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PHYSICAL AND BIOLOGICAL FEATURES ACROSS AN UPWELLING FRONT IN THE SOUTHERN BENGUELA

D. A. ARMSTRONG*, B. A. MITCHELL-INNES*†, F. VERHEYE-DUA†, H. WALDRON‡ AND L. HUTCHINGS*

The upwelling front of the Cape Columbine upwelling centre was intensively studied, physically and biologically, along a repeated transect during December 1984 following a quiescent phase in the upwelling cycle. Three distinct zones were evident, an inshore zone influenced by upwelling, an offshore warm oligotrophic zone and a transitional frontal zone separating the two. Salinity proved to be a useful indicator of recent water movements. There was evidence of intrusions and mixing of water types within the frontal zone, possibly accounting for the elevated phytoplankton biomass recorded there. Floral and faunal changes occurred between the frontal and offshore zones, corresponding to the thermal front. The predominant flow was alongshore, with strong equatorward jet currents, making the interpretation of cross-shelf gradients difficult in this dynamic area. Aspects of the distributions of organisms and their productivity across the upwelling front are described with respect to the hydrographic parameters and associated flow-field.

Die opwelfront van die opwelsentrum by Kaap Columbine is t.o.v. van die fisika en biologie intensief bestudeer langs 'n herhaalde transek gedurende Desember 1984 ná 'n rusfase in die opwelsiklus. Drie duidelike sones kon onderskei word: 'n kussone beïnvloed deur opwelling, 'n aflandige, warm, oligotrofiese sone en 'n oorgangsone by die front wat die twee skei. Soutgehalte het 'n nuttige aanduider van onlangse waterbewegings geblyk. Daar was bewys van binnedringing en vermenging van watertipes binne die front-sone, wat moontlik die verhoogde fitoplanktonbiomassa aldaar verklaar. Floristiese en faunistiese veranderings het tussen die front- en die aflandige sone ingetree, in ooreenstemming met die termiese front. Die hoofvloei was kuslangs, met sterk ewenaarwaartse snelstrome wat die vertolking van oordwarse gradiënte op die vastelandsplat in hierdie dinamiese streek bemoeilik het. Aspekte van die verspreiding van organismes en hul produktiwiteit dwars oor die opwelfront word beskryf met inagneming van die hidrografiese parameters en die geassosieerde stroomveld.

The existence of pronounced fronts in the southern Benguela between cold upwelled water inshore and warm offshore water has long been recognized. However, apart from the earlier pioneering work by Bang (1971, 1973, 1976) and Bang and Andrews (1974), relatively few measurements have been made with the frontal interface as the primary target of investigation. Remote sensing by satellites (Lutjeharms 1981, Shannon and Anderson 1982, Van Foreest *et al.* 1984) and Airborne Radiation Thermometry (Andrews and Cram 1969, Jury 1985, Taunton-Clark 1985) have greatly increased awareness of the large-scale features and variability of the area, and from such images sites of interest can be identified and targeted for finer-scale investigation during oceanographic surveys.

Episodic, longshore equatorward winds are the primary driving force of the southern Benguela system. They cause upwelling of cold, nutrient-rich South Atlantic Central Water into the euphotic zone

thereby elevating the isopycnals and creating a prograde front which outcrops at the surface as a frontal zone (Andrews and Hutchings 1980, Nelson and Hutchings 1983). A series of papers describing the relationship that exists between the local wind field and the distribution of physical and chemical properties (Bailey and Chapman 1985, Jury 1985) and between the fluctuation in wind velocities and current regime (Holden 1985, Nelson 1985) has recently been published as part of the South African Ocean Colour and Upwelling Experiment (CUEX). It has also become evident that marked changes observed in the development of phytoplankton blooms and the distribution of zooplankton are closely related to wind events (Hutchings 1981, Brown and Hutchings 1985). For further information on the southern Benguela, readers are directed to the recent reviews on various aspects of the system: physical (Shannon 1985), chemical (Chapman and Shannon 1985) and biological (Shannon and Pillar

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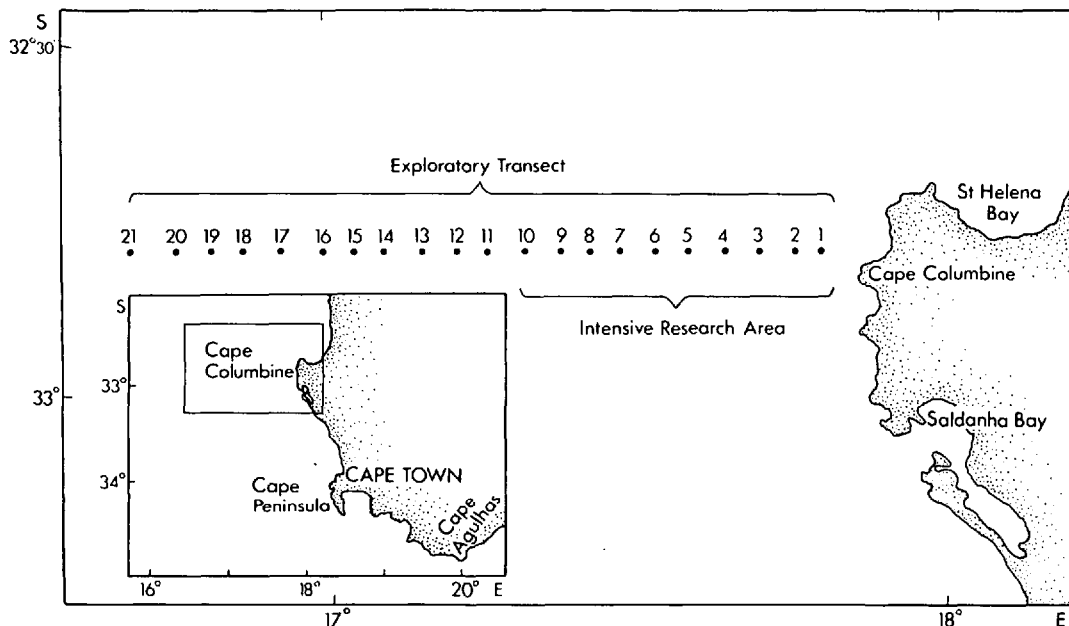
Fig. 1: The study area showing stations occupied during the exploratory and intensive transects of the Frontal Zone cruise in December 1984

1986, Crawford *et al.* 1987).

The superficial frontal features within the southern Benguela are also highly responsive to changes in physical forcing of the local wind field (Bang 1973, Andrews and Hutchings 1980). Bang (1974) distinguished two fronts within the system, the upwelling front and the shelf-break front, which can coexist because their dynamics are not mutually exclusive (Mooers *et al.* 1978). The surface manifestation of the upwelling front is highly variable in position, responding rapidly to changes in wind stress and direction, moving offshore during upwelling-favourable winds and onshore during reversals or quiescent periods. The shelf-break front appears to be more permanent and can persist off the Cape Peninsula as a subsurface structure for most of the year (Hutchings *et al.* 1984). The two fronts coalesce during periods of sustained upwelling in the austral summer, creating intense thermal gradients in the vicinity of the shelf-break (Hutchings *et al.* 1986).

In comparison with other eastern boundary current systems (Brink *et al.* 1983, Huyer 1983, Mittelstaedt 1983) the frontal gradients encountered in the southern Benguela are particularly strong, often of the order of 1°C per nautical mile but occasionally several degrees over a few hundred metres (Bang 1973). Several factors contribute to this intensification

of horizontal thermal gradients. The upwelling process itself is influenced by topographic irregularities in the form of capes and canyons, modifying the local wind patterns and funnelling very cold water (<10°C) up to the surface, creating distinct upwelling plumes. The close proximity of the warm water Agulhas regime in the south-east exerts a substantial influence on the system. Northward advection of these waters around the Cape during the upwelling season (Duncan and Nell 1969) intensifies the horizontal gradients around the Cape Peninsula and Cape Columbine upwelling centres (Bang and Andrews 1974) and modifies the plankton community structure off the West Coast (De Decker 1984). Associated with the upwelling fronts in these two areas are strong equatorward jet currents (Bang 1971, Bang and Andrews op. cit., Nelson 1985). Velocities of up to 120 cm·s⁻¹ have been recorded off the Cape Peninsula where the jet often coincides with the shelf-break (Bang and Andrews op. cit.).

These jet currents have been implicated in facilitating the transport of pelagic fish eggs and larvae from spawning grounds on the Agulhas Bank to recruitment areas off the West Coast (Shelton and Hutchings 1982). The recent focus on the frontal zone was partly stimulated by the need to assess the possible impact of this region on larval survival and

also by the increased recognition of frontal boundaries as potential regions of high productivity (e.g. Floodgate *et al.* 1981, Holligan 1981, Kahru *et al.* 1986, Smith *et al.* 1986). Evidence of the biological consequences of fronts is extensive, and they have been shown to influence the distribution of organisms over a wide spectrum of trophic levels, from phytoplankton (Fournier 1978, Packard *et al.* 1978) through to higher predators (Uda 1973, Haney and McGillivary 1985). The ecological response to such interfaces is diverse, and the modification of community composition or productivity varies depending on the type of front and its persistence in space and time.

