Fish spawning strategies in the variable southern Benguela Current region

by

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Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Cape Town

To my friend Larry who inspired this study throughout, to my family Lynette, Jeremy and Matthew for love and understanding whilst it was being undertaken, and to my parents Gwen and Alfred for sacrifice and encouragement from the beginning.

DECLARATION

I hereby declare that this thesis to a large extent represents my own work, both in concept and execution. The initial data collection was carried out over 12 cruises of about 12 days each between August 1977 and August 1978. I participated in many of these cruises, mostly in the position of Chief Scientist. Analysis of data and samples collected at sea for temperature, salinity, chlorophyll and surface drift were routinely conducted at the SFRI Physical/Chemical Laboratory. Dr L. Hutchings and Dr V. Shannon, who acted as Project Co-ordinators, undertook preliminary analysis of the chlorophyll and temperature data at regular intervals during the project. I had complete responsibility for all ichthyoplankton sampling and analysis. Sorting of samples for fish eggs and larvae was undertaken by a technical team over a 7 year period under my direction. Section 1.3, "The influence of large-scale environmental processes on neritic fish populations in the Benguela Current system", is a published co-authored paper read by invitation at the 1984 CalCOFI meeting in California. Mr Boyd was responsible for the description of the physical oceanography in the northern Benguela region and contributed considerably to the remaining sections. Dr Armstrong carried out most of the simulation modelling and the description of the results obtained. Section 3.1, "Spatial and temporal distribution of chlorophyll in southern African waters as deduced from ship and satellite measurements and their implications for pelagic fisheries", is a second published co-authored paper included as part of this thesis. I wrote the section on the implications for fisheries and had minor input in the rest of the paper. In all other respects I lay claim to uncited ideas, concepts, hypotheses or conclusions contained in this thesis.

Signed by candidate

25-8-86

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ACKNOWLEDGEMENTS

In the initial planning stages the Cape Egg and Larval Programme (CELP) benefitted from the chairmanship of Dr G. Newman and the expert input of Drs Shannon, Hutchings and De Decker. Members of the SWA group, particularly Dr O'Toole and Mr King brought valuable experience to bear on the early discussions. The technical group under the management of Mr Robertson, particularly Messrs Crous, Kriel, Horstman, Alexander, Cooper, Wehmeyer, Van der Westhuizen, Jeenes, Giddey and Ms Illert played a major role in the project. A large body of technical assistants moved through the sorting laboratory over the years when analysis was underway and some left a bigger mark than others. In particular the hard work by Messrs Giddey, Hart and Ms Herbet, Ms Ford, Ms Dirker and Ms Lewis is strongly appreciated. For the most part the sorting team was supervised by Mr J. van der Westhuizen. Some colleagues became closely involved in the identification of larvae and the hard work in this regard undertaken by Messrs Van der Westhuizen, Jeenes, Prosch and Ms Davies is thankfully acknowledged. Most of the artwork was carried out by Ms S. Wright. Dr V. Shannon provided wise council and germs of ideas on many occasions and Drs Crawford and Armstrong patiently allowed me to discuss many of my more esoteric ravings with them. Dr C. Brownell advised on the identification of some fish eggs. Mr C. Holden advised on the methodology for calculating surface Ekman velocity vectors. Senior Management at SFRI, including Mr Stander, Drs Newman and Botha and Mr de Villiers provided solid encouragement throughout. American friends associated with the Southwest Fisheries Center and Pacific Fisheries Environmental Group of the National Marine Fisheries Service are thanked for freely discussing their ideas with me. In particularly Dr P. Smith provided much advice in the early stages and Dr G. Moser and his group assisted with the identification of some problematical taxa. The finanacial support of the Fisheries Development Corporation is highly appreciated. I am indebted to my supervisor, Prof J. Field, for the steady hand he placed on this study and the wise counsel he provided throuthout. I am particularly greatful to Dr L. Hutchings who, from my earliest days at SFRI, has inspired, directed and encouraged much of my actions and thinking regarding the early life history of fish.

ABSTRACT

A 120 station grid was surveyed at monthly intervals in the southern Benguela Current system between August 1977 and August 1978. Plankton was collected at each station by means of a double oblique tow behind the ship at 2 knots down to 100m or 5m off the bottom. Plankton displaced volume was determined and all fish eggs and larvae were removed and identified to the lowest possible taxon. Water samples were collected at each station by means of 5 litre bottles from 5 depths down to a maximum depth of 75m. Microplankton (37–100 μm fraction) particle concentration, chlorophyll concentration and salinity were determined from the samples. A vertical temperature profile was obtained at each station using a bathythermograph. Twenty plastic drift cards were released at each station and recoveries plotted. Wind measurements were made on board the ship and also obtained after the cruise from land sites at Cape Point and Cape Columbine. After August 1978, the CELP grid was resurveyed in November 1978, November 1981 and November 1982. In November 1979 and November 1980 a number of stations were sampled in the vicinity of the Cape Peninsula to determine the vertical abundance pattern of anchovy eggs. In November 1983, 1984 and 1985 a much larger portion of the southern Benguela Current system was surveyed to determine the spawner biomass of anchovy using the egg production and acoustic methods. In these surveys anchovy eggs were sampled by means of a vertical tow with a CalVET net and at some stations on the Agulhas Bank the vertical abundance of anchovy eggs was sampled using a multiple opening and closing RMT sampler. The ichthyoplankton and environmental data were interpreted to reveal any similarity in pattern. Anchovy, hake and laternfish were selected for special attention because of their different spawning strategies, and were shown to have seasonal and spatial patterns of egg and larval abundance which could be related to the environment. The major environmental process influencing ichthyoplankton abundance patterns appeared to be the seasonal advection of warm western boundary current water into the system from late spring to early autumn, causing the development of a temperature front along the west coast and a thermocline over the Agulhas Bank. Plankton standing stocks were elevated between the front and the coast and in the thermocline. In order to place their spawning strategies into perspective, a simulation model was used to explore the performance of anchovy, hake and lanternfish life history strategies in filtering out environmental variability. Results suggested that anchovy and hake are adapted to cope with variability whereas lanternfish are less well adpated, and therefore spawn in winter when the system is most homogeneous. Conclusions are drawn as to the kinds of environmental anomalies likely to cause poor year class strength in the three species.

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1 INTRODUCTION

1.1 Background to this study

The objective of the Cape Egg and Larval Programme (CELP) was "to gain knowledge on the composition, distribution, and temporal variability in the ichthyoplankton in the survey area and the relationship between this and the environment" in order to "lead to a better understanding of the mechanism of recruitment of important fish species" (SFRI, unpublished document). Implicit in this objective was that a one year study, conducted from August 1977 to August 1978 in the southern Benguela Current region (Fig. 1.1) would isolate environmental factors, the monitoring of which would prove useful, either singly or in combination, for predicting year class strength of important fish stocks. This theme was accentuated, both during the survey and subsequently, under the influenced by a number of empirical studies which showed relationships between fish year class strength and various environmental parameters in other systems (e.g. Nelson et al. 1977, Parrish and McCall 1978, Boyd 1979).

In planning the survey, insufficient thought was given to the difference in the amount of time required to process physical data compared to plankton data, with the result that while most of the physical data was available for interpretation by the end 1978, it was not until the end of 1984 that processing of the ichthyoplankton had been completed and combined interpretation of both physical and plankton data sets could be undertaken. While preliminary analysis of the temperature data was carried out by Shannon (SFRI, unpublished MS) and the chlorophyll data by Hutchings (SFRI, unpublished MS), this thesis represents the first comprehensive interpretation of all the data collected during CELP.

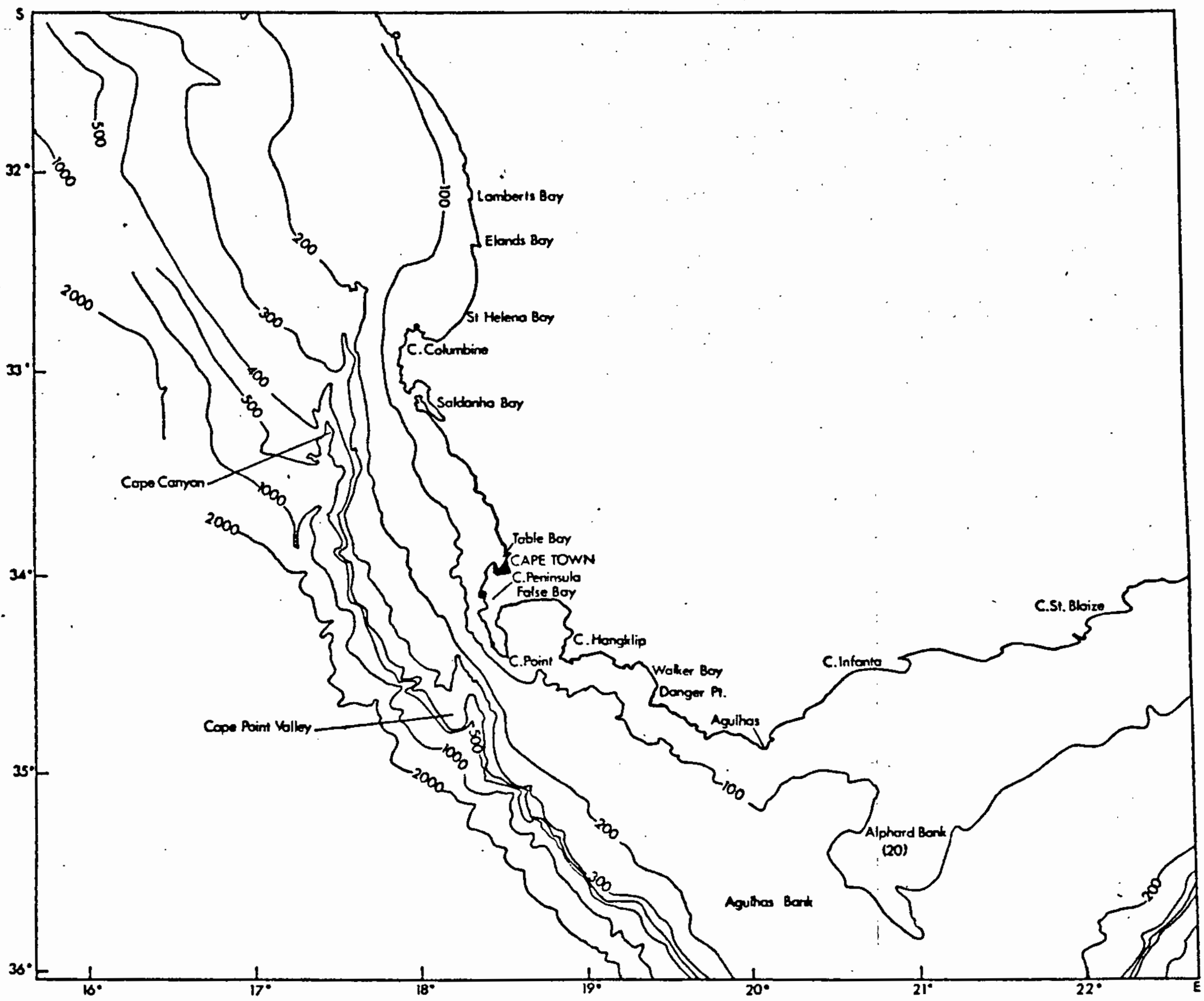

Fig. 1.1 The CELP study area within the Benguela Current system, showing the topography (depth in metres) and main place names.

1.2 Spawning and recruitment

Marine fish typically reproduce by means of spawning large numbers of spherical eggs less than 2mm in diameter which rapidly hatch into small larvae, and then develop more slowly into juvenile forms, and finally recruit into the adult population. Species differ with regard to the length of the egg phase and to the level of development reached within the egg before hatching. Except for a few marine species which give birth to well developed progeny and omit the egg stage altogether, or which attach their eggs to the substrate, the reproductive products are initially totally planktonic.

Since large numbers of eggs are produced, mortality must, by implication, be high between the egg stage and maturity, as only two progeny need, on average, to survive to maturity during the entire life span of each female, assuming an equal proportion of males and females, in order to replace the population. Part of this mortality is independent of the population density and part varies as a function of population density. Density-dependent mortality may be expected to be highest shortly after spawning before the eggs disperse in the plankton, or later on when fish group in schools or in favoured habitats. In addition to mortality, the initial number of progeny produced by the parent population may also vary in a density-independent or -dependent manner. The existence of a density-dependent or compensatory response forms the conventional theoretical basis for sustained harvests of wild fish populations, whereas density-independent variability may explain why high levels of sustained harvesting have seldom been achieved for extended periods. In order to rationally harvest wild fish populations in a prescriptive manner, it is therefore desirable to understand both components of variability and adjust harvest rates accordingly.

Thus a major objective in research for fisheries resource management is to understand the environmentally induced (or density-independent) variability in recruitment, firstly so that the underlying density dependent functional response can be revealed (Shepherd et al. 1984), given adequate measurements of spawner stock size and recruitment, and secondly so that the residual variance can be predicted on the basis of environmental monitoring. It has been argued (e.g. Smith 1985) that until effective predictions of recruitment strength are available, resource management must rely, especially in the case of short-lived clupeoid populations, on assessments of stock size and direct estimates of recruitment. Walters (1984) proposes that since climatic factors are largely unpredictable, a probability distribution is likely to be more useful than a single prediction of recruitment. In some instances environmental variability may be dominated by low frequency, autocorrelated fluctuations at the time scale of decades which may allow more useful prediction in fisheries management (Shepherd et al. 1984). This is given some consideraton in Section 1.3. Walters (1984) points out that in order to establish the credibility of a probability distribution for future variations it will be necessary to look at historical patterns of variation, and that this probability distribution can be used without making any special assumptions about causality. Despite the arguement of Walters (1984), considerable research effort is being channeled into studies of the causation of recruitment variability in fish (e.g. Bakun et al. 1982) with the objective of determining the underlying density dependent population response and predicting the residual variance.

Mechansims that have the potential to cause recruitment variability have been reviewed in the context of eastern boundary currents by Bakun and Parrish (1980), and in the context of clupeoids by Smith (1985). Bakun (1985) presented a useful summary table which is repeated as Table 1.1 in this Section.

Table 1.1

Some hypothetical controls on surivival of early life stages of fishes (from Bakun 1985)

I Starvation hypotheses
- Turbulent mixing of fine scale food particle strata
- Low productivity of the system
- Wrong type of food organisms
- Dispersion of food due to divergent flow pattern
- Mismatch with seasonal food succession caused by anomalies in growth rate

II Predation hypotheses
- Incidence of small planktonic predators
- Incidence of large planktonic predators (e.g. coelenterates)
- Incidence of predatory adult fish
- Incidence of predatory larval fish
- Variations in growth with size-dependent predation

III Advection hypotheses
- Offshore transport (removal of drifting larvae from favourable habitat)
- Onshore transport (exposure of larvae to damage in surf zone, etc.)
- Disruption of normal current patterns to which reproductive habits are tuned

IV Physiological stress hypotheses
- T, S or O_2 conditions are not within physiological range
- Effects of environmental pollution

V Disease hypotheses
- Infectious outbreaks, etc.

Examination of recruitment data sets shows that the frequency distribution is approximately log-normal (Hennemuth et al. 1980, in Shepherd et al 1984). It follows from the Central Limit Theorem that this kind of distribution will result when a number of different factors act multiplicatively to determine survival, and therefore recruitment is unlikely to be the result of only one of the factors listed in Table 1.1, but rather of a number acting at different times during the early life history stages. In keeping with this idea there has been a tendency to build multiple linear regression models to predict recruitment from spawner population size and varying numbers of environmental variables similar to those listed in Table 1.1 (e.g. Nelson et al. 1977, Parrish and MacCall 1978). While a number of these regressions have been able to explain significant amounts of the variability in the fitted data sets, they have seldom provided useful predictions for management. This is not unexpected, not only because of the probable complexity of the processes determining recruitment, but also because fish adapted to a specific range of environmental variability are likely to show highly nonlinear responses to both positive and negative anomalies.

In most instances the underlying density dependent population response in fish populations is obscured by the environmentally caused variability and by error in both the measurement of recruitment and spawner stock size. MacCall (1980) has estimated that as little as 10% of the variation in mortality rate in the northern anchovy could be attributed to density dependent as apposed to environmental causes. Error in the estimation of spawner stock and recruitment are seldom reported in the literature. The fitting of stock-recruit curves to data series subject to environmentally induced variability and measurement error cannot even be guaranteed to provide poor, but unbiased, estimates of the functional responses. For example Walters and Ludwig (1981), Walters (1985) and Shelton et al. (1985, see Section 1.3) and Armstrong and Shelton (in prep.) have shown that random errors in the measurement of stock size, correlations between deviations and subsequent levels of recruitment and autocorrelation in the deviations may be serious sources of bias. Thus the prediction of recruitment on the basis of spawner stock size alone is unlikley, especially in the case of clupeoids, to be very useful in the context of fisheries management.

Most time series of recruitment estimates do not differentiate between error associated with the estimate and actual variance in recruitment strength due to combined density-dependent and -independent effects. In Beddington and Cooke (1983) the variance of the logarithm of recruitment strength is given for 61 fish stocks, including Clupeiformes, Pleuronectiformes, Gadiformes and Perciformes.

Log variances range from 2.84 for the Georges Bank stock of Melanogrammus aeglefinus (haddock) to 0.07 for a number of other stocks. A variance of approximately 0.12 corresponds to a range in recruitment of about half to double. Beddington and Cooke (1983) warn that the values are only an approximate guide to the level of variability in recruitment as at least 20 successive years of mutually independent recruitment values would be required to estimate the S.D. within a factor of two. Many of the estimates are derived from cohort or virtual population analyses and the assumptions in some of these analyses may lead to underestimates of variability. For example, the estimate of the variance in the log of recruitment for the anchovy population in the southern Benguela Current region of 0.1, based on virtual population analysis, is estimated using a single age key, a constant for natural mortality and various simplifying assumptions about terminal fishing mortality.

Thus in many populations the true recruitment variability can only be guessed at. Since fish are presumebly adapted to the environment which they inhabit, it is likely that in most instances environmental variability is at least partly filtered out as a result of life history adaptations, and that the variability in population size is less than that of the environment. However, since it is impossible for fish to be adapted to the complete power spectrum of environmental variability in the ocean, certain perturbations in the environment may not be filtered out and may indeed be amplified by the population. The monitoring of variability in the environment to which a fish population is not adapated will be of significance to fisheries management whereas monitoring environmental variability which is treated largely as "noise" by the fish population is unlikely to be of much use. Therefore a comparison of the temporal and spatial patterning of environmental variability with the life history characterstics of the species may be more important than determining small scale causal relationships. In the following section (1.3) some progress is made in this direction by examining the possible influence of large-scale, low frequency environmental variability on fish populations within the Benuela Current system. This study uses data additional to that collected during CELP and to some extent provides a broader background against which to view the patterns of environmental variables and plankton abundance described and discussed in the subsequent sections.

1.3 THE INFLUENCE OF LARGE-SCALE ENVIRONMENTAL PROCESSES ON NERITIC FISH POPULATIONS IN THE BENGUELA CURRENT SYSTEM

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ABSTRACT

Environmental variability in the Benguela eastern boundary current system appears to result from variability in mesoscale processes like upwelling, as well as from lower-frequency variability forced by periods of alternate stronger and weaker advection of warm tropical or subtropical water. Warm events can be more extensive in the northern region, where the seasonal advection occurs during an upwelling minimum. In the south the concurrent seasonal effect of warming and maximum upwelling may inhibit extensive warm events. The effects of SST anomalies on fish populations within the area indicate that moderate advection of warm water may be advantageous, whereas exceptionally strong warming may cause diminished reproductive success. High-frequency variability can be incorporated into fish population models as a stochastic term in order to evaluate the risk associated with alternative management strategies, but these models have no predictive value. Fish populations like the anchovy seem buffered against high-frequency variability. If environmental variability affecting recruitment is autocorrelated, it will modulate the central tendency of the recruitment, and the appearance of stock-recruit scatter will vary in a manner dependent on the fishes' generation time and the biomass growth pattern. A population like the anchovy will track the autocorrelated signal and be susceptible to depletion, particularly under a constant catch policy.

RESUMEN

La variabilidad ambiental en el sistema de la Corriente de margen oriental de Benguela parece ser el resultado de la variabilidad de procesos de mesoescala tales como afloramientos, así como de la variación de baja frecuencia causada por períodos alternos de fuerte y débil advección de aguas cálidas tropicales o subtropicales. Los eventos cálidos pueden ser de mayor envergadura en la región norte, donde la advección estacional ocurre durante los períodos de mínimo afloramiento. En el sur, el efecto estacional conjunto del calentamiento y el afloramiento máximo pueden inhibir eventos cálidos extensos. Los efectos de las anomalías térmicas superficiales sobre las poblaciones de peces locales indican que advecciones moderadas de aguas cálidas pueden ser beneficiosas, mientras que calentamientos muy pronunciados pueden provocar disminuciones en el éxito reproductivo. Las variaciones de alta frecuencia pueden ser incorporadas en los modelos poblacionales de peces en la forma de una variable estocástica con el fin de evaluar el riesgo asociado con estrategias de manejo alternativas, pero estos modelos carecen de valor predictivo. Las poblaciones de peces como la anchoveta (*Engraulis capensis*) parecen estar protegidas contra la variabilidad de alta frecuencia. Si la variabilidad ambiental que incide sobre el reclutamiento está autocorrelacionada, ello modelará la tendencia central del reclutamiento en función del tiempo de generación del pez y de las características del aumento de la biomasa. Una población como la anchoveta se guiará por la señal autocorrelacionada y será susceptible de agotamiento, especialmente en condiciones de una política constante de captura.

INTRODUCTION

The Benguela eastern boundary current region (Figure 1) has yielded large catches of pilchard (*Sardinops ocellata*), horse mackerel (*Trachurus trachurus*), mackerel (*Scomber japonicus*), hake (*Merluccius capensis/paradoxus*) and, more recently, anchovy (*Engraulis capensis*) (Butterworth 1983; Crawford et al. 1983). In most instances peak catches appear to have followed the entry of a number of good year classes into the fishery (Figure 2), and have not been maintained during subsequent population downswings. This pattern of recruitment variability may be related to the influence of large-scale climatic events rather than to mesoscale, intra-annual processes like upwelling.

The influence of large-scale, low-frequency climate variability on fish populations has been considered by a number of authors (Iles 1973; Soutar and Isaacs 1974; Cushing and Dickson 1976; Cushing 1978; Smith 1978; Lasker 1978; Caddy 1979; Bernal 1981; Chelton et al. 1982; Kawasaki 1983), and convincing supporting evidence has been presented. In turn, mesoscale (within season) variability in coastal dynamic processes has been successfully related, retrospectively, to fish population variability over short

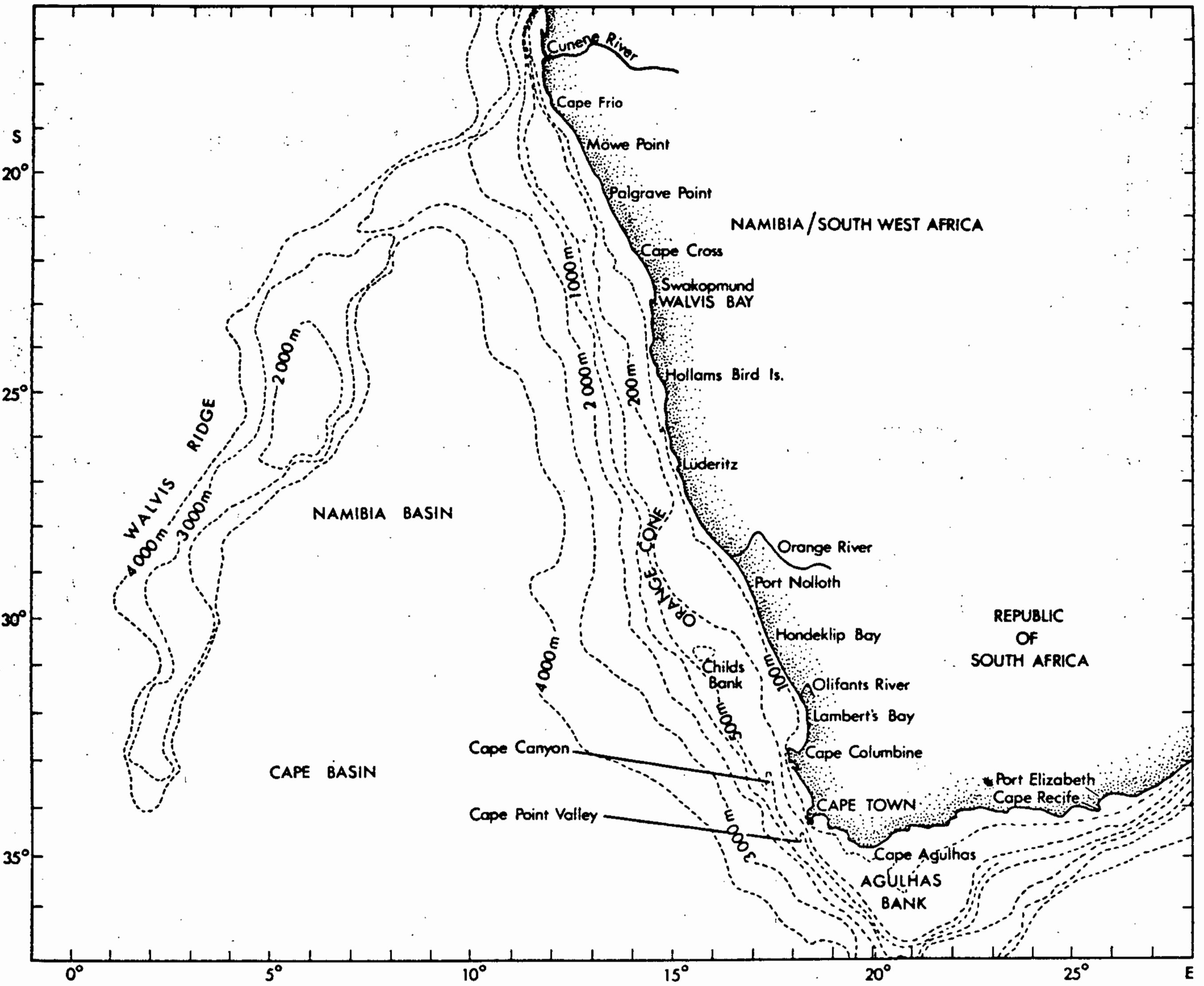

Figure 1. Bathymetry of the Benguela eastern boundary current region.

time periods for various fisheries (Parrish and MacCall 1978; Nelson et al. 1977; Schaaf 1979; Boyd 1979) although Hutchings and Nelson (in press) found no clear relationship between upwelling processes and pelagic fish population size variations in the southern Benguela region. There are few comparisons of the various scales of forcing on marine biota and even fewer occasions of successful forecasting.

Different scales of variability have important implications for fish population dynamics and consequently for management. It is relatively easy to incorporate a high-frequency component as stochastic recruitment variability into a model in which recruitment is functionally related to spawner stock size or egg production. This approach is valuable for demonstrating the dangers inherent in deterministic modeling and for comparing the risks associated with different harvesting strategies (Beddington and May 1977; Armstrong 1984), but it has no predictive value. In contrast, incorporating low-frequency variability into population models may allow some short-term prognosis based on the current position in the cycle, provided the underlying density-dependence of stock productivity has been elucidated.

In this paper, aspects of the average seasonal large-scale pattern of physical and biological processes in the Benguela region are described, and large-scale environmental anomalies are related to variability observed in neritic fish populations. The possible effect of an autocorrelated signal on the dynamics of fish populations is considered, by means of a theoretical model.

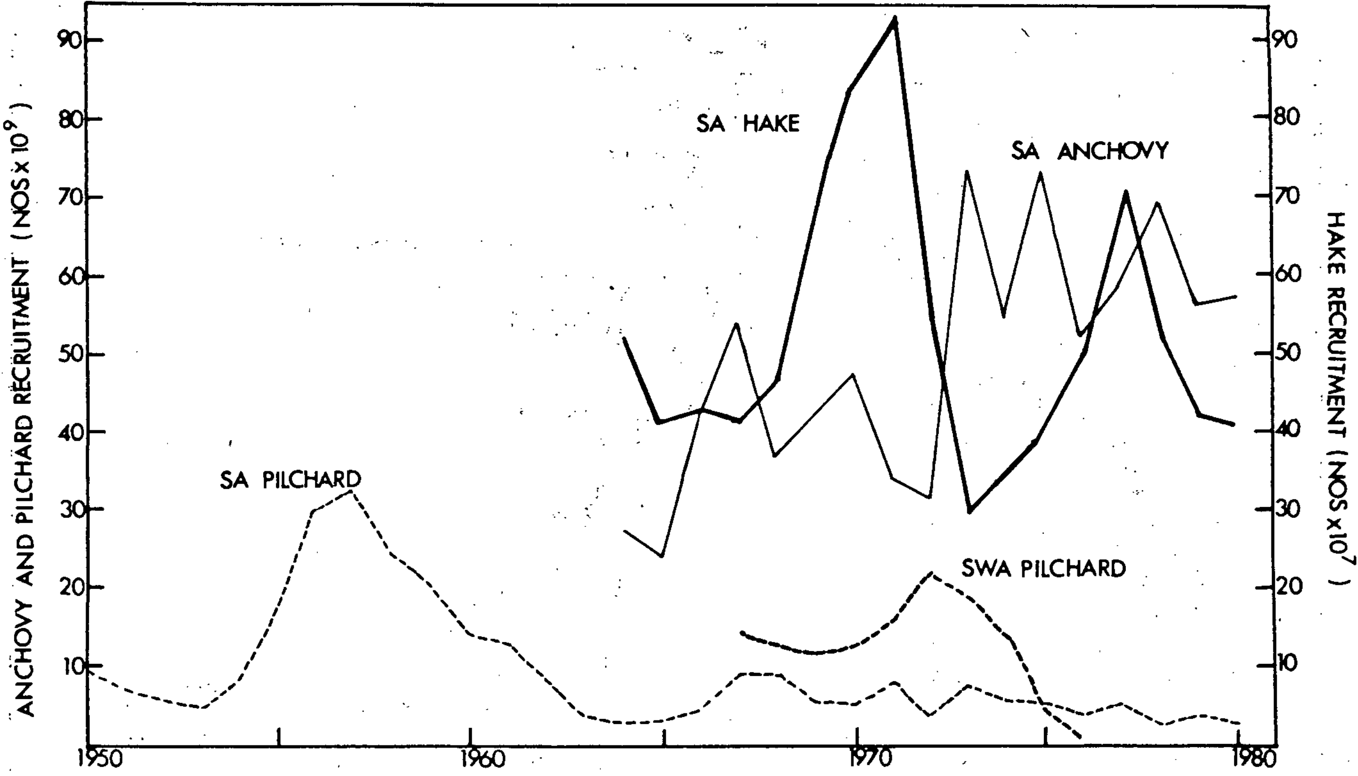

Figure 2. Recruitment calculated by cohort analysis for a number of neritic fish populations inhabiting the Benguela system.

SYSTEM DESCRIPTION

System Boundaries

In general terms, the Benguela is a cool, eastern boundary current, with equatorward flow at the surface, off the west coast of southern Africa. The longshore boundaries are formed by warm water of subtropical/tropical origin to the north *and* south, in contrast to other eastern boundary current regions, whereas the offshore boundary is formed by a circulation of warm subtropical water associated with the South Atlantic Gyre (Hart and Currie 1960; Shannon 1966). Bang (1971) adds the interesting but arguable caveat that the Benguela Current is the area east of the offshore divergence within which processes are dominated by short-term atmospheric interactions rather than longer-scale climatic influences.

The cool surface waters of the Benguela Current originate by upwelling of South Atlantic central water from depths generally between 100 and 300 m (Stander 1964; Shannon 1966). In contrast to the eastern boundary currents off the Americas (Chelton et al. 1982), these surface waters are not contributed to by surface advection of cool water from higher latitudes. The migratory nature of the offshore boundary is generally acknowledged (Shannon 1966; Bang 1971), and large, stationary eddies extending up to 500 km offshore are a feature of satellite imagery (Van Foreest et al. 1984).

