichment of source water as it moves across the shelf (Bailey and Chapman 1985). Variation in the oxygen concentration of bottom mixed water (mean 4,0 dm^3·m^{-3}, range 2,77–4,82 dm^3·m^{-3}) may also reflect differences in the degree of organic decomposition.

Low concentrations of chlorophyll a (including phaeopigments) in the bottom mixed layer (Table III) suggest that the decay processes responsible for the high nutrient concentrations had long since taken place. An exceptionally high value of chlorophyll a (9,4 mg chll a·m^{-3}) recorded in shallow water along Drogue track A (Station 26) was probably mainly detritus, because chlorophyll a measurements were not corrected for phaeopigments. Using the more discriminatory HPLC techniques, Monteiro (1986) found that such deep secondary chlorophyll a maxima in Benguela waters were due to chlorophyll a breakdown products such as chlorophyllide a, phaeophorbide a and phaeophytin a.

Comparison of mean temperature and salinity and mean concentrations of nutrients, oxygen and chlorophyll a in the bottom mixed layers along the five drogue tracks with mean values for "upwelling" water given by Andrews and Hutchings (1980) — see Table III — suggests that bottom mixed water is similar to and may be representative of upwelling source water. However, variation in nutrient concentrations (Fig. 18) and ratios (Brown and Hutchings 1987) in deep water suggests that the bottom water sampled at each station was unlikely to be the same body of water along each drogue track. Instead, surface water in which the drogue was suspended probably sheared over a bottom layer of somewhat variable nutrient composition.

Changes in the euphotic zone

HYDROGRAPHIC CONDITIONS AT COMMENCEMENT OF DROGUE STUDIES

The existence of at least a weak thermocline (see Fig. 16) at the commencement of each study, suggests either that upwelling was not actively taking place at the site where the drogue was deployed (active upwelling close to the shore can usually be recognized by cold, isothermal water), or source water was coming from mid-depths. Comparison of surface with deep hydrological measurements (Table IV) indicates that surface water had been in the euphotic zone at least long enough for photosynthesis to reduce the nutrients and to increase oxygen concentrations. Differences in temperature and salinity and in nitrate and silicate concentrations suggest that the water at the beginning of Cruises A, C and D was more recently upwelled and uniform than that for Cruises B and E. Initial chlorophyll a concentrations were correspondingly low during Cruises A, C and D whereas, at Station 1 of Cruise B, surface chlorophyll a was high (4,4 mg·m^{-3}), in keeping with the reduced nitrate concentration.

The hydrography of the water into which the drogue was deployed in Cruise E is curious. A well defined thermocline (20–35 m) separated surface from deep water; the latter, as in the other studies, reflects the characteristics of Andrews and Hutchings' (1980) "upwelling" water (see Table III). How ever, the salinity of the surface water was 35,01 × 10^{-3}, somewhat higher than that for "upwelling" water but within the range for "mixed" water, the characteristics of which lie between those of "up-welling" and "oceanic" water (Andrews and Hutchings op. cit.). Perhaps the less vigorous offshore winds (see Fig. 7), which preceded the study, were responsible for "mixed" water being close to the shore. Moreover, the upwelling season (September–April) had only just commenced, and the oceanic front was not as firmly established as it tends to be later in the season (see Fig. 9). This is supported by the t/s data in Figure 11, which reveal that the salinity of the deep water (temperature < 11,5°C) was higher than expected when compared with Nelson's (1985) t/s relationship. However, salinity values greater than 35 fall either above (owing to solar warming) or near the line PQ (see Fig. 11), thus suggesting that the surface water at least had similar characteristics to those of line PQ.

As in the other studies, nutrient and oxygen concentrations along Drogue track E suggest that some photosynthesis had already occurred when the

Table III: Mean values (and ranges) of parameters measured in the "bottom mixed" layer along the five drogue tracks, and in "upwelling" and "oceanic" water as calculated from Table I of Andrews and Hutchings (1980)