Hutchings *et al.* (1986) reviewed the literature and presented preliminary results from a frontal zone cruise in December 1984 to summarize the possible biological significance and implications of the frontal zone within the southern Benguela system. A broad approach was adopted for this cruise, involving several disciplines and Institutes in a first direct investigation of the manner in which physical and biological processes interact to generate and control biological production and spatial distribution of organisms in the frontal zone. In this paper the overall cruise strategy is reported and general descriptive results are presented to provide a background for later detailed analyses of specific aspects.

MATERIALS AND METHODS

Cruise description

A Frontal Zone (FZ) cruise during the period 6–13 December 1984 was designed to cross and study the front associated with the Cape Columbine upwelling centre (Fig. 1). The sampling was carried out on board R.S. *Africana*, a multidisciplinary research ship owned by the Sea Fisheries Research Institute. The position and the extent of the front were defined during an exploratory transect (Leg 1) along latitude 32°48′S out to the shelf-break, 120 km offshore. Vertical profiles of temperature and salinity were obtained by means of a CTD at 21 stations 3 nautical miles (~ 5,5 km) apart. Additional information was obtained from satellite thermal imagery (METEO-SAT) on 27 November 1984.

Three repeated transects (Legs 2, 3 and 4) across this frontal feature were then restricted to the inner 10 stations of the original transect, encompassing inshore, frontal and offshore zones. Sampling was shorewards on Leg 2 (Stations 2–10 to 2–01) and Leg 4 (Stations 4–10 to 4–01), and seawards on Leg 3 (Stations 3–02 to 3–09). During this part of the study

intensive hydrological and biological sampling was undertaken on a 24-h basis. All routine sampling procedures involving CTD/rosette sampling and zooplankton net hauls were carried out at each station. At seven selected stations (1–16, 2–07, 2–03, 3–03A, 4–10, 4–04 and 4–05A), phytoplankton and bacterial productivity measurements were also made during daylight. Infra-red satellite imagery of sea surface temperature on 8 December 1984 was obtained after the cruise from the Remote Sensing Centre at Hartebeesthoek.

Data collection

METEOROLOGICAL

Information on the prevailing local wind velocity and direction before and during the cruise was obtained from hourly observations at the Cape Columbine lighthouse. This was supplemented with anemometer measurements taken from the vessel during the cruise. There was close agreement of simultaneous wind measurements between these two sources.

PHYSICAL

Continuous profiles of temperature and salinity through the whole water column were obtained from the CTD and these data were then used to calculate density. Surface temperature and salinity were monitored continuously by means of a thermosalinograph which was annotated hourly. The horizontal surface thermal features over a much larger area during the cruise were obtained from the NOAA-7 overpass on 8 December 1984.

During the intensive part of the survey an acoustic current meter was deployed with the second cast of the CTD/rosette assembly. The ship was allowed to drift freely for at least one hour, taking note of the position at the beginning and end of the drift period.

CHEMICAL

Water samples were collected during ascent of the CTD/rosette sampler at a maximum of 10 discrete depths of 5-, 10-, or 20-m resolution in the upper 100 m. The sampling depths at routine stations were selected according to the real-time temperature profile displayed on the shipboard computer during deployment of the CTD. Sampling depths for the "productivity stations" corresponded to the depths at which 100, 50, 25, 10 and 1 per cent of the incident light penetrated, as estimated by Secchi disc readings.

Subsamples were removed for analysis of oxygen, inorganic nutrients and CHN. Oxygen titrations were carried out immediately by means of the standard Winkler technique. Two 10-ml water samples were deep-frozen and stored for analyses ashore of phosphate, silicate, nitrate and nitrite on an autoanalyser (Mostert 1983). Between 0,5 and 1,0l of water was filtered onto pre-ashed Whatman GF/F filters which were then frozen and stored. In the laboratory the particulate carbon and nitrogen were determined by high temperature oxidation in an elemental analyser with cyclohexanone (20,14%N: 51,79%C) as a standard.

PHYTOPLANKTON BIOMASS AND PRODUCTION

Chlorophyll samples were collected on Whatman GF/F filters, wrapped in aluminium foil and frozen for later spectrophotometric analysis of chlorophyll a by the method of SCOR/UNESCO Working Group 17 (1966). Estimates of phytoplankton biomass were also obtained by counting and sizing particles on a 16-channel Coulter counter with a 280-μm aperture tube following the method described by Sheldon and Parsons (1967). Details of the practical application of this method at sea are given in Olivieri (1983). In each instance an additional 200 ml of water was preserved with Lugol's solution for later microscopic examination.

At the "productivity stations", two Niskin bottles were triggered at each predetermined light depth to provide sufficient water for all routine procedures in addition to the experimental determination of rates of production. Primary productivity was measured by the uptake of ^{14}C-bicarbonate over 4-h incubation periods under simulated *in situ* conditions on deck (Brown 1984).

BACTERIAL NUMBERS, BIOMASS AND PRODUCTION

Subsamples of water (20ml) were preserved with 1,25-per-cent gluteraldehyde. They were later used for determination of bacterial numbers by means of the acridine orange direct counting technique (AODC) after filtration onto 0,2 μm Nuclepore filters (Hobbie *et al.* 1977). Bacterial biomass and cellular carbon were estimated from mean cell volumes for seven categories of bacterial morphs (Painting *et al.* 1985), using a specific gravity of 1,1 g·cm^{-3} (Doetsch and Cook 1973, as cited in Linley *et al.* 1983) and a wet biomass to carbon ratio of 0,11 (Troitsky and Sorokin 1967, Linley *et al.* op. cit.).

Bacterial production was measured by small-volume (< 3 μm diameter), predator-reduced incubations (Sorokin and Kadota 1972). Details and critical analysis of estimates of bacterial production based on population growth are given by Linley *et al.* (1983) and Painting *et al.* (1985).

ZOOPLANKTON NUMBERS AND BIOMASS

A second cast of the CTD/rosette assembly was made at each station, and samples were collected during the ascent from 100 m at specified depth intervals of 5, 10 or 20 m during the current-profiling operation. Each 5-l sample was then concentrated through a 37-μm filter and the concentrate preserved in 5-per-cent buffered formalin for later microscopic examination of microzooplankton.

Mesozooplankton and ichthyoplankton samples were collected with a multiple-net Rectangular Midwater Trawl (RMT 1 × 6), of mouth area 1 m^2 and fitted with 200-μm mesh netting. The net was towed obliquely at 2 knots, and five depth strata were sampled during the ascent of the net from just above the sea bed. These strata were selected on the basis of the predetermined temperature profile. The samples were then preserved in 5-per-cent buffered formalin for later processing. In the laboratory, all fish eggs and larvae were removed, identified to the lowest taxon possible and measured, before splitting and fractionating the samples for biomass determination and zooplankton species identification. Because of a malfunction in the trigger mechanism of the RMT, it was necessary to pool data from the samples collected in the upper two strata for subsequent analyses.

Throughout the cruise, a 38-kHz echosounder was in operation to record sound-scattering layers and to detect fish targets and areas of dense zooplankton.

RESULTS AND DISCUSSION

Physical aspects

During the week preceding the cruise, variable light-to-moderate winds at Cape Columbine lighthouse were recorded, with frequent changes in direction and with no period of sustained southerly winds (Fig. 2a). These quiescent conditions persisted into the initial exploratory phase of the cruise, but throughout the remainder of the investigation more consistent southerly winds prevailed (Fig. 2b). Maximum wind speeds of 15 m·s^{-1} were recorded during the third leg on the 10th December, but these abated towards the end of the cruise. This sequence of events in the wind record illustrates the passive and
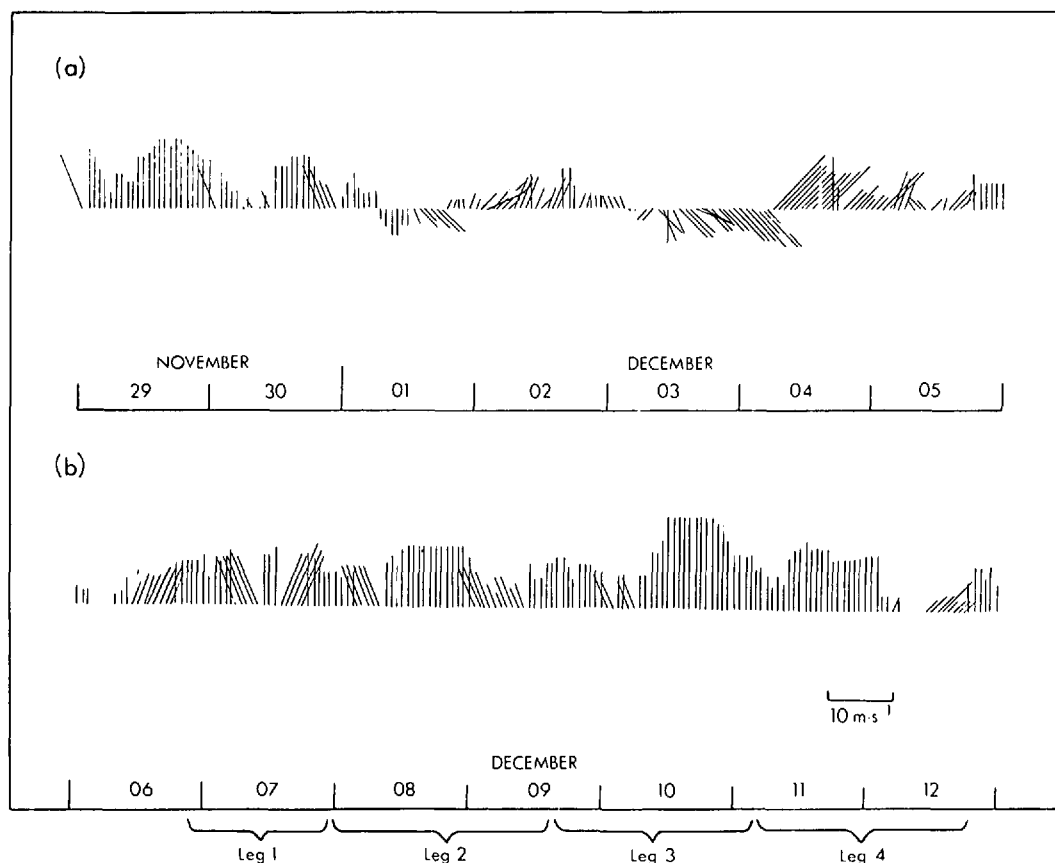
Fig. 2: Stick vector diagrams of hourly wind measurements recorded at Cape Columbine lighthouse (a) prior to and (b) during the cruise