Both the warm, western boundary Agulhas Current in the south and the warm Angolan water to the north form mixing areas of variable extent (O'Toole 1980; Nelson and Hutchings 1983) and are loci for the spawning of a number of neritic fish species. Pelagic eggs and larvae in the Benguela may drift substantial distances from the site of spawning as a result of mixing or transport (Shelton and Hutchings 1982). Stock separation in fish species may require distinct larval retention areas (Iles and Sinclair 1982); Badenhorst and Boyd (1980) and Boyd and Hewitson (1983) have presented evidence from anchovy larval distribution compatible with a southern retention area for anchovy extending as far north as Lüderitz. Catch-based information indicates anchovy recruitment epicenters in Walvis Bay and St. Helena Bay (Crawford et al. 1983; Crawford 1980). The Lüderitz region, a site of intense perennial coastal upwelling, lies between these two epicenters. Larvae must also be retained within the Agulhas Bank region in significant numbers, because juvenile anchovy and pilchard are eaten by inshore predators in the vicinity of Algoa Bay (Batchelor and Ross 1984); however, the relative strength of recruitment to the east of Cape Town has not been assessed.

Topography

The most striking difference between the Benguela region and other eastern boundary current regions is the termination of the land mass at a relatively low latitude, resulting in an overall convex shape in the south (Figure 1). These features allow easterly moving cyclones an unimpeded passage south of the continent (Nelson and Hutchings 1983), and the penetration of warm western boundary current Agulhas water onto the west coast under certain conditions, particularly in summer and early autumn (Shannon 1966). This latter feature is unique among eastern boundary current regions.

The bottom topography is characterized by a double shelf break over much of the coast, with strong gradients in the vicinity of the 100-m to 200-m and beyond the 500-m contours (Figure 1). The inner shelf is relatively wide in the vicinity of the Orange River (Orange River Cone), and to the southeast of Cape Town over the extensive Agulhas Bank; at these places the double break largely disappears. Off the Cape Peninsula (on which Cape Town is situated), Cape Columbine, Hondeklip Bay, Lüderitz, and Cape Frio, the 200-m contour lies particularly close to the coast, and a steep bottom slope occurs. Off Cape Columbine and the Cape Peninsula the outer break is contorted into the Cape Canyon and Cape Point Valley, respectively.

The general flow of the Benguela is considered to be topographically steered (Nelson and Hutchings 1983), with regions of enhanced flow resulting from baroclinic jet currents associated with regions where the shelf break is particularly steep (Bang and Andrews 1974). Shannon et al. (1981) have suggested that the Cape Point Valley may act as a conduit for cold water entering the system, and the Cape Canyon off Cape Columbine may have a similar role. The narrowing of the shelf at a number of localities along the coast coincides with areas of enhanced upwelling activity (Nelson and Hutchings 1983), particularly at Cape Frio, Lüderitz, Hondeklip Bay, Cape Columbine, and the Cape Peninsula.

Climatic Influences

The main climatic influences on the system are the South East Atlantic high-pressure anticyclone, which lies off the west coast of southern Africa causing perennial equatorward winds over the Benguela region north of 32°S, and the eastward-moving cyclones to the south of the continent. The possible influence of the Indian Ocean High on the Benguela system has not been investigated in any detail.

The South Atlantic High moves southeastward in spring to lie closer to the coast in summer (December to February) and retreats to the northwest in autumn to lie farther north and offshore in winter (June to August). The movement of the South Atlantic High is responsible for decreasing the equatorward wind stress over the region 25°-35°S in winter and increasing it in spring, summer, and, to a lesser extent, autumn. Therefore, the southern sector of the Benguela region, which includes the Lüderitz upwelling center at 27°S, has maximum upwelling in these seasons, in contrast to the northern Benguela region, which has a summer upwelling minimum (Stander 1963; Parrish et al. 1983).

The passage of easterly moving cyclones south of the continent (often accompanied by the rapid southward movement of a coastal low-pressure system formed in the Lüderitz vicinity) modulates the seasonal trends in upwelling winds on a time scale of 3 to 6 days in the southern Benguela region (Nelson and Hutchings 1983). A similar time scale of variation has been noted in the winds at Walvis Bay. Nelson and Hutchings (1983) describe in detail the sequence of events following the passage of a summer low-pressure center: the South Atlantic High elongates and ridges round the south of the continent, causing intense southeast wind stress in the southern Benguela region along both the south and west coasts. Schumann et al. (1982) showed that upwelling occurred at capes along the south coast as far east as Cape Recife under these conditions.

Large-Scale Circulation

Discussion of the water movement within the Benguela region by Nelson and Hutchings (1983) and Shannon (in press) underscores the complexity of the system. In this paper, a more generalized overview will be given.

Direct measurement of surface currents (in the upper 20 m) between 18° and 35°S by means of drift cards (Duncan and Nell 1969; Shelton and Kriel 1980) and drogues (Harris and Shannon 1979; Shelton and Hutchings 1982; Brown and Hutchings, in press; Boyd and Agenbag, in press) indicate that movement of the surface waters in the Benguela region is generally in the direction of the wind forcing and therefore equatorward. In the vicinity of a front between dense upwelled water and less dense oceanic water, this northward movement can take the form of a baroclinic jet current (Bang and Andrews 1974), which may persist for an entire season (Brundrit 1981). Inshore, a countercurrent has been observed to occur between 32° and 34°S, particularly in autumn and winter (Duncan and Nell 1969; Brown and Hutchings, in press).

Recently obtained current meter data indicate dominant southward flow over the shelf in the subsurface layer (deeper than 40 m) in the southern Benguela region between 32° and 34°S (Nelson and Hutchings 1983). In the northern Benguela the existence of a southward-flowing subsurface compensation current was proposed by Hart and Currie (1960). Although direct current measurements are sparse in this area, indirect evidence from analysis of low-oxygen water and dynamic topography convincingly supports the existence of such a countercurrent north of Walvis Bay and possibly as far south as Lüderitz (Stander 1964; Moroshkin et al. 1970; Nelson and Hutchings 1983). In the region between Walvis Bay and 32°S, De Decker (1970) showed that southward advection can also be detected by tracing low-oxygen water, but Bailey (1979) found the situation more variable in the Lüderitz region.

In the far north (15°-18°S) warm, high-salinity Angolan water regularly advances at the surface as far as Cape Frio in summer and early autumn (Stander 1964; O'Toole 1980; Badenhorst and Boyd 1980), but the presence of this water mass (with salinities > 35.5%; O'Toole 1980) is seldom recorded farther south, other than as a thin tongue or without substantial mixing having occurred. In 1984 Angolan water advanced much farther south than usual, with drastic effects on the biota (Boyd and Thomas 1984; Boyd et al., in press), and this event will be discussed later. In the south, Agulhas Current water and Agulhas Bank mixed water (a mixture of Agulhas Current water and South Atlantic surface water) frequently penetrate the west coast, particularly in summer and early autumn (Shannon 1966; Bang 1973; Bang and Andrews 1974).

The extensive western boundary between upwelled water and oceanic water has recently been shown by satellite imagery to contain dynamic features that have been largely overlooked in previous studies (Shannon et al. 1983; Van Foreest et al. 1984). The spatial scale suggests that this boundary may be important in the interannual variability of the productive zone's extent within the Benguela system. The offshore eddies described by Van Foreest et al. (1984) may be important leaks of productive eastern boundary current water off the shelf and may result in a loss of neritic larvae. However, these eddies may maintain zooplankton populations as food sources for large populations of mesopelagic fish, which are thought to exist offshore of the shelf break.

SEASONAL SIGNAL

Large-scale studies, which may be most relevant to the recruitment processes of neritic fish populations within the Benguela system, have been few (Wooster[1]; Parrish et al. 1983; Christensen 1980; Boyd and Agenbag, in press; McLain et al. 1985). However, these studies present a clear seasonal "average" sea-surface temperature pattern, which can be related to the observed pattern of fish distribution, spawning, and recruitment, and against which climatic perturbations can be measured.

Sea-Surface Temperature

Wooster[2] examined monthly averages of sea-surface temperature for one-degree squares (which often do not reveal coastal upwelling sites like those off the Cape Peninsula) for the entire west coast of southern Africa. The data (Figure 3) show two temperature minima, one centered between Cape Frio and Möwe Point, and the other off Lüderitz, from July through September. These minima correspond to the winter-spring upwelling centers of Cape Frio and the perennial upwelling center at Lüderitz. Water warmer than 18°C occurs north of Walvis Bay in summer (December-March) and in the Cape Town region in January and February. Between these two regions the perennially cold water centered at Lüderitz dominates the pattern.

In the most comprehensive analysis of its kind, Parrish et al. (1983) averaged one million sea-surface temperature measurements in the Benguela region to obtain bimonthly values for one-degree squares. They selected January and February to represent summer, and July and August to represent winter. Their data (Figure 4) support and extend the earlier perspective obtained by Wooster[3]. In particular, they show that in winter the area covered by water < 16°C is extensive both in the longshore and offshore directions, whereas in summer the 18°C isotherm encapsulates the Lüderitz to Cape Columbine area within a narrow segment close to the coast, with water warmer than 20°C forming a pincerlike pattern from the north and south. The isotherms from the north seem linked to subtropical Angolan water, whereas those from the south seem linked with the Agulhas Current.

Christensen's (1980) charts of monthly average sea-surface temperature, constructed from 10-day mean data spanning 1968-78, emphasize the apparent extension of warm water of Agulhas Current origin onto the west coast in summer (Figure 5). They also show the pronounced temperature front and the divergence of isotherms offshore in the vicinity of Cape Columbine. By comparison, in winter the front is weaker, and the cool coastal water extends farther offshore.

The data presented by Boyd and Agenbag (in press) extend Christensen's analysis and demonstrate that an

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[1] Wooster, W.S. 1973. Upwelling in the Eastern Atlantic. Abstracts of the South African National Symposium, Cape Town, 6-10 August 1973.

[2] Ibid.

[3] Ibid.

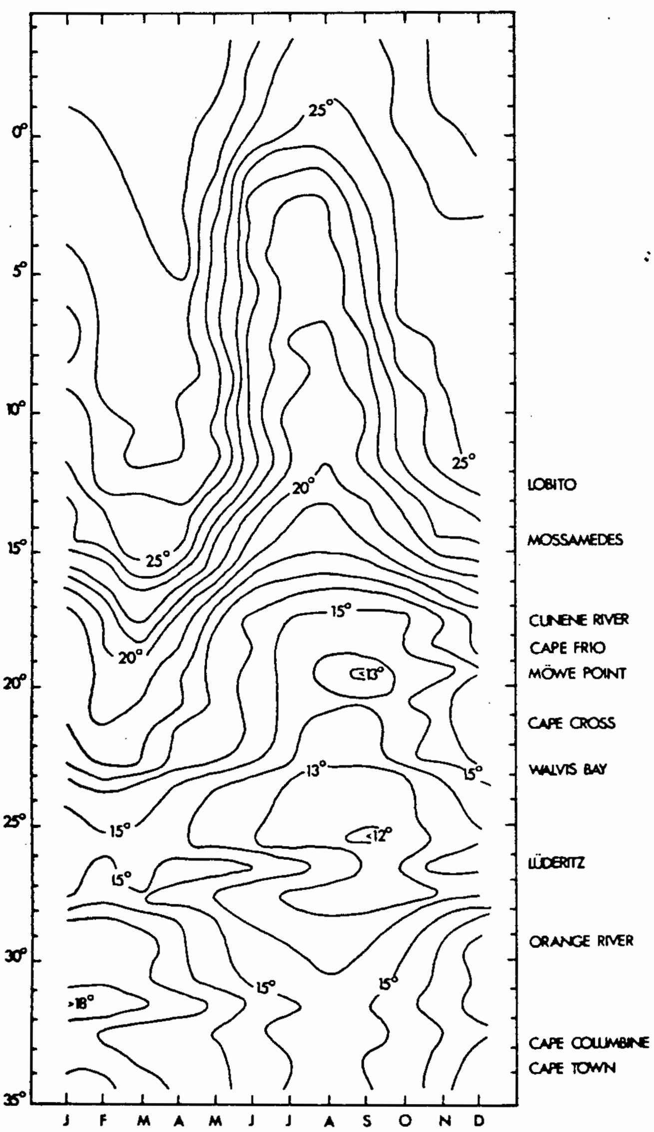


Figure 3. Monthly mean SST measurements for the coastal area of the Benguela system (from Wooster, W.S. 1973. Upwelling in the Eastern Atlantic. Abstracts of the South African National Symposium, Cape Town, 6-10 August 1973).

area of water cooler than 16°C extends along the entire coast between 18°S and 34°S up to 220 km offshore in winter (Figure 6). This cool area is considerably contracted in summer, with stronger offshore gradients set up by warmer water offshore.

Although the data from large-scale sea-surface temperature studies suggest that summer warming can be linked to the increased advection of water of subtropical and tropical origin onto the west coast, a component is due to solar heating of oceanic water. However, data from over 2,000 hydrocasts spanning 12 months taken in the southern Benguela region show that the warm water in summer can occur as a substantial layer of up to 60 m deep (e.g., Figure 7), indicating a strong advected component of Agulhas Current origin in the south. The observation that Agulhas Current water is advected considerable distances up the west coast can be substantiated from the distribution of certain Agulhas Current copepod species described by De Decker (1984).

Plankton Abundance and Distribution

As a result of having warm water close to the coast in summer and strong upwelling inshore, an exceptionally strong thermal gradient can be set up in the southern Benguela, particularly off the Cape Peninsula and off Cape Columbine. This feature takes the form of a front during upwelling (Figure 8a) and as a strong thermocline during lulls in upwelling (Figure 8b). Low levels of chlorophyll were found beyond the front in January 1978, but the chlorophyll concentration was high where upwelling displaced the nutricline toward the surface close to the coast (Figures 8a and 9a). During summer lulls in upwelling, the warm water advances as a substantial layer resulting in low chlorophyll levels with a weak subsurface maximum associated with the thermocline (Figures 8b and 9b).

The change in the distribution of high chlorophyll and plankton concentrations resulting from seasonal changes in temperature structure can be clearly seen in Figures 10 and 11. In winter, surface temperature is relatively isothermal, and chlorophyll is fairly widespread, but concentrations are low because of mixing and weak solar irradiation (Figure 10). Plankton concentrations in winter are most abundant north of the Cape Peninsula, particularly in the St. Helena Bay region (Figure 11a). As light levels and upwelling increase in spring, high concentrations of chlorophyll and plankton are encountered over a larger area. In summer, warm water close to the coast results in a strong thermal front and a severe reduction in the extent of the productive area. This area becomes limited to the vicinity of the upwelling centers off the Cape Peninsula and Cape Columbine, as well as St. Helena Bay—immediately downstream. Relaxation of the front in late autumn allows an expansion of the productive area and a return to winter conditions of relatively widespread concentrations of chlorophyll and plankton. As a result of this "bellows" effect, the distribution of plankton changes dramatically. Although the standing stock of plankton may increase in winter, the production may be less because of low light levels and reduced nutrient regeneration. Plankton standing stocks are consistently high in the inshore area north of the Cape Peninsula and particularly in St. Helena Bay (Figure 11b).

From the data presented by Kruger (1983) and Kruger and Boyd (1984), phytoplankton displaced volume

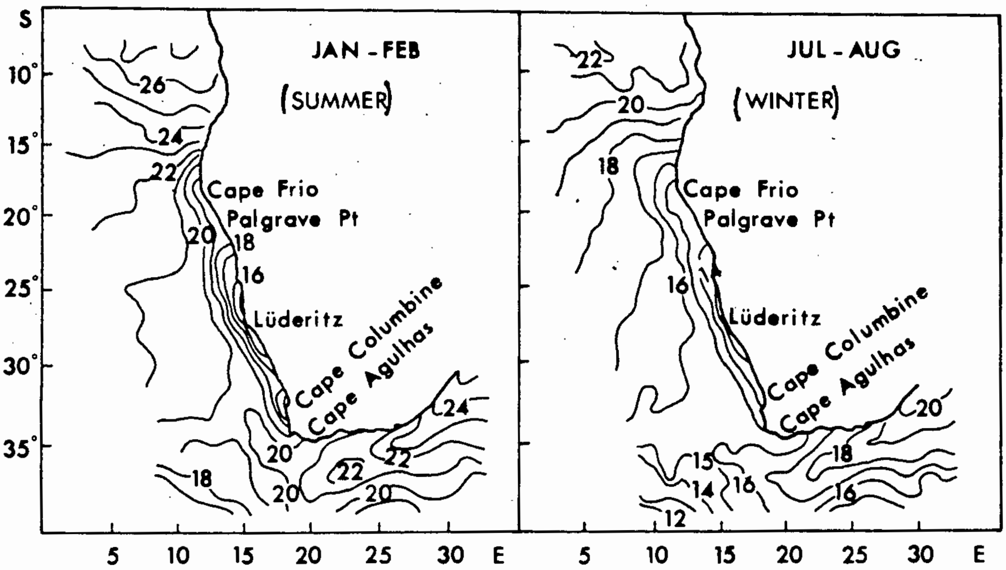


Figure 4. Summer and winter mean SST measurements for one-degree squares in the Benguela system (from Parrish et al. 1983).

in the northern Benguela region appears to be consistently high in the coastal area between Lüderitz and Walvis Bay, just north of the center of perennially strong upwelling. Zooplankton displaced volume is most often highest farther offshore and farther north between Walvis Bay and Cape Frio. During upwelling in the region north of Walvis Bay, the productive zone expands northwards (Figure 12a), whereas advection of warm surface water from the north and west results in generally lower productivity. (Figure 12b).

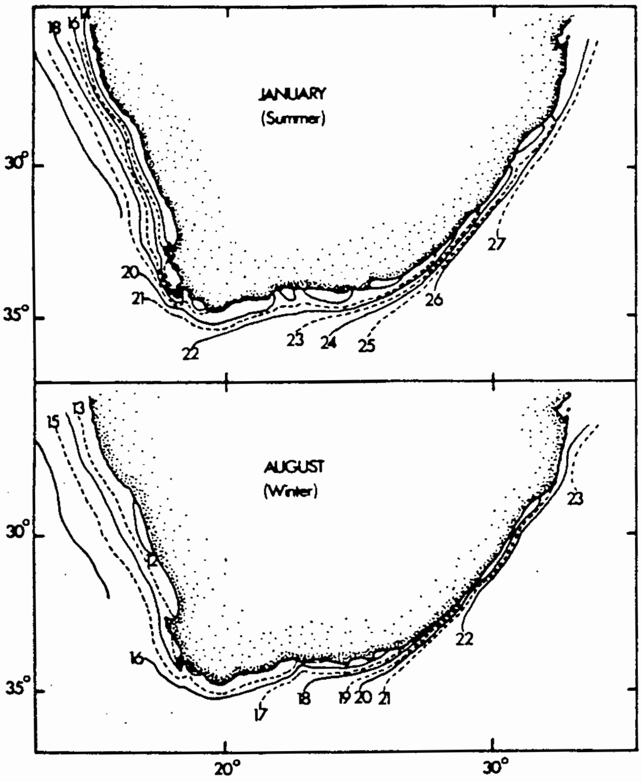


Figure 5. Summer and winter mean SST from an analysis of ten-day mean values from 1968 to 1978 for the coastal area off southern Africa (from Christensen 1980).

Fish Distribution, Spawning, and Recruitment

In both the northern and southern Benguela regions, spawning of a number of commercially important neritic species like pilchard, anchovy, and hake occurs mostly from spring to autumn, and is associated with the mixing areas between Benguela Current water and warm surface water advected into the system (O'Toole 1976, 1977; Crawford 1980; Crawford et al. 1983; Shelton and Hutchings 1982; Shelton 1984). Sites of strong offshore transport are avoided, even though productivity may be highest in these areas. Rapid egg development in the warmer water may result in increased early survival, and first-feeding larvae may benefit from food concentrated in strong fronts and thermoclines set up by the interplay between upwelling, advective processes and solar heating.

Dispersal after spawning is predominantly northwards in both regions, following the general equatorward flow of the Benguela Current at the surface. But accelerated transport of anchovy eggs and early-stage larvae has been recorded in a frontal jet off Cape Town (Shelton and Hutchings 1982) and may occur at other sites of strong horizontal temperature gradients, such as off Cape Columbine. In the southern region, recruitment of 0-year-old anchovy takes place along the west coast from midautumn onwards and is initially strongest to the north of St. Helena Bay (Crawford et al. 1983). Recruits may benefit from the consistently high plankton standing stock in the inshore region between Lamberts Bay and Cape Town (Figure 11b). In the northern region, anchovy and pilchard 0-year-

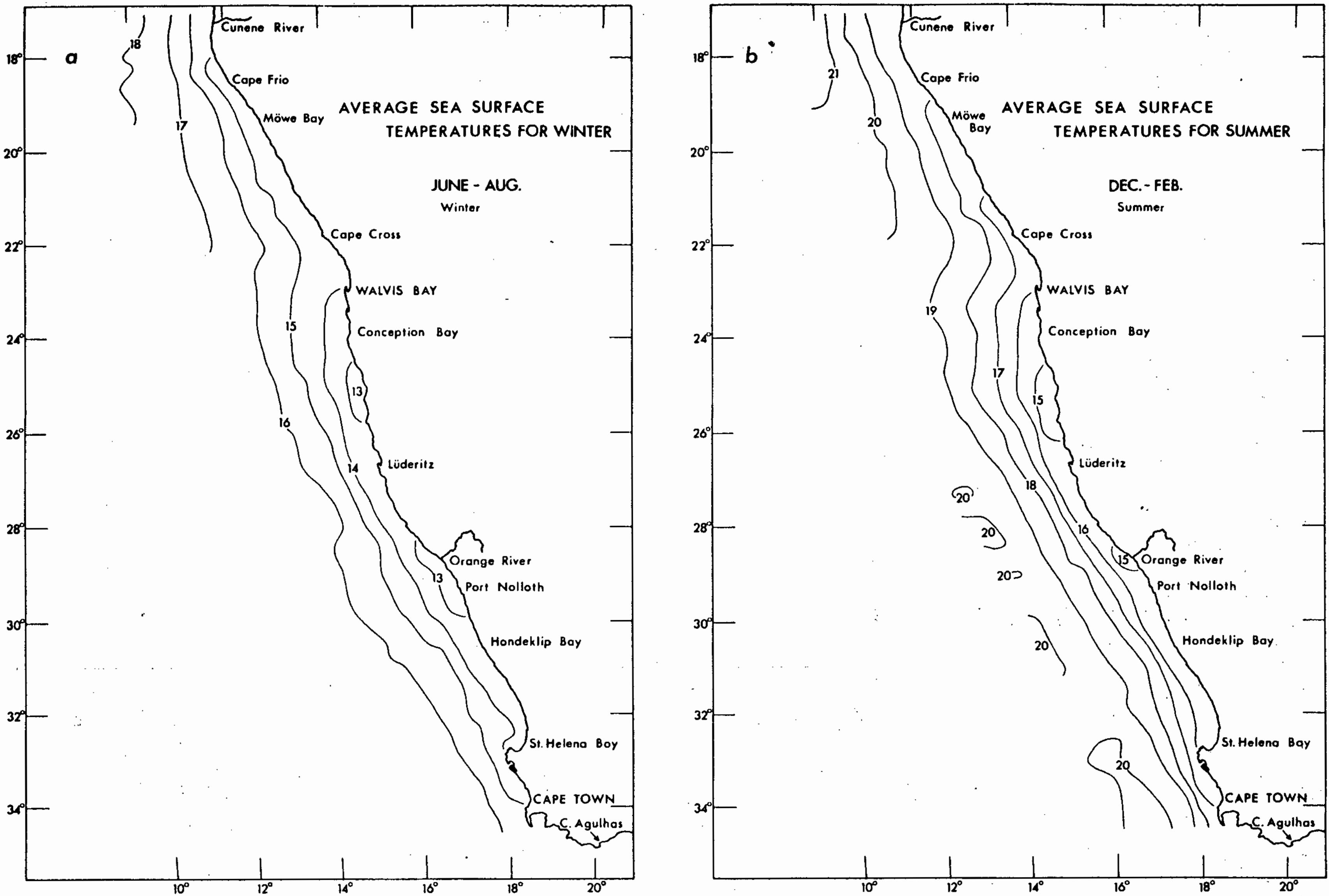


Figure 6. Winter and summer mean SST from an analysis of ten-day mean values for the Benguela system (from Boyd and Agenbag, in press).

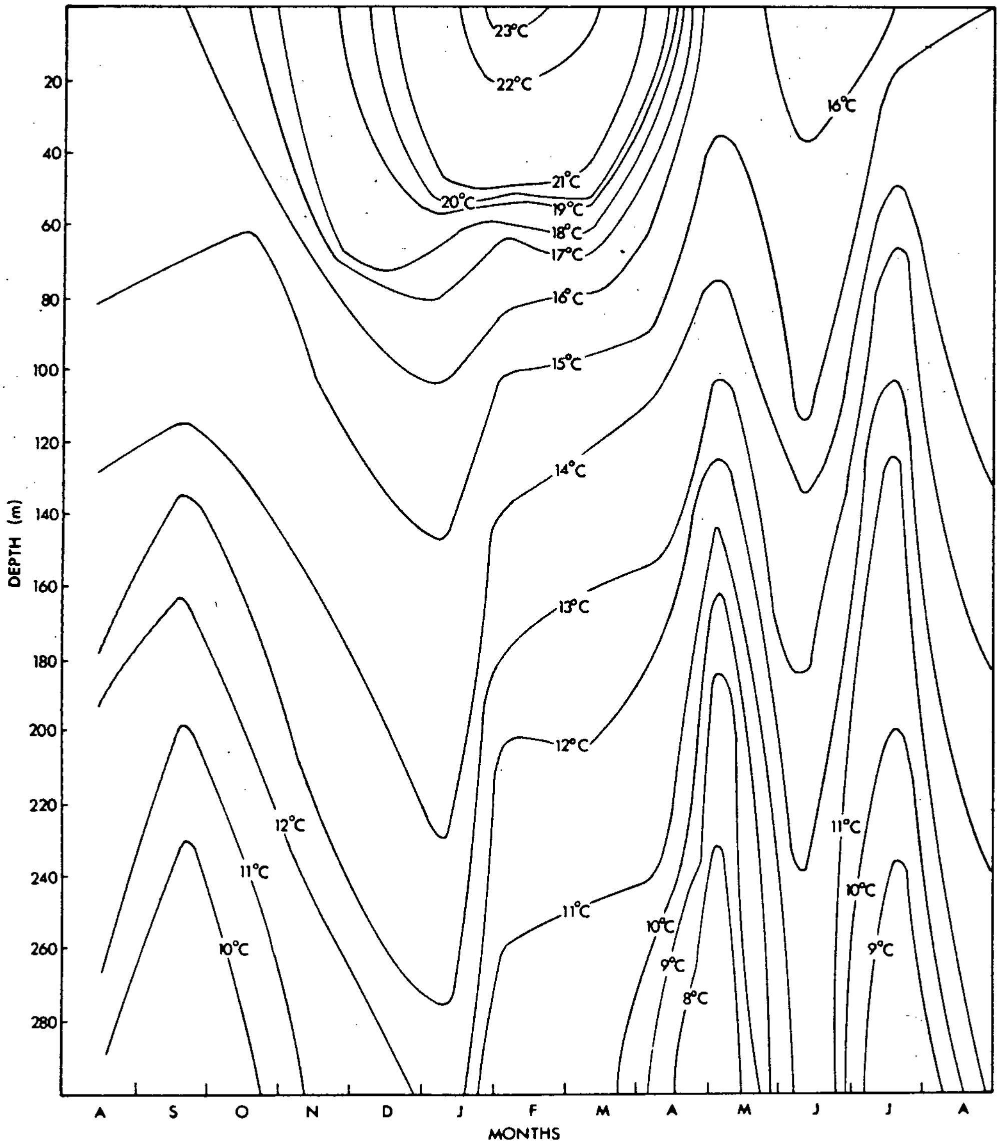


Figure 7. Temperature section from monthly measurements taken about 110 kilometers west of Cape Columbine between August 1977 and August 1978.

olds recruit into the fishery in the vicinity of Walvis Bay from May onwards (Crawford et al. 1983). Southward movement of shoals of 0-year-old fish detected by fishing boats at this time of year may be facilitated by inshore countercurrents in the two regions.

In the southern Benguela region, the southward migration is initially into the productive coastal zone, where the fish feed before moving offshore onto the Agulhas Bank to spawn. There, moderately warm 17°-18°C water is widespread in spring and early summer (Figure 10). Anchovy in the northern Benguela region recruit over several winter months off Walvis Bay before reappearing in the spawning ground farther north. This return migration may occur in northerly flowing water offshore of the main fishing ground, which is confined to the area close to the coast. Recruitment patterns are similar in both the northern and southern regions, but in the south anchovy larvae reach the recruitment ground by the northward-flowing Benguela Current and the spawning ground via a countercurrent; whereas in the northern Benguela region a countercurrent may assist the recruitment migration, and the main flow of the Benguela Current may aid the spawning migration.

The occurrence of water warmer than 20°C on the Agulhas Bank in late summer and early autumn (Figures 5 and 10) appears to reduce the area suitable for spawning and concentrate adult spawning fish closer inshore, since very few anchovy eggs are found in the warm water, and the catch rate of adult anchovy by the purse seine fleet operating inshore increases at this time. A rapid decline in the catch rate of adult

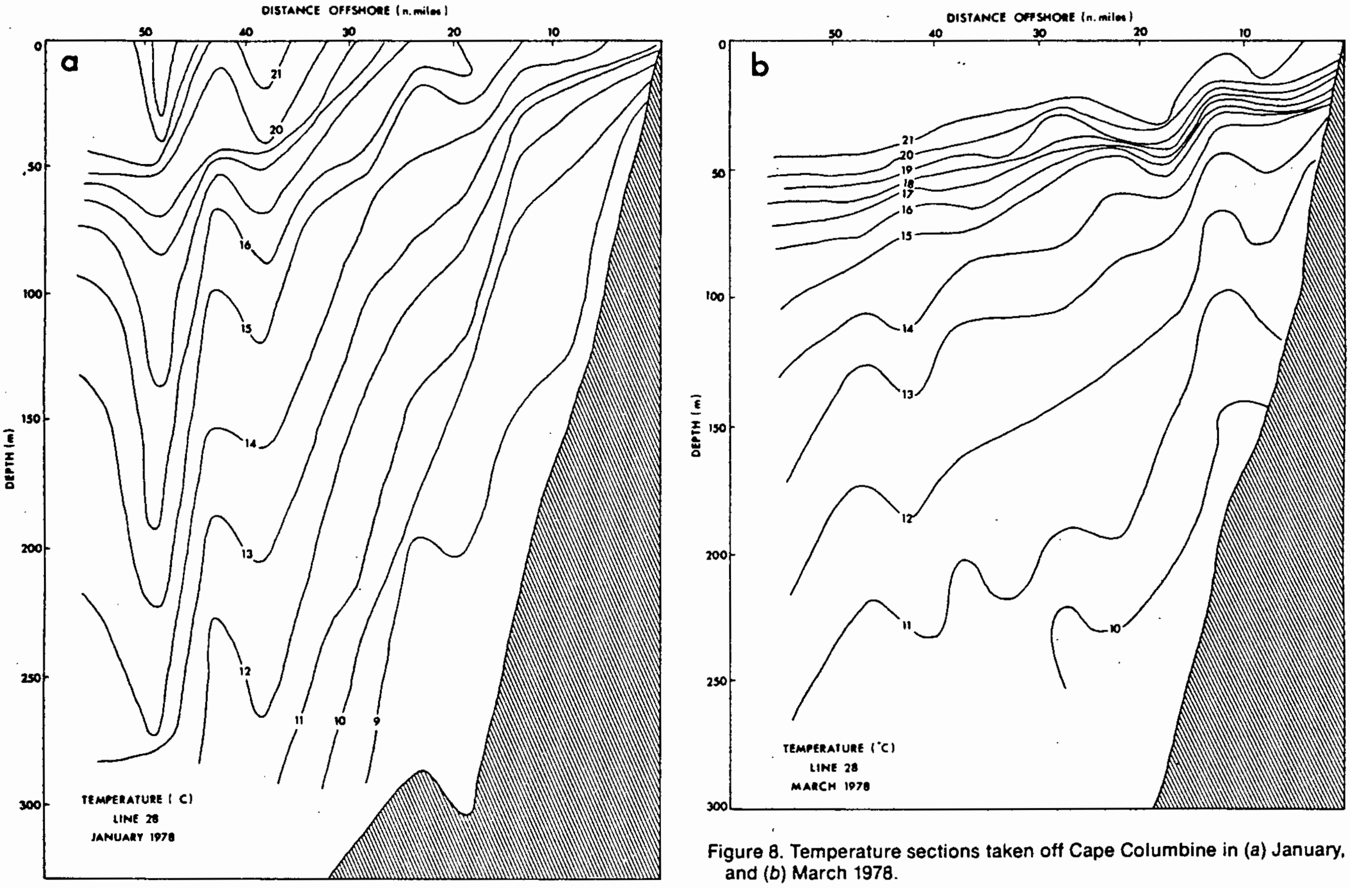


Figure 8. Temperature sections taken off Cape Columbine in (*a*) January, and (*b*) March 1978.

anchovy in late autumn is coincident with the seasonal cooling of surface waters on the Agulhas Bank. By winter the warm water is confined to the body of the Agulhas Current (Figure 5). There is a marked eastward movement of anchovy and pilchard up the coast in autumn (Crawford 1981a, b).