Data set	Temperature (°C) Mean	(Range)	Salinity (×10⁻³) Mean	(Range)	Density (σt) Mean	(Range)	Nitrate (mmol·m⁻³) Mean	(Range)	Silicate (mmol·m⁻³) Mean	(Range)	Phosphate (mmol·m⁻³) Mean	(Range)	Oxygen (dm³·m⁻³) Mean	(Range)	Chlorophyll a (mg·m⁻³) Mean	(Range)
Cruise A	8,55	(8,2–8,9)	34,65	(34,65–34,70)	26,93	(26,87–26,97)	20,4	(15,6–26,8)	14,1	(10,3–21,3)	2,24	(1,60–2,74)	3,83	(3,41–4,12)	1,5	(0,1–9,4)
Cruise B	9,15	(8,5–9,9)	34,60	(34,55–34,72)	26,78	(26,63–26,86)	19,8	(10,4–25,3)	suspect data		2,13	(1,23–2,64)	4,40	(3,61–4,75)	0,4	(0–0,7)
Cruise C	8,98	(8,7–9,2)	34,77	(34,71–34,94)	26,95	(26,87–27,11)	21,9	(16,5–25,3)	15,9	(10,0–22,9)	1,82	(1,35–2,20)	4,07	(2,77–4,82)	0,7	(0,3–1,3)
Cruise D	9,09	(8,6–9,9)	34,74	(34,71–34,79)	26,90	(26,81–26,96)	21,0	(15,4–26,0)	20,2	(11,8–25,1)	1,47	(0,44–1,12)	3,89	(3,26–4,62)	0,3	(0,1–0,8)
Cruise E	8,80	(8,6–9,1)	34,83	(34,79–34,84)	27,01	(26,98–27,23)	20,9	(16,9–23,6)	16,4	(13,2–19,4)	1,74	(1,23–2,10)	3,82	(3,21–4,29)	0,3	(0–1,5)
Cruises A–E	8,90	(8,2–9,9)	34,72	(34,55–34,94)	26,91	(26,63–27,23)	20,8	(10,4–26,8)	16,6	(5,8–25,1)	1,88	(0,44–2,74)	4,00	(2,77–4,82)	0,6	(0–9,4)
"Upwelling" water	9,06	—	34,69	—		—	20,0	—	16,0	—	1,43	—	4,34	—	0,7	—
"Oceanic" water	18,80	—	35,40	—		—	0,8	—	4,67	—	0,4	—	5,57	—	0,4	—

Table IV: Sea surface and deep measurements at the first station after release of the drogue

Cruise	Depths (m)	Temperature (°C)	Salinity (×10⁻³)	Density (σt)	Nitrate (mmol·m⁻³)	Silicate (mmol·m⁻³)	Phosphate (mmol·m⁻³)	Chll a (mg·m⁻³)	Oxygen (dm³·m⁻³)
A	0–63	10,84–8,43	34,75–34,66	26,61–26,94	20,7–25,7	11,6–13,4	2,29–2,23	0,1–0,1	5,12–4,11
B	0–85	11,97–8,93	34,84–34,69	26,47–26,89	9,8–21,5	—	1,73–2,43	4,4–0	5,92–4,49*
C	0–80	10,00–8,72	34,79–34,83	26,79–27,03	18,8–21,2	14,8–15,4	2,05–1,35	1,6–0,3	5,42–4,26
D	0–93	10,62–8,62	34,75–34,71	26,65–26,95	17,6–20,8	16,6–22,5	1,13–1,83	0,9–0,1	4,28–3,45
E	0–70	12,74–8,62	35,01–34,81	26,45–27,03	12,7–22,5	10,3–16,0	1,27–1,54	0,7–0	4,83–4,16