active phases in the upwelling cycle. The passive phase or period of quiescent conditions prior to and at the start of sampling was followed by a more active period when upwelling-favourable winds $> 5\mathrm{m\cdot s^{-1}}$ (Shannon 1985) were recorded. Frontal dynamics under these pulsing conditions are not well understood and interpretation must include the possible changes resulting from longshore water movements.

GENERAL FEATURES

The large-scale thermal surface features are depicted on the infra-red satellite image recorded during 8 December 1984 (Fig. 3). The image is calibrated, atmospherically corrected and filtered, giving temperatures accurate to within 0,5°C. The front was convoluted, containing irregularities of various shapes and sizes with indications of intrusions of one water type into another. Eddies and meanders in the frontal region are common and have been observed and described from numerous satellite images (Lutjeharms 1981, Shannon et al. 1985). Lutjeharms (op. cit.) considered certain eddies to be a persistent feature, while Shannon et al. (op. cit.) found frontal perturbations to be more prevalent after reversals in the upwelling-favourable longshore wind. These eddies probably contribute significantly to the exchange and mixing of properties across the front and therefore have major consequences for biological processes occurring near the frontal boundary. An understanding of the evolution and formation of eddies and other frontal instability features is being developed through extensive simulations in the laboratory (e.g. van Heijst 1986). The presence of cold-water upwelling plumes, extending northwards from Cape Columbine and the Cape

Fig. 3: NOAA-7 satellite infra-red image of the southern Benguela system, 8 December 1984 at 14h56, with station positions superimposed (●). Each colour spans 1°C. Light blue = 10,0–10,9°C
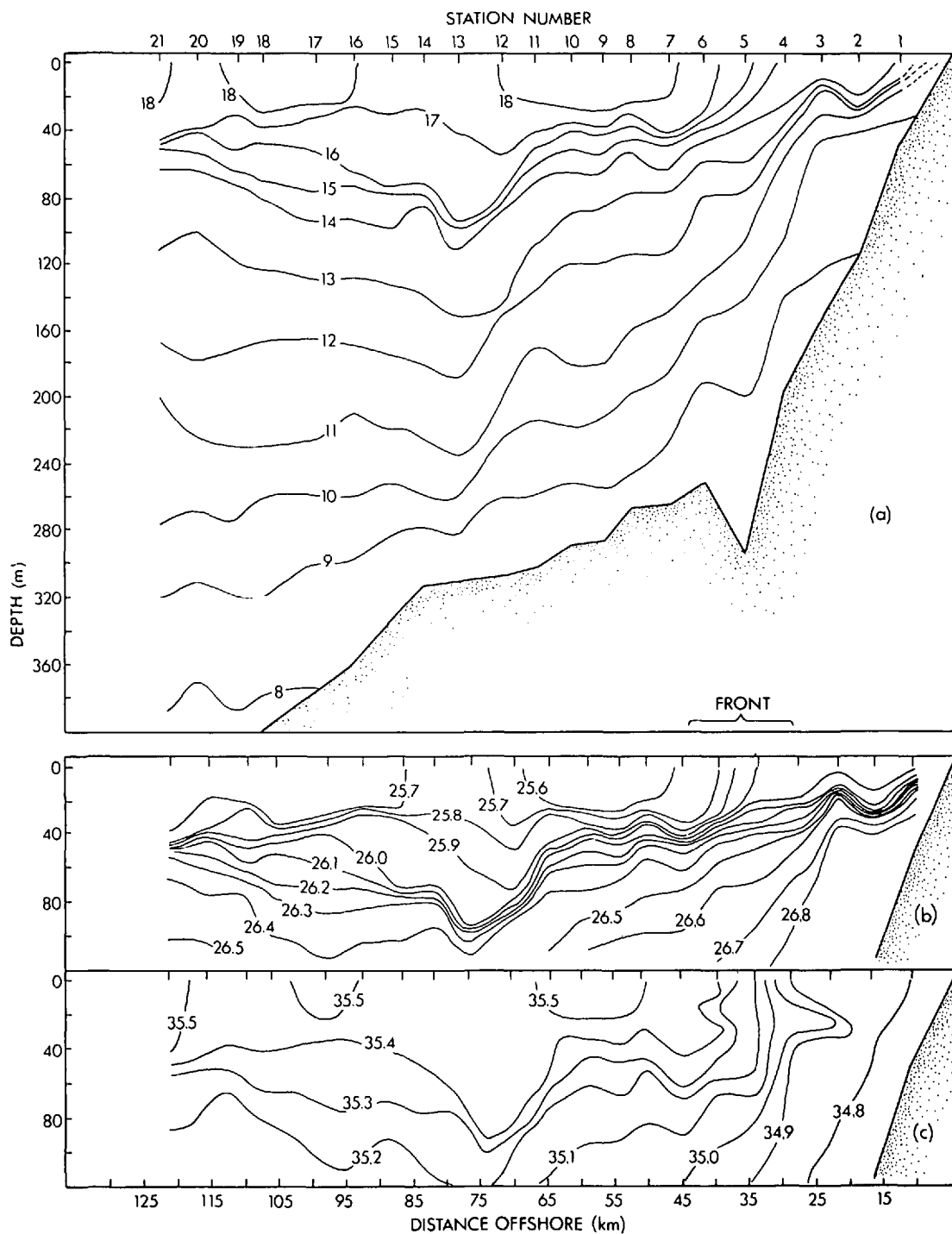
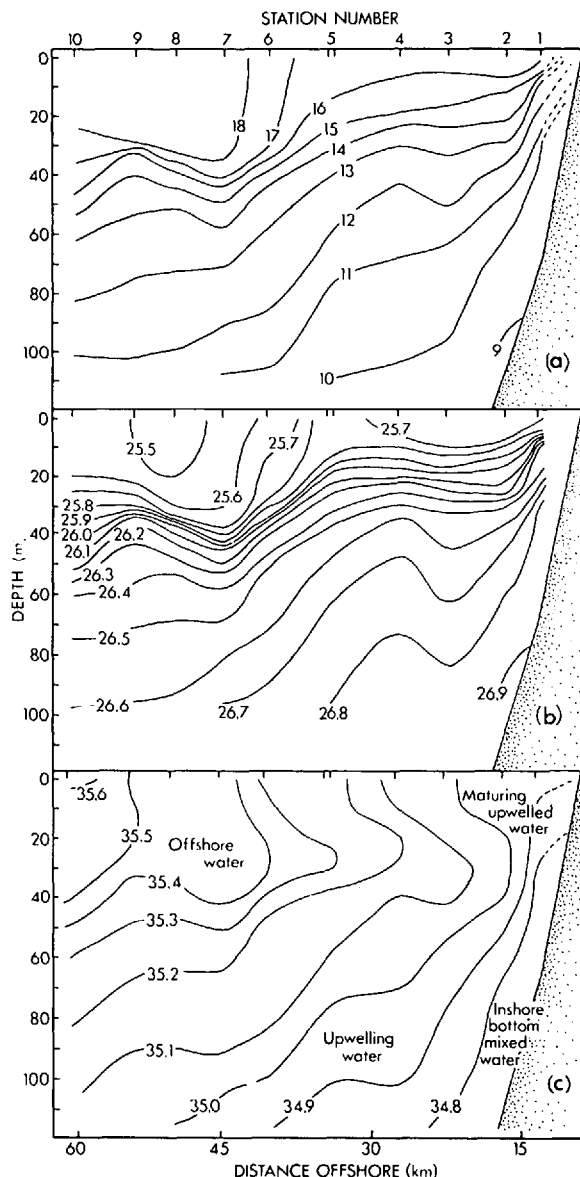Fig. 4: Vertical sections of (a) temperature (°C), (b) density (σt) and (c) salinity (×10⁻³) along the exploratory transect (Leg 1), showing the position of the front

Fig. 5: Vertical sections of (a) temperature (°C), (b) density (σt) and (c) salinity (×10⁻¹) from Leg 4 of the cruise. Water types are included on the salinity section

Peninsula, are obvious features on the image, and the greatest horizontal thermal gradients ocurred in these two regions (Fig. 3). Warm surface water had intruded into the south and compressed the plume off the Cape Peninsula towards the coast.