Neritic species inhabiting the Benguela system generally avoid winter spawning. This may be because in winter, onshore advection of warm water is at a minimum; temperature near the surface is cool and relatively isothermal; offshore transport is not constrained by strong fronts; and plankton is distributed over a large area rather than concentrated close to the coast. In the southern region, lantern fish, *Lampanyctodes hectoris*, and round herring, *Etrumeus teres*, are normally associated with the shelf edge and appear to spawn predominantly in winter (Figure 13), possibly in response to the more widespread distribution of plankton in this season.

INTERANNUAL SIGNAL

If the strong seasonality in plankton distribution as well as the distribution, spawning, and recruitment of pelagic fish in the Benguela system is linked to the seasonal influence of warm water, interannual variability in the strength and extent of warm conditions may have a major effect on year-class strength. Extensive occurrence of warm water could severely limit plankton production and concentrate fish in a restricted environment where density-dependent population responses may be intensified. Alternatively, during a cool period, spawning and dispersal of eggs and early-stage larvae, as well as food for first-feeding larvae may be adversely affected. The influence of within-season departures from the seasonal average of onshore, warm-water advection or upwelling may be difficult to detect in terms of year-class strength and may require intensive sampling of differential mortality within a cohort subsequent to spawning. However, prolonged periods of warming or cooling could be expected to have a more apparent influence on spawner biomass and recruitment strength.

Guano Record

A historic time series of the annual amount of guano collected on islands off Namibia and off South Africa (Figure 14) may reflect past fluctuations in the combined pilchard, anchovy, and horse mackerel biomass

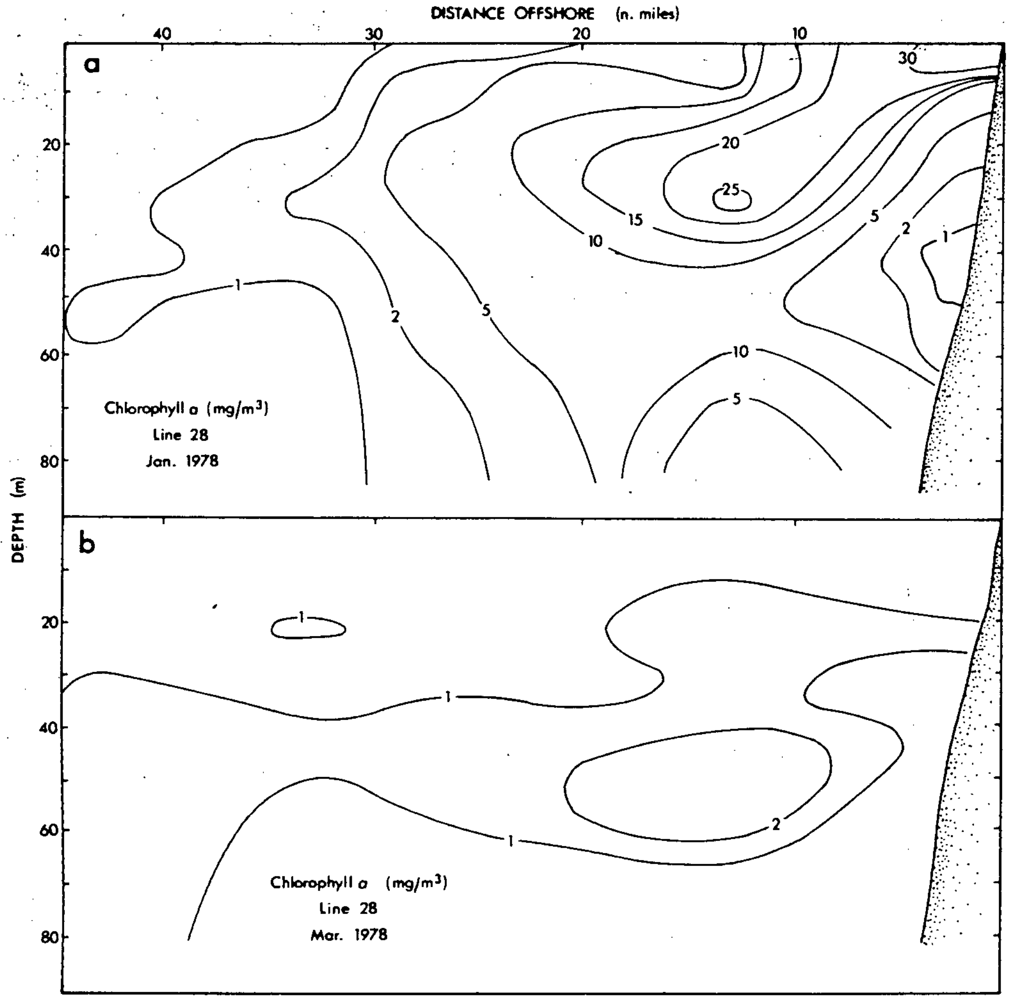


Figure 9. Chlorophyll *a* section off Cape Columbine in (*a*) January, and (*b*) March 1978.

(Crawford and Shelton 1978), in the absence of any more direct historic record. The Namibian and South African guano records are significantly positively correlated ($r = 0.37$, $n = 73$). This could be a result of similar trends in the abundance of pelagic prey species off both Namibia and South Africa, which in turn could have resulted from large-scale environmental phenomena that impacted the whole system over periods of decades.

The individual guano records for Namibia and South Africa show significant autocorrelation with time lags of up to five years (Figure 15). This could be attributed to similar autocorrelation in the prey biomass resulting from the smoothing of random environmental variability by the multiple age-group prey spawner populations, or by smoothing within the seabird populations themselves. Alternatively, autocorrelation in the guano records could be caused by low-frequency environmental effects directly on the seabird populations or on their prey. While no unequivocal interpretation of the guano record is possible, the argument that environmental autocorrelation in the Benguela system is an important signal is not invalidated.

Sea-Surface Temperature and Sea Level

In the southern Benguela region, advection of warm water outside the upwelling front is most marked during the seasons of strongest upwelling and is aided by the prevaling upwelling-favorable wind stress, whereas in the northern Benguela region the normal seasonal advance of Angolan water occurs during the upwelling minimum, tending to oppose the wind forcing. Hence the mechanisms for advection of warm water differ within these two regions in the Benguela Current system. In the south, advection of Agulhas Current and Agulhas Bank mixed water outside the coastal upwelling zone would tend to reinforce the frontal feature, whereas in the north, a southward intrusion tends to deepen the thermocline and suppress upwelling. The

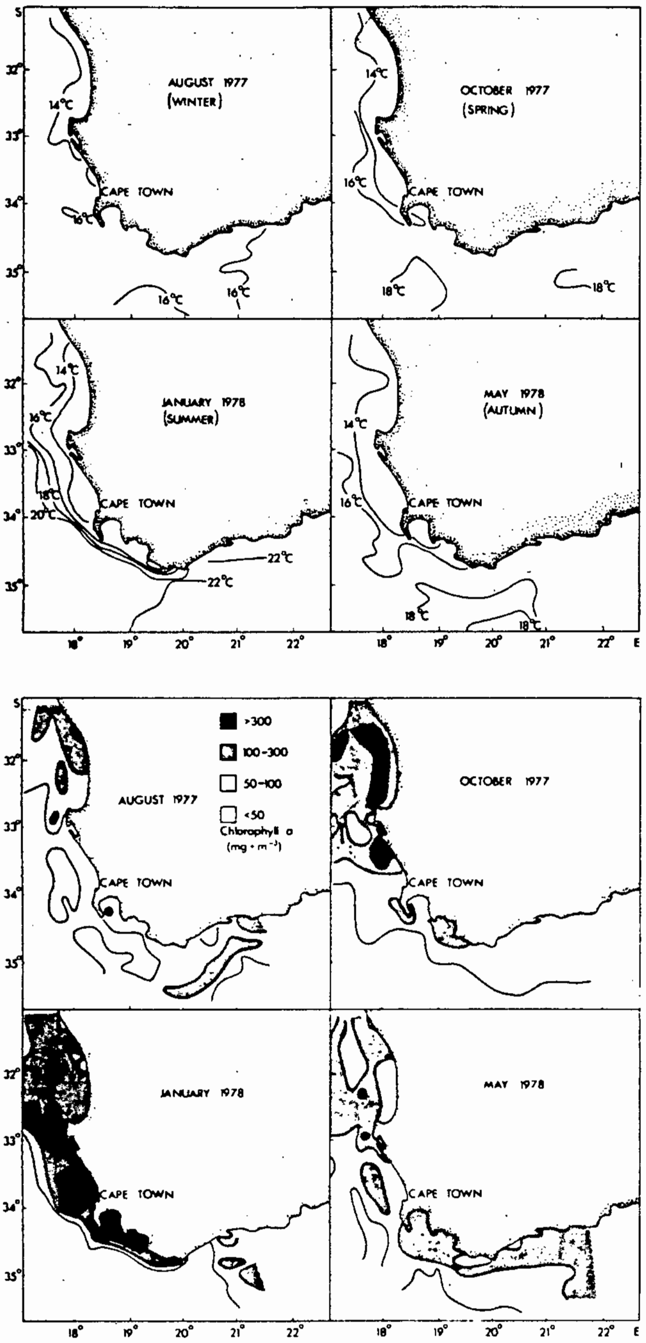


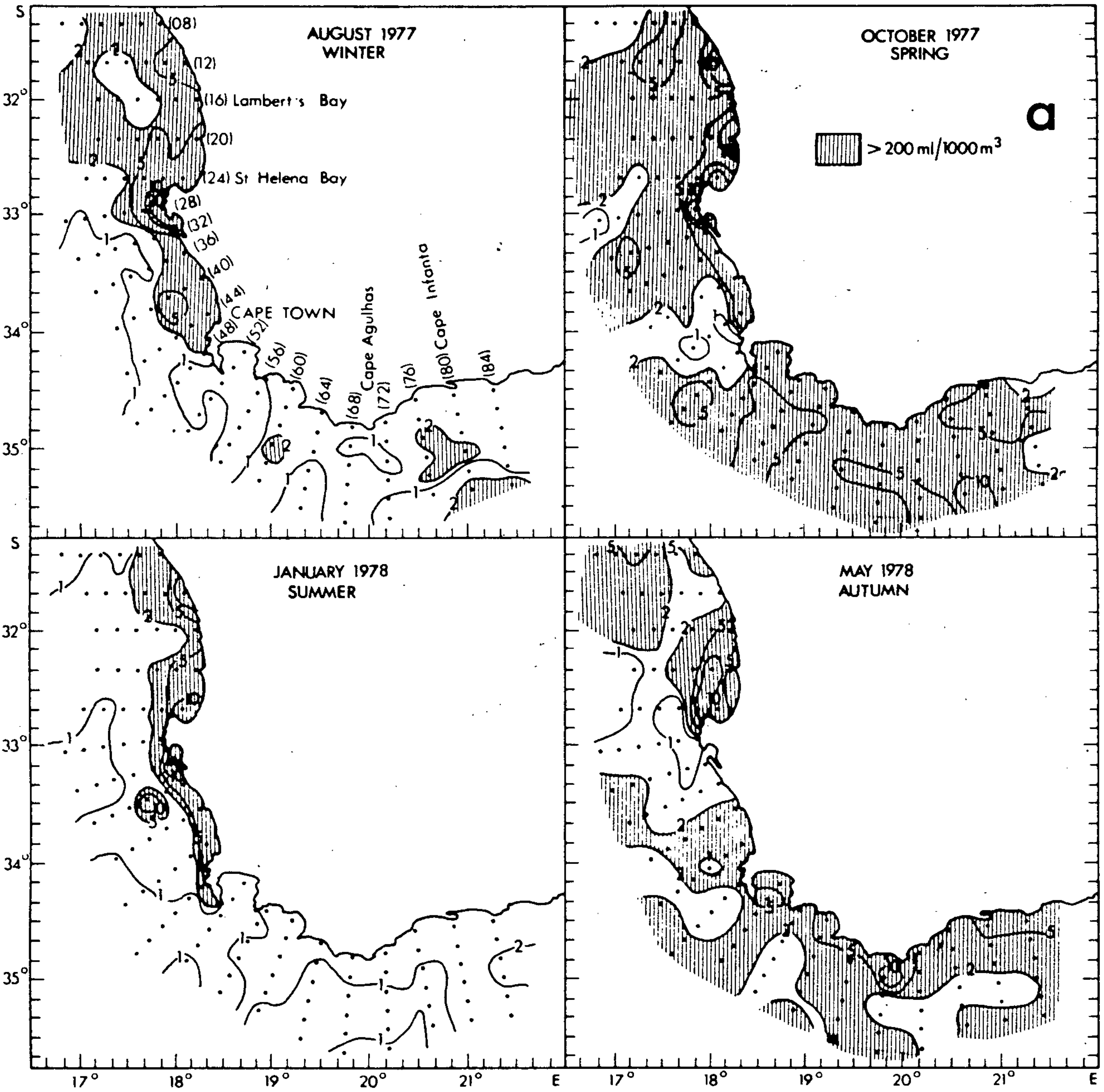
Figure 10. Seasonal pattern of surface temperature and chlorophyll a distribution in the southern Benguela region in 1977-78 (from Shannon et al. 1984).

northern Benguela region would therefore seem more susceptible than the south to a large-scale El Niño-type anomaly, although a high incidence of onshore (westerly) winds or periods of calm in the south during summer and early autumn could be expected to have a measurable effect in terms of SST anomaly in the coastal zone.

A major warm event was recorded in the northern Benguela region in 1963 and was well documented by Stander and De Decker (1969). Brundrit (1984) found that this coincided well with a mean sea-level peak that is clearly visible in the records from Walvis Bay and Lüderitz and detectable as far south as Cape Town. Annual mean SST measurements recorded in the vicinity of Walvis Bay from 1955-67 and from 1969-79 from two different sources (Figure 16) show that 1963 was the warmest year in a warm period that began in 1961. A similar but less intense warm period began in 1972 and peaked in 1974 (Figure 16) and is reflected by increased sea levels at Lüderitz (Figure 2 in Brundrit 1984). McLain et al. (1985) present mean SST data for three-degree squares for the entire west coast of southern Africa from 1971-84. Their data show that a large portion of the Benguela system was subject to a positive temperature anomaly between 1972 and 1977.

Boyd and Thomas (1984) and Boyd et al. (in press) report a further major warm event in 1984 when warm, saline Angolan water penetrated particularly far south, suppressing upwelling and leading to extremely low volumes of phytoplankton. In March and April 1984, water temperatures were 3° to 6°C warmer than average over large areas, but conditions appeared to return to normal in May. However, monthly monitoring cruises in the winter of 1984 showed warmer and more-saline-than-average water off Walvis Bay in June and August 1984, indicating a sustained warm period throughout the winter. The 1984 anomaly in the northern Benguela region is particularly clear in the data presented by McLain et al. (1985) as a southward projecting tongue of Angolan current water that raised temperatures by more than 2°C from the mean shown in the three-degree-square analysis.

Although SST anomalies as strong as those that occurred to the north of Lüderitz in 1963 and 1984 are not apparent in data records for the southern Benguela region, SST measurements made in Table Bay at Cape Town from 1956-80 (Figure 17) and mean annual SST values for three-degree squares for the period from 1971-84 (McLain et al. 1985) show that a generally warm period spanned the late 1950s and early 1960s, with a maximum SST anomaly in September and November 1963. A second warm period from 1972-77 is evident in the three-degree-square analysis as well as the Table Bay data. The three-degree-square analysis also shows that a substantial cool period extending over much of the Benguela system began in 1978 but may have terminated in 1984, coinciding with the warm event north of Lüderitz. The cooling in SST corresponds to decreased sea levels measured at Simons Bay near Cape Town (Figure 3 in Brundrit et al. 1984).



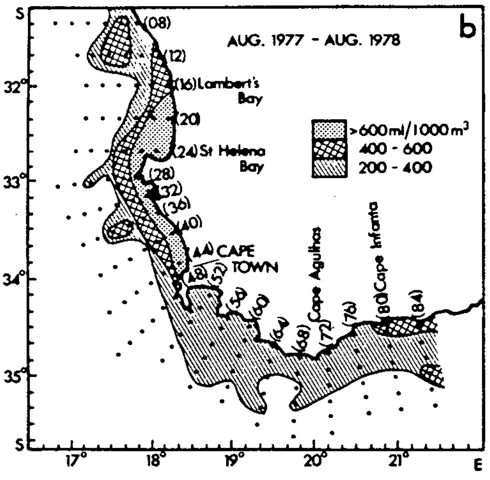


Figure 11. Southern Benguela region: (*a*) seasonal pattern of plankton standing stock from a double oblique tow with a bongo net fitted with 300-micron mesh, taken down to a maximum depth of 100 m; (*b*) mean distribution of plankton retained by the 300-micron mesh net from monthly surveys conducted between August 1977 and August 1978.

The mechanisms causing prolonged warm and cool periods in SST and changes in sea level in the Benguela system may be linked to changes in large-scale climatic processes, such as deviations in the seasonal change in the position of the South Atlantic high-pressure system, which may affect both upwelling and advection. The Pacific El Niño is known to be forced by the Southern Oscillation phenomenon (Philander 1983), and Walker et al. (1984) have quoted Van Loon

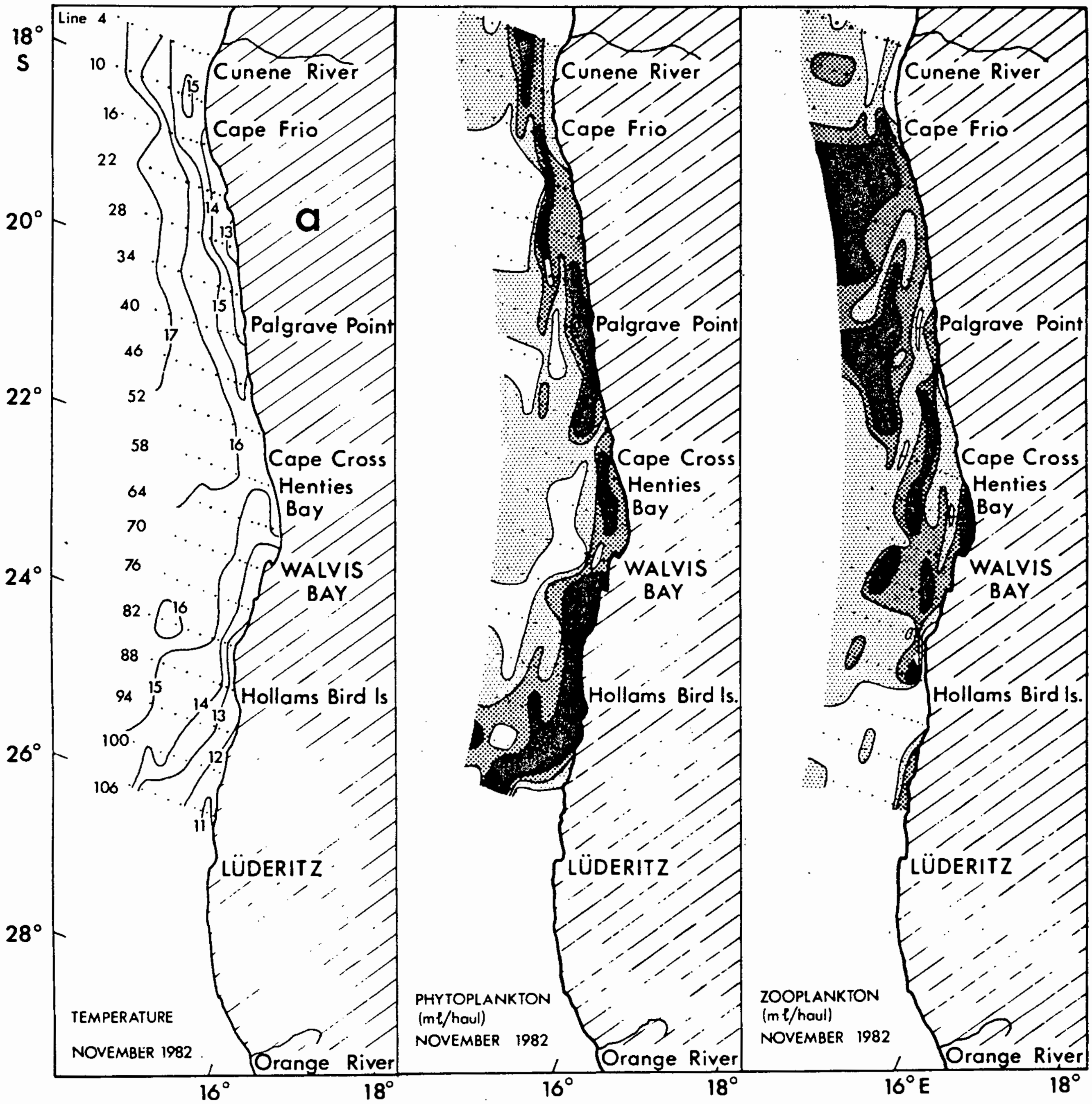


Figure 12a. Northern Benguela region surface temperature and plankton displaced volume from vertical tows from 50 m to the surface with a 50-cm-diameter net fitted with 80-micron mesh for November 1982 (from Kruger and Boyd 1984).

and Madden (1981) as demonstrating that during a Pacific warm event, negative atmospheric pressure anomalies arise over the central South Pacific Ocean in phase with negative anomalies over the South Atlantic Ocean, south of 35°S. Walker et al. (1984) also show a close relationship between annual (1976-83) SST measurements in the southern Benguela region and the southerly extent of the Subtropical Convergence. Northward displacement of the Subtropical Convergence was found by Gilooly and Walker (1984) to indicate increased frequency of cold fronts to the south of the continent and a northward shift in the mean position of the South Atlantic High. This represents an annual shift toward winter conditions.

Tyson (1981) has examined the occurrence of extended wet and dry spells over the southern African

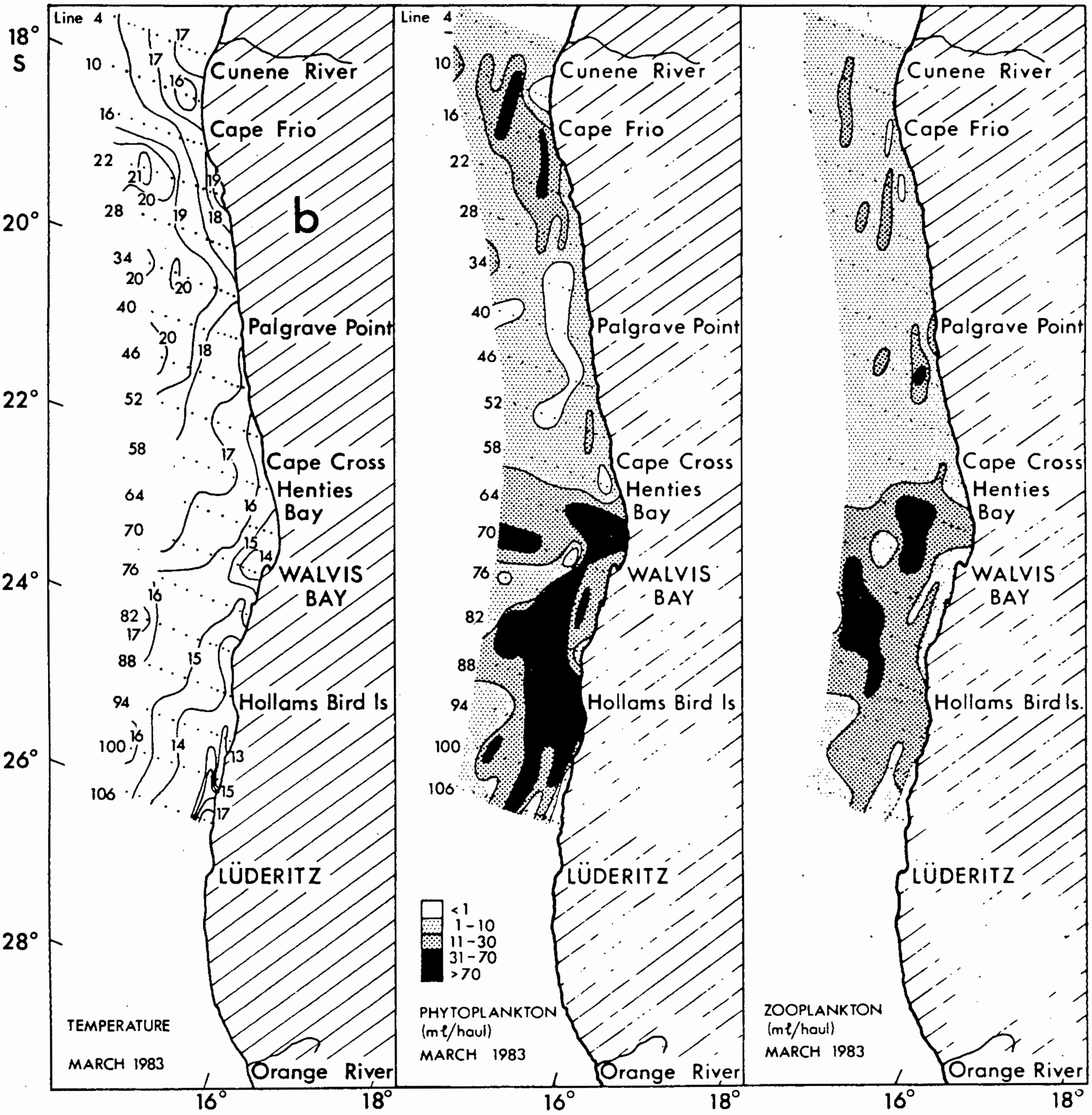


Figure 12b. Northern Benguela region surface temperature and plankton displaced volume from vertical tows from 50 m to the surface with a 50-cm-diameter net fitted with 80-micron mesh for March 1983 (from Kruger and Boyd 1984).

subcontinent, which is predominantly a summer rainfall area, and reports that 1963-72 was a dry spell and 1973-79 a wet spell. Since 1979, the southern African subcontinent has experienced severe drought conditions, which may have only recently been broken. The dry spells coincide with cold SST, and the wet spells with warm SST shown in both Figure 17 and in the analysis of McLain (1985).

Tyson (1981) showed that the subcontinental wet and dry spells have occurred in association with atmospheric circulation variations, which impart a quasi-18-year oscillation in rainfall. However, he also identified a 10-11-year rainfall oscillation for the winter rainfall area near Cape Town. A cycle fitted to the Cape rainfall data by Vines (1980), shown in Tyson (1981), is in phase with the variability shown in Figure

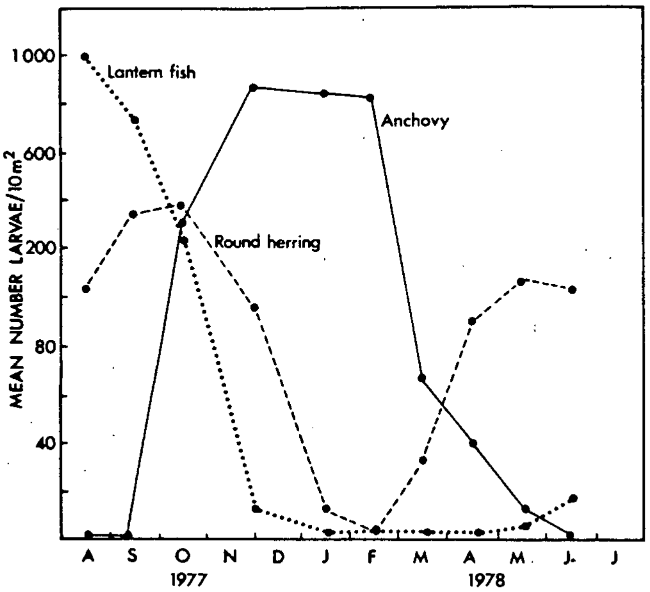


Figure 13. Mean number of anchovy, lantern fish, and round herring larvae from monthly bongo net tows in the southern Benguela region between August 1977 and June 1978.

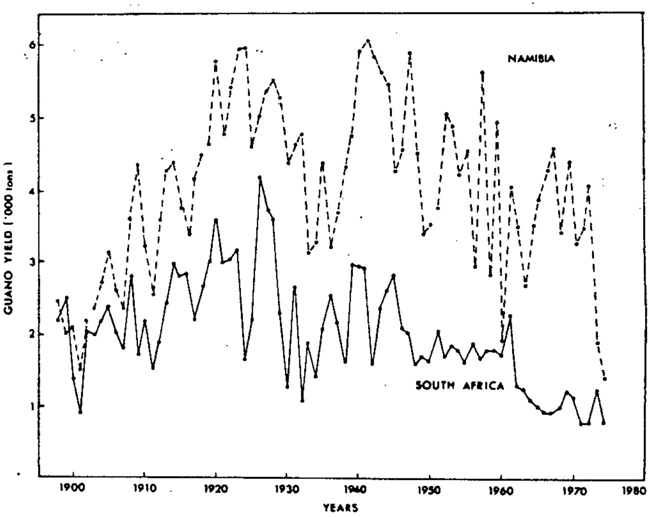


Figure 14. Guano yield from islands off South West Africa/Namibia and South Africa.

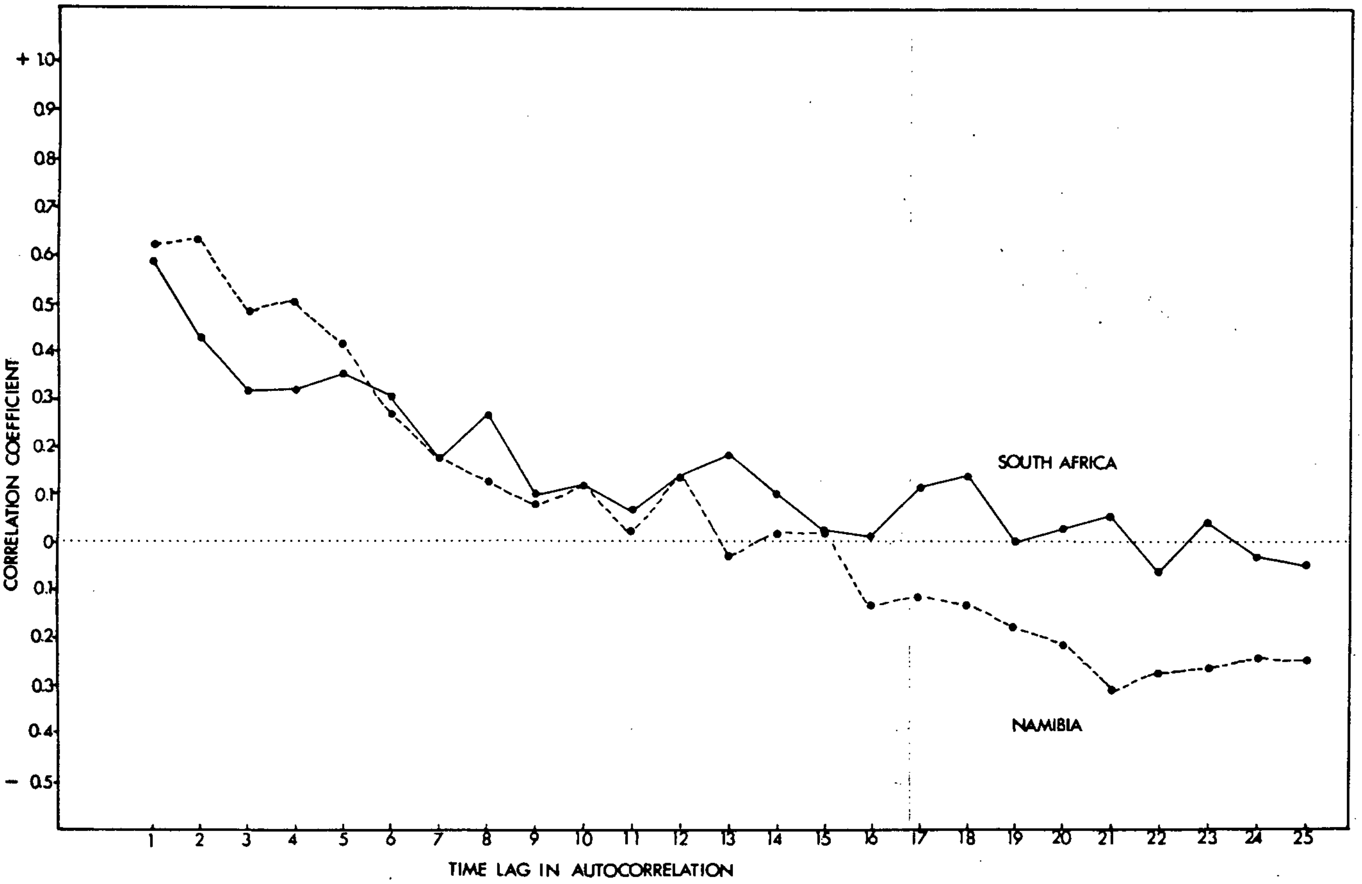


Figure 15. Time-lagged autocorrelation of guano yield data from islands off Namibia and South Africa.