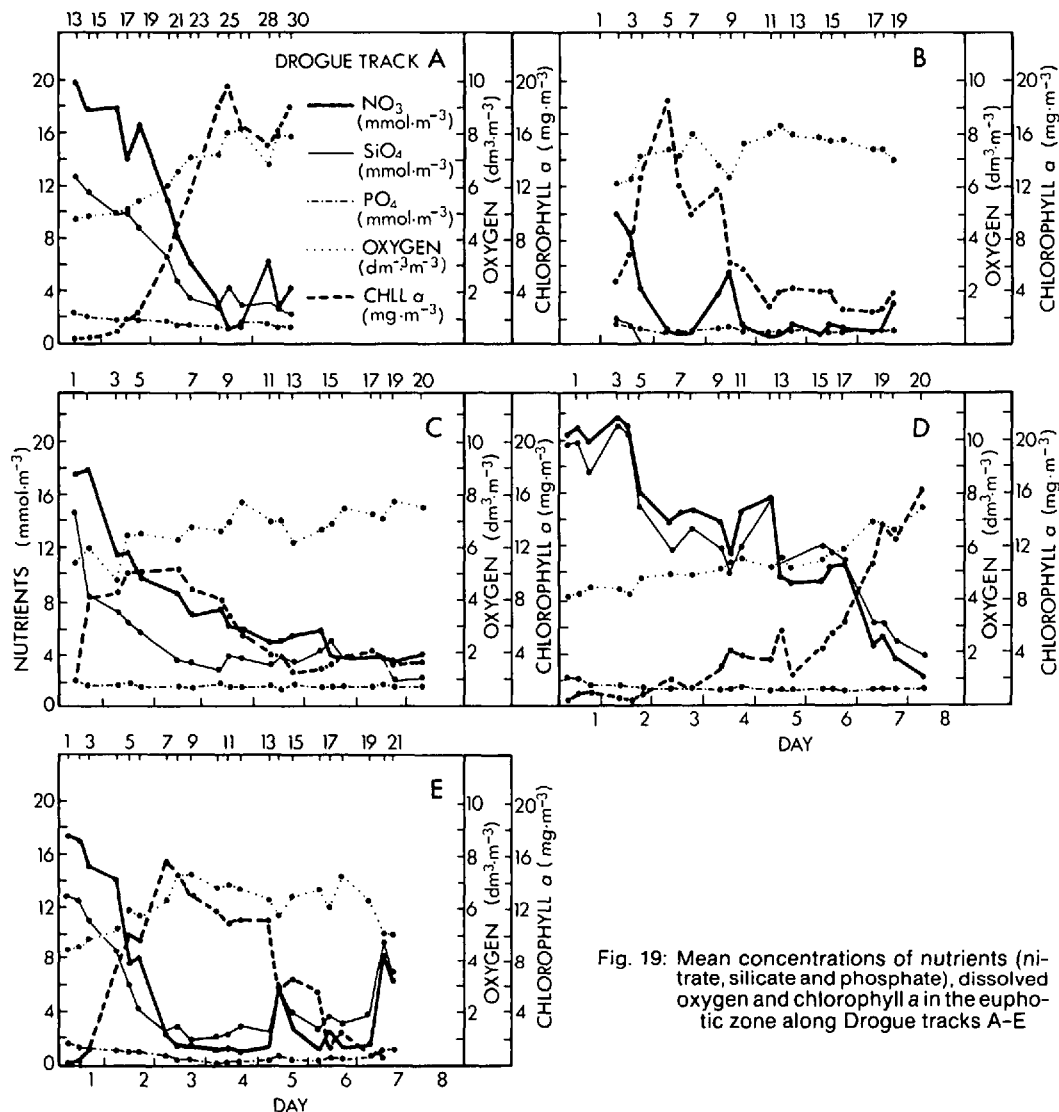*As oxygen was not measured at Station 1, data from Station 2 are presented

Fig. 19: Mean concentrations of nutrients (nitrate, silicate and phosphate), dissolved oxygen and chlorophyll a in the euphotic zone along Drogue tracks A-E

drogue was deployed. However, the very low euphotic zone chlorophyll *a* concentrations (0–0,7 mg·m⁻³), which are suggestive of more newly upwelled water, may be a reflection either of poor phytoplankton seeding or of zooplankton grazing having prevented the build-up of phytoplankton stocks before commencement of the study.

PHYTOPLANKTON BLOOM DEVELOPMENT

Changes in mean concentrations of nutrients, oxygen and chlorophyll *a* in the euphotic zone are presented for the five drogue tracks in Figure 19. Increases in oxygen and chlorophyll *a* along each track illustrate increased primary productivity and the build-up of phytoplankton blooms. After reaching a maximum, chlorophyll *a* concentrations decreased, thus indicating the decline of the bloom, whereas oxygen concentrations levelled out close to saturation. Bloom development during each cruise is assessed in the following sections in terms of chlorophyll *a* concentration. Factors affecting development, such as the depths of surface mixing and the euphotic zone (see Fig. 16), nutrient concentrations (see Figs

13 and 19) and zooplankton grazing (as assessed from Table II of Olivieri and Hutchings 1985b for Cruises B–E) are also discussed.

Cruise A — Low wind speeds, resulting in a stable water column with a shallow upper mixing layer (mean depth 6 m, range 0–15 m), allowed rapid phytoplankton growth along Drogue track A. Chlorophyll *a* concentrations in the euphotic zone increased from 0,18 mg·m⁻³ on Day 1 to 19,4 mg·m⁻³ on Day 4, with sharp decreases in nitrate and silicate concentrations. The euphotic zone was deep (54 m) in the cold, clear newly upwelled water, but decreased to 11 m at the chlorophyll *a* peak on Day 4 (Station 25). Low nutrient concentrations at Stations 25–26 were accompanied by a decrease in chlorophyll *a*. However, an increase in the depth of mixing (to 15 m) at Station 28 increased nutrient concentrations in the euphotic zone, delaying the decline of the bloom, as is evident from the renewed increase in chlorophyll *a*.