A relatively broad surface thermohaline and density front was encountered during the 21-h exploratory transect of CTD stations (Fig. 4). The front was located close inshore, 30–40 km from the coast, consistent with the quiescent wind history of the preceding week (see Fig. 2a). A shelf-break subsurface front was not evident during this transect and the detailed biologically orientated studies were confined to the inner 10 stations encompassing a coastal, frontal and offshore zone. The inner edge of the front was considered to be between Stations 4 and 5 and the outer edge between Stations 6 and 7 during Leg 1 of the transect (Fig. 4). The term frontal zone will be used throughout to refer to the region affected significantly by phenomena associated with an inclined density discontinuity (Mooers *et al.* 1976).

For the purpose of this report, data are presented from Leg 4, but including productivity measurements derived during Legs 2 and 3 to provide information from contrasting areas across the front. The changes between the three legs and the implications of the observed variability of parameters in response to fluctuations in the meteorological regime are aspects for future analysis.

DETAILED PHYSICAL STRUCTURE

The temperature, salinity and density vertical sections from Leg 4 are presented in Figure 5. The thermal front had lost some definition in comparison with Leg 1 (Fig. 4a), with inshore surface waters appreciably warmer and the inner edge indistinct (Fig. 5a). Density is determined chiefly by temperature in this area, and the density section therefore reflects the same features as the temperature section (Fig. 5b). The depth of the pycnocline decreased shorewards. The salinity section displays a relaxation in structure from that observed during the exploratory transect (Leg 1), creating a diffuse haline front with the strongest gradients occurring between Stations 4 and 5, and between Stations 6 and 7 (Fig. 5c).

Brundrit (1986) and Waldron (1985) have emphasized the value of salinity as a conservative property in revealing information on the origins and movements of water within the system. The haline signature of the water column is particularly useful in identifying maturing upwelled water and in resolving the post-upwelling structure in the surface layers, where temperature values are modified by sun-warming. Waldron (op. cit.) used salinity to refine Andrews and Hutchings' (1980) classification of water types in the southern Benguela; application of this revised classification to the data set enabled the water types to be defined and boundaries to be delineated (Fig. 5c).

Evidence of lamination and interleaving of water types in the frontal zone can be seen in the salinity section (Fig. 5c) and from the salinity inversions
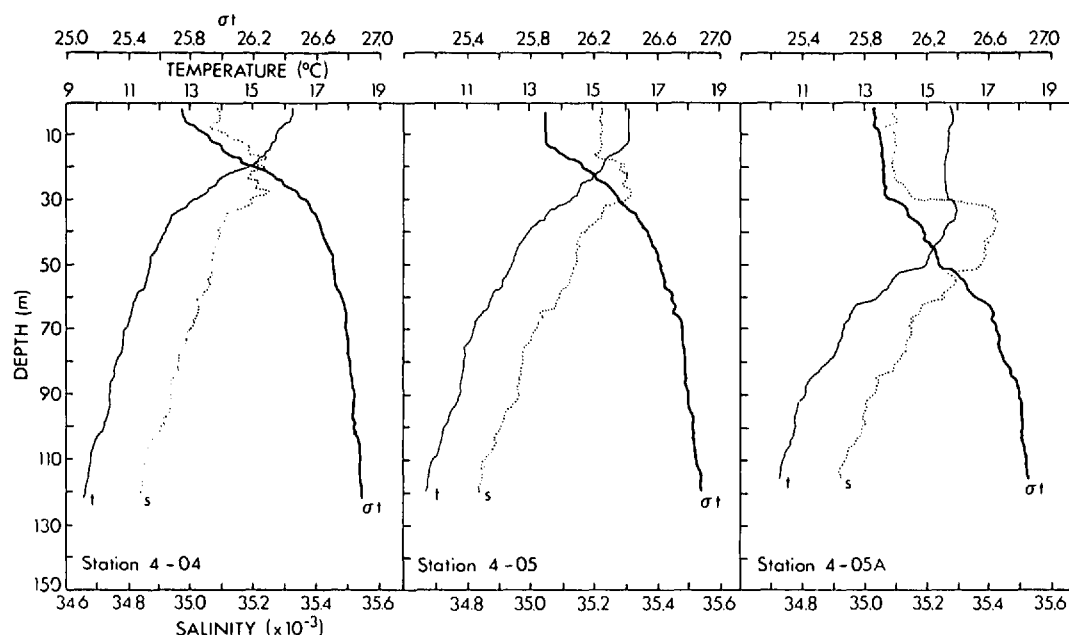
Fig. 6: Temperature, salinity and density depth profiles from three frontal zone stations, showing salinity inversions

depicted in the CTD profile at stations within and close to the front (Fig. 6). These frontal interleaving layers suggest possible regions of intensified localized mixing and exchange of properties. They have been recorded by numerous other workers as predominant features of CTD profiles through oceanic thermohaline fronts (e.g. Horne *et al.* 1978, Tang 1983). This zone is clearly very dynamic and subject to rapid change, as can be observed from the differences in vertical profiles taken at stations three hours apart in the same location (4–05 and 4–05A) — see Fig. 6. Such rapid changes effectively invalidate any assumption of observational synopticity.

Transects across the shelf can be misleading in that they are interpreted with the focus on cross-shelf gradients with little consideration for longshore effects. Current measurements clearly showed that along-shelf currents dominated the flow in this region during the cruise (Fig. 7). A strong north-flowing jet current, with speeds in excess of 90 cm·s^{-1} and extending to a depth greater than 200 m, was located seawards of the outer boundary of the front. This confirmed the existence of an equatorward coastal jet with a core located just offshore of the surface front documented by, among others, Mooers *et al.* (1978) off Oregon and Nelson (1985) off the Cape Peninsula. A second, shallower and slower jet current was associated with the inner edge of the front. These two

jets were present, although variable in location and intensity, during all transects across the front. The zones of high shear associated with the jet currents are potentially active sites for turbulent mixing across the front. Information was available from current meters moored at 32°47'S, 17°42'E, 10 km north of Station 3 (C. J. Holden, Sea Fisheries Research Institute, pers, comm.). The direction of currents measured by profiling from the ship was confirmed by these data but, as a consequence of uncertainty in the ship's drift calculations, the northward velocities may have been overestimated by some 10 cm·s^{-1} in the shipboard measurements (see Nelson [op. cit.] for discussion of the limitations of this technique).

The differential alongshore advection created a complex mosaic of water structure in cross-section, with water originating from different localities upstream, and made cross-shelf transects difficult to interpret. The area investigated was more dynamic than most other frontal systems described in the literature, for instance the Bering Sea fronts which Iverson *et al.* (1979) described as "hydrographically sluggish". Even in comparison to other upwelling fronts (Mooers *et al.* 1976, Brink *et al.* 1983), the southern Benguela front appears to be very dynamic. The pulsed nature of upwelling in the southern Benguela system is an additional dynamic feature, with contortions and irregularities developing in the
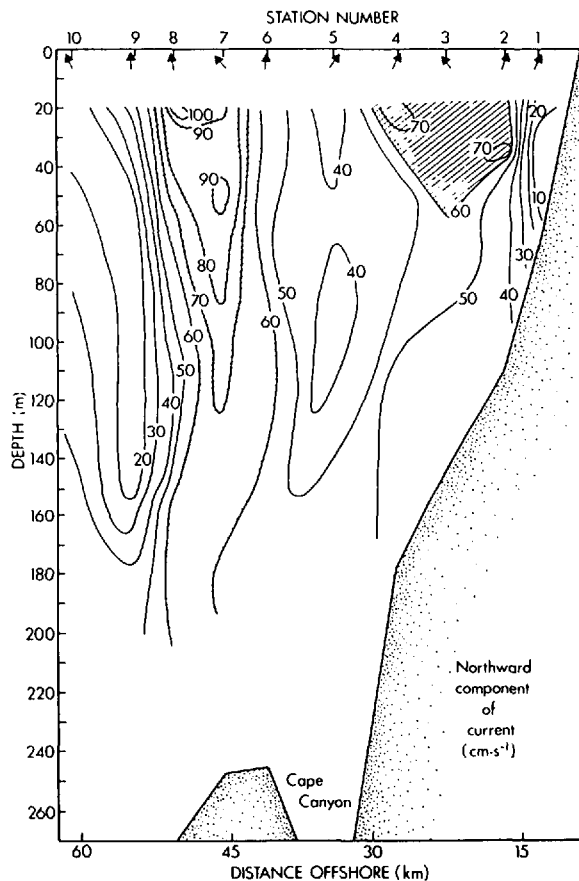
Fig. 7: Section of the northerly component of the currents measured during Leg 4 (actual directions are given by an arrow)

front during quiescent periods.