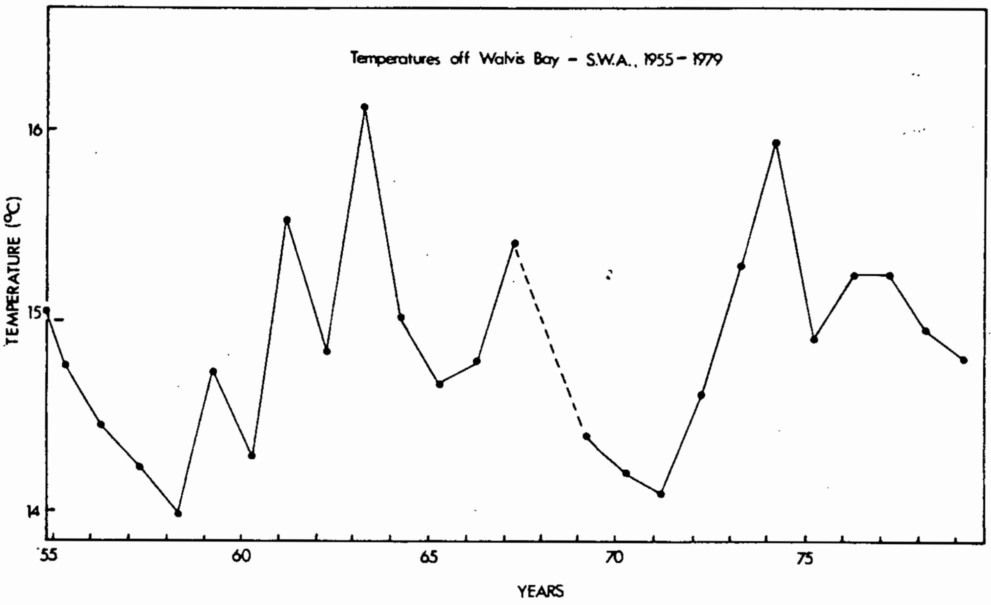


Figure 16. Mean annual SST measurements from a site near Walvis Bay for the period 1955-79. The temperatures for 1955-67 were from hydrological data, those from 1969-79 from general shipping. The latter data were adjusted to have the same mean as the former. Means were computed for each 12-month period beginning in September and extending through the following August; the resulting annual mean value was then plotted in the position corresponding to February on the time axis.

16 and links cool annual temperatures at Walvis Bay with increased rainfall in the Cape.

Effect on Fish Populations

The 1963 warm event in the northern Benguela region shifted shoals of pilchard southwards in the Walvis Bay region. These fish were in poor condition, gave low oil yields, and had reduced gonad development with consequently diminished egg production over the spawning grounds (Stander and De Decker 1969). The major warm event that occurred in the northern Benguela region in 1984 also caused pilchard to concentrate close to Walvis Bay, leading to high catch rates. There was a failure of anchovy recruitment caused apparently by reduced spawning activity accompanied by low survival of larvae in the excessively warm water of up to 26°C (Boyd and Thomas 1984).

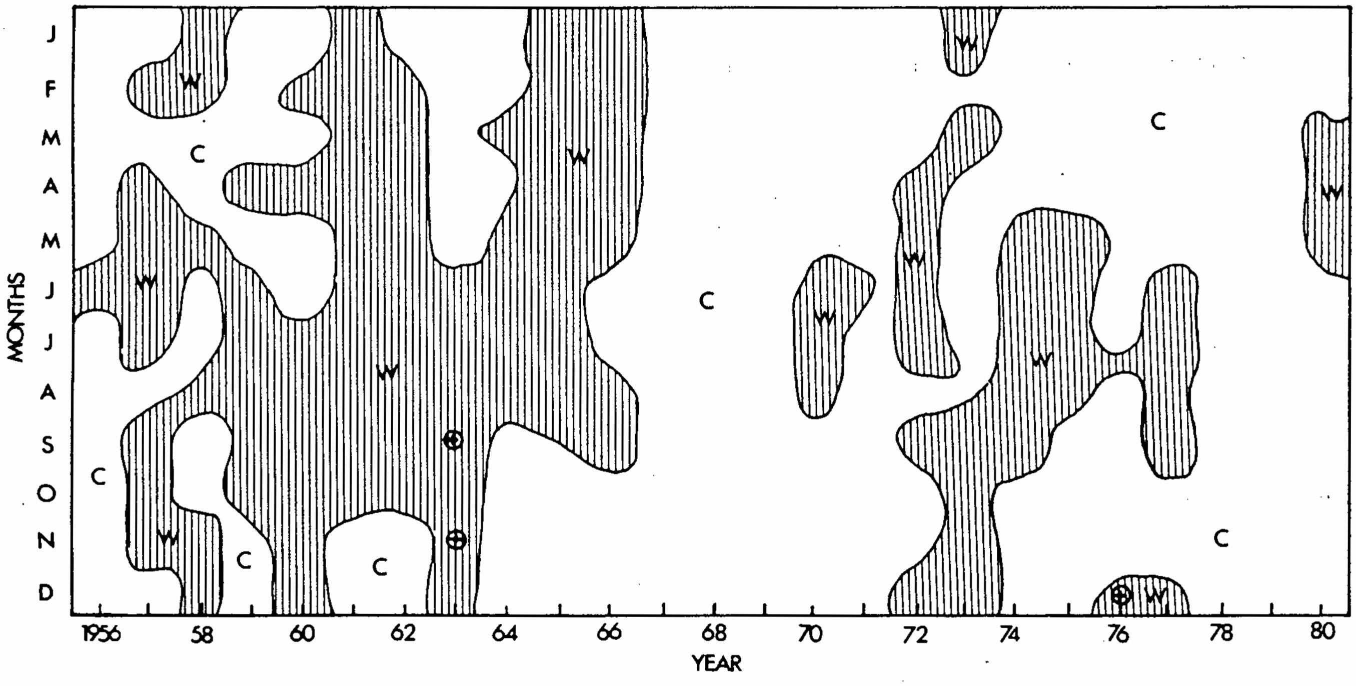


Figure 17. Mean monthly SST measurements from Table Bay near Cape Town for the period 1956-80, showing positive (hatched) and negative temperature anomalies. The (+) indicates a positive anomaly of more than 2°C (from M. Jury, Sea Fisheries Research Institute, Cape Town, unpublished data).

Boyd (1979) suggested that consistent and warm December-April temperatures from 1972-75 favored anchovy recruitment, whereas highly variable temperatures in 1976 and 1977 coincided with poor recruitment. Increased variability in SST has been observed to result from either intense upwelling events in summer (e.g., Stander 1963) or a major advection phenomenon (e.g., Stander and De Decker 1969; Boyd and Thomas 1984).

In the southern Benguela region the pilchard resource collapsed over the period 1960-67, with very low recruitment resulting from the spawning that took place in the summer of 1963-64 (Figure 2). This coincides with a maximum SST anomaly of more than 2°C in Table Bay in September and November 1963 (Figure 17). The warming that began in the southern Benguela region in 1972 corresponds to years of apparently good recruitment of anchovy (Figure 2).

However, an alternative interpretation of the anchovy response may be that availability of adult fish increased in the inshore fishing zone because of the increased influence of Agulhas Current water on the Agulhas Bank. The elevation of adult catchability under such conditions is not accounted for in the cohort analysis performed to estimate year-class strength and biomass. The period of cooling over the early 1980s coincided with a marked decline in the catch of adult anchovy in the southern Benguela. This has conventionally been attributed to poor recruitment, whereas a relaxation of advection may have reduced the incidence of adult anchovy close inshore.

Although the relationship between the Benguela system's neritic fish populations and periods of warming and cooling still must be rigorously examined, it can be inferred from this descriptive study that the populations do respond to low-frequency environmental forcing. Further, there is some evidence that periods of exceptionally strong SST anomaly adversely affect year-class strength, whereas moderate warming may be advantageous to some neritic fish.

Incorporation into Population Models

High-frequency and essentially unpredictable environmental variability can only be incorporated as a stochastic "noise" term in fish population models. These models have no predictive value, but can be used in Monte Carlo simulations to estimate the risk of collapse associated with alternative management strategies, provided the statistical description of the variability is adequately known. The central tendency of the variability can be expected to be strongly modulated if, in addition to random variability on a short time scale, autocorrelation over a longer period occurs. Swartzman et al. (1983) developed an approach for managing the Pacific whiting fishery in which separate stock-recruit curves could be used during periods of ocean warming or cooling, and risk of overfishing could be assessed according to stochastic recruitment variability around the appropriate curve.

The potential importance of autocorrelation of en-

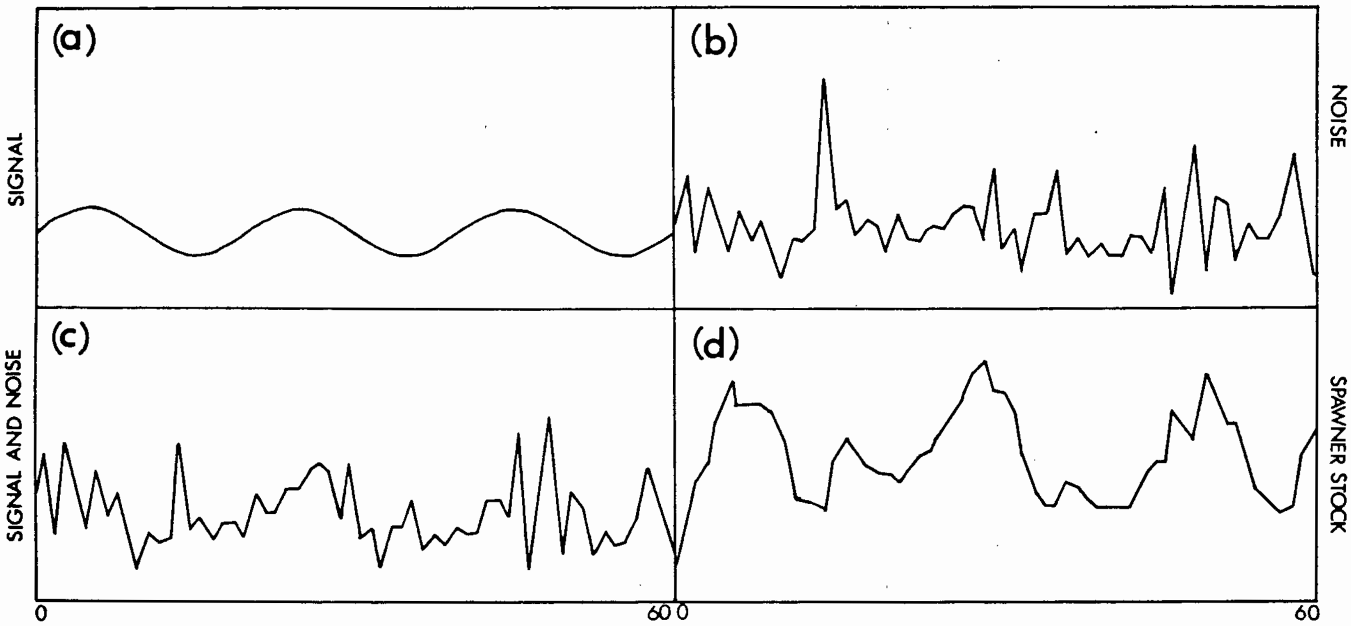


Figure 18. A sine wave with a wavelength of 20 years and an amplitude of 0.67 to 1.33 of the mean value (*a*), used multiplicatively to vary the central tendency of a log-normally distributed random number sequence with a range of 0.5 to 2.0 times the mean value (*b*). This resulted in the signal (*c*), which was used to modify recruitment generated in the model from which the spawner stock (*d*) was obtained.

vironmental variability that modifies recruitment success has been examined by means of a theoretical model of the anchovy population, which uses the same population parameters as those in Armstrong (1984):

$$R = (e^{\epsilon}\alpha) P\exp(-\beta P^{c})$$

where R is the number of anchovy recruits,
- P is the parent biomass,
- α is a parameter expressing density-independent prerecruit mortality and specific fecundity of spawners,
- $\epsilon(0,\sigma)$ is a random number from a normal distribution with mean of zero and standard deviation σ,
- β is a parameter expressing density-dependent prerecruit mortality, and
- c is an exponent modifying the severity of density-dependence (MacCall 1980).

To simulate the response to an autocorrelated environmental variable, the density-independent term (α) of the stock-recruit function was made to follow a sine wave with a wavelength of 20 years and minimum and maximum values of 0.67 and 1.33 times the mean value (Figure 18a). To simulate the unpredictable component of environmental variability, this term was perturbed using a multiplicative log-normally distributed random number sequence with a mean of 0.0 and a standard deviation of 0.35, which resulted in a range of values of about 0.5 to 2.0 (Figure 18b). The resulting signal was used to modify recruitment generated by the model, which assumes an asymptotic stock-recruit curve, age at maturity of one year, and an instantaneous rate of natural mortality of 1.0. The spawner stock biomass sequence generated by the model shows that the population filters out the random variability and returns the autocorrelated signal (Figure 18d). This demonstrates that a population with parameters like those assumed in the model will be well buffered against random variability but strongly modulated by an autocorrelated signal.

The periodicity of any cyclical change will affect population growth according to the generation time of the fish and the biomass growth pattern of each year class. The spawner biomass of short-lived species will react quickly to changes in recruitment, whereas long-lived species may exhibit a considerable time lag between a period of enhanced or depressed reproductive success and its effect on subsequent spawner biomass levels.

Fish species with delays of several years between hatching and the maximum reproductive output of a year class may oscillate out of phase with an environmental cycle if the wavelength of the cycle is approximately double the average age of the spawning population. Reduced spawner biomasses following years of depressed year-class strength would coincide with a period of favorable environment for spawning and recruitment, giving the impression of high productivity at small spawner stock sizes (Figure 19b). This would result in an overestimate of the severity of density-dependence, and an overestimate of maximum average yield (MAY).

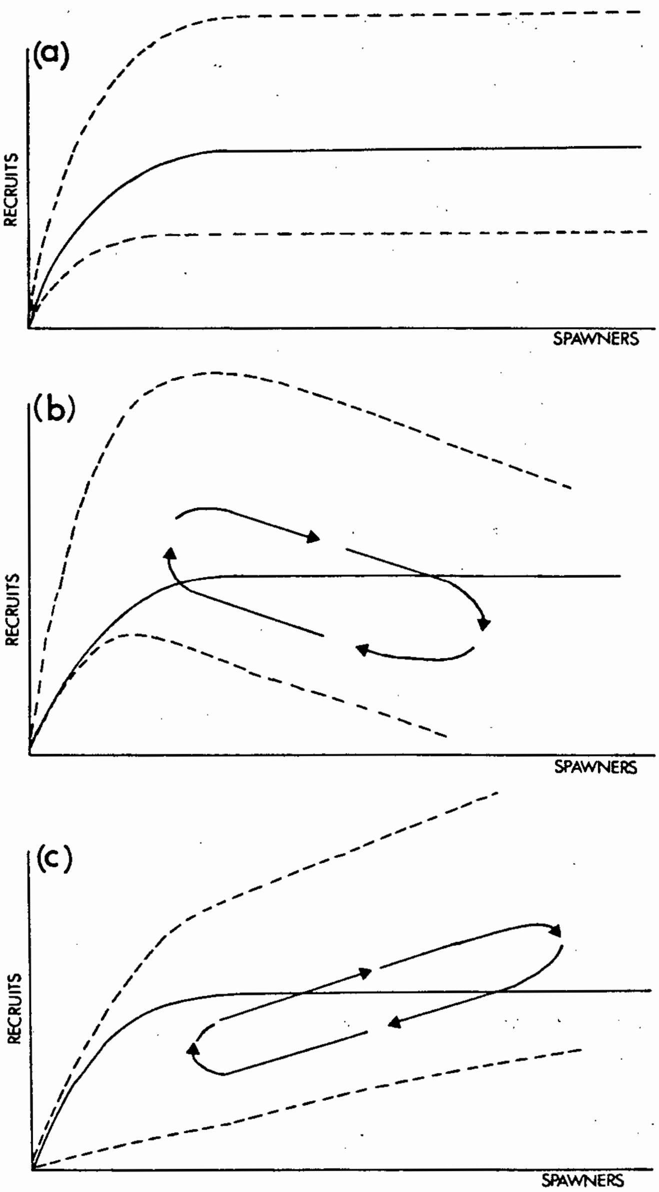


Figure 19. Theoretical stock-recruit functions for fish species, showing possible ranges of recruitment variability (broken lines): (*a*) with no autocorrelation in the environmental variable affecting recruitment, (*b*) with autocorrelation in environment exhibiting a periodicity of approximately double the average age of the spawner population, and (*c*) autocorrelation in environment exhibiting a periodicity of approximately eight times the average age of the spawning population. Arrows indicate temporal progression of stock-recruit values under the influence of the autocorrelated environmental signal without random variability.

If the environmental cycle is of long wavelength in relation to the average age of fish in the spawning population, the spawning biomass will tend to come into phase with the cycle, and the stock-recruit data will suggest low productivity at reduced biomass and high productivity at elevated biomass levels (Figure 19c). This will result in an underestimate of the degree of density-dependence and an underestimate of MAY. In either case, the influence of autocorrelation in year-class strength would increase the probability of severe stock depletions, particularly under constant catch policies.

The theoretical examination of the potential effect of autocorrelated environmental variability makes it seem important to improve the description of the larger-scale variability component in the Benguela system and in other eastern boundary current systems, and to develop appropriate harvesting strategies that are robust to runs of years in which environmental conditions adversely affect recruitment. If cycles in environmental conditions, similar to those found by Tyson (1981) for rainfall over the southern African continent, can be determined in the marine environment, and shown to consistently affect recruitment, then a measure of recruitment prediction may be feasible.

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1.4 Objectives and approach of this study

Although a number of fish populations in the southern Benguela region have been harvested commercially for a considerable period of time, very little information exists on the temporal and spatial patterns of abundance of the egg and larval stages. An attempt to describe the patterns of abundance of pilchard Sardinops ocellata, and later the anchovy Engraulis capensis, eggs and larvae was made between 1950 and 1969. These results have only been partially analysed and therefore never fully documented. However Stander and Le Roux (1968) and Crawford (1980a) have discussed some of the egg data from the surface plankton net tows. Thus the primary objective of this study was to document, for the first time, the patterns of abundance of the egg and larval stages of the commercially exploited, potentially exploitable and other abundant species in the plankton over a full year and relate this to patterns in the environment. It was anticipated that coherence in, and similarity between, ichthyoplankton and environmental patterns would allow the selection of suitable environmental variables for monitoring with a view to predicting recruitment. As a consequence of this it was necessary to give consideration to the kinds of anomalies likely to adversely inluence recruitment in the different populations. In the process of achieving the main objective, a number of subsiduary objectives became feasible. Apart from those species caught commercially, little is known about the relative abundance of the various components of the neritic ichthyofauna. As most fish produce planktonic egg and larval stages with roughly equal catchability by plankton nets, the study provided the first oppurtunity to roughly determine the relative abundance of nearly all members of the ichthyofauna in the southern Benguela Current region. The nearly complete species composition data also provided a basis for examining ichthyoplankton species associations within the region.

At the commencement of the study there was no review of the seasonal variability in the physical environment of the Benguela Current system. This has subsequently been rectified by Parrish et al. (1983), Shelton et al. (1985, see Section 1.3), Shannon (1985) and McLain et al. (1985). However, the repeated sampling of the CELP survey grid over a 13 month period in 1977/78 provided an opportunity to examine seasonal changes in the environment at a scale intermediate to that of the large scale averaging studies (e.g. Parrish et al. 1983) and the more detailed mesoscale oceanographic investigations (e.g. Shannon et al. 1981). Similarly the sampling strategy adopted during CELP allowed the first description to be made of large scale seasonal changes in the pattern of abundance of plankton, as measured by the displaced volume of plankton net samples and the concentration of chlorophyll and microplankton, for the southern Benguela Current region.

The approach adopted to fulfil the major objective was repeated monthly sampling of both the physical environment and the plankton over a broad area of the southern Benguela Current region (Fig. 1.2) for a one year period. Vertical profiles of temperature were obtained by means of a bathythermograph and water samples were collected at discrete depths from casts of 5 litre bottles for the analysis of salinity, chlorophyll, and microplankton. Drift cards were released in order to determine the general circulation of surface water. Plankton was collected with a double oblique tow with a Bongo sampler. As a result of the commercial importance of the anchovy resource the spawning and larval abundance patterns of this species was subject to further analysis at regular intervals after the intial one year programme. From 1983 onwards the area surveyed was expanded to cover the full spawning range of the species in the southern Benguela region to allow spawner biomass estimates to be made using acoustics and the egg production method (Lasker 1985). Surveys directed towards the

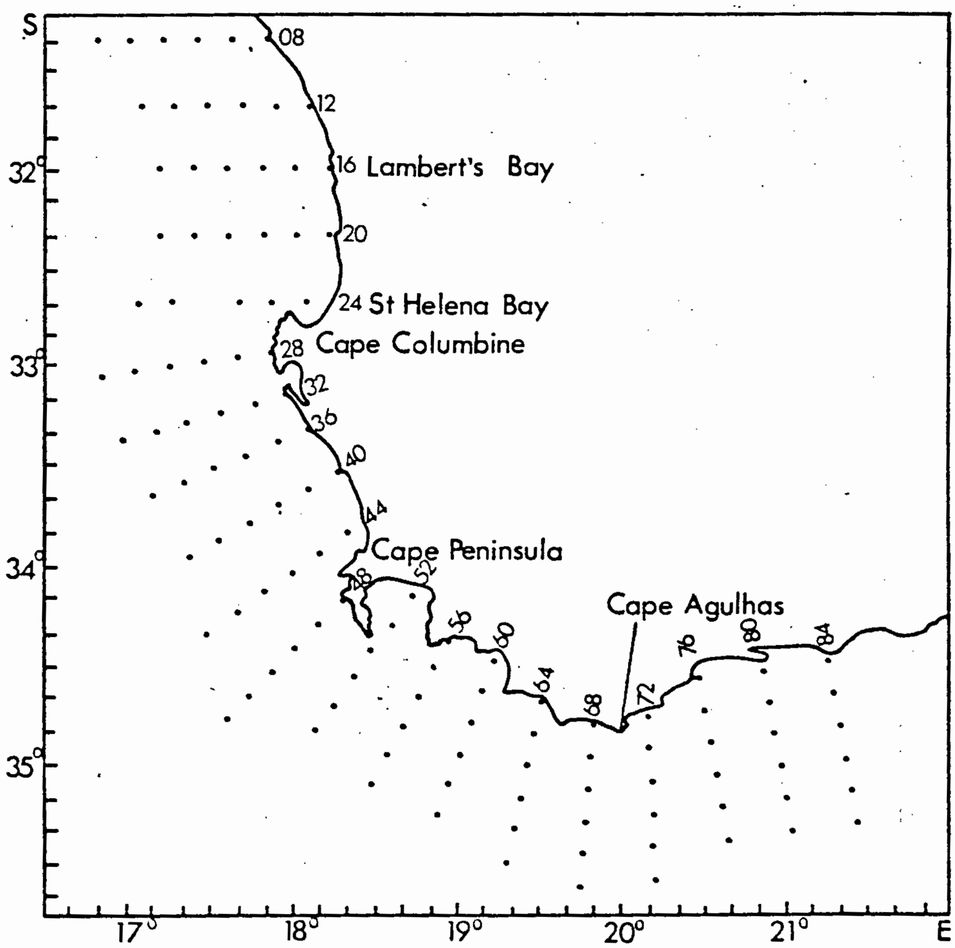

Fig. 1.2 Station grid surveyed during the Cape Egg and Larval Programme.

sampling of fish eggs and larvae since the start of CELP are summarized in Table 1.1.

Table 1.1

General details of ichthyoplankton surveys conducted between August 1977 and November 1984.

Month	Year	Duration	Area	Stations	Parameter	Net
August	1977	18 - 29	CELP	119	T,S,Chl,Mi	B,N
September	1977	16 - 29	CELP	120	T,S,Chl,Mi	B,N
October	1977	14 - 26	CELP	140	T,S,Chl,Mi	B,N
Nov/Dec	1977	19 - 11	CELP	120	T,S,Chl,Mi	B,N
January	1978	7 - 20	CELP	138	T,S,Chl,Mi	B,N
February	1978	1- 12	CELP	140	T,S,Chl,Mi	B,N
March	1978	7 - 18	CELP	140	T,S,Chl,Mi	B,N
April	1978	6 - 17	CELP	140	T,S,Chl,Mi	B,N
May	1978	2 - 14	CELP	140	T,S,Chl,Mi	B,N
June	1978	7 - 21	CELP	140	T,S,Chl,Mi	B,N
July	1978	17 - 21	CELP	70	T,S,Chl,Mi	B,N
August	1978	4 - 16	CELP	132	T,S,Chl,Mi	B,N
November	1978	4 - 14	CELP	120	T,S,Chl,Mi	B
November	1979	5 - 6	Cape Peninsula	10	T,S,Chl	M
November	1980	20 - 21	Cape Peninsula	5	T	M
December	1980	11 - 14	Walker Bay	24	T	B,M
January	1981	27 - 29	Cape Peninsula	16	T,S,Chl	B,M
October	1981	10 - 11	Cape Peninsula	10	T	B,M
November	1981	5 - 18	CELP	69	T,Chl	B
November	1982	18 - 24	CELP	119	T	B
November	1983	1 - 29	Ext CELP	271	T,S	C,RMT6
November	1984	5 - 29	Ext CELP	308	T	C,RMT6
November	1985	11 - 26	Strat. Rand. Grid	364	T	C

T=temperature, S=salinity, Chl=chlorophyll, Mi=microplankton
B=Bongo net, M=Miller net, RMT6=multiple opening and closing research midwater trawl net, N=neuston net, C=Calvet net.
Ext CELP = extended CELP grid used for egg production estimate of anchovy spawner biomass, Strat. Rand. Grid = roughly the same area covered as extended CELP but lines positioned on a stratified random basis.

The data from the surveys are interpreted in Sections 2 to 4 in order to determine broad spatial and seasonal patterns within the southern Benguela Current region of the physical properties, the plankton in general and the ichthyoplankton in particular. Although it is acknowledged that the description of seasonal events from a one year data set could be construed as tenuous under certain circumstances, there is strong evidence from the analysis of Andrews and Hutchings (1980) and the description of sea surface temperature variability in McLain et al. (1985) to suggest that the seasonal signal is a strong and regular forcing agent in the southern Benguela region. Furthermore the study period of 1977/78 was apparently not associated with any major anomaly, although Shannon et al. (1984a) indicate that the sea temperature in 1978 was somewhat cooler than average and that there was a negative atmospheric pressure gradient anomaly. In Section 5 ichthyoplankton and environmental patterns are compared. In Section 6 consideration is given to the kind of environmental anomaly likely to adversely affect the survival of fish eggs and larvae produced by adults displaying different life history strategies and occupying different habitats within the southern Benguela Current region. In Section 7 the major conclusions of this thesis are discussed.

2 INTRA-ANNUAL ENVIRONMENTAL VARIABILITY

2.1 Temperature and salinity structure of the southern Benguela region

2.1.1 Introduction

The oceanography of the southern Benguela region may be expected to be complex due to the complicated topography, large seasonal changes and variable meteorological conditions described in Shannon (1985). Previous interpretations of hydrographic data from the area by Shannon (1966), Andrews and Cram (1969), Jones (1971), Bang (1971, 1973), Bang and Andrews (1974), Andrews and Hutchings (1980) and Shannon et al. (1981) have tended to emphasise the mesoscale temporal and spatial heterogeneity rather than processes at the larger scale (>50Km, >10 days, Barber and Smith 1981) which may be more relevant to the dynamics of neritic fish populations within the Benguela system. The few studies that have concentrated on the larger scale are reviewed in Section 1.3. In most instances they are based on large scale temporal and spatial averaging from which it is not easy to deduce the causative mechanisms of anomalies. In contrast, the CELP data allows a large scale seasonal discription of the southern Benguela system to be made without losing the resolution required to investigate the causative processes. It therefore provides a valuable bridge between mesoscale studies and those analyses involving large temporal and spatial averaging.

This describes a new set of temperature and salinity data from over 2 000 hydrocasts taken on regular monthly surveys between August 1977 and August 1978, and thereafter at less regular intervals until November 1985, at an appropriate scale for understanding the life history stategies of neritic fish species in the southern Benguela system, and for determining some of the mechansisms causing anomalies in SST time series.

2.1.2 Methods

Data were collected over the CELP survey grid at monthly intervals between August 1977 and August 1978. The grid was resampled in November 1978, November 1981 (southern half only) and in November 1982. In November 1979 (Shelton 1984) and November 1980 data were collected along a single line of stations which intersected the thermal front close to the Cape Peninsula. In November 1983 and 1984 an Extended CELP grid was surveyed with additional stations positioned both further offshore and further east in order to cover the full spawning range of the anchovy for application of the egg production technique of biomass estimation (Lasker 1985). In November 1985 roughly the same area was surveyed as in 1984, but lines were positioned in a stratified random manner to increase sampling intensity in known areas of abundant anchovy spawning.

With the exception of the November 1983 to 1985 surveys, which were carried out on the RS Africana, the temperature data were collected from bathythermograph (BT) casts down to a maximum depth of 275m. Water samples for salinity were collected from casts of 5 litre bottles with a maximum of 8 samples distributed between the surface and 100m, with samples positioned just above, within and just below the thermocline, where one could be clearly detected. Salinity samples were stored in glass bottles and returned to the laboratory ashore for analysis with an inductively-coupled Autolab salinometer. On the November 1983 to 1985 surveys temperature was monitored using an electronic temperature/depth probe linked to a microprocessor in the laboratory. Water samples for salinity analysis were not collected on cruises after August 1978, except at certain stations in November 1983.

2.1.3 Results

The mean monthly and mean spatial sea surface temperature (SST) over the survey grid is shown in Fig. 2.1. There is a distinct seasonality in SST with a peak of about 20°C in January (summer) and a trough of about 14°C in August (winter). The S.D. increased with increasing temperature indicating more variability in SST during summer as compared to winter. The mean spatial pattern for the year clearly shows that water with an SST of less than 17°C occurred mostly east of Cape Agulhas and that water less than 15°C occurred predominantly north of the Cape Peninsula, along the west coast. The pattern of mean SST shows that a surface front formed by 15 to 17°C isotherms occurred between the Cape Peninsula and Cape Columbine. North of line 24 the 16 and 17°C isotherms diverged offshore. Water with a mean SST warmer than 18°C was found at offshore stations on the west coast between lines 32 and 48, and over the Agulhas Bank in the south.