The low concentrations of chlorophyll *a* and oxygen on Day 1 suggest that little phytoplankton growth had taken place at the time of drogue deployment. Consequently, the three-day period between Stations 13 and 25 may be considered a reasonable estimate of bloom development time after upwelling, when turbulence does not limit primary productivity.

Cruise B — The upper mixing layer along the drogue track was moderately deep on Day 2 (20–37 m), but it shallowed from Day 3 (Station 5) to average 9,5 m (range 0–17 m) for the remainder of the cruise. Relatively high concentrations of chlorophyll *a* (4,6 mg·m⁻³) and oxygen (6,08 dm³·m⁻³) and low nitrate (9,7 mmol·m⁻³) concentrations at the beginning of the study indicated that significant phytoplankton growth had already occurred in the patch of upwelled water selected for monitoring. Consequently, the build-up period of the bloom cannot be estimated. Nonetheless, rapid growth (indicated by the sharp increase in chlorophyll *a* and decrease in nitrate) culminated in a peak in chlorophyll *a* on Day 3 (Station 5) followed by very low nitrate concentrations (0,7 mmol·m⁻³). The euphotic zone decreased rapidly to a minimum at the peak of the bloom (7 m), then increased as the bloom declined to approximately 20 m after Station 9.

As the depth of mixing after the peak in the bloom was either the same as or markedly shallower than the 1-per-cent light depth, bloom decline is considered to have taken place during stable conditions associated with low nutrient concentrations. As zooplankton grazing had a minimal effect on the

phytoplankton community (less than 2 per cent of the phytoplankton daily productivity and biomass being consumed each day), bloom decline was probably caused by phytoplankton sinking out of the euphotic zone. Inspection of discrete data (see Fig. 14) reveals that chlorophyll *a* levelled out after Station 14 to concentrations of between 1 and 1,9 mg·m⁻³ in the upper mixed layer, thus indicating a bloom decline period of about three days. The distinct subsurface maximum in chlorophyll *a* at 20–30 m was due either to phytoplankton sinking from surface waters into the stable layer or the upper layers (and the drogue) shearing over a more mature water mass.

Cruise C — During the first half of Cruise C, the upper mixing layer was relatively deep (mean 32 m, range 25–40 m) 1,3–3,2 times as deep as the 1-per-cent light depth (mean 14,6 m, range 12,5–19 m). The large increase in concentration of chlorophyll *a* between Stations 1 and 2 seems unrealistic, because it represents 13,5 doublings per day. The drogue may have moved into another patch, indistinguishable in terms of temperature and salinity (see Figs 10 and 12) and nitrate concentration, but with lower silicate and higher chlorophyll *a* concentrations. Deep mixing appears to have prevented phytoplankton stocks in the euphotic zone from attaining the high concentrations found in the other four cruises, despite substantial decreases in nutrient concentrations. During this cruise, bloom development appears to have been light-limited, because deep mixing would reduce the mean light levels to which phytoplankton cells were exposed. Consequently, although gross productivity may have been similar to that in the other cruises, high respiration (resulting from cells spending relatively longer periods below the compensation depth) was probably responsible for the less intense bloom. The time of bloom development is difficult to estimate here, because substantial growth had already occurred when monitoring commenced. However, the build-up period was at least 1½ days, probably longer.

The water column stabilized on Day 4 (Station 9), when the drogue reversed direction and moved south. The bloom was already declining presumably due to light limitation resulting from the combined effect of deep mixing (to 35–40 m) and shallow euphotic zone (12,5–14 m) at Stations 6–8. Despite water column stabilization and moderate nitrate and silicate concentrations, chlorophyll *a* concentrations continued to decrease steadily until Day 5. During the period of bloom decline (Days 4–5), zooplankton consumption of phytoplankton was estimated at less than 2 per cent of the phytoplankton daily producti-

vity and biomass in the euphotic zone, and thus its effect on bloom decline was hardly significant.

A shallow upper mixing layer (mean depth 3,5 m, range 0–10 m) persisted during the second half of the cruise, with silicates maintaining constant concentrations (mean 3,6 mmol·m^{-3}), and nitrates decreasing from 5,9 to < 2 mmol·m^{-3}. Although there was no clear chlorophyll *a* peak, the decline of the bloom took place within about 2–3 days. The factors limiting production in the latter stages of bloom decline are not clear, although changes in species composition (Olivieri *et al.* 1985) may partially account for the change in productivity.