Chemical and biological aspects

Nutrients were depleted in the surface layers, the depleted layer shoaling towards the coast with slightly elevated levels at Station 4-01 indicative of recent upwelling (Fig. 8). A deviation from this trend was the increase in nitrate values observed at 10–15 m at Stations 4-05A, 4-06 and 4-07. No sharp gradient in nutrient concentrations was associated with the front. The only difference between inshore upwelled waters from which the nutrients had been recently stripped and offshore "old" nutrient-poor waters was the depth of the depleted layer (< 1 μM nitrate), which deepened beyond the front from ~10 m inshore to > 20 m offshore (Fig. 8a). The main gradient was in the vertical plane, concentrations
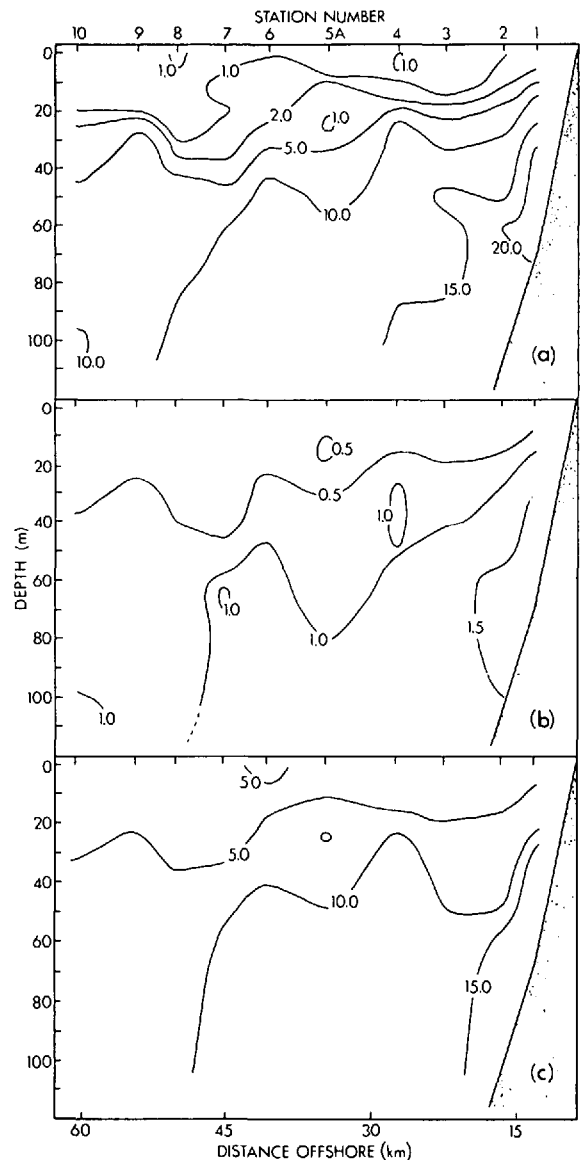

Fig. 8: Vertical sections of (a) nitrate, (b) phosphate and (c) silicate, all in μg-at$\cdot l^{-1}$ from Leg 4

increasing with depth as temperature decreased. From this static picture it is difficult to resolve whether nutrients are indeed limiting or whether they are maintained at a low level by rapid turnover, despite constant replenishment. The impact of the passage of internal waves on the structure of the water column and distributions of properties is evident in the vertical sections, notably the doming of isolines at Station 4-04 (see Figs 5 and 8). This feature suggests another possible source of mixing through
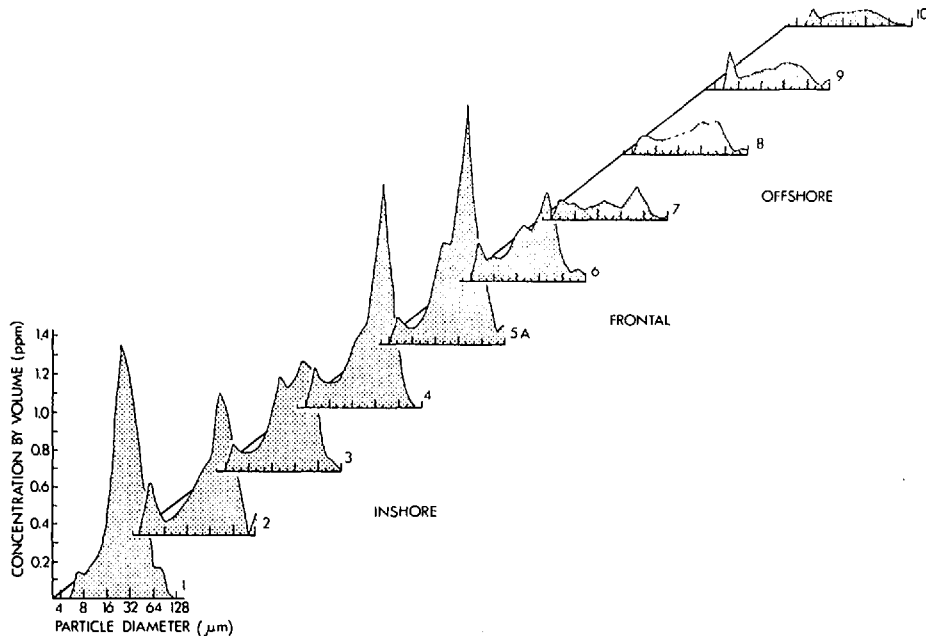
Fig. 9: Particle spectra of samples from the particle volume maximum in the water column, at stations along the transect (Leg 4)

the breaking of internal waves in the region of sloping pycnoclines (Wang and Mooers 1977, as cited by Brink 1983).

Nutrient values higher than those typical of true South Atlantic Central Water (10–18 μM nitrate, 0,8 1,5 μM phosphate and 6–15 μM silicate [Jones 1971]), were recorded at the inshore stations in the bottom mixed water (IBMW), indicative of *in situ* regeneration processes. Bailey and Chapman (1985) and Waldron (1985) have described this water body with a concurrence of opinion regarding its local formation. Water deficient in oxygen ($<$ 2m$\ell\cdot\ell^{-1}$) was not detected during this cruise but there were pockets of oxygen-depleted water (2–4mℓ O$_2\cdot\ell^{-1}$) inshore in this bottom mixed layer and in the water column at Stations 4–06 and 4–07. Highest concentrations of particulate organic carbon were measured at the inshore and frontal stations (maximum 647,7 mg C·m^{-3} at Station 4–04), declining offshore to ~100 mg C·m^{-3} in surface waters.

PHYTOPLANKTON POPULATION SIZE STRUCTURE

The different size structures of the phytoplankton assemblages along the transect are shown by particle-size spectra (Fig. 9). The particle spectra provide a convenient means of identifying the types of populations present, whether predominantly net-plankton

($>$20-μm diameter) or nanoplankton ($<$ 20 μm). At coastal and frontal zone stations (4–01 to 4 06) phytoplankton populations were dominated in terms of volume by diatoms, whereas in offshore waters diatoms were fewer and a relatively larger proportion of the population volume was contributed by nanoplankton, identified from microscopic examination as being mostly small flagellates $<$ 10 μm in diameter. The fraction $<$ 10 μm in diameter comprised, on average, 17,3 per cent (range 11,4–24,0 per cent) of the population volume at inshore and frontal stations and 32,9 per cent (range 30,8–37,2 per cent) at offshore stations.

Diatoms were most abundant in surface waters in inshore and frontal areas, but with increasing depth their concentrations declined and nanoplankton assumed relatively greater importance. This change in community structure has been observed across other fronts, where flagellates (often mainly dino-flagellates) occur in stratified water and diatoms dominate in well mixed and transitional zones between different water masses (Holligan 1981, Beardall *et al.* 1982).