The most distinctive large scale feature with regard to the temperature and salinity measurements from the individual surveys was the variability in discontinuity zones which formed horizontal gradients (fronts) and vertical gradients (thermoclines and haloclines).

Horizontal gradients

There is a clear seasonal pattern of surface temperature structure in the southern Benguela region. In winter (e.g. August 1977, Fig. 2.1.2) the surface water within the CELP survey grid was relatively isothermal between 14 and 16°C. Warmer water was encountered at the southern edge and the eastern

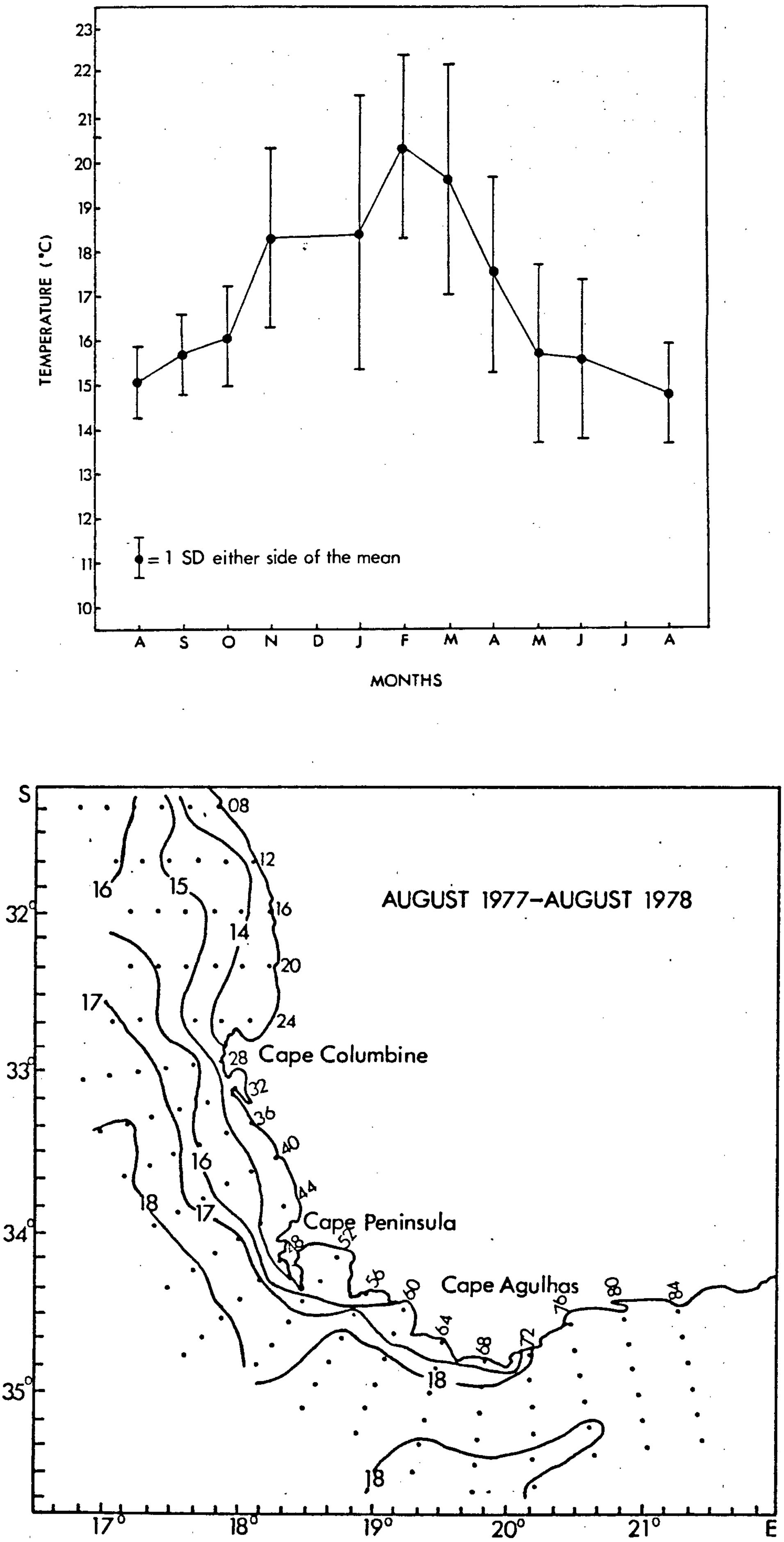

Fig. 2.1.1 Mean monthly and spatial SST over the CELP survey grid, August 1977- August 1978.

extremity of the survey grid. Upwelling activity in winter (e.g. June 1978, not shown) only gave rise to a moderate temperature front because of the cool temperature of surface oceanic water in winter. In spring (e.g. October 1977, Fig. 2.1.2), an increase in temperature offshore combined with an increased occurrence of coastal upwelling gave rise to a more complex temperature structure and a well developed thermal front extending from Cape Town (line 48) to Cape Columbine (line 24). North of Cape Columbine the front weakened and 15 and 16°C isotherms diverged offshore, whereas the 13 and 14°C isotherms bent into St Helena Bay. In summer (e.g. January 1978, Fig. 2.1.2) there was a dramatic increase in the surface temperature offshore, particulary south of Cape Columbine extending over the Agulhas Bank. The January 1978 survey took place during active upwelling and as a result an intense thermal front had developed from Cape Columbine (line 28) to Cape Agulhas (line 72) with a temperature change of 8°C within 40Km of the Cape Peninsula (line 48). Relaxation of upwelling off the Cape Peninsula and further east to Cape Agulhas during the February 1978 survey (not shown) allowed water of 19°C to 21°C to advance to the coast. In January 1978 the divergence of surface isotherms in the vicinity of Cape Columbine was again apparent. By late autumn (e.g. May 1978, Fig. 2.1.2) temperatures offshore had decreased and even though some upwelling activity was encountered along the west coast, only a moderately strong thermal front developed and the area covered by water with a temperature of less than 16°C expanded offshore.

The surface salinity structure (Fig. 2.1.3) shows that a haline front was present in the Cape Columbine to Cape Peninsula area in all 4 seasons, although it was best developed in spring and summer. In these two surveys there was a divergence of surface isohalines in the vicinity of Cape Columbine with more saline water moving offshore and less saline water moving into St Helena Bay. The strong salinity front which developed in January 1978 occurred between

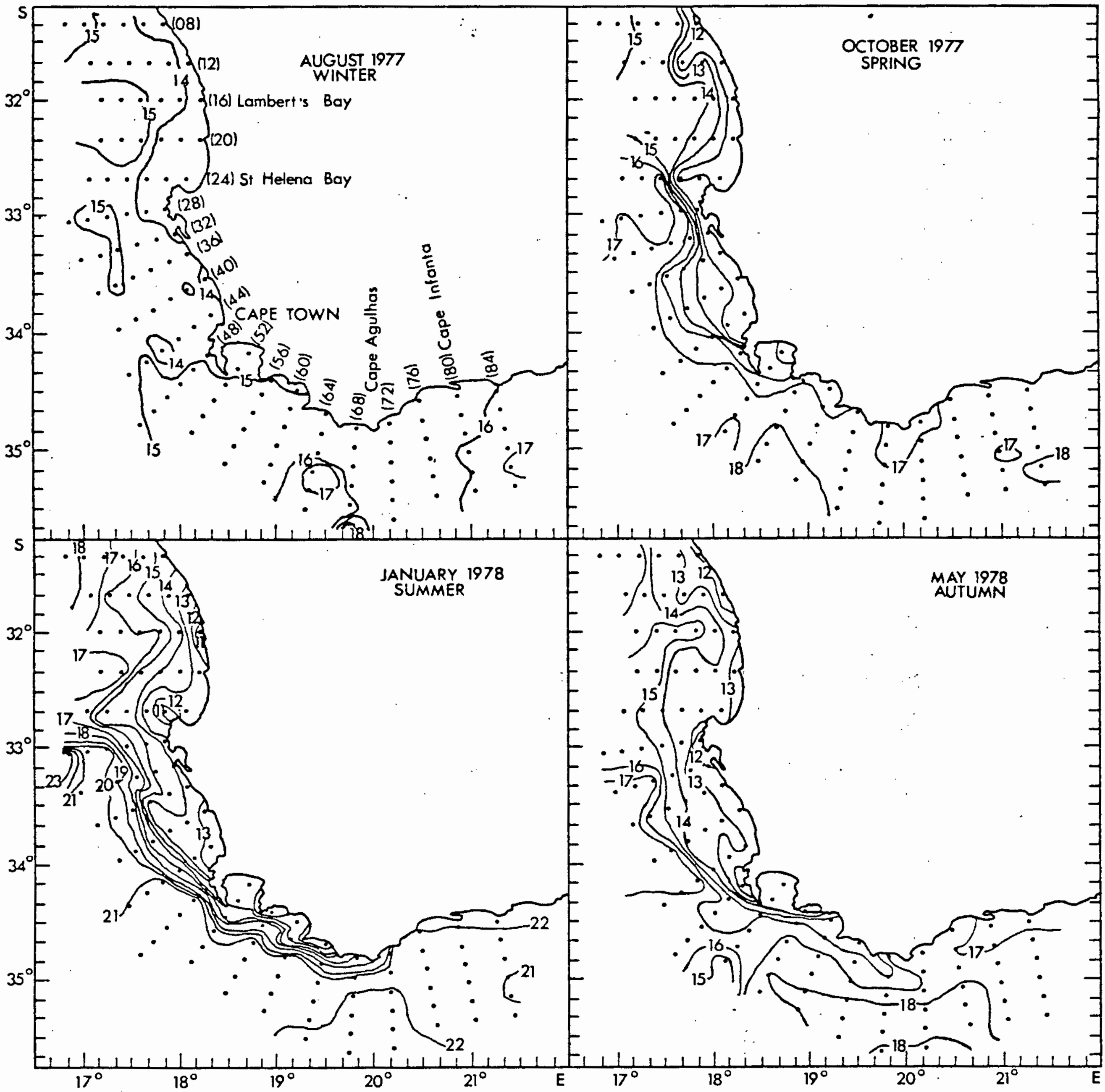

Fig. 2.1.2 Sea surface temperature measurements during selected CELP surveys showing the seasonal pattern of horizontal gradients.

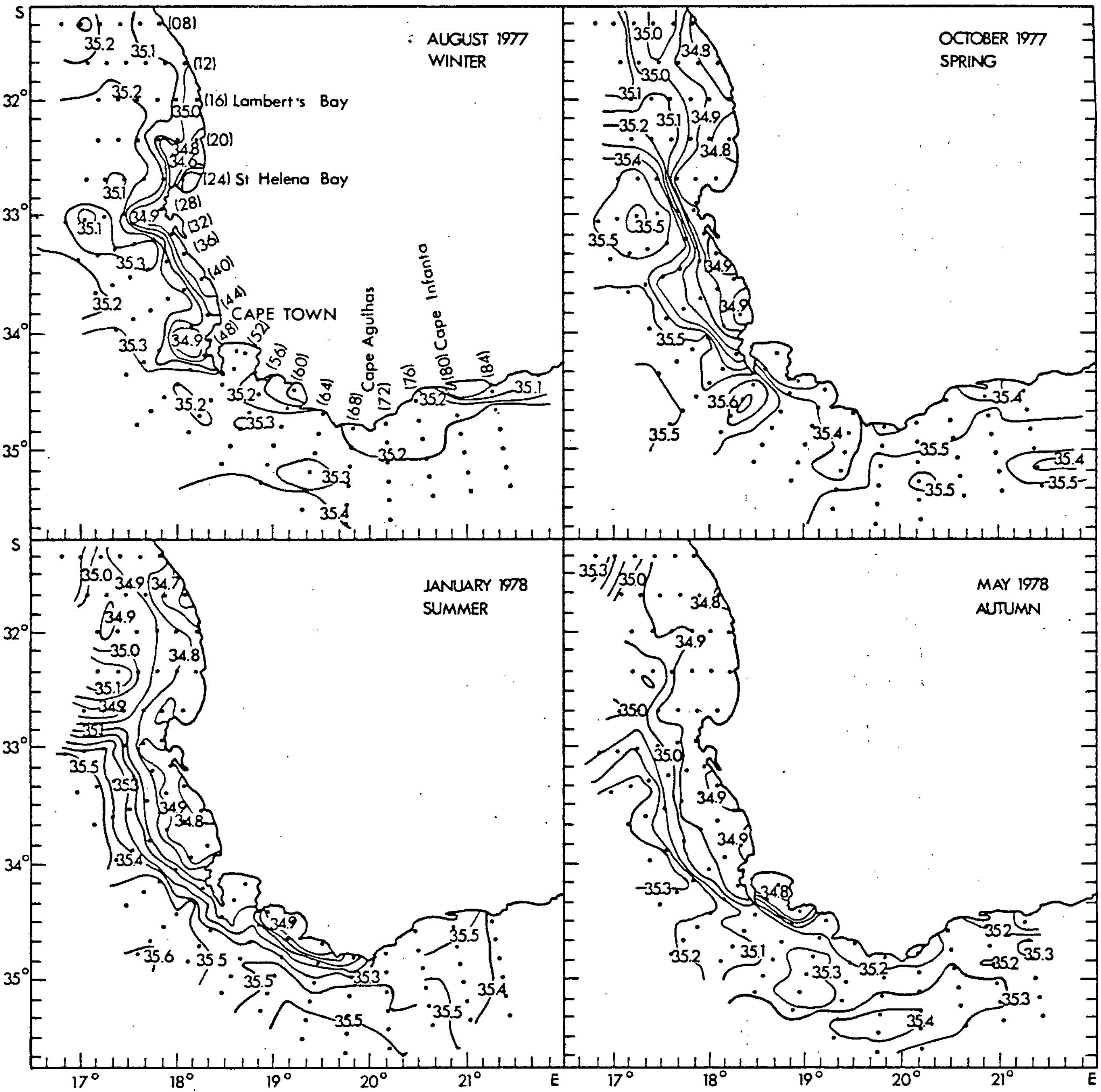

Fig. 2.1.3 Surface salinity measurements during selected CELP surveys showing seasonal changes.

newly upwelled water with a salinity of less than 34.8°/oo and water warmer than 21°C offshore which had a salinity of more than 35.5°/oo. During all seasons there was a tendency for the salinity to be highest over the Agulhas Bank.

A comparison of surface temperature structure over 7 November surveys (Figs. 2.1.4, - 2.1.6) shows that the degree of offshore warming at this time of the year resulted in variations in the intensity of horizontal gradients and the size of the area covered by water with a temperature of less than 16°C. In the November/December 1977 survey 21°C water was encountered offshore on the west coast, whereas in November 1978 this same area was covered by 17°C water, and in November 1984 by 16°C and 17°C water. The size of the area covered by water with a temperatue of less than 16°C appeared to be inversely related to the degree of offshore warming and directly related to upwelling activity.

From surface temperature measurements made during the Extended CELP surveys (Figs 2.1.5 and 2.1.6) it is clear that upwelling as far south as Cape Agulhas in November prevents warm water from advancing right up to the coast. East of Cape Agulhas warm water tends to dominate the inshore area except for in the vicinity of Plettenberg Bay where a slight alteration in the angle of the coastline towards a north-south orientation was associated with relatively strong upwelling in both the November 1984 and 1985 surveys (Fig. 2.1.6). The Bank is relatively narrow in this region and Agulhas Current water was encountered along the shelf edge outside of the cool water which upwelled in the vicinity of Plettenberg Bay, giving rise to a moderately strong thermal front. In the November 1983 and 1984 surveys the 18°C, and in November 1985 the 19°C isotherm intruded closer to the coast in the vicinity of line 84 on the Agulhas Bank. This warming occurred in close association with the Alphard Bank which is

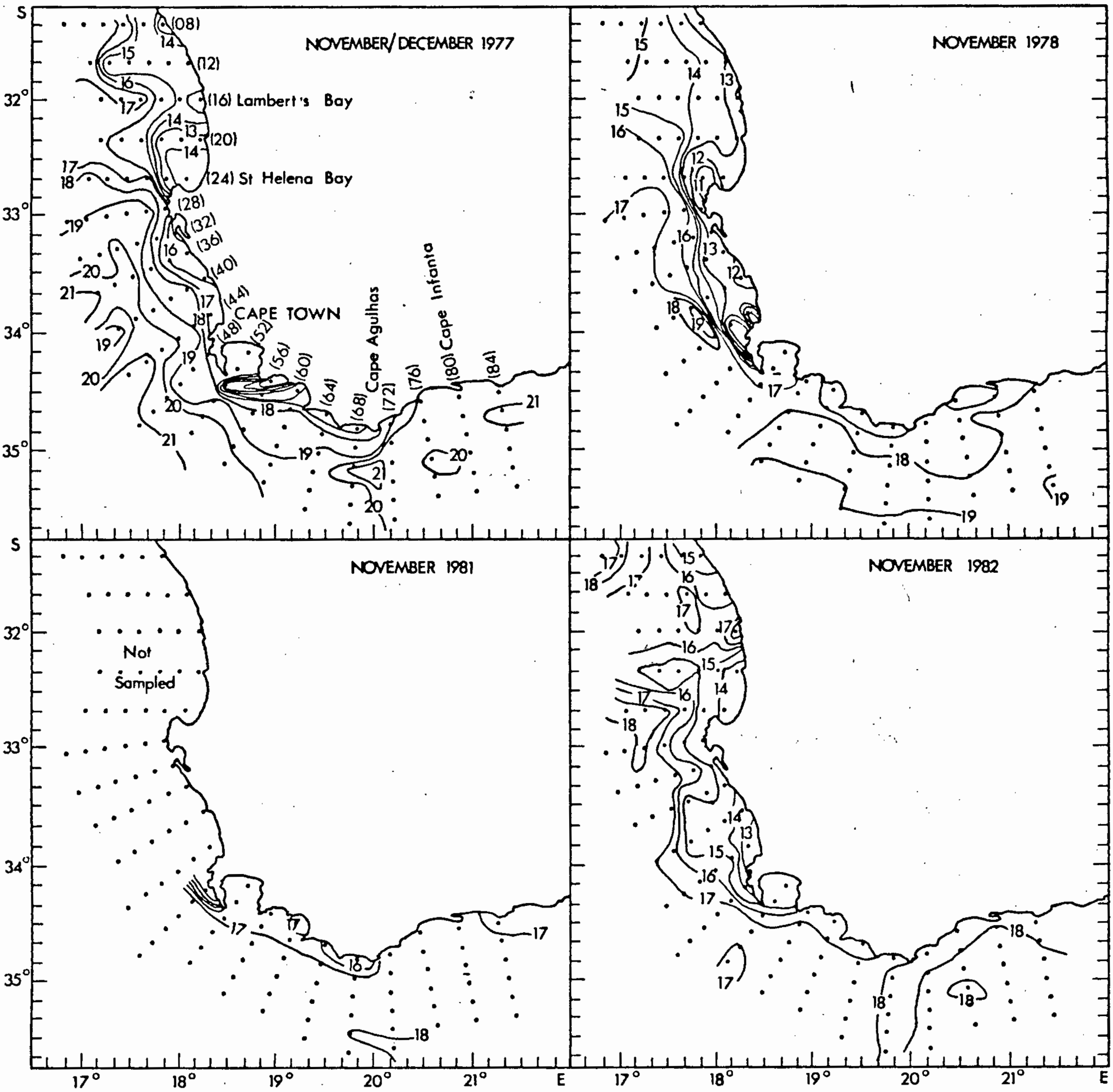

Fig. 2.1.4 Surface temperature structure in November 1977, 1978, 1981 and 1982.

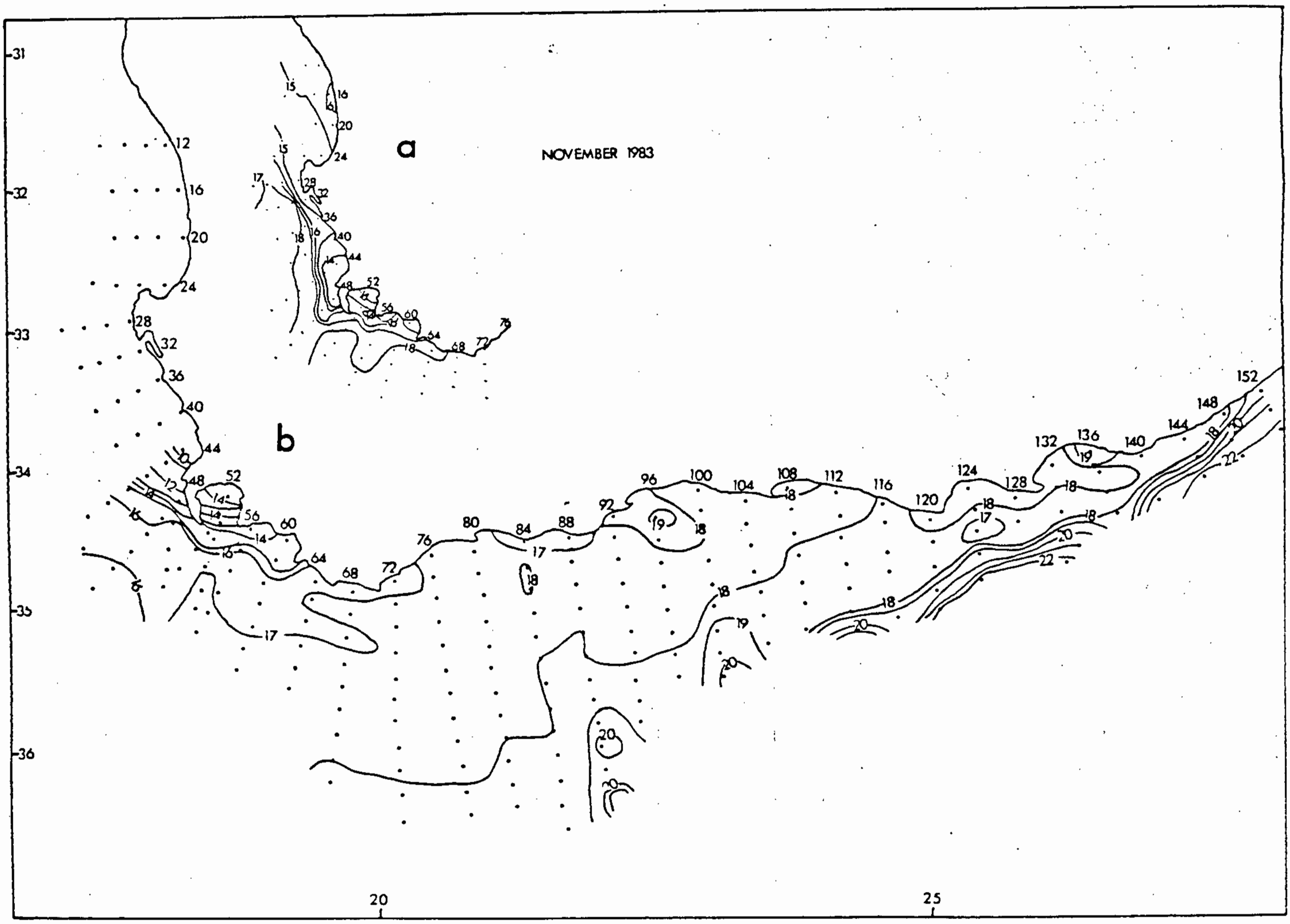

Fig. 2.1.5 Surface temperature structure during the Extended CELP survey in November 1983. (a) shows the surface temperature during the first leg of the cruise which partly overlapped the second leg shown in (b).

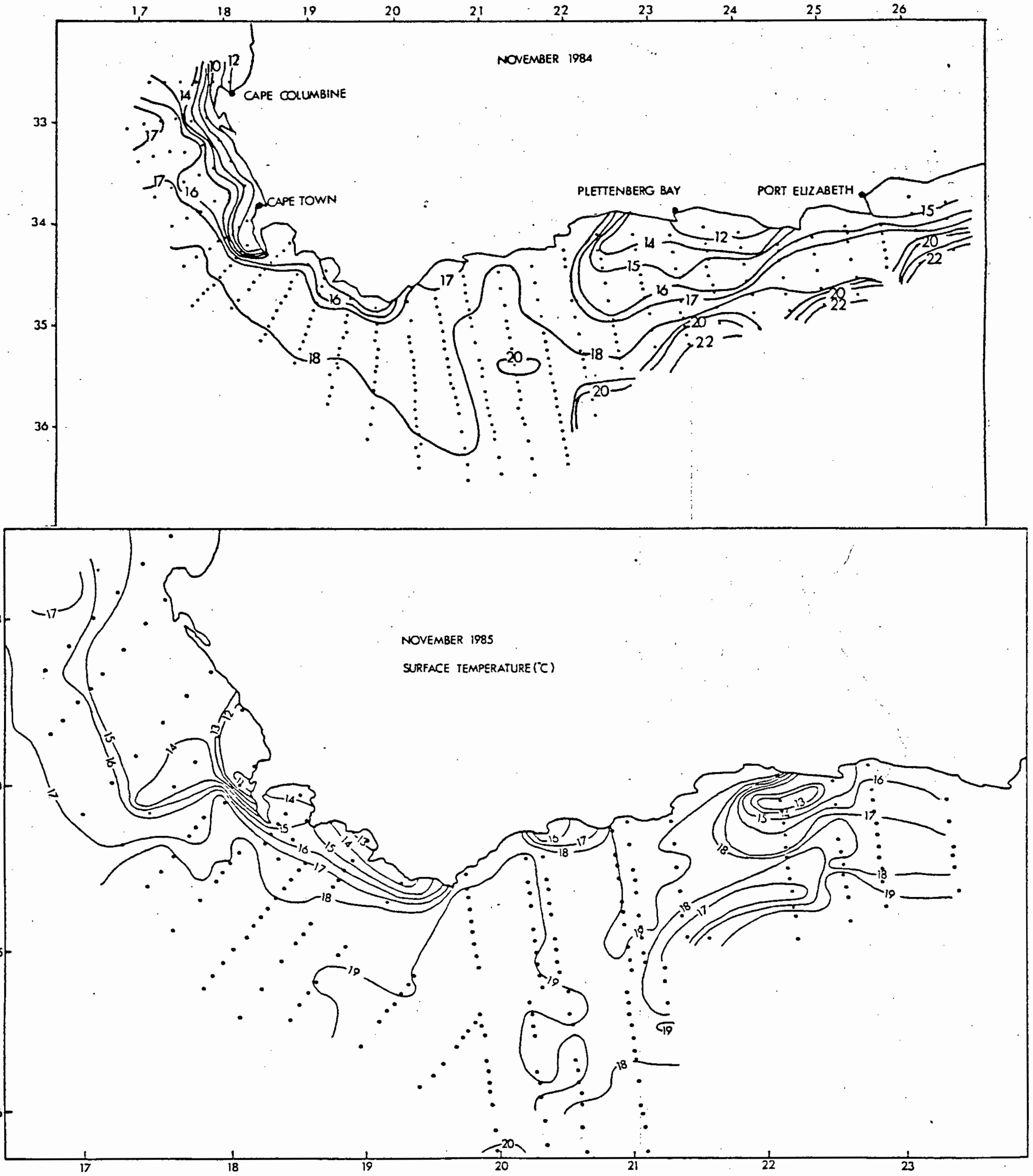

Fig. 2.1.6 Surface temperature structure during the Extended CELP and the Stratified Random surveys in November 1984 and 1985.

a particulary shallow area over the Agulhas Bank suggesting that the Alphard Bank may influence circulation in the area or alternatively increase the effect of surface warming within a reduced water column.

Vertical gradients

Six survey lines (16, 28, 44, 48, 64 and 80) were selected to show spatial and seasonal changes in the vertical temperature structure (Figs. 2.1.7 - 2.1.13). On line 16 off Lambert's Bay (Fig. 2.1.7) the vertical temperature structure remained fairly constant throughout the year with a maximum vertical temperature range of 8°C. The 10°C isotherm was situated within 50m of the surface in spring, summer and autumn but was deeper in winter. In summer a moderately strong front developed between upwelled water inshore and 15-16°C water further offshore. A lens of warm water about 40 and 50km from the coast in the January 1978 survey may indicate that an anticyclonic eddy existed in the area at this time.

On line 28 off Cape Columbine the steeply sloping shelf break caused an upward tilt to isotherms close to the coast throughout the year (Fig. 2.1.8), although the inclination was least steep in winter and autumn. In spring and summer water warmer than 16°C advanced towards the coast and a strong surface front developed. In winter the warm layer retreated and the front weakened even though the 12°C and cooler isotherms continued to be tilted towards the surface inshore. Further offshore the 12°C isotherm lifted towards the surface in autumn and winter with the result that a considerably greater portion of the water column comprised water cooler than 12°C, in contrast to summer. Down-tilting of isotherms about 90km from the coast in summer may be evidence that a poleward flow occurred in this region.

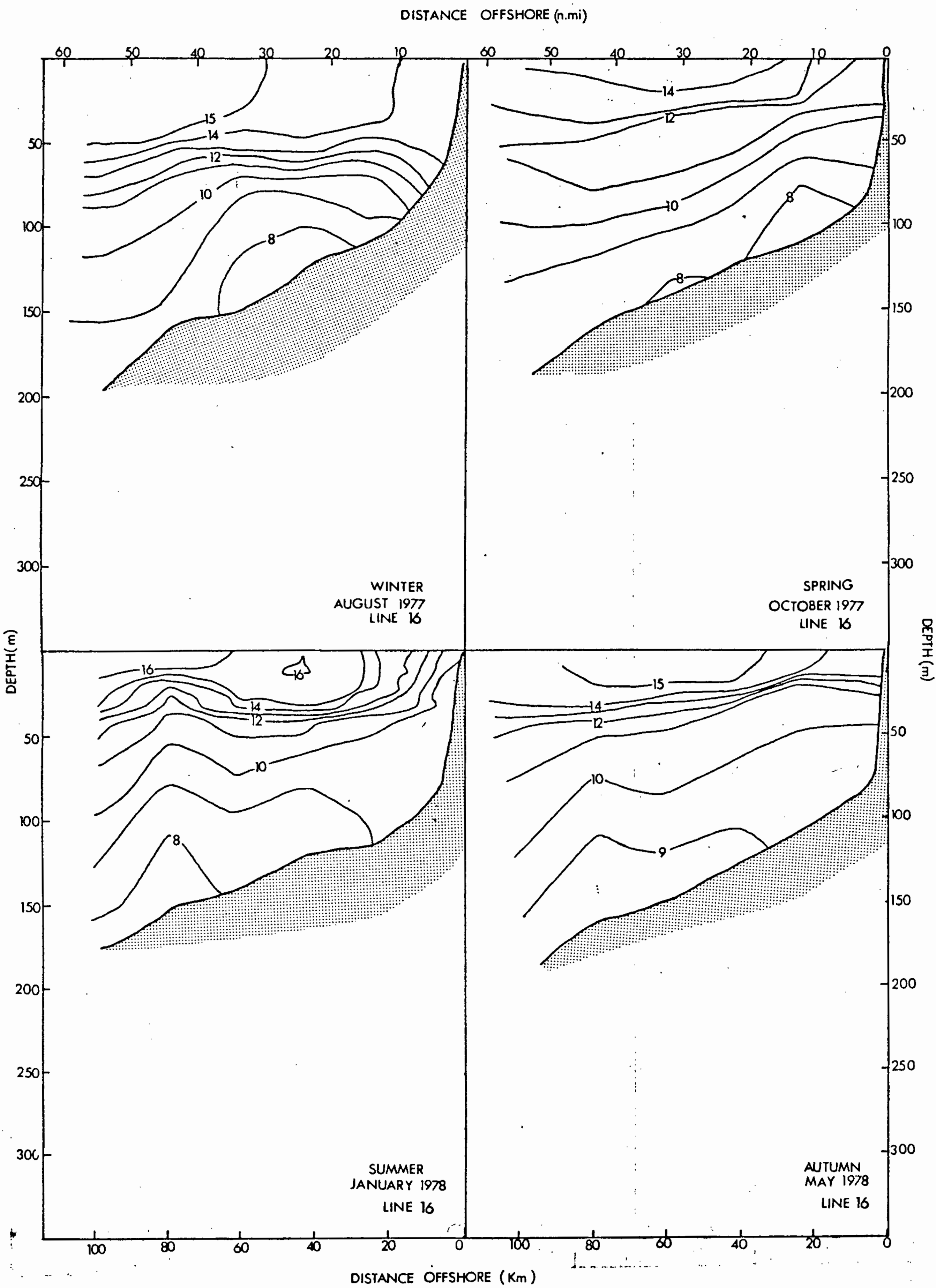

Fig. 2.1.7 Seasonal change in vertical temperature gradients along line 16 off Lambert's Bay.