Cruise D — Very low chlorophyll *a* (0,36 mg·m^{-3}), low oxygen (4,1 dm^3·m^{-3}) and high nutrient concentrations (20,4 mmol·m^{-3} nitrate, 19,6 mmol·m^{-3} silicate) in the euphotic zone at the commencement of monitoring suggest that little phytoplankton productivity had occurred since upwelling, despite the depth of surface mixing (30 m) being shallower than that of the euphotic zone (63 m). As previously cautioned, chlorophyll *a* changes during the cruise are interpreted with particular care because of the irregular salinity changes along Drogue track D (see Fig. 12). The initiation of surface stabilization was reflected by a small but definite increase in chlorophyll *a* on Day 1. The subsequent decrease in chlorophyll *a* and increase in nutrients (Day 2) were probably due to the entrainment of more recently upwelled water as the drogue moved away from the coast off Slangkop (see Fig. 6), and not to deep mixing, because a very definite thermocline was present. However, the sudden drop in nutrient concentrations from Day 2 to 3, with virtually no increase in chlorophyll *a*, is difficult to explain. The drogue may have moved into a different patch of water previously subjected to grazing or deep mixing (this would have prevented a build-up of phytoplankton, but not a decrease in nutrients). The delay in chlorophyll *a* build-up on Day 3 is strange, particularly because the euphotic zone depth was considerably greater than the depth of mixing and grazing rates were low throughout the study period. However, the increase in chlorophyll *a* on Day 4 appears to have been temporarily retarded by deep mixing down to 63 m on Day 5 (1-per-cent light depth was 26 m). A change in the chlorophyll *a* depth profiles on Day 6 suggests that Stations 15 and 16 were in yet another patch of water. However, chlorophyll *a* and nutrient depth profiles from Stations 17 to 22 (Days 6–8) indicate that, during this period at least, the drogue probably maintained itself in a consistent patch of water in which a rapid increase in chlorophyll *a* from 5,4 to 16,2 mg·m^{-3} was

accompanied by a sharp drop in nutrients and a decrease in the depth of the euphotic zone from 25 m (Stations 17–18) to about 11 m (Stations 19–22). The depth of mixing was variable but unlikely to limit primary productivity significantly. Monitoring of the water body was unfortunately stopped before a definite chlorophyll *a* peak was attained. The build-up period of the final bloom was at least two days, probably more.

Prior to Station 17 (Day 6), the water mass appeared rather patchy. With the vigorous winds, strong upwelling and moderately deep mixing that occurred, it is likely that the chemical changes were caused by physical mixing and advection rather than by biological activity. The sharp changes in salinity (Fig. 12) support this view.

Cruise E — The water column along Drogue track E was stable, with a shallow upper mixed layer (mean depth 6,3 m, range 0–15 m) and a well established thermocline present throughout the cruise. At the commencement of the study, chlorophyll *a* concentrations were low (0–0,7 mg·m^{-3}) and the euphotic zone was moderately deep (35–45 m) stretching well below the thermocline. The overnight increase in chlorophyll *a* from Day 1 to 2 seemed too large to be due to phytoplankton growth alone, and thus probably gives an underestimate of bloom build-up time (2 days).

The peak in chlorophyll *a* at Station 7 was accompanied by a sharp drop in nutrients and a decrease in the euphotic zone depth to 12 m. For the two days following the peak, the euphotic zone (10–13 m) maintained a depth similar to the depth of mixing (0–15 m), whereas nutrient concentrations remained low. Irregular peaks in nutrient concentrations between Stations 14 and 21 (Days 5–7) are somewhat artificial and are attributed to the variable euphotic zone depth (13–35 m), because the nutricline was generally between 10 and 20 m. The bloom decline spanned 3–4 days and was associated with low nutrients (nitrates were consistently < 2 mmol·m^{-3}), and marginally higher grazing rates (mean 5 per cent, range 3–11 per cent of phytoplankton daily productivity and biomass combined) than in the other cruises.

DISCUSSION

Drogue movements

Rough similarity between the wind PVDs and corresponding drogue tracks suggest that the move-

ment of near-surface water (i.e. upper 10 m) tended to be influenced mainly by the prevailing winds (southerly). This is perhaps not surprising, because the same larger scale meteorological processes are responsible for both (Nelson 1985). However, detailed inspection of the data showed some obvious deviation of the drogue tracks from the wind as measured from the ship (see progressive and stick vectors in Figs 3-7 and 16). Interpretations based on local current patterns as described by Nelson (op. cit.) and Nelson and Hutchings (1983), and on actual current measurements during Cruise E (October 1981) by Holden (1981), may better explain the drogue movements. For comparative purposes the five drogue tracks are presented together in Figure 20, along with the Upwelling Monitoring (UM) line of stations (Andrews and Hutchings 1980) and a schematic diagram of currents in the area (Nelson and Hutchings op. cit.). The drogue tracks, which were within 50 km of the coast, show that the path taken by upwelled water varies somewhat from the UM line. This implies that, to equate spatial changes offshore (as did Andrews and Hutchings [1980] along the UM line) with temporal changes (associated with phytoplankton bloom development), may be misleading. However, drogue movements appear to be consistent with the major current patterns associated with the study area.