PHYTOPLANKTON BIOMASS AND PRODUCTION

Both chlorophyll *a* and particle volume may be considered as estimates of phytoplankton biomass in
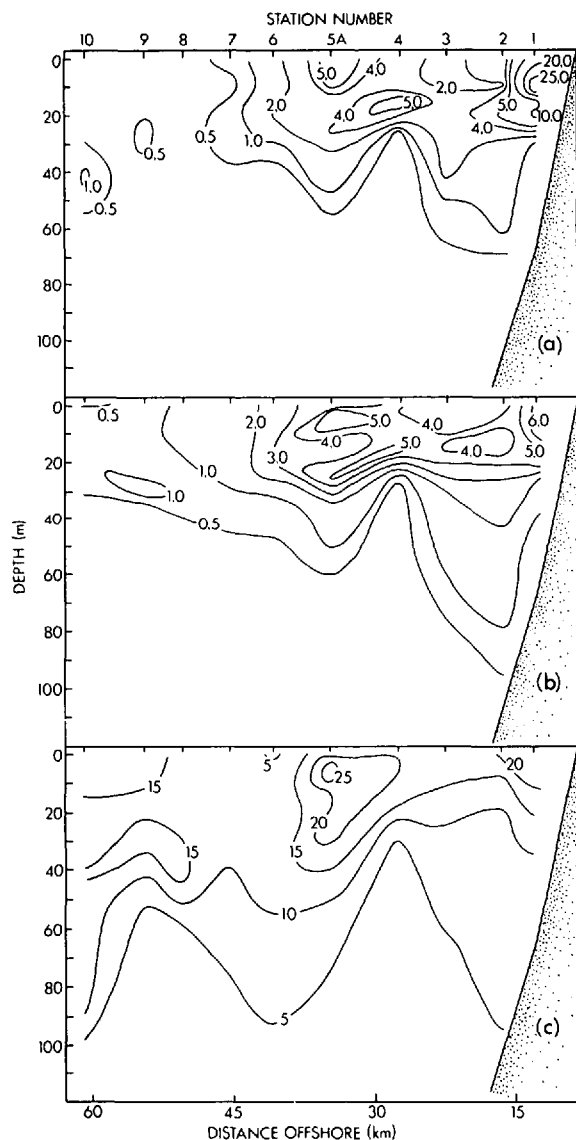
Fig. 10: Vertical sections of (a) chlorophyll a in mg·m⁻³, (b) particle volume in mm³ 10³·m⁻³ and (c) bacterial biomass in mg C·m⁻³ from Leg 4

the southern Benguela (Olivieri 1985), and their distribution along the transect was similar (Fig. 10a, b). Greatest biomass was found closest inshore at Station 4–01, where values of chlorophyll a of 25,2 mg·m⁻³ and particle volume of 6,3 ppm were recorded at 10 m, as a consequence of upwelling of nutrients into the euphotic zone. It is also possible that production can be maintained at the innermost

station through the introduction of nutrients from the IBMW by vertical mixing processes. Values of chlorophyll $a > 0,5$ mg·m⁻³ extended to about 60 m deep in the nearshore region, a possible remnant of the relaxation event. Away from the coast, concentrations declined sharply, although there was a region high in concentration of chlorophyll a (maximum 6,8 mg·m⁻³) and in particle volume (maximum 5,8 ppm) at Stations 4–04 and 4–05A. From the sections of both chlorophyll a and particle volume, two patches can be distinguished within this region, a subsurface patch extending between Stations 4–04 and 4–05A and a surface patch at Station 4–05A. The subsurface patch in phytoplankton biomass occurred within the frontal zone in an area of pronounced lateral interleaving of water types (see Fig. 5c), where potential pathways for the transference of nutrients by vertical mixing across the interfaces exist (e.g. Horne *et al.* 1978, Fedorov 1980, Tang 1983). Evidence for both turbulent and diffusive fluxes across similar boundary regions in the southern Benguela has been documented by Waldron (1985).

Offshore values of chlorophyll a were generally below 0,5 mg·m⁻³, similar to Andrews and Hutchings' (1980) mean value of 0,4–0,6 mg·m⁻³ in offshore waters. Higher values of chlorophyll a (0,5 – ~1,0 mg·m⁻³) were found in areas of potential nutrient enrichment, in a subsurface chlorophyll maximum layer which coincided with the thermocline at Stations 4–08 to 4–10, and in a zone extending 4–6 km beyond the outer edge of the frontal zone at Station 4–07. This zone of slightly elevated chlorophyll a was in an area of a high-speed frontal jet current, and shear-induced turbulence associated with this jet may have contributed to the nitrate enrichment in the upper water column at Stations 4–06 and 4–07 (Fig. 8a), thereby enhancing phytoplankton growth. This zone had large assemblages of nauplii and copepodites (see section on zooplankton), which suggests that substantial grazing pressure could have been exerted on the phytoplankton.

At all stations offshore from Station 4–01, there was a subsurface maximum layer of chlorophyll a and particle volume, which was especially pronounced at the coastal and frontal Stations 4–02 to 4–05A. It is best illustrated in the vertical section of particle volume (Fig. 10b). The depth of the maximum layer increased offshore; at Stations 4–02 to 4–07 it was between 15 and 25 m deep and at Stations 4–08 to 4–10 it lay between 35 and 40 m, following the pycnocline. Only at Station 4–05A were concentrations of chlorophyll a and particle volume in the upper 10 m higher than at 30 m, where a secondary maximum occurred; at all other stations the subsurface maximum was the water column maximum.
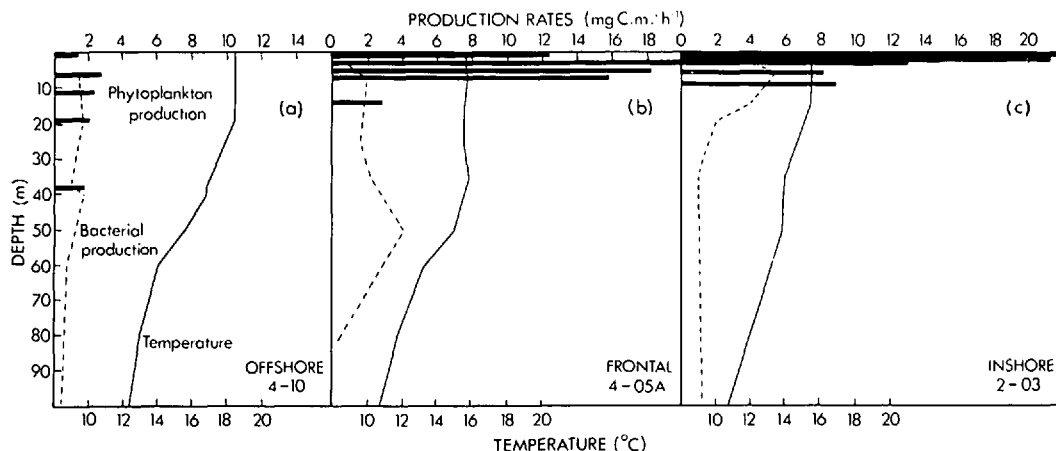
Fig. 11: Depth profiles of phytoplankton and bacterial production rates from (a) inshore (Station 2-03), (b) at the front (Station 4-05A) and (c) offshore (Station 4-10)

The subsurface chlorophyll maximum appeared to be finely balanced between vertical flux of nutrients and decreasing light availability. In offshore waters it occurred within or just above the thermocline whereas, at frontal and inshore stations where there was a less pronounced thermocline, it lay above a nutricline associated with a layer of inversions. Highest concentrations of chlorophyll a and particle volume were found at Stations 4-04 and 4-05A where the most pronounced interleaving (see Fig. 6) and presumably the greatest nutrient entrainment into the upper water column occurred.

Measurements of primary production were made in the three zones (viz. coastal, frontal and offshore) at selected stations along the transects. The depth of the euphotic zone increased with distance offshore, from 9 m at a nearshore station to 14-19 m at frontal stations and 27-38 m offshore (Table I). The highest rates of unit volume production (>20 mg $C \cdot m^{-3} \cdot h^{-1}$)

were at Stations 3-03A and 4-05A, both within the frontal zone, and at 2-03, a coastal station (Fig. 11). At coastal stations, light penetration was the major factor that limited production in the water column. For instance, at Station 2-03, although unit volume production rates were high (Fig. 11), the production integrated through the water column was relatively low (112,8 mg $C \cdot m^{-2} \cdot h^{-1}$). At the frontal stations where the highest biomass occurred, integrated production rates for the euphotic zone ranged from 80,9 mg $C \cdot m^{-2} \cdot h^{-1}$ at Station 4-04 to 258,9 mg $C \cdot m^{-2} \cdot h^{-1}$ at Station 3-03A (Table I). Lowest rates of production ($< 3,0$ mg $C \cdot m^{-3} \cdot h^{-1}$; Fig. 11) were offshore (Stations 2-07, 4-10 and 1-16), where integrated rates in the euphotic zone ranged from 27,3 to 81,0 mg $C \cdot m^{-2} \cdot h^{-1}$ (Table I). At these stations the thermocline was well developed and, as a consequence, nutrient availability in the euphotic zone was the main factor that limited primary production.