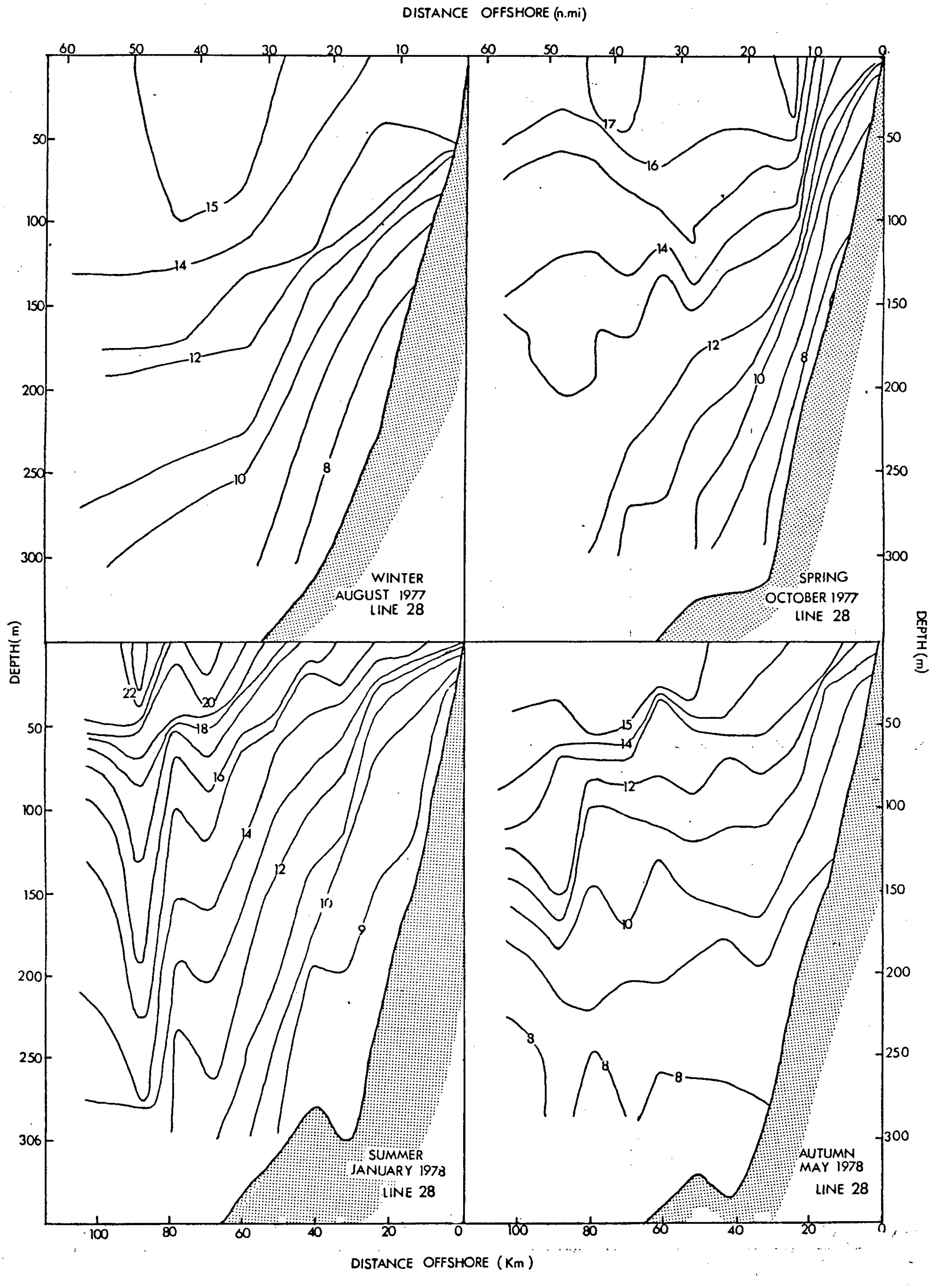

Fig. 2.1.8 Seasonal change in vertical temperature gradients along line 28 off Cape Columbine.

The seasonal change in temperature structure along line 44 west of Table Bay (Fig. 2.1.9) showed a similar sequence of events to that which occurred at line 28. Because of the steep bottom topography, isotherms tended to slope towards the surface throughout the year, although in winter there was a marked downwelling of isotherms inshore of a strong sub-surface front, with the result that the top 20m of the water column was fairly isothermal. In spring upwelling inshore, together with 16°C water within 20Km of the coast, resulted in the formation of a moderately strong front at the surface. The front was intensified in summer by the presence of 20°C water within 30Km of the coast. The weaker front in winter corresponded to a cooling of water in the top 100m offshore. Whereas in summer water cooler than 10°C appeared to be limited to a thin layer close to the bottom as a result of the advection of warm water onto the coast, a larger volume of cool water was able to move up onto the shelf in winter. The dynamic nature of the front in summer is evident from the temperature section along line 44 in February 1978 when upwelling was minimal (Fig. 2.1.10). Without cold water being lifted to the surface by offshore Ekman drift, the warm layer was able to advance towards the coast over the cooler water. As a result the surface front weakened substantially and the temperature discontinuity was strongest in the vertical plane in the form of a strong thermocline.

At line 48 off the Cape Peninsula (Fig. 2.1.11) the shelf is particulary narrow and this appears to allow warm water to advance as a fairly deep layer particularly close to the coast, even during upwelling. In winter isotherms 70 to 90Km offshore were tilted downwards, indicating the possibility of poleward flow around Cape Point in winter (see Section 2.2). Compared with the temperature sections off the west coast, the more gently sloping bottom topography at line 64 corresponded to reduced upward inclination of isotherms (Fig. 2.1.12). In winter the water was well mixed down to 100m. The progressive increase in temperature

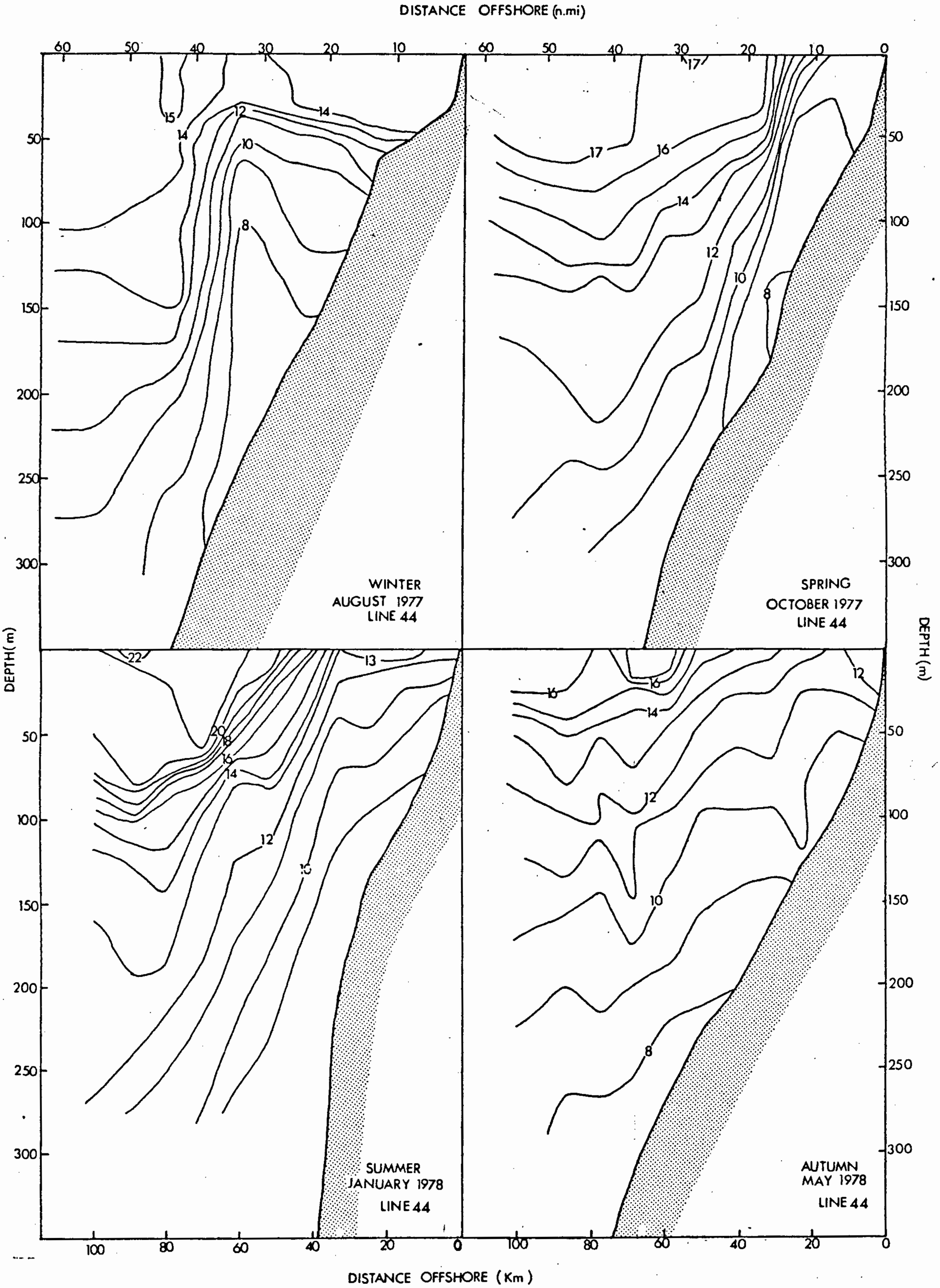

Fig. 2.1.9 Seasonal change in vertical temperature gradients along line 44 off Table Bay.

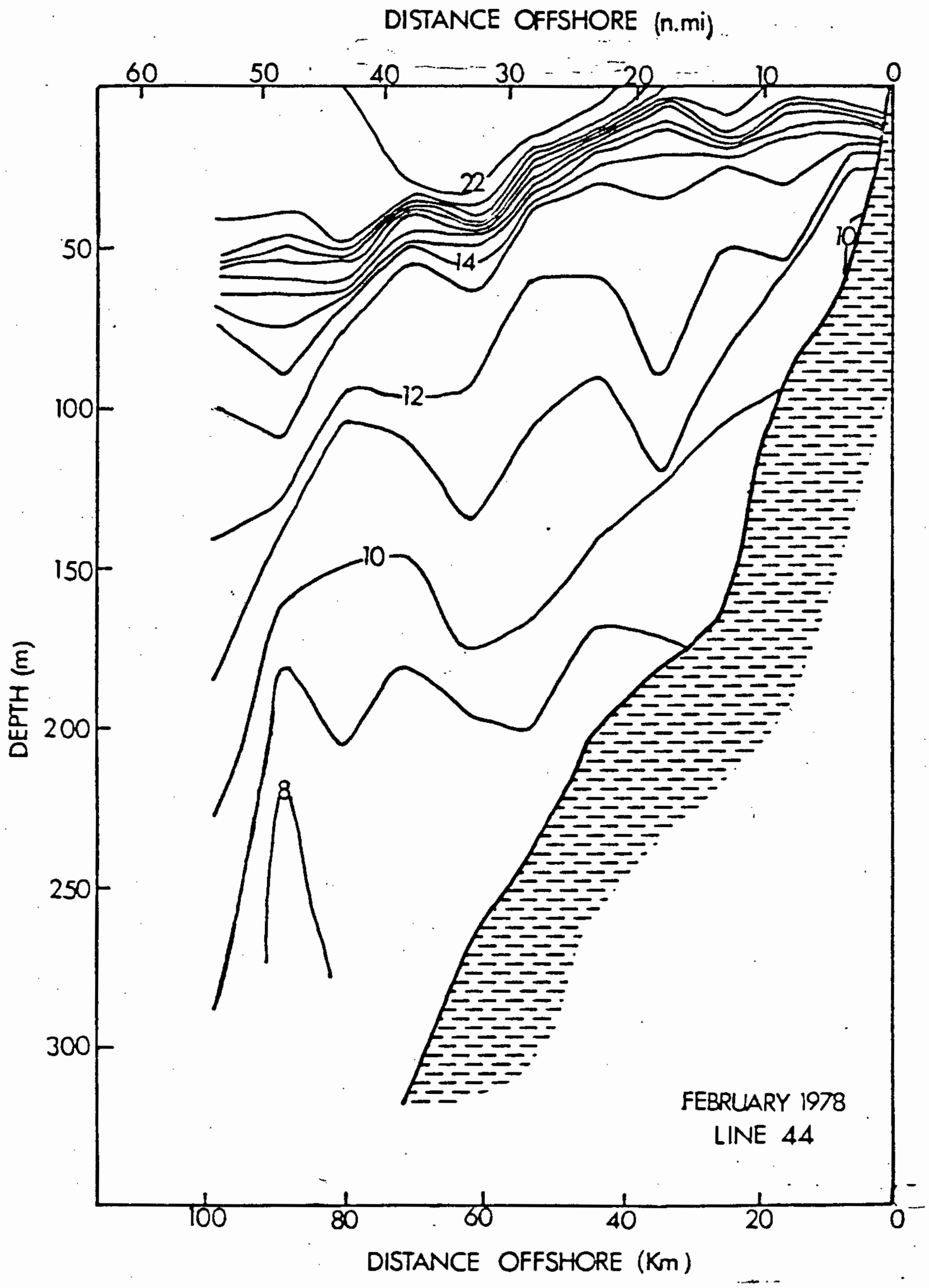

Fig. 2.1.10 Temperature section along line 44 in February 1978 showing quiescent upwelling conditions which resulted in weakening of the surface front allowing warm water to advance towards the coast.

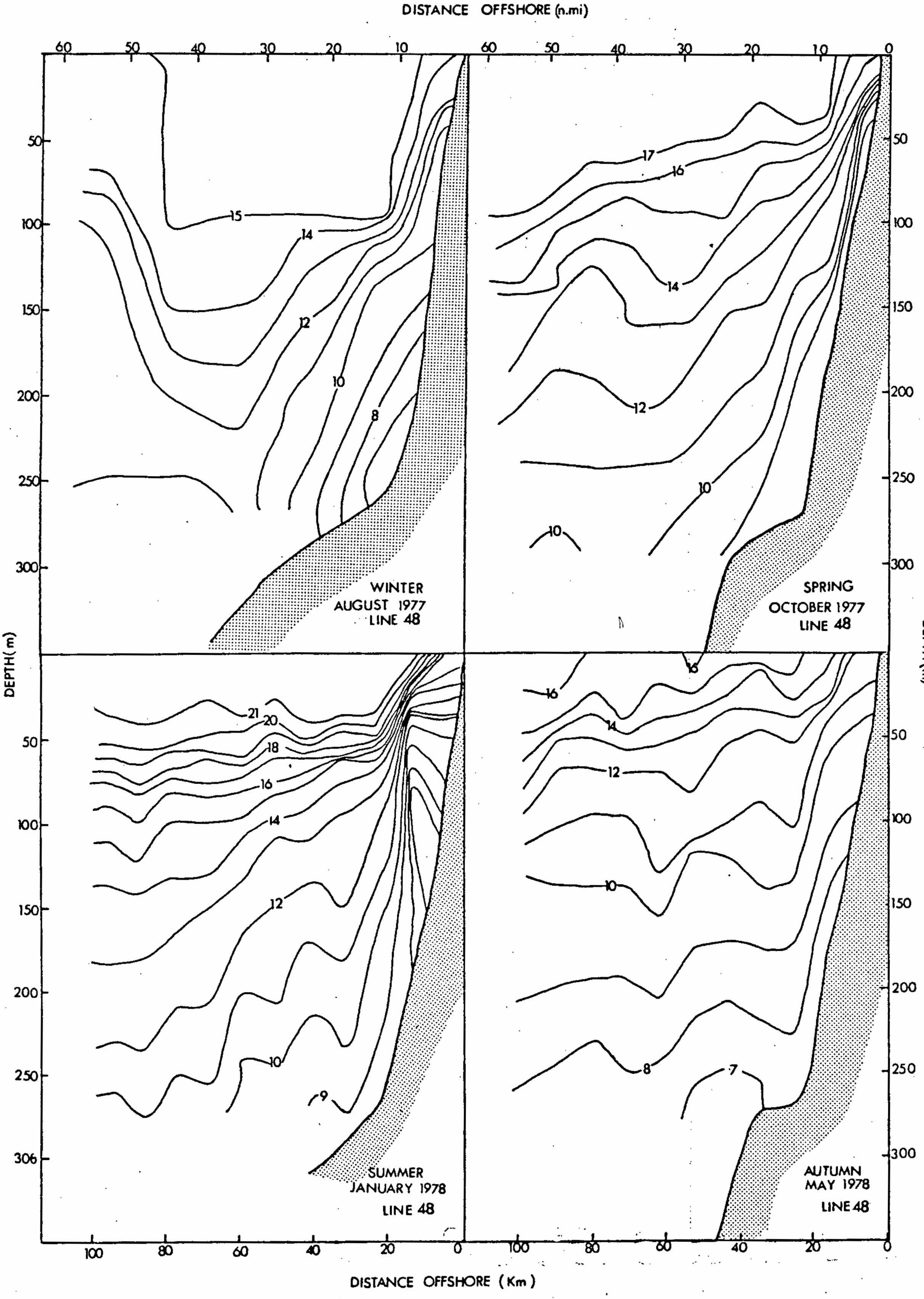

Fig. 2.1.11 Seasonal change in vertical temperature gradients along line 48 off the Cape Peninsula.

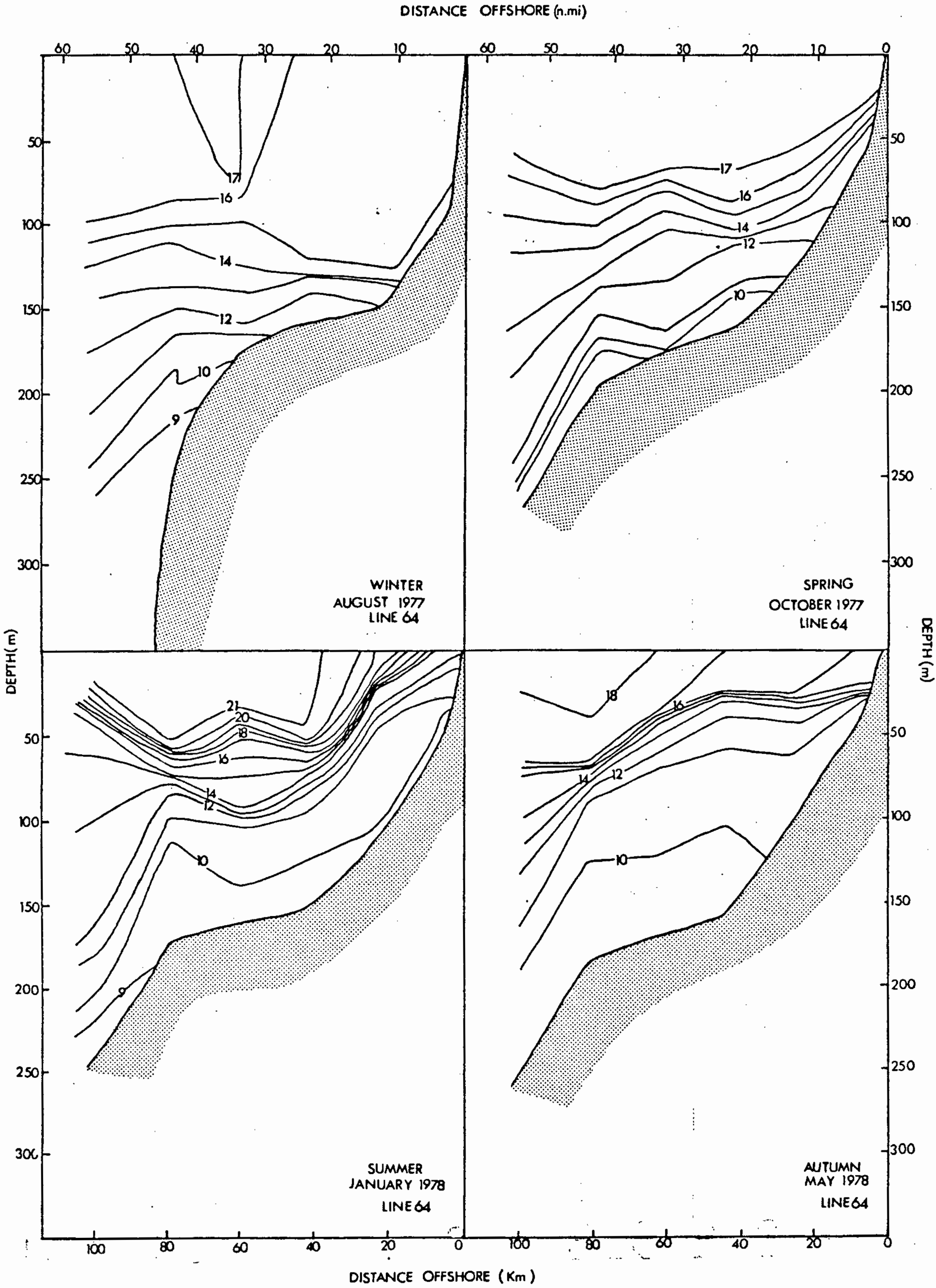

Fig. 2.1.12 Seasonal changes in vertical temperature gradients along line 64 just west of Cape Agulhas.

of the surface layer as summer approached as well as a substantial movement of cold water onto the Agulhas Bank along the bottom corresponded to an increase in the intensity of the thermocline. Upwelling conditions during the January 1978 survey caused isotherms near the coast to tilt upwards and a fairly strong front developed between 21°C water offshore and 13°C water inshore. At line 80, east of Cape Agulhas, upwelling was absent throughout the year (Fig. 2.1.13). In winter and spring the entire water column was well mixed with a temperature of 16 to 17°C, whereas in summer cold water moved onto the Agulhas Bank along the bottom and the top 40m increased in temperature to above 21°C giving rise to a strong thermocline at about 50m. These conditions persisted during autumn but would have been disrupted by increased mixing and reduced influence of cold water over the Agulhas Bank during winter (e.g. August 1977).

The Extended CELP surveys provided temperature sections to the edge of the Bank (Fig. 2.1.14 and 15). The section along line 84 shows that the top 30m was relatively isothermal during both surveys, although the warm tongue, supposedly associated with the Alphard Bank, is visible as an 18°C layer of about 20m thick. In both surveys the thermocline was situated between 30 and 50m, showing very little variability along the entire length of the sections. Further east at line 108 (Fig. 2.1.15) the shelf is narrower and the temperature structure was more variable. In November 1983 very little 9°C water was apparent on the shelf and only mixed Agulhas Current water occurred at the surface. Inshore there was evidence of downwelling. In November 1984, 9°C water had lifted right onto the shelf and upwelling was taking place inshore. Offshore, 20°C water was encountered down to 20m.

Time series data from the monthly sampling of stations was used to examine seasonal events at certain locations. Changes in the temperature structure in

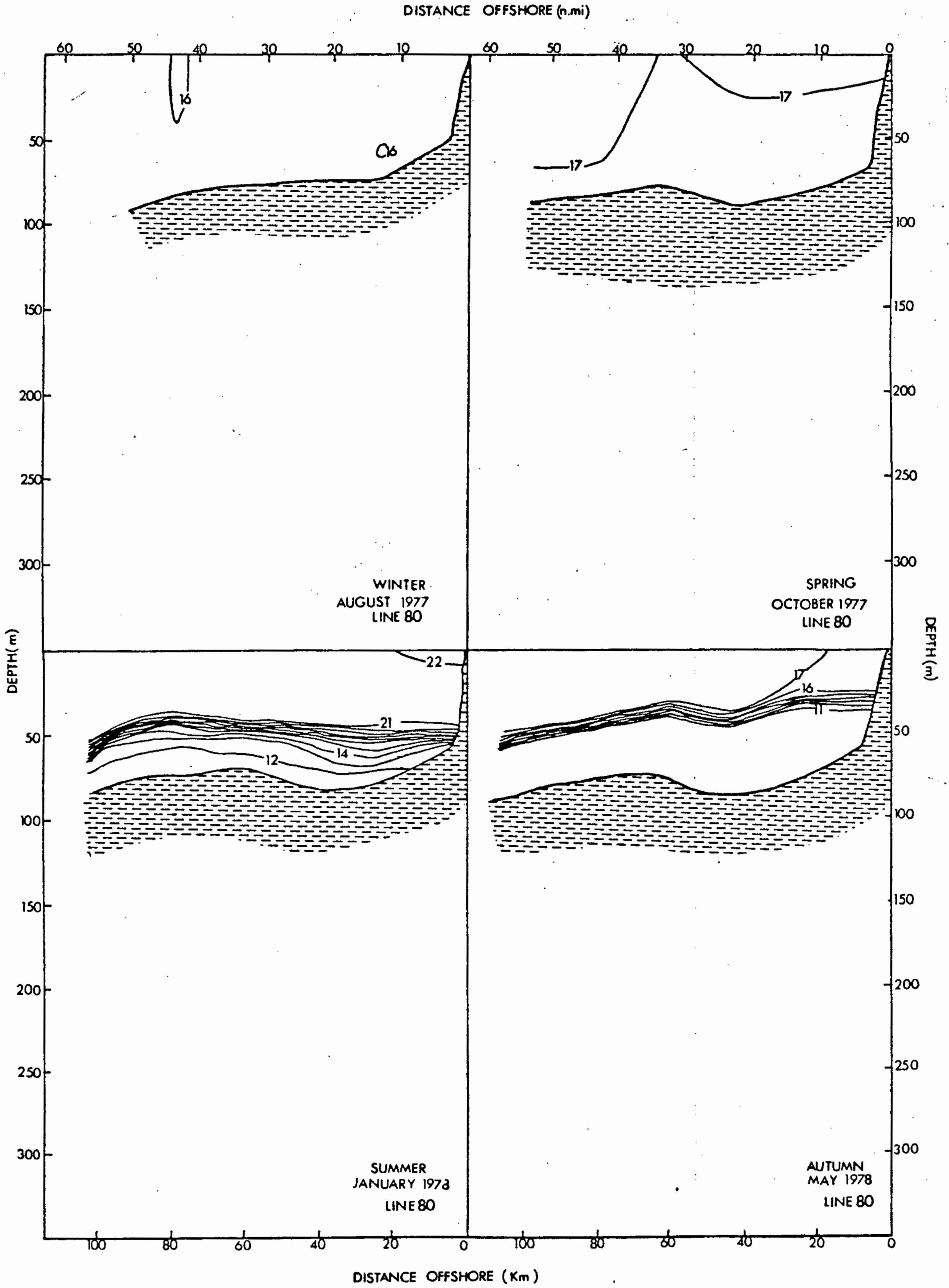

Fig. 2.1.13 Seasonal changes in vertical temperature gradients along line 80 off Cape Infanta.

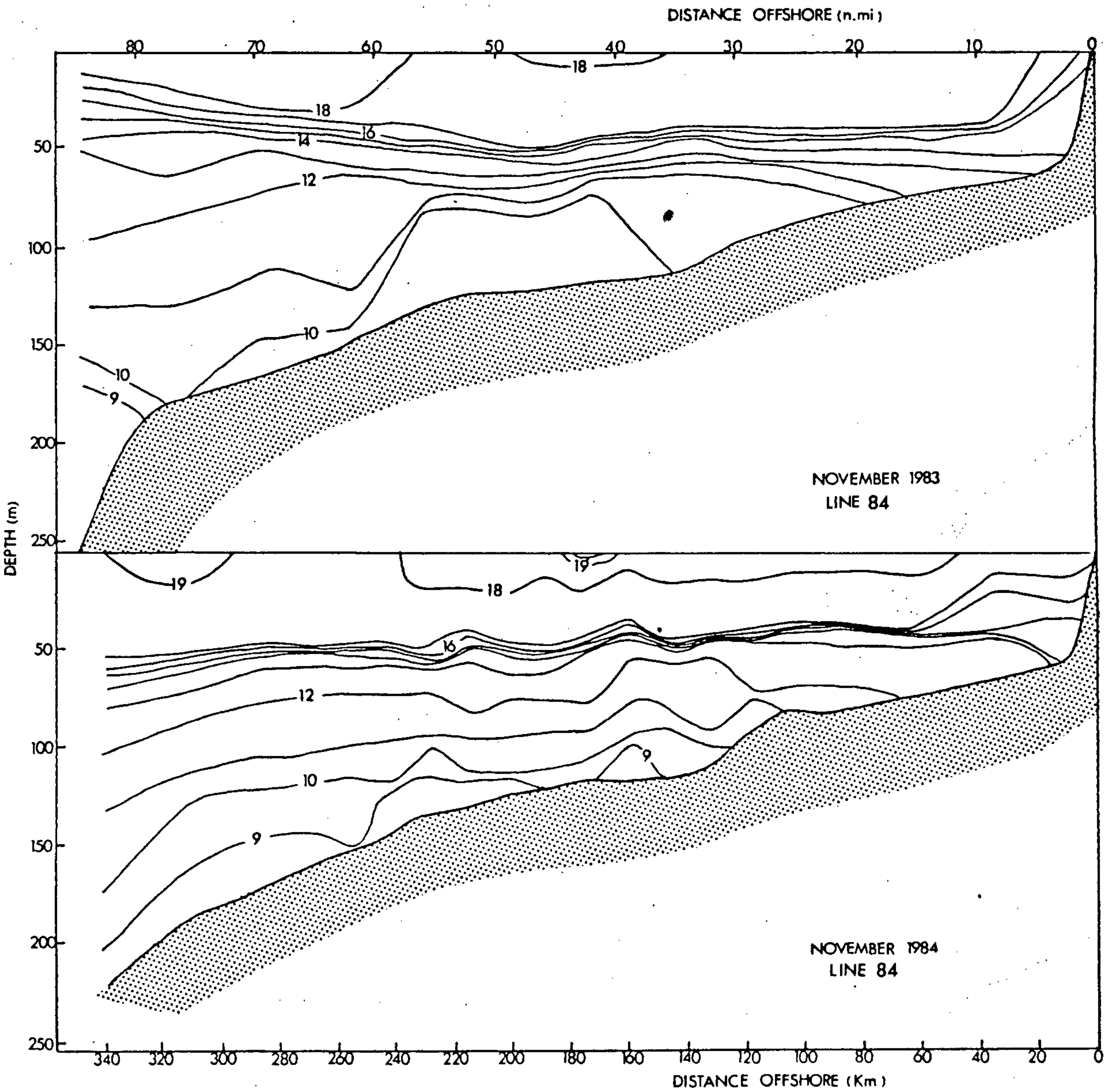

Fig. 2.1.14 Temperature section along line 84 in November 1983 and November 1984. See Figs. 2.1.5 and 2.1.6 for position of the section.