During Cruise B, for example, the drogue appears to have been entrained into a north-flowing jet which develops as a result of complex interactions between upwelling cells, entrainment of Agulhas water offshore, general northward drift of water in the Benguela and shelf topography (Bang 1973, Bang and Andrews 1974). On the other hand, in March 1981 (Cruise D), the drogue was deployed in a southerly nearshore counter-current the existence of which has been noted on many occasions between Cape Columbine and Slangkop; its sudden reversal offshore on the second day coincided with its reaching the Slangkop retroflection area. During Cruise C (February 1981) the drogue reversal was reminiscent of the sudden switching of currents reported by Nelson (1985) to be a common feature of the area, the paths of two of his radio-tracked drogues showing a similar pattern in November 1978.

The meanderings of the drogue during Cruise E (October 1981) partly result from the weaker and more variable (compared with the other studies) winds blowing at the time. However, probably more important was the presence of juxtaposed north- and south-flowing currents creating a shear zone in the vicinity of the drogue, so that entrainment of the drogue into either current would result in drogue movement being independent of wind. Moreover, the study was conducted during the transition from winter to spring, when the increased dominance of southerly winds initiates the upwelling season. The quiescent periods, frequent fluctuations in wind during October 1981 and lack of strong horizontal temperature gradients reflect the less stable meteorological pattern typical of seasonal transition periods.

High frequency changes in the meteorology are more likely to be closely reflected in the winds than by the ocean, which has far more inertia than the atmosphere and which, at a depth of about 200 m, has been found to have a response time of approximately four days (Nelson 1985). However, response times of currents near the sea surface are likely to vary with such prevailing conditions as the slope of the sea surface, direction of wind reversal and the extent to which the ocean has been "primed" for upwelling. Taunton-Clark (1985), for example, reports that the sea surface (down to about 30 m) may respond to wind events in a matter of hours. Although prevailing winds do influence water movement in this area, other factors also play a part in setting up currents and thus determining drogue movements. For instance, periodic reversals in currents in the Cape Columbine region appear to be caused by coastally trapped waves moving polewards, with some remote forcing functions such as coastal lows, or movements in the location of the South Atlantic high pressure cell (Holden 1987, Shannon *et al.* 1987). Because of the unstable meteorological and circulation patterns off the Cape Peninsula, simulation models by G. Nelson (pers. comm.) show that small temporal or spatial variation in drogue deployment may result in considerable variation in the path traced by the drogue (Nelson and Hutchings 1987). Results from the present study support this view.