Table I: Water type, sea surface temperature (SST), 1-per-cent light depth ($D_{1\%}$), phytoplankton production rates (with mean values), chlorophyll a and bacterial production rates integrated through the euphotic zone and the percentage ratio of bacterial to phytoplankton production

Station	Water type	SST (°C)	$D_{1\%}$ (m)	Phytoplankton production		Chlorophyll a (mg·m^{-2})	Bacterial production	B/A
				A (mg $C \cdot m^{-2} \cdot h^{-1}$)	Mean (mg $C \cdot m^{-3} \cdot h^{-1}$)		B (mg $C \cdot m^{-2} \cdot h^{-1}$)	(%)
2 03	inshore	15,3	9	112,8	12,5	17,5	39,2	34,7
4 04	frontal	16,3	16	80,9	5,1	58,9		
3 03A	frontal	16,2	19	258,9	13,6	108,5		
4 05A	frontal	15,7	14	187,0	13,4	73,4	21,4	11,4
2 07	offshore	18,1	33	65,4	2,0	20,3		
4 10	offshore	18,5	38	81,0	2,1	15,5	54,5	67,3
1 16	offshore	18,0	27	27,3	1,0	13,1		

As emphasized previously, the frontal zone is dynamic and subject to rapid change. Shannon *et al.* (1985) illustrated the variability of the front from their work on satellite imagery. They found good agreement between the positions of the surface thermal and chlorophyll (colour) fronts during the upwelling season, but only occasionally did they observe elevated concentrations of surface chlorophyll associated with the oceanic thermal front (e.g. in December 1978 — Fig. 4 of Shannon *et al.* op. cit.). Numerous examples exist in the literature of high phytoplankton biomass at fronts, estuarine (e.g. Kahru *et al.* 1986), shelf-break (e.g. Herman *et al.* 1981) and tidal (e.g. Fogg *et al.* 1985), although the mechanisms and processes involved are different. Mooers *et al.* (1978) and Dengler (1985) found the most intense concentrations of phytoplankton biomass and high primary productivity just seawards of an upwelling front. In contrast, during this study the relative enhancement on the stratified seaward side of the expanded front was only slight compared with the enhancement found within the frontal zone. The fact that the upwelling front was relaxed and poorly developed could account for this apparent discrepancy in observations, with the degree and location of enhancement dependent upon the stage of the upwelling cycle. Hutchings *et al.* (1986) suggested that an anticlockwise circulation cell could facilitate the uplift of nutrients into the euphotic zone and lead to the enhanced production observed at the inner edge when the upwelling front was coincident with the shelf-break. Clearly, considerable additional exploration over the entire upwelling cycle is required.

BACTERIAL BIOMASS AND PRODUCTION

Bacterial biomass distribution across the transect showed three near-surface maxima: inshore, frontal and offshore (Fig. 10c). There was also a subsurface maximum in bacterial biomass at the offshore stations associated with the chlorophyll *a* subsurface maximum (Figs 10a, c). At Station 4–01 in recently upwelled water, bacterial growth had responded to the development of the phytoplankton bloom, probably stimulated by the exudation of photosynthetically derived dissolved organic carbon or PDOC (Jensen 1983, Smith *et al.* 1977). The high concentrations of chlorophyll *a* (maximum 25,2 mg·m^{-3}, Fig. 10a) relative to the bacterial biomass (maximum 22,9 mg C·m^{-3}) suggest that there is a lag in bacterial population development, as demonstrated in microcosm studies in newly upwelled water (Painting *et al.* 1985). At frontal stations 4–04 and 4–05, a second peak in bacterial biomass was found, coinciding with the phytoplankton patch there (Fig. 10a, b). High

ratios of bacteria : phytoplankton, and the highest bacterial biomass (30,3 mg C·m^{-3}), were observed in this mature water. The close coupling between the distributions of bacteria and phytoplankton biomass suggests a strong relationship between bacterioplankton growth and phytoplankton standing stocks. This relationship could have been stimulated either directly by photosynthate release from phytoplankton cells or indirectly from zooplankton feeding activity. Other workers have also found a good correlation between the distribution of chlorophyll *a* and bacterial biomass (e.g. Fuhrman *et al.* 1980, Fuhrman and Azam 1982).

Beyond the front in offshore waters, chlorophyll *a* declined to concentrations < 1 mg·m^{-3}, but bacterial biomass remained relatively high with a maximum of 19,7 mg C·m^{-3} at Station 4–10. The higher-than-expected bacterial biomass in these waters, on the basis of chlorophyll *a* values, may have been due to the presence of relatively high concentrations of particulate organic carbon (some 100 mg C·m^{-3}). This suggests that offshore bacteria are utilizing other dissolved organics and particulate material which may be derived from a number of sources including detritus, zooplankton excretion and so-called "messy feeding" by herbivores (Williams 1981, Joint and Morris 1982).

Depth profiles of bacterial and phytoplankton production estimates for an inshore, frontal and an offshore station are given in Figure 11. Highest rates of bacterial production were recorded in the inshore and frontal regions (maximum 5,5 mg C·m^{-3}·h^{-1} and 4,11 mg C·m^{-3}· h^{-1} respectively). The maximum rate occurred 6 m deep at Station 2–03 inshore, corresponding to a region of high phytoplankton production, but at 50 m at Station 4–05A in the front. Such high activity recorded below the euphotic zone and chlorophyll maximum at Station 4–05A was in the vicinity of a density discontinuity at the base of the thermocline (see Fig. 6) and may be indicative of a region of accumulation. Fuhrman and Azam (1982) also found fastest rates of bacterial growth below the depth of maximum photosynthesis, and they suggested that decomposition of sinking particles and also photosynthate release from physiologically stressed phytoplankton could account for the growth.

Integrated values of phytoplankton and bacterial production over the euphotic zone are given in Table I. Bacterioplankton have been shown to be dependent upon both DOC and POC as carbon sources, but they will preferentially utilize the dissolved substrate of low molecular weight (Joint and Morris 1982). Difficulty in quantifying the release of DOC by phytoplankton has led to a controversy regarding the extent of exudation of organic material by phyto-

plankton, and thus to the quantity available to the bacteria for growth. Commonly accepted values are in the range 5–40 per cent of production released as DOC (Fogg 1983), although higher values have been recorded during the decline of a bloom (Lancelot 1983). In the euphotic zone at inshore and frontal stations, most of the bacterial production can be attributed to the utilization of the PDOC released by the large actively growing phytoplankton populations in these areas. However, in offshore waters, where the highest ratios of integrated bacterial to phytoplankton production rates were recorded (Table I), the carbon requirements of the heterotrophic bacterial community cannot be met by PDOC alone, even assuming a higher percentage release. Therefore, in offshore waters, the bacteria must use particulate detrital material or non-photosynthetic sources of DOC in order to obtain sufficient carbon to sustain their production rates.

Bacterial and microbial predator-prey interactions are known to be important in the supply of reduced nitrogen to primary producers, particularly in strongly stratified systems (e.g. Williams 1981, Newell and Field 1983, Probyn and Lucas 1987), and may also conceivably play a significant role in the regeneration of nutrients within the frontal zone. However, the bacteria could also act as potential competitors with phytoplankton for a limited nitrogen source. Indications of increased heterotrophic activity in the vicinity of tidal fronts have been reported by Floodgate *et al.* (1981) and Fogg *et al.* (1985). Dengler (1985) attributed the high primary productivity measured at an upwelling front to the availability of ammonium as a nitrogen source. Unfortunately ammonium concentrations were not measured during this investigation.

ZOOPLANKTON

Mesozooplankton biomass was highly variable along the transect and with time of sampling during the transects (range 0,54–3,76 g dry mass·m⁻²). There was no obvious relationship between zooplankton distribution and the hydrographic conditions, and the only consistent feature was that zooplankton concentrations reached a maximum at the two inshore stations. Biomass data will be considered in more detail when the species composition of the zooplankton assemblages has been determined and spatial gradients in abundance at the species level assessed.

There is much literature indicating that frontal zones may support increased zooplankton populations (e.g. Owen 1981 [shelf-break front], Floodgate *et al.* 1981 [tidal front], Walsh *et al.* 1980 [upwelling front]). Some evidence is available to suggest higher

zooplankton biomass associated with the front in the southern Benguela. On further examination of the raw data summarized by Hutchings (1981), it appears that there was a peak in zooplankton in the upper mixed layer at the front after prolonged upwelling, when the upwelling front was coincident with the shelf-break (Hutchings *et al.* 1986). Pillar (1986), in analysing data from an extensive monthly sampling programme, found a significant increase in copepod biomass offshore during the upwelling season in the St Helena Bay area. From a more localized study farther south, Hutchings (1979) recorded slightly enhanced zooplankton stocks along the intense frontal zone off the Cape Peninsula. However, there are also numerous instances when no effect of a frontal zone on zooplankton biomass has been detected (e.g. Foster and Battaerd 1985, Scrope-Howe and Jones 1985). The conflicting evidence again emphasizes the necessity for investigating such phenomena over the whole range of frontal manifestations and through an entire cycle of events in order to determine when there is an effect.

Microscopic analysis of the microplankton (> 37 μm) bottle samples provided information on the distribution of the different larval stages of copepods, because these dominated the zooplankton fraction of the samples. Copepod eggs were concentrated inshore and in the upper 40 m, exceeding values of 50 eggs·l^{-1} at Stations 4–01 and 4–02 and with a second patch at 10 m at Station 4–04, but declining sharply to lower levels offshore (Fig. 12a). This distribution corresponded with that determined for phytoplankton biomass (see Fig. 10a, b), suggesting a reproductive response of female copepods to increasing food availability. Experimental studies have found copepod egg production to be strongly correlated with chlorophyll *a* concentration (Ambler 1986), and in particular chlorophyll in the size fraction > 10 μm (Peterson and Bellantoni 1987).