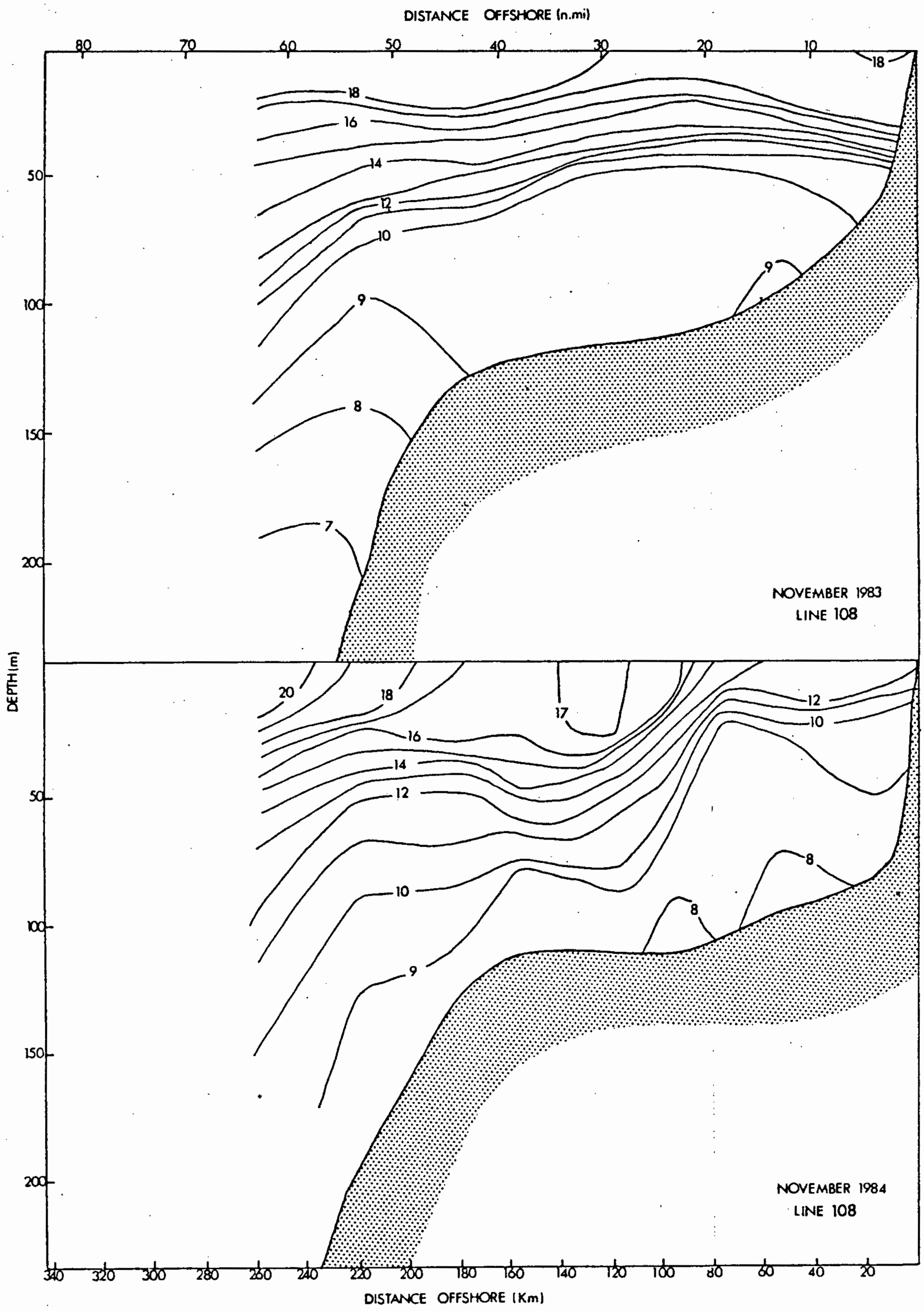

Fig. 2.1.15 Temperature section along line 108 off Plettenberg Bay in November 1983 and November 1984. See Figs. 2.1.5 and 2.1.6 for position of the section.

the top 100m appeared to be largely seasonal, but at a deeper level cold water moved onto the shelf with a less regular pattern which may be related to internal waves (L. Hutchings, SFRI, pers. comm.). At station 28-12 off Cape Columbine (Fig. 2.1.16), the clearest feature is the seasonal increase in surface temperature to values above 16°C over the period October to April. Although a component of this of this heat may be due to sun-warming, the depth of the layer over the late spring to early autumn period indicates that warm water was advected into the area. This warming resulted in the intensification of the thermocline between 40 and 80m. Below 100m cold, deep water pushed onto the shelf for brief periods in September, April/May and July. In April/May the 11°C isotherm rose from below 275m to 150m.

Off the Cape Peninsula at station 48-12 (Fig. 2.1.17) the changes near the surface were similar to those which occured at station 28-12 off Cape Columbine, but three pulses of cool water were centered in October, January/February and May. In May the 13°C isotherm rose by at least 200m from below 275m to 80m. Closer inshore at station 48-04 (Fig 2.1.18) cold water pulsing was less clear and instead there was a general shallowing of the isotherms during summer, which, together with the advection of warm water into the area, resulted in the formation of a strong thermocline in the top 80m of the water column.

At station 64-06, situated on the Agulhas Bank considerable warming of surface water occurred concurrently with the accumulation of cold water on the shelf in late summer/autumn (Fig. 2.1.19). This led to the formation of a particularly intense thermocline from January to April. Cooling of the surface waters from May onwards contributed to the weakening of the thermocline and by June the upper 80m was relatively isothermal.

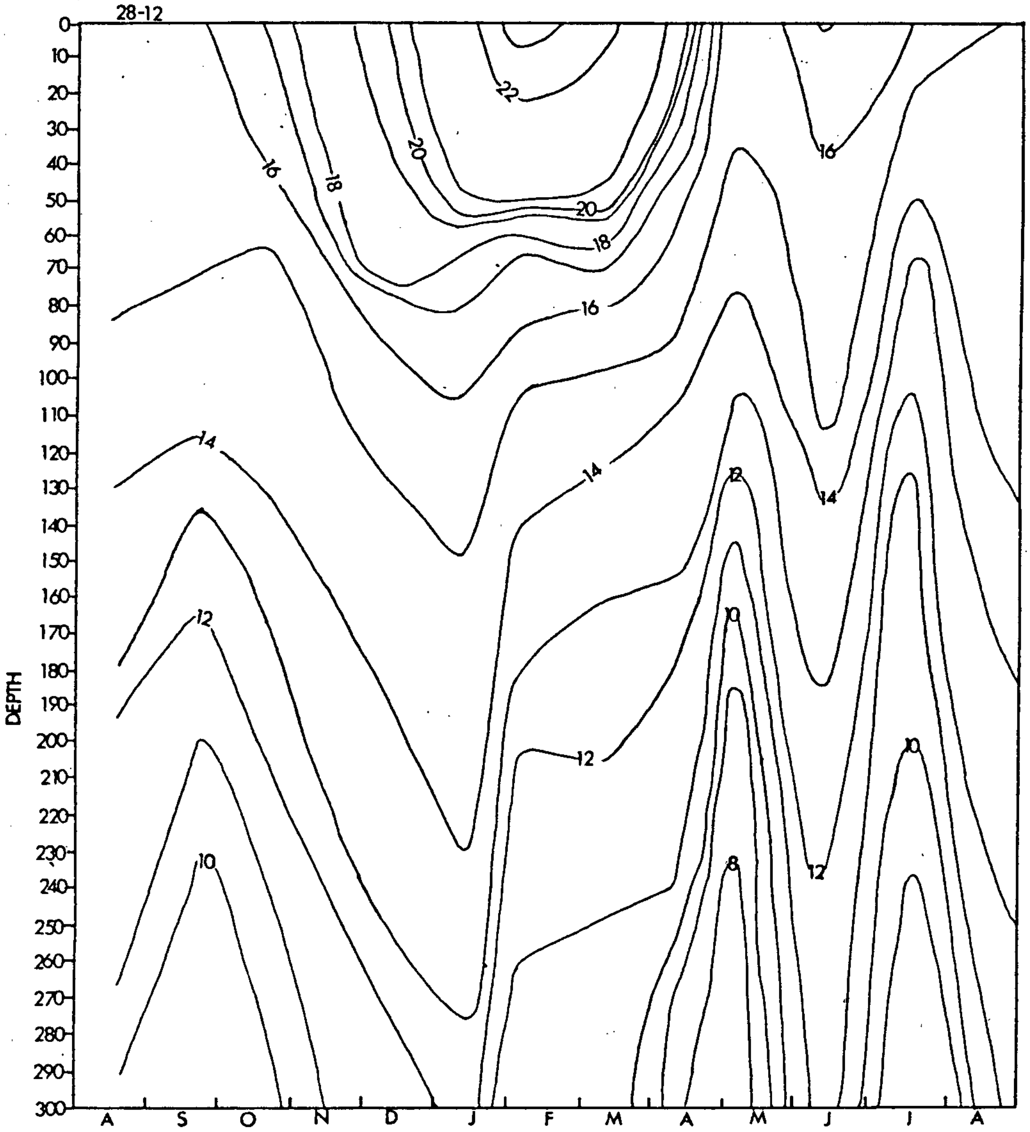

Fig. 2.1.16 Monthly changes in the vertical temperature structure at station 28-12 off Cape Columbine.

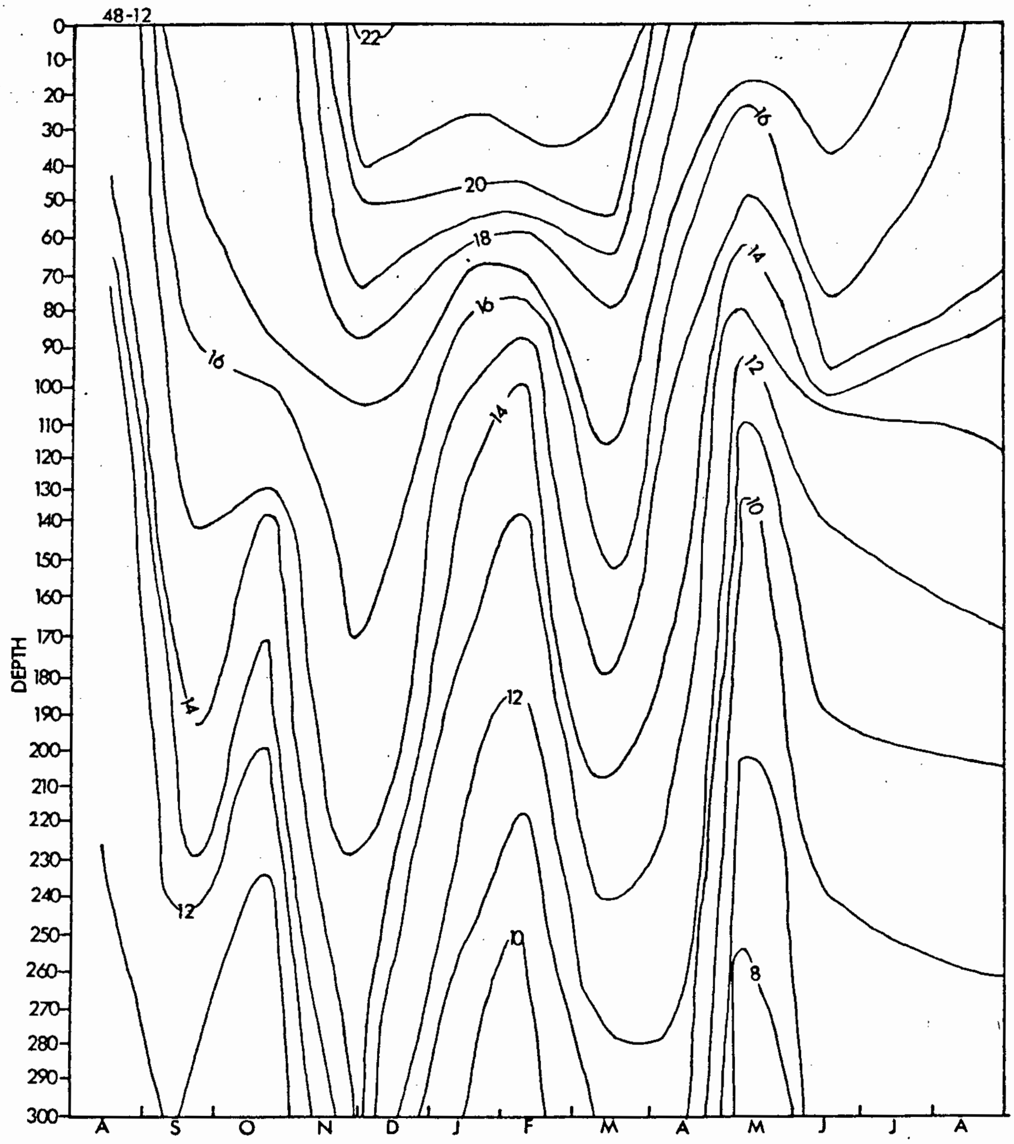

Fig. 2.1.17 Monthly changes in the vertical temperature structure at station 48-12 off the Cape Peninsula.

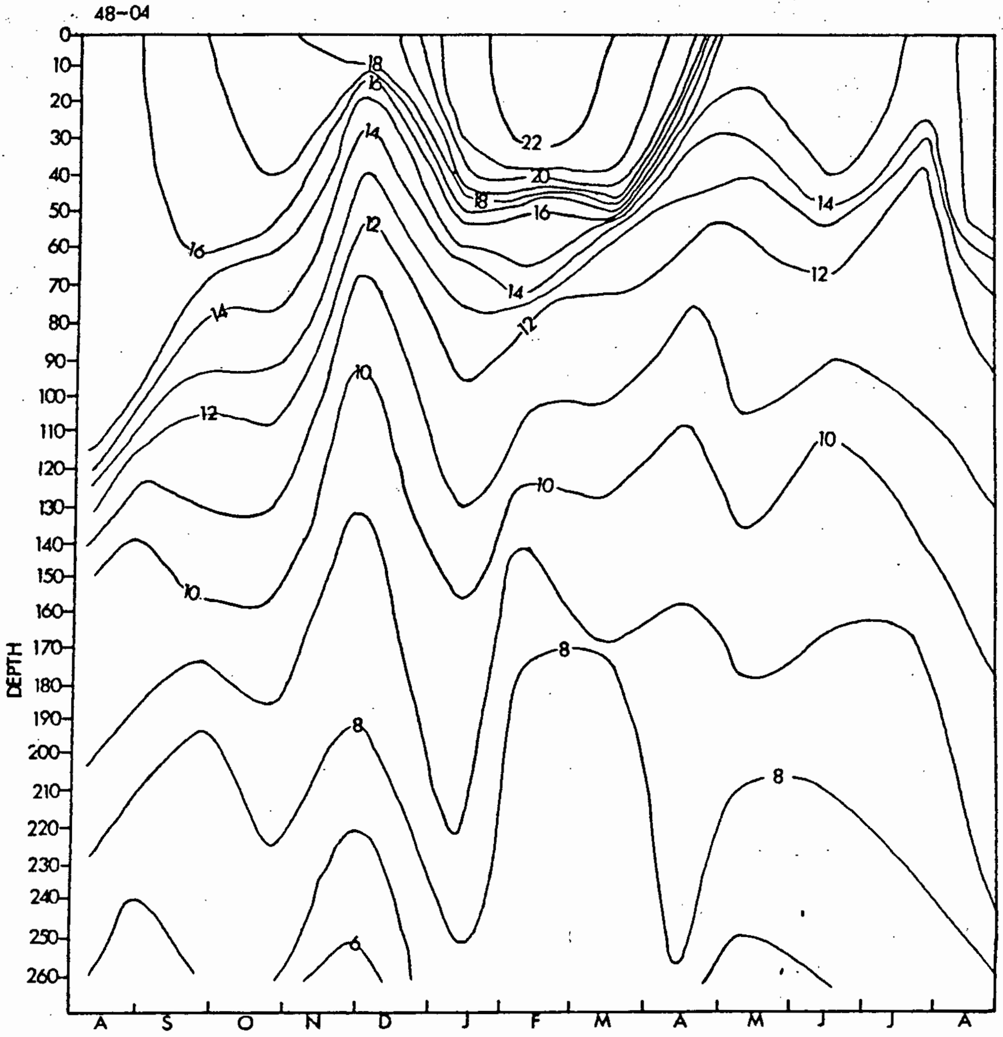

Fig. 2.1.18 Monthly changes in the vertical temperature structure at station 48-04 off the Cape Peninsula.

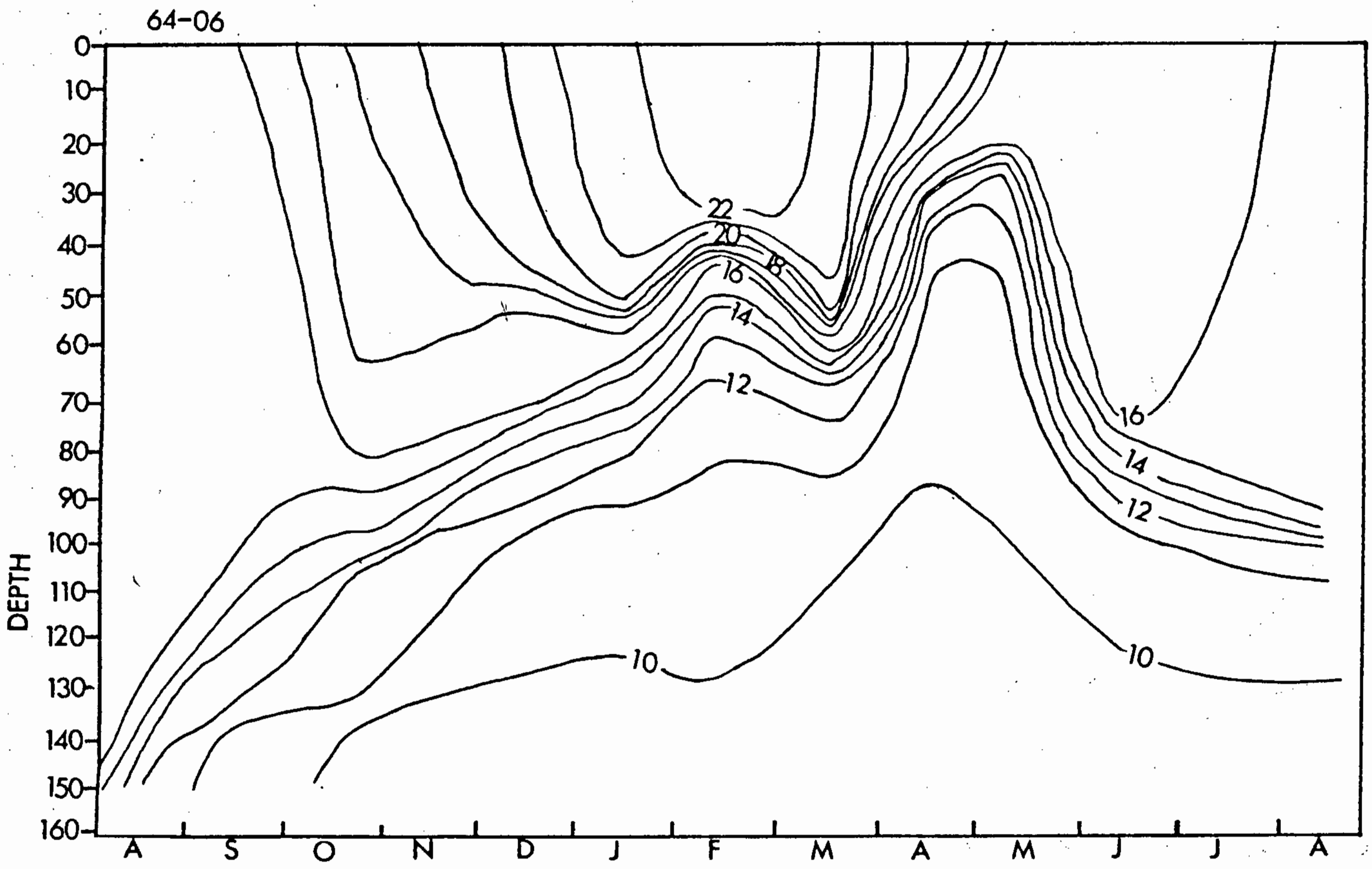

Fig. 2.1.19 Monthly changes in the vertical temperature structure at station 64-06.

T/S analysis of the warm water

From examination of horizontal and vertical temperature gradients, it would appear that the particulary intense fronts and thermoclines, which characterize the southern Benguela region, formed during summer when the incidence of upwelling is maximum and when the temperature of water at the outer stations of the survey grid increases. From surveys where salinity data are available, recently upwelled water with a temperature of 12°C or less at the surface (mean = 11.5°C, SD = 0.49, n = 26) had a corresponding salinity of less than 34.89°/oo (mean = 34.81°/oo, SD = 0.059). These values fall within the temperature and salinity range given by Clowes (1950) for South Atlantic Central Water and are within the temperature range given by Shannon (1966) for upwelled water on the west coast. Temperature and salinity characteristics for different water masses in the southern Benguela region obtained from the literature are illustrated in (Fig. 2.1.20).

The characteristics of the warm saline water which penetrated the survey grid from the west or south-west is more complex than the cold, upwelled water, as illustrated by the T/S scatter diagrams for stations with a surface temperature greater than 20°C between Cape Columbine and Cape Point (Fig 2.1.21). During the November/December 1977 and January 1978 surveys, very few of the data points at temperatures above 21°C fell below 35.5°/oo Instead, most of the surface water fell within the range given for South Atlantic Surface Water by Shannon (1966). At cooler temperatures associated with water below the surface, a number of the January 1978 data points fell within the range suggested for Agulhas Bank Mixed Water by Penrith and Cram (1974), but might also have arisen from the mixing of South Atlantic Surface and Central Waters.

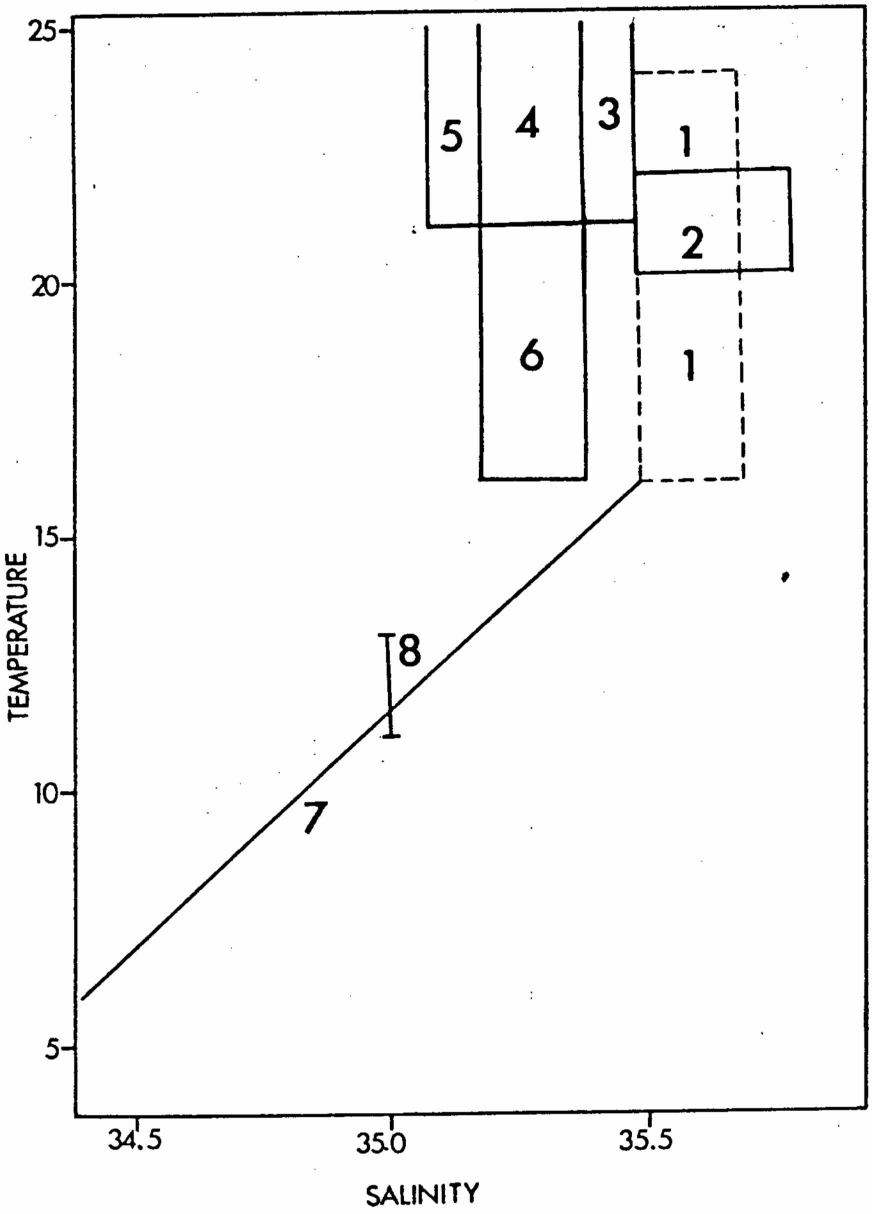

Fig. 2.1.20 Temperature and salinity ranges of the major water types found in the southern Benguela region:

(1) South Atlantic Surface Water (Darbyshire 1966)
(2) South Atlantic Surface Water (Shannon 1966)
(3) Agulhas Current Water off Port Elizabeth (Shannon 1966)
(4) Agulhas Current Water (Darbyshire 1966)
(5) Agulhas Current Water (Pearce 1977)
(6) Agulhas Bank Mixed Water (Penrith and Cram 1974)
(7) South Atlantic Central Water (Clowes 1950)
(8) Typical South Atlantic Central Water (Shannon 1966).

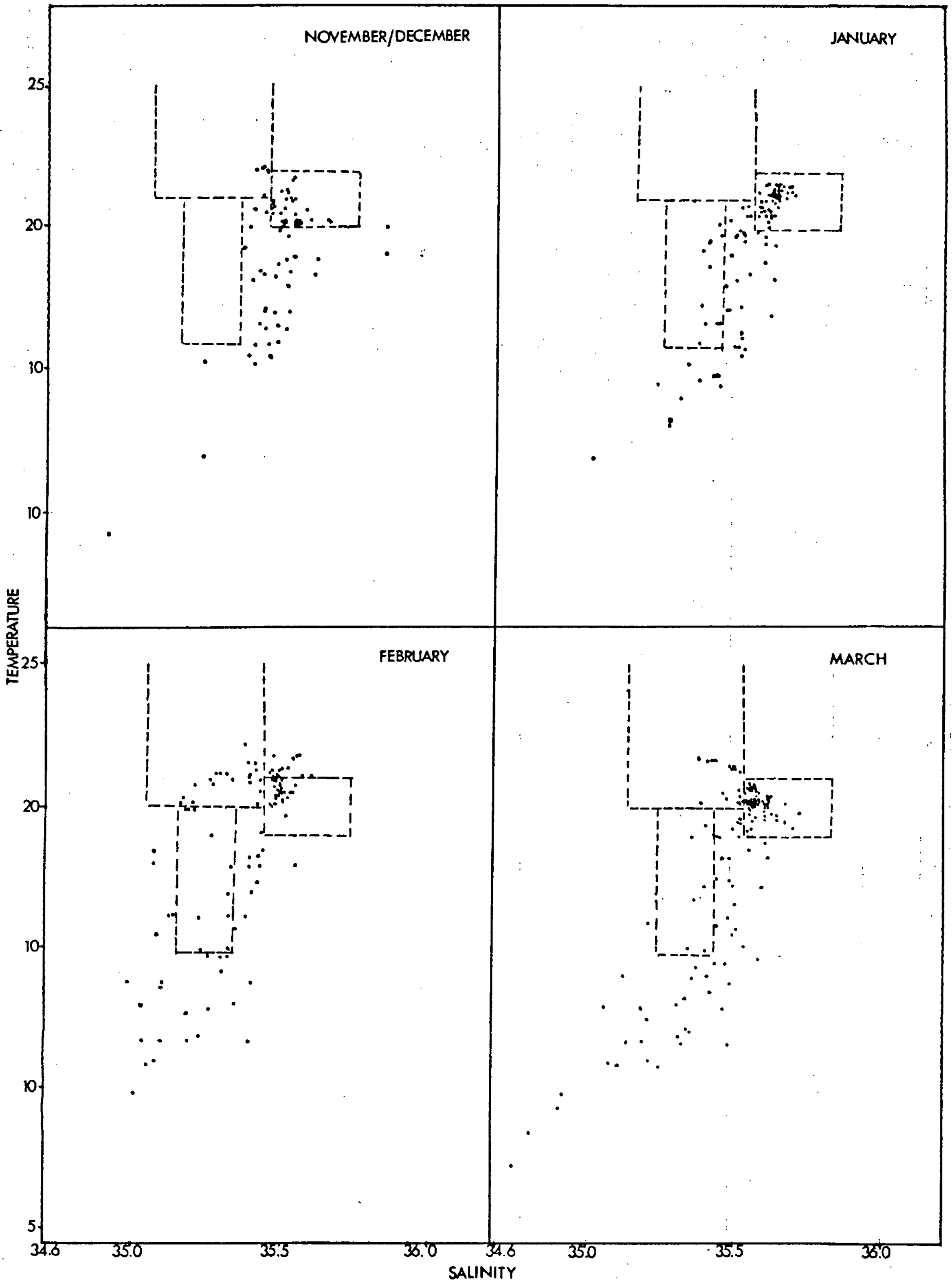

Fig. 2.1.21 T/S scatter of water with a surface temperature of more than 20°C found on the west coast between Cape Columbine and Cape Point. Boundaries for Agulhas Current Water (3,4,5), Agulhas Bank Mixed Water (6) and South Atlantic Surface Water (2), taken from Fig. 2.1.~~19~~, are shown.
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In February and March 1978 a substantial number of T/S data points fell within the temperature and salinity ranges attributed to Agulhas Current Water by Shannon (1966), Darbyshire (1966) and Pearce (1977). It therefore appears that a least part of the cause of the intensification of fronts and thermoclines between Cape Columbine and Cape Point in late summer and early autumn may be the increased influence of water of Agulhas Current origin.

2.1.4 Discussion

Upwelling has formed a focus for oceanographic research in the southern Benguela region for some time, and it is thought to dominate physical and biological processes in the near-shore area (Andrews and Hutchings 1980). The upwelling "plume" off the Cape Peninsula is particulary well studied (e.g. Andrews and Cram 1969, Bang and Andrews 1974, Andrews and Hutchings 1980, Hutchings 1981, Shannon et al. 1981), with one line of stations bisecting the plume having been resampled 45 times (Hutchings et al. 1984). These mesoscale studies followed the earlier larger scale surveys of the Benguela system (Hart and Currie 1960) and the southern Benguela region (Shannon 1966, Jones 1971, Bang 1971).

Seasonal changes across the Cape Peninsula upwelling plume are comprehensively dealt with in Andrews and Hutchings (1980) in which their Fig. 9 suggests that the influence of the upwelling plume expands in summer. Seasonal changes inferred from large scale temporal and spatial averaging of SST data, however, suggest that events are dominated by the summer warming and winter cooling of sea surface temperatures within the southern Benguela region (e.g. Wooster 1973, Christensen 1980, Parrish et al. 1983, McLain et al. 1985, Shelton et al 1985, see Section 1.3). Thus offshore warming may be a more vigorous and constraining influence on coastal upwelling than has hitherto been inferred on the basis of mesoscale studies. Although this coarse scale of SST analysis is very useful for monitoring in order to determine when anomalies arise (e.g. McLain et al. 1985), the processes determining the average picture are not always apparent. Data from the CELP surveys allows the large scale seasonal pattern of temperature and salinity to be described without obscuring the causative processes and should prove useful in interpreting anomalies in data of the Kind presented by McLain et al. (1985).

West coast

The southern Benguela region can be divided into two areas - the west coast area extending as far south as Cape Agulhas where strong upwelling is a frequent feature, and the south coast area from Cape Agulhas east as far as Algoa Bay where, because of the orientation of the coastline, upwelling is less evident. On the west coast the contraction of the area occupied by cool water in summer and the expansion of this zone in winter is the most noticeable feature and is elucidated here for the first time. The seasonal expansion and contraction resembles the action of a set of bellows, and suggests that the influence of upwelling is modulated or squeezed by offshore warming from late spring to early autumn. The increase in temperature of oceanic water in summer is partly related to sun warming and partly to the increased influence of Agulhas Current water on the west coast, as noted by Shannon (1966), Andrews and Hutchings (1980) and Shannon et al. (1981).

The T/S analysis of CELP stations with warm water at the surface suggests that the influence of Agulhas Current water on the west coast is greatest in late summer and early autumn, confirming the findings of Shannon (1966). The penetration of western boundary current water into an eastern boundary current region is unique to the Benguela current system. Offshore warming together with strong upwelling inshore and a steep shelf break situated close to the coast combine to cause the formation of exceptionally strong thermal fronts and thermoclines in the vicinity of the Cape Peninsula, as well as off Cape Columbine, from late spring to early autumn. There is considerable interannual variability in the degree of surface warming on the west coast and over the Agulhas Bank, as can be seen by comparing the 7 surveys of the region during the month of November (Figs. 2.1.4-6). However, within each spring to autumn period it is likely that the contribution of Agulhas Current water plays an important role in stabilizing the coastal region by strengthening the front and the thermocline.