Upwelling filaments, which have been described both off California (Mooers and Robinson 1984, Flament *et al.* 1985) and in the Benguela (Lutjeharms and Stockton 1987), are clearly visible as elongated cool structures in satellite images of these regions. These filaments are responsible for advecting upwelled water rapidly and far offshore (Mooers and Robinson op. cit.). However, as the inner limit of the filamentous region in the southern Benguela is about 1° latitude from the coast (see Fig. 2 of Lutjeharms and Stockton op cit.), filaments themselves probably did not play a major role in drogue movements during this particular study, the drogue always remaining within 50 km of the coast (Fig. 20). However, the importance of filaments in the circulation of upwelling zones, as stressed by Lutjeharms and Stockton (op. cit.), should not be underestimated.
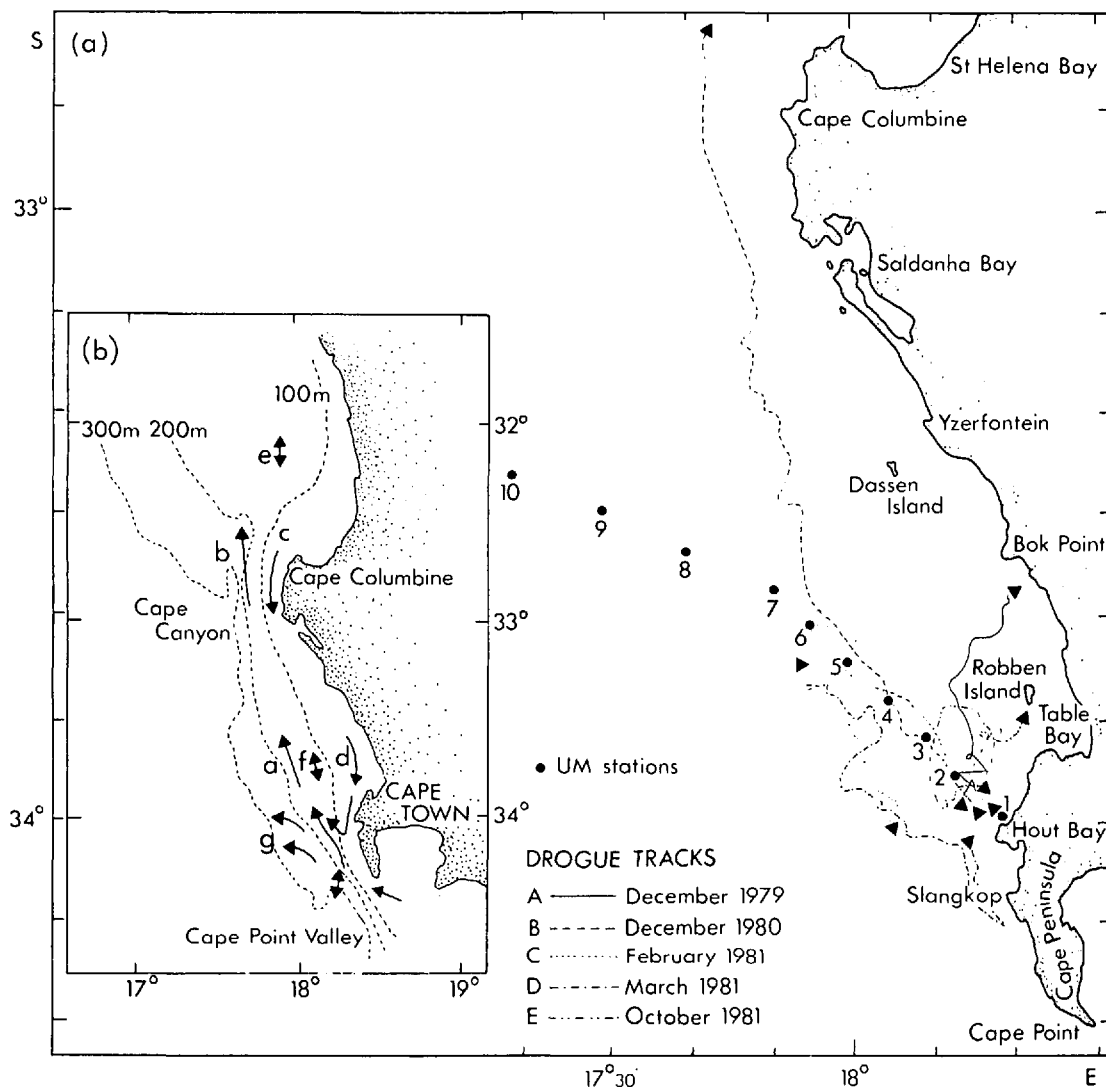
Fig. 20: (a) The five drogue tracks during the Plankton Dynamics cruises, and the station positions for the Upwelling Monitoring (UM) cruises; (b) a schematic diagram of currents off the Cape Peninsula and Cape Columbine (from Nelson and Hutchings 1983), showing permanent shelf-edge baroclinic jets (a and b), nearshore net southward currents (c and d) with distinct retroflection at Slangkop, weak variable currents (e and f), and intermittent westward flow which occurs when the shelf-edge jet accelerates (g)

Hydrography and phytoplankton bloom development

Relative to the physical characteristics (temperature and salinity) of the deep water along each drogue track, nutrient concentrations were more variable. This suggests that the "patch" of water which the drogue was following was shearing over a deeper layer of variable nutrient content, because the changes were too irregular to be attributed to normal biological activity in a single water column. Near the sea surface, temperatures increased along the drogue tracks, thereby increasing the stability of the water column. Wind caused surface mixing, but in only one

Table V: Growth and decline cycles of phytoplankton blooms in upwelled water and a summary of conditions influencing bloom development