The distribution of copepod nauplii was quite different (Fig. 12b). Highest densities were not found inshore, but maximum concentrations (> 200 nauplii·l^{-1}) were in the vicinity of the two jet currents at Stations 4–04 and 4–07. The naupliar densities declined rapidly with depth and with distance offshore beyond Station 4–07. The inner patch at Station 4–04 was associated with the patch of phytoplankton and copepod eggs found in a region of pronounced lateral interleaving. The presence of copepod nauplii within the outer jet current suggests that both primary and secondary production could have occurred recently within this water body, with mixing processes farther south being responsible. Smith *et al.* (1986) found highest concentrations of copepod nauplii in frontal zones as opposed to non-frontal zones, particularly
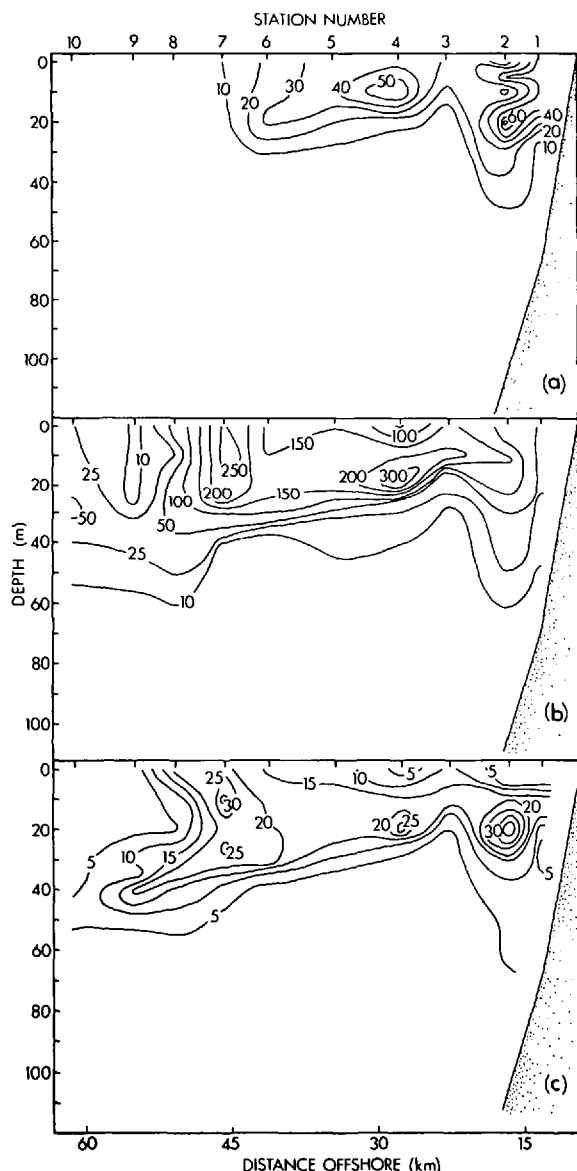
Fig. 12: Vertical sections of (a) copepod egg, (b) copepod nauplii and (c) copepodite densities, all in number·l⁻¹, along the transect (Leg 4)

during downwelling events, and they suggest that these areas were sites of enhanced secondary production. Scrope-Howe and Jones (1985) also noted that, on the two occasions when they recorded high concentrations of zooplankton within the frontal region at a tidal mixing front, they were found to be caused by large quantities of copepod nauplii. These peaks they attributed to increased secondary production stimulated by elevated phytoplankton levels at the surface.

The distribution of copepodites (mainly *Oithona* and *Paracalanus* species in the present samples) reflected the distributions of eggs and nauplii to differing degrees; an inner patch corresponding to the location of the high egg densities inshore, a middle patch at Station 4-04 and a third patch coinciding with the elevated nauplii densities at Station 4-07 in the jet current, which extended offshore along the thermocline (Fig. 12c). These maxima were all sub-surface and associated with the chlorophyll *a* sub-surface maxima.

ICHTHYOPLANKTON

Distinct changes in species composition of the ichthyoplankton community occurred along the transect and with depth (Fig. 13a, b). In the warm offshore surface waters beyond Station 4-06, pelagic fish larvae (anchovy *Engraulis capensis*, pilchard *Sardinops ocellatus* and round herring *Etrumeus whiteheadi*) constituted more than 90 per cent of the total population of fish larvae. The offshore extent of these larvae was not determined during this transect, but there was an indication that densities were declining at the outermost station. Maximum densities in excess of 1 400 larvae·100 m⁻³ of these three species alone were recorded in the region of the outer jet current (Station 4-08). This fact supports the hypothesis of Shelton and Hutchings (1982) that frontal jet currents are important for transporting pelagic fish larvae from spawning to recruitment areas. Copepod nauplii and copepodites were abundant in the area (Station 4-07, Fig. 12b, c), providing a food supply for the developing larvae.

Fish eggs of the same pelagic species were distributed closer inshore than the larvae, maximum egg densities being recorded in the frontal zone (Fig. 13b). Below the thermocline offshore, and inshore of Station 4-06 throughout the water column, lightfish (*Maurolicus muelleri*) larvae were dominant in the larval fish assemblage, except at Station 4-01 where sparid fish larvae predominated (Fig. 13a). Other fish eggs, predominantly of lightfish, were most abundant in the surface water at frontal stations. Similar observations of high concentrations of fish eggs and larvae around frontal boundaries have been reported elsewhere (Scrope-Howe and Jones 1985, Richardson *et al.* 1986), and such findings highlight the possible importance of these zones for larval survival.
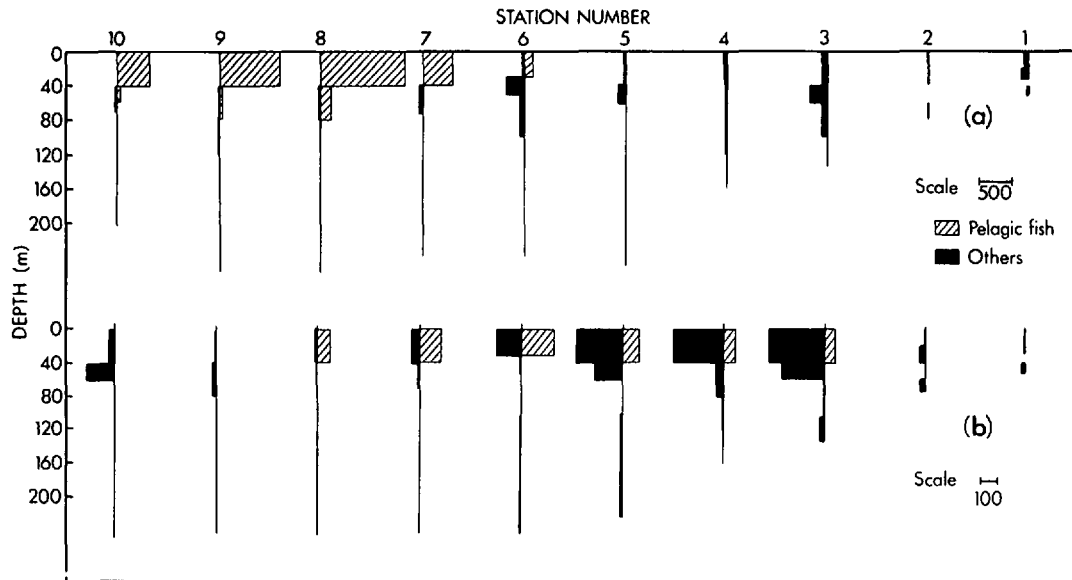
Fig. 13: Vertical distributions of (a) fish larvae and (b) fish eggs, in number·100 m^{-3}, along the transect (Leg 4)

CONCLUSIONS

The Cape Columbine upwelling front investigated during December 1984 was a relatively broad, diffuse feature following a period of quiescent conditions. Recent water movements and evidence of lateral interleaving between water types were distinguishable from the salinity structure. Distinct relationships were observed between the various components of the biota and hydrographic features and related water types, thereby implying that physical processes are the dominant factors controlling plankton distribution and heterogeneity.

Phytoplankton biomass was at a maximum at the innermost station with a secondary peak within the frontal zone, where highest rates of production were measured. Cross-front mixing and entrainment processes associated with the interleaving layers in the vicinity of the weakened frontal structure may be important mechanisms in enhancing phytoplankton growth in this maturing water body.

Bacteria and zooplankton responded to the stimulated phytoplankton production with elevated levels of bacterial biomass and with copepod eggs and nauplii coinciding with peaks of chlorophyll.

The distributions of diatom/nanoplankton ratios and ichthyoplankton reflect the contrast between inshore/frontal and offshore waters, the transition corresponding to the position of the temperature/density front. However, caution must be used in the interpretation of cross-shelf gradients because the predominant flow-field was in the longshore direction and was associated with pronounced jet currents, creating a mosaic of water from different origins upstream. Some of the cross-shelf distributions reflected this differential longshore advection. Copepod nauplii and copepodites were concentrated in the strong jet current along the outer edge of the front, suggesting that enhancement and mixing processes farther south could have been responsible. Such a relationship could have major implications for the survival of pelagic fish larvae occurring there.

The results presented provide new insights into the question of the importance of the frontal zone to the trophic dynamics of the region and they suggest avenues of future research. Certainly, considering the dynamic nature of the region and the difficulty in making effective measurements, it is essential that further investigations employ more synoptic and rapid-sampling techniques (preferably underway devices) in a three-dimensional study to cover alongshore gradients and to encompass all phases of the upwelling cycle. Only then can the biological and physical processes operating within the front be better understood.

ACKNOWLEDGEMENTS

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