Cruise	Bloom development cycle (days)			Conditions influencing development
	Growth	Decay	Total	
A	3	>1	>4	Stable water column allowed rapid bloom build-up; nutrient-induced bloom decline delayed by entrainment of nutrients into euphotic zone
B	>1,5	3	>4,5	Bloom peaked rapidly after deeply mixing water stabilized at Station 2. Low nutrients associated with bloom decline
C	>1,5	2–3	3,5–4,5	Low light levels resulting from deep mixing did not prevent bloom initiation, but limited its extent in that chlorophyll concentrations did not increase to levels as high as other cruises. Limiting factors in latter stages of bloom are not clear
D	>2	—	2	Slow build-up of phytoplankton stocks artefactual; water around drogue was replaced by more recently upwelled (chlorophyll-poor) water. After Station 17, bloom development was similar to that in other stable water masses. Monitoring ceased before bloom declined
E	>2	3–4	6	Stable water column permitted rapid bloom development. Drogue appeared to move into patch of water rich in chlorophyll *a*; thus, apparent two-day build-up period is probably an underestimate. Low nutrients associated with bloom decline
A–E	3	3–4	6–7	Estimated periods of bloom build-up and decline are combined to obtain a complete bloom development of cycle about 6–7 days

case (the first half of Cruise C) was the depth of mixing markedly greater than the euphotic zone depth, thus resulting in light-limitation of the phytoplankton community (see below).

While nutrient concentrations in the upwelling source water were high, phytoplankton biomass was low. High levels of light at the sea surface allowed nutrients in newly upwelled water to be rapidly taken up by phytoplankton, so that concentrations in surface waters were reduced to low levels after a few days once the bloom started. Although a complete cycle of bloom development was not attained during any one cruise, some idea of the variation in build-up and decline periods was obtained by superimposing the peaks of the five chlorophyll *a* curves presented in Figure 19. The growth and decline cycles are summarized in Table V together with brief comments on prevailing conditions and limiting factors. The complete cycle of bloom development in upwelled water appeared to be completed within 6–7 days. Chlorophyll *a* increased from concentrations of usually less than 1 mg·m⁻³ in upwelling water to 10–20 mg·m⁻³ at the peak of the bloom. It then decreased to concentrations of 1–3 mg·m⁻³ after the bloom, when recycling of nutrients probably maintained phytoplankton stocks at moderately low levels. Turbulence may, of course, entrain nutrients up into the euphotic zone and so prolong the bloom.

It is interesting that, first, the rate of phytoplankton consumption by zooplankton was low in these studies, failing to account for bloom decline, and,

second, that in only one of the five cruises did light-limitation as a result of deep mixing influence bloom development. In this case (Cruise C) the initiation of the bloom was not impeded, but its development was limited so that only moderately high concentrations of chlorophyll *a* were attained. It follows that high nutrient levels and a relatively stable water column after upwelling are responsible for the intense blooms of phytoplankton encountered in the Cape Peninsula upwelling region. Conversely, however, the association of low nutrients with decreasing chlorophyll *a* concentrations is not sufficient evidence to attribute bloom decline to nutrient limitation of phytoplankton productivity alone (Brown 1986). Other processes such as sinking or dispersion, may be important factors controlling the decline in blooms in this area.

The system as a whole

Active upwelling in the southern Benguela region results in the formation of clearly defined tongues of cool water extending offshore from upwelling centres (Nelson 1981, Nelson and Hutchings 1983) as well as cool filaments, plumes and eddies farther offshore (Shannon *et al.* 1985, Lutjeharms and Stockton 1987). It is tempting to assume that the main flow of water close to the coast is along the major axis of the upwelling tongue. However, near-surface temperature distribution indicates little of the complexity associated with tongue formation and decay (Nelson

1981, 1985, Brink 1983). Initially, in the present studies, the drogue usually followed the main axis of the tongue during southerly winds, but there were significant variations in the form of eddies or reversals which were sometimes contrary to wind direction. In contrast to similar drogue studies off North West Africa (Herbland *et al.* 1973, Herbland and Voituriez 1974), each drogue track was different.

The present study has shown that changes in local winds and more distant forcing functions may play an important role in the timing and position of the sequence of biological events following upwelling. Each upwelling event appears to invoke a sequence of phytoplankton development which varies mainly with the relative stability of the upwelled water. The destination of the biological products of upwelling may vary quite considerably and, thus, may have significant effects on the planktonic and nektonic consumers in the southern Benguela ecosystem.

Within an individual patch of water "tagged" by the drogue, phytoplankton growth and decline took place over a period of 6–7 days, whereas the cycle of upwelling pulses typically lasts for 3–10 days (Nelson and Hutchings 1983, Hutchings and Nelson 1985). Consequently, in the area in which the newly upwelled water is transported and mixed, one could expect high chlorophyll levels to persist for periods of 10–16 days after the start of an upwelling cycle. During strong winds, the shearing action in the upper few metres may spread the phytoplankton over a wide area, thereby creating large patches of chlorophyll-rich water commonly observed in CZCS imagery in the southern Benguela region (Shannon *et al.* 1985, Lutjeharms and Stockton 1987). Only when upwelling-favourable winds cease for periods longer than 6–7 days would a decline in phytoplankton concentrations become generally apparent in the coastal zone.

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