During lulls in upwelling in summer the warm layer of water advances towards the coast and the front may weaken or disappear at the surface. The temperature discontinuity is then most apparent in the form of a strong thermocline. The steep bottom topography found off the Cape Peninsula, and to a lesser extent off Cape Columbine, maintains the subsurface upward tilt of the isotherms even in the absence of offshore Ekman transport. The front between Cape Point and Cape Agulhas appears to be more ephemeral during summer than the front to the north, and warm water intrusions into False Bay and Walker Bay are more frequent. This is primarily due to the more east-west orientation of the coastline which reduces offshore Ekman tranport during the dominant summer south easterly winds, and the more gently sloping bottom topography.

The commonly observed divergence of isotherms offshore in the vicinity of Cape Columbine during spring to autumn has been described by Shannon (1985) and Shelton et al. (1985, see Section 1.3). Shannon (1985) suggests that the front divides into two components at Cape Columbine as a result of the divergence of isobaths into an inner and outer shelf break. The front between cool water and oceanic water tends to follow the outer break and, as noted by Shannon (1985), often bends acutely westward in the vicinity of 33°S, whereas the inner component tends to turn cyclonically into St Helena Bay. Since the CELP survey grid only extends about 100Km off Cape Columbine, it is not possible to determine the conformation of the front after it bends westwards, but reference to published satellite images of chlorophyll in Shannon et al. (1983), Shannon and Anderson (1982) and Shannon et al. (1984b) shows that the chlorophyll front may move some distance offshore in this region. Van Foreest et al. (1984) have shown that the front may have a number of offshore eddies or filaments during the winter months, although the front is weaker and further offshore at this time of the year. A satellite tracked drougue released off Cape Town moved westward off Cape Columbine (Harris and Shannon 1979) following the outer shelf break as far as Luderitz where it moved westwards and then passed through the gap in the Walvis Ridge, from which Nelson and Hutchings (1983) concluded that the Benguela flow is topographically steered. Shelton and Hutchings (1982) have shown that anchovy eggs and larvae are funnelled into the frontal jet current off the Cape Peninsula from the western Agulhas Bank and transported northwards towards Cape Columbine. The divergence at Cape Columbine represents a potential leak of coastal water and associated ichthyoplankton out of the neritic system to areas where mortality of the ichthyplantkton may be expected to be high. In comparison, larvae that are advected into St Helena Bay will be in an area of constistently high plankton standing stock (see Section 3) with a far better probability of survival.

South coast

The area east of Cape Agulhas has reduced upwelling activity, although Schumann et al. (1982) have shown that some upwelling activity is associated with crenulated capes in this area. In particular, the slight north-south orientation of the coast between Cape Seal and Cape St Francis either side of Plettenberg Bay appears to promote upwelling, as was recorded during the November 1984 and 1985 surveys, and the area should be considered as an additional discrete site of upwelling to add to those reviewed by Nelson and Hutchings (1983), and a potentially important source of nutrients for sustaining plankton production on the Agulhas Bank. The narrow shelf off Plettenberg Bay allows Agulhas Current water to approach close to the coast and strong surface temperature gradients are set up in this area.

The dominant feature over the Agulhas Bank is the seasonal formation of a strong thermocline in spring and its weakening and disappearence in autumn, resulting in very strong vertical stratification in summer and an almost isothermal water column in winter. There is evidence that in the eastern portion of the Agulhas Bank, outside the CELP survey grid, the thermocline is perennial in nature (National Research Institute for Oceanology, Stellenbosch, unpublished data), probably as a result of the greater influence of Agulhas Current water throughout the year. The seasonal variablity in vertical stratification over the Agulhas Bank has been examined by Pugh (1982) and Schumann and Beekman (1984), and is attributed by them to solar heating of the surface water in summer which builds up the stratification, and wind mixing in winter which, together with reduced solar heating, weakens the stratification. In addition, results from the CELP survey suggest that the intensification of the thermocline in summer and autumn can partly be attributed to the deeper movement of water less than 16°C onto the Bank at this time of the year. It seems unlikely that this movement compensates for offshore Ekman transport of the surface layers and therefore it is more likely to be the result of remote forcing.

Shannon and Chapman (1983) and Shannon (1985) have noted a "divide" or transition zone over the Bank at 21°E. Schumann and Beekman (1984) have suggested that the divergence may be caused by eddies shed from the Agulhas Current. It seems likely that the tongue of 18°C–19°C water in the vicinity of Cape Infanta may be associated with the Alphard Bank which is a particularly shallow southward projecting ridge on the Agulhas Bank. The exact influence of the Alphard Bank on circulation in the area needs to be examined by more detailed sampling. Any surface flow of the Agulhas Current onto the Bank in summer would intensify the thermocline and increase the stability of water column.

2.1.5 Conclusion

The oceanography of the southern Benguela region is dominated by the seasonal intensification of the front on the west coast and the seasonal intensification of the thermocline east of Cape Point. The strengthening of the front in spring is caused primarily by upwelling but is strongly enhanced by Agulhas Current or Agulhas Bank Mixed water which combines with solar heating to raise temperatures offshore. The onshore advection of cold bottom water onto the shelf on the west coast at irregular intervals throughout the year and onto the Agulhas Bank in winter intensified the gradient. The process whereby western boundary current water mixes onto the east coast, and the resulting extremely strong surface front, is unique to the southern Benguela eastern boundary current region. Off Oregon the front is formed by the seasonal outcropping of the permanent pycnocline (Mooers et al. 1976). A seasonal pycnocline formed by the seasonal thermocline and a halocline resulting from Columbia River water is nearly level, except for close inshore where it merges with the pycnocline to form the surface front. Off Peru winds are normally upwelling favourable and the front remains far offshore and is relatively indistinct (Brink 1983). From data presented in Mittlestaedt (1983) and Parrish et al. (1983), the Northwest African system would appear to be dominated by the dynamics of the tropical frontal zone between warm tropical water and cooler termperate water with only a weak surface front developing as a result of the coastal upwelling of comparitively warm South Atlantic Central Water and North Atlantic Central Water to the north of the tropical front.

The extent of offshore warming and the position of the front may have a strong modulating influence on the near-shore zone in the southern Benguela region, particularly if the dynamics follows the two celled model of circulation proposed by Mooers et al. (1976), and convergence or sinking occurs at the front. There is evidence from the distribution of chlorophyll (Shannon et al. 1984c, see Section 3.1), plankton and microplankton (see Section 3.2) that particles are retained within the coastal zone by the front. Although the incidence and strength of upwelling is greatest from late spring to early autumn, its spatial influence is limited by the front. Lulls in upwelling weaken the front and allow warm water to advance towards the coast. This may result in a strong thermocline with a subsurface cholrophyll maximum. In winter, although upwelling is weaker, The influence of water less than 16°C extends further offshore and plankton is less concentrated. The seasonal and interannual dynamics of the front are therfore likely to play a major role in determining the amount and distribution of plankton production and in influencing the development of the lifehistory strategies of fish inhabiting the southern Benguela system, and anomalies in the seasonal pattern are likely to have a measurable influence.

East of Cape Point the front is more ephemeral and the area over the Agulhas Bank is dominated by the seasonal formation of a strong thermocline which only occasionally outcrops at the surface as a result of surface offshore Ekman transport close to the coast. During summer enchanced chlorophyll concentrations are limited to the thermocline layer (Shannon et al. 1984c, see Section 3.1) and the dynamics of the thermocline may be equally important over the Agulhas Bank as the front is on the west coast in determining suitable feeding areas for fish. In addition, the warm isothermal layer above the thermocline provides a suitable environment for the rapid development of early life history stages of fish.

2.2 Near-surface circulation patterns in the southern Benguela region deduced from drift cards, wind stress and density gradients in 1977/78

2.2.1 Introduction

The strong influence of the wind field on the near surface circulation in the southern Benguela Current region has been acknowledged since the earliest studies of Gilchrist (1904). Subsequently Duncan and Nell (1969) showed the existence of a definite seasonal variation in surface currents in the region, and Andrews and Hutchings (1980), in a description of the dynamics of upwelling adjacent to the Cape Peninsula, described a seasonal wind cycle which could be expected to generate seasonal changes in drift. Harris (1978) reviewed coastal currents in the region using information from ship's drift, moored current buoys, tracked floats, current meters and drift cards, and confirmed the distinct seasonality of events and concluded that coastal currents away from the immediate influence of the shoreline could be predicted largely on the basis of wind. In addition to direct wind driven circulation of the surface waters, the underlying geostrophic current field may have a substantial effect on near-surface flow. Bang and Andrews (1974) described an intense jet current in the southern Benguela region off the Cape Peninsula which they attributed to geostrophic processes and it is likely that accelerated flows occur within the southern Benguela Current region wherever there are significant density gradients.

In reviewing mesoscale processes in the Benguela system related to upwelling, Nelson and Hutchings (1983) described recent results of current meter work and constructed a generalized diagram of flow for the region from Lambert's Bay to

Cape Hangklip. This approach was extended to the whole Benguela system using all available information on currents in a comprhensive review of the oceanography of the system by Shannon (1985). In addition, Parrish et al. (1983) have compared a number of environmental processes, including Ekman drift and turbulence, in the Benguela system with conditions in other eastern boundary current regions of the world, building on the comparative approach of Wooster and Reid (1963) and adding substantially to the large scale analysis of the Benguela system by Wooster (1973).

In this study a broad scale description of the temporal and spatial characteristics of surface flow in the southern Benguela region is attempted on the basis of wind stress, drift card trajectories and density gradients from data collected during CELP, in order to extend the generalized descriptions of Duncan and Nell (1969), Nelson and Hutchings (1983) and Shannon (1985), and to identify processes that may play a role in determining recruitment of neritic fish. While drift card trajectories and temperature structure may be expected to partially integrate out high frequency variability and give an average seasonal picture, wind events in the southern Benguela region have a characteristic periodicity of 3 to 6 days (Nelson and Hutchings 1983) so that interpretation from non-synoptic cruise data requires caution.

2.2.2 Methods

From August 1977 to August 1978 twenty plastic drift cards (Duncan 1965) were released at each station of the Cape Egg and Larval Programme (CELP) survey grid. All recoveries were plotted on monthly charts by joining the point of release with the recovery location, choosing an arbitrary trajectory. Quasi-geostrophic flow was deduced from vertical temperature sections on selected lines. Temperature and salinity are closely correlated in the southern Benguela region (Bang 1973) and therefore temperature is a good index of density.

Wind strength and direction was measured at each station using the ship's anemometer. Progressive wind vectors from measurements made at Cape Columbine and at Cape Point were used to interpret events during the cruise which were complicated by the lack of synopticity. The cube of the wind speed was used as an index of turbulence (Bakun and Parrish 1982) and related to the depth of the upper mixed layer. Wind stress and Ekman velocity vectors were calculated using the following formulations (Pond and Pickard 1978):

Wind stress (y, dynes. cm^{-2})

$$y = pa * CD * W^{-2} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

Where pa = density of air (0.0013 $g.cm^{-3}$)

CD = drag coefficient (0.0014)

W = wind speed ($cm.sec^{-1}$)

Ekman velocity (Vo, $cm.sec^{-1}$)

$$Vo = \frac{0.0127 \, . \, W}{\sqrt{\sin /\theta/}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2)$$

Where θ = latitude in decimal degrees

Depth of Ekman layer (De, metres)

$$De = \frac{4.3 * W}{\sqrt{\sin /\phi/}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(3)$$

Direction of Ekman velocity vector at the surface (A, deg.)

$$\mathrm{Tan}\ A = \frac{\sinh(2\pi/De.d) - \sin(2\pi/De.d)}{\sinh(2\pi/De.d) + \sin(2\pi/De.d)} \quad \ldots\ldots\ldots\ldots(4)$$

Where A = angle of Ekman velocity vector at the surface relative to the direction of the wind. This is to the left of the wind forcing due to Coriolis Force in the southern hemisphere.

d = sounding or depth of the water column in metres.

2.2.3 Results

2.2.4.1 Temporal variability

Four months, August 1977, October 1977, January 1978 and May 1978 have been selected to illustrate respectively winter, spring, summer and autumn trends in wind stress, turbulence, depth of the upper mixed layer, Ekman velocity and drift card trajectories.

Wind stress

Progressive vector diagrams constructed from wind measurements made at Cape Columbine and at Cape Point during CELP (Fig. 2.2.1) show that the wind at Cape

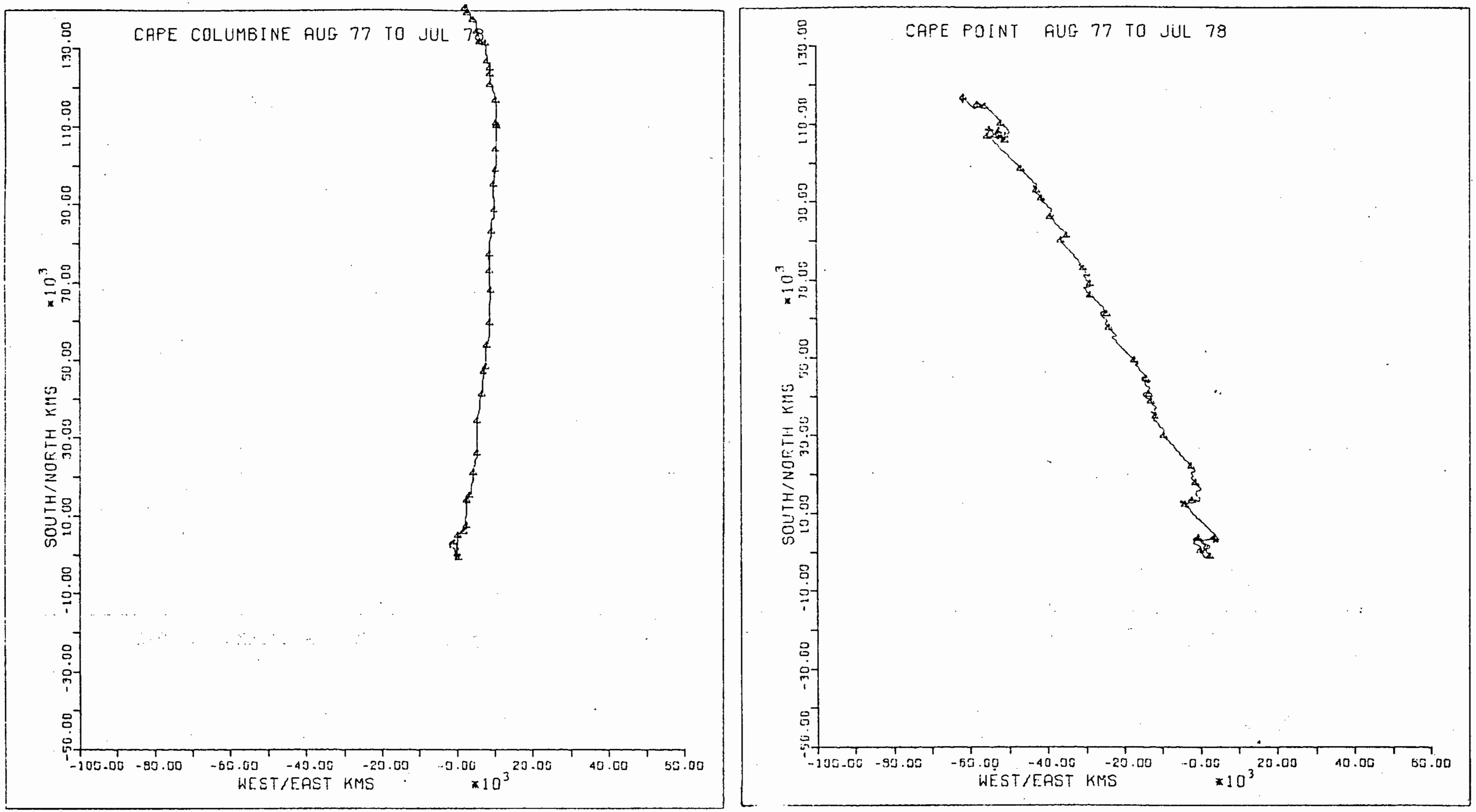

Fig. 2.2.1 Progressive wind vectors (km) from wind measurements made at Cape Columine and Cape Point from August 1977 to July 1978. The vector is marked off in 10 day intervals.

Columbine was generally directly from the south with very few reversals and maximum displacement in summer. In contrast the progressive vector from measurements at Cape Point shows that the wind was generally from the south east with more frequent wind reversals, especially during the winter months.

In a little more detail, progressive vector diagrams of wind for the months selected as representitive of the four seasons (Fig. 2.2.2) show that in winter and autumn wind reversals were relatively common and that strong blows were rare. In May 1978 the wind at Cape Point had a net~~t~~ easterly displacement due to a north westerly wind gale in the middle of the month. Spring and summer were characterized by southerly winds. In October 1977 the wind measured at Cape Point had an easterly displacement over the early part of the month due to westerly winds. The vector for Cape Point in January 1978 shows that 4 wind reversals took place interspersed with blows of south east wind. In Table 2.2.1 the duration of each of the 4 cruises is given for comparison with Fig. 2.2.2.

Table 2.2.1

Start and end date for each of the four selected CELP cruises. The CELP grid was surveyed from north to south.

Month	Duration
August 1977	19 - 28
October 1977	15 - 25
January 1978	7 - 19
May 1978	3 - 12

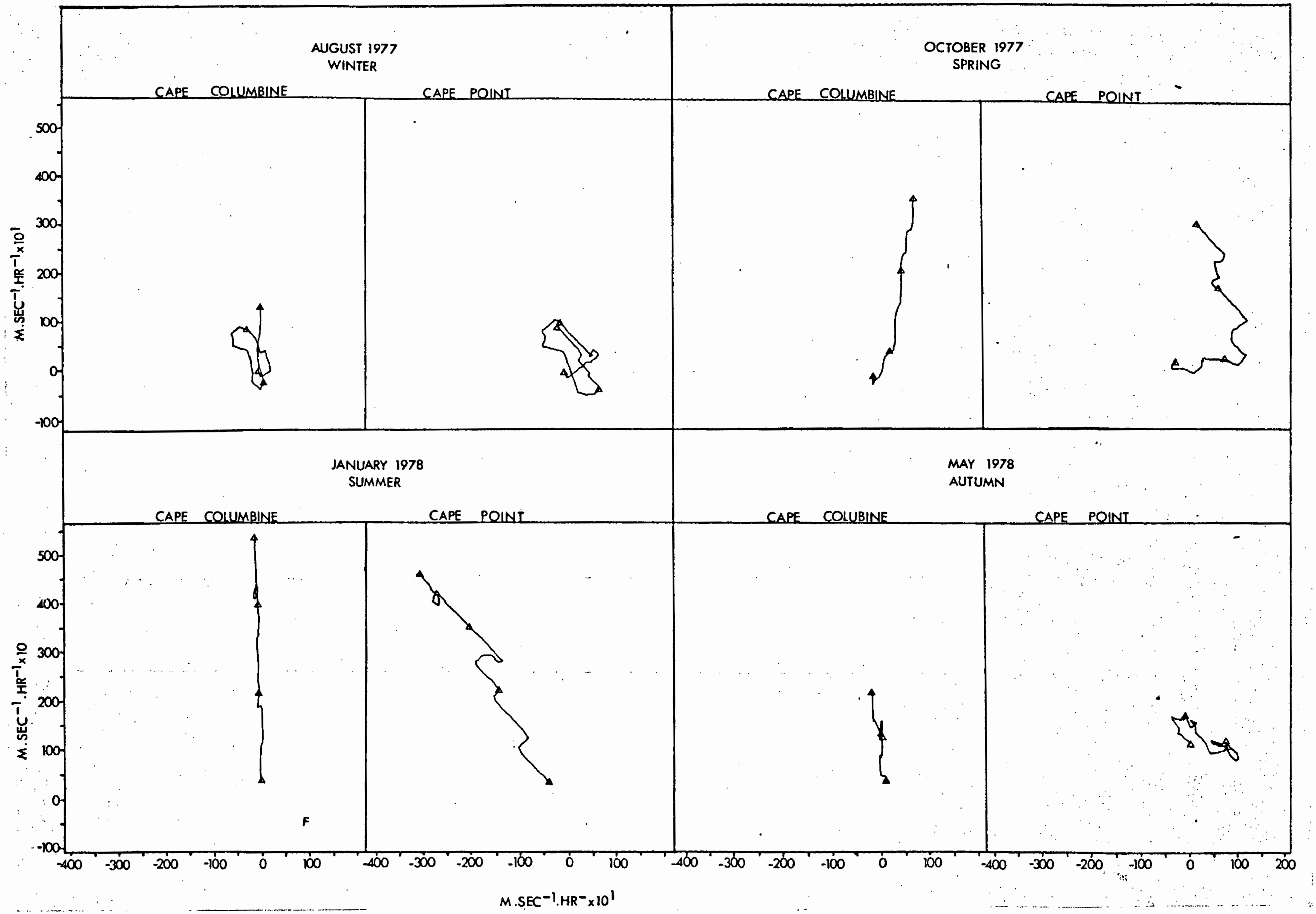

Fig. 2.2.2 Progressive wind vectors (Km) from wind measurements made at Cape Columbine and at Cape Point for months selected as representitive of the seasons. Triangles mark 10 day intervals.

Measurements of wind stress were made at each station during the survey and the wind fields for the 4 selected months are given in Fig. 2.2.3. During the August 1977 cruise there was a divergence in the wind field in the vicinity of Cape Agulhas with westerly winds between lines 72 and 84, and easterly to south easterly winds between lines 52 and 64. The wind stress along the west coast was generally south easterly and therefore normal to the coastline, but with a marked reduction in wind stress north of Cape Columbine, particulary in St Helena Bay, and a reversal in wind direction to north westerly on lines 8 to 16. The progessive wind vector analyses from measurements made at Cape Columbine and Cape Point (Fig. 2.2.2) show that a wind reversal occurred during the early part of the cruise after which the wind stress was fairly consistantly southerly at Cape Columbine and south easterly at Cape Point. Despite the influence of this wind reversal, the pattern of wind stress in St Helena Bay and the northern part of the grid was similar in June and August 1978 suggesting that this may be a fairly common winter situation.

The spring wind field (e.g. October 1977) was characterized by south easterly winds along the west coast between Cape Point and Cape Columbine but with calm conditions in St Helena Bay (Fig. 2.2.3). The divergence in the wind field during the survey in the vicinity of line 60 corresponded to a weakening in the wind stress measured at Cape Point and a change in direction from south east to south west during this part of the survey .

Progressive wind vector measurements made at Cape Columbine and Cape Point (Fig. 2.2.2) show that during January 1978 the wind was predominantly southerly and south easterly respectively, although at Cape Point two wind reversals and two changes in wind direction to the south west ocurred. The wind stress measured during the January cruise was normal to the coastline over much of the

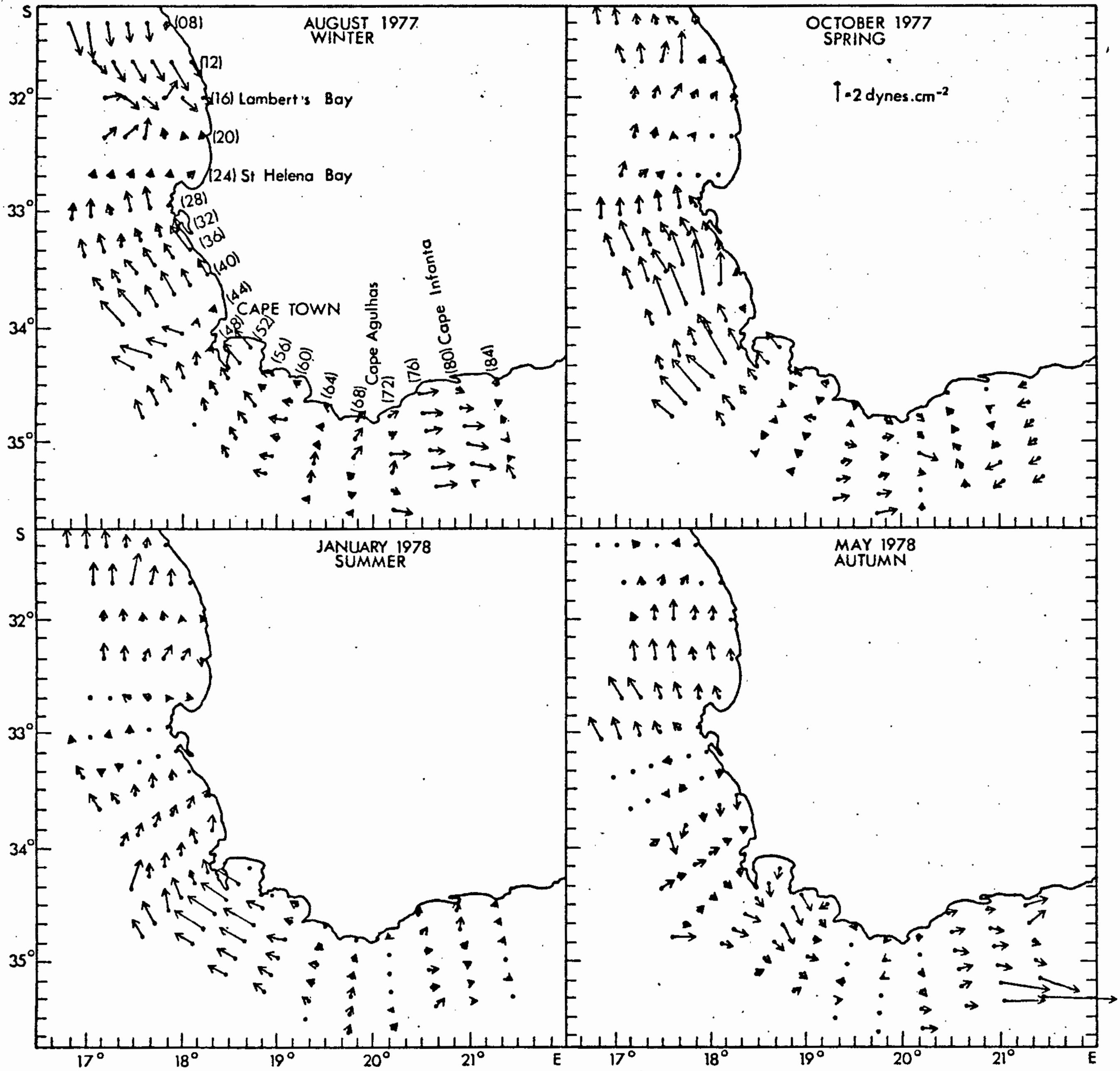

Fig. 2.2.3 Wind stress in dynes. cm-2 measured on board the ship during the surveys.

survey grid (Fig. 2.2.3). A reduction in the wind stress and a divergence in the wind field occurred in the vicinity of Cape Agulhas, similar to that encountered in winter, with weak westerly winds on lines 76 to 84. Reduced wind stress was encountered in the vicinity of Cape Columbine and in St Helena Bay where westerly winds were encountered.

In keeping with the progressive wind vector measurements made at Cape Columbine and at Cape Point in May 1978 (Fig. 2.2.2), the wind stress measured onboard the ship during the cruise was southerly in the area north of Cape Columbine and north westerly from line 36 to line 84, with a lull in wind on lines 64 to 72 (Fig. 2.2.3). Strong westerly winds were ecountered at offshore stations on lines 80 and 84.

Turbulence and mixed layer depth

Corresponding to the wind stress, the index of turbulence (wind speed cubed) showed three main areas of potential vertical mixing in August 1977 (Fig. 2.2.4). The pattern to the north of Lambert's Bay and to the east of Cape Agulhas may be fairly typical of winter conditions during strong blows of westerly or north westerly winds. The depth of the upper mixed layer over the Agulhas Bank (Fig. 2.2.5) was about 40m where the wind speed cubed was less than 500 $m^3.sec^{-3}$ and about 60m within the turbulent area. Where the water depth exceeded 100m west of line 80 the upper mixed layer was deeper than 60m. The very deep thermocline on line 32 was not associated with wind-induced turbulent mixing but ocurred at the top of the Cape Canyon (Fig. 2.2.1) where other mixing processes may occur. Although the area between Cape Columbine and Cape Point was turbulent, the depth of the upper mixed layer at inshore stations remained shallow (Fig. 2.2.5).

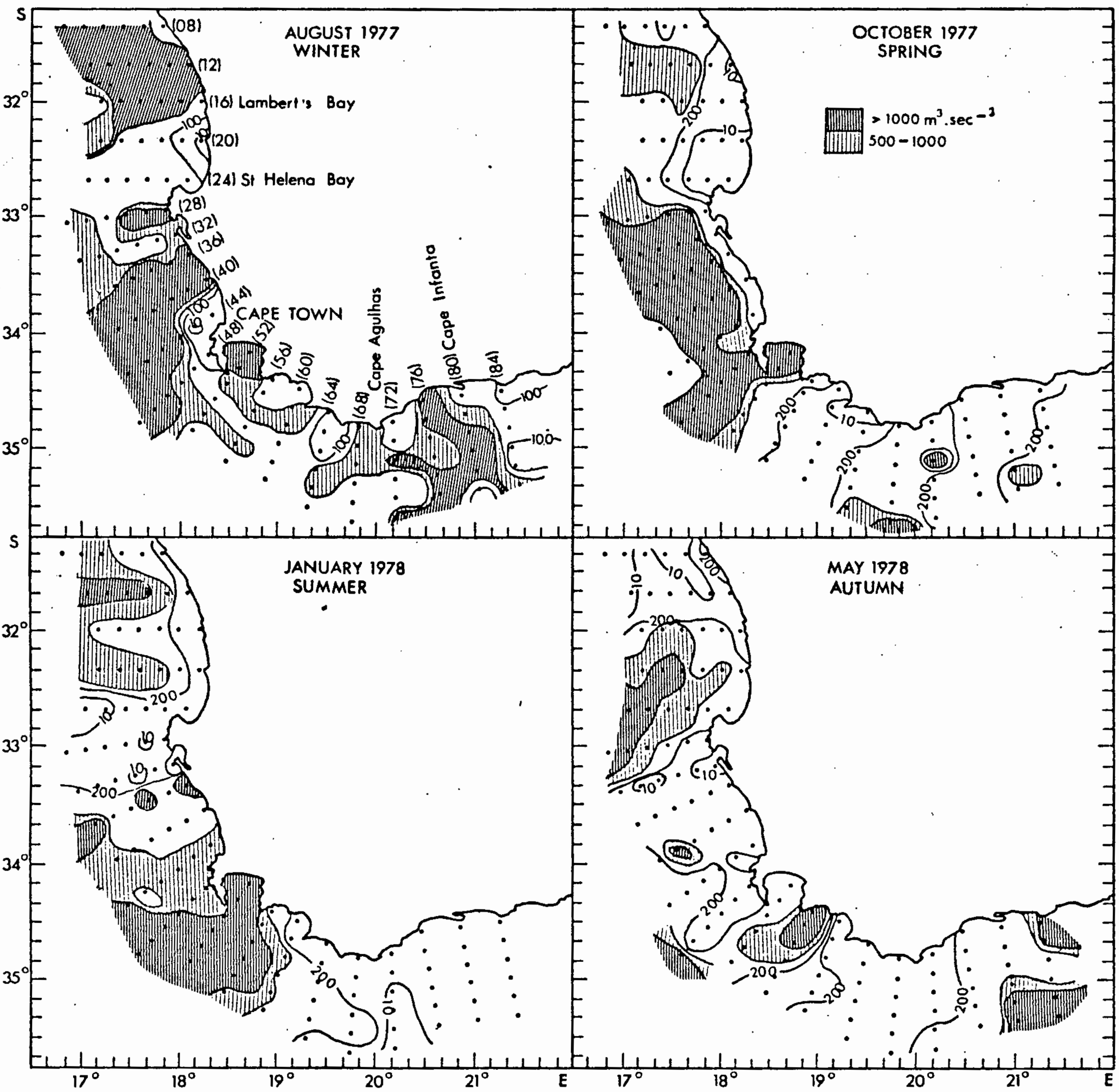

Fig. 2.2.4 Index of turbulence ($m^3.sec^{-3}$) calculated from the wind speed measured on board the ship during the surveys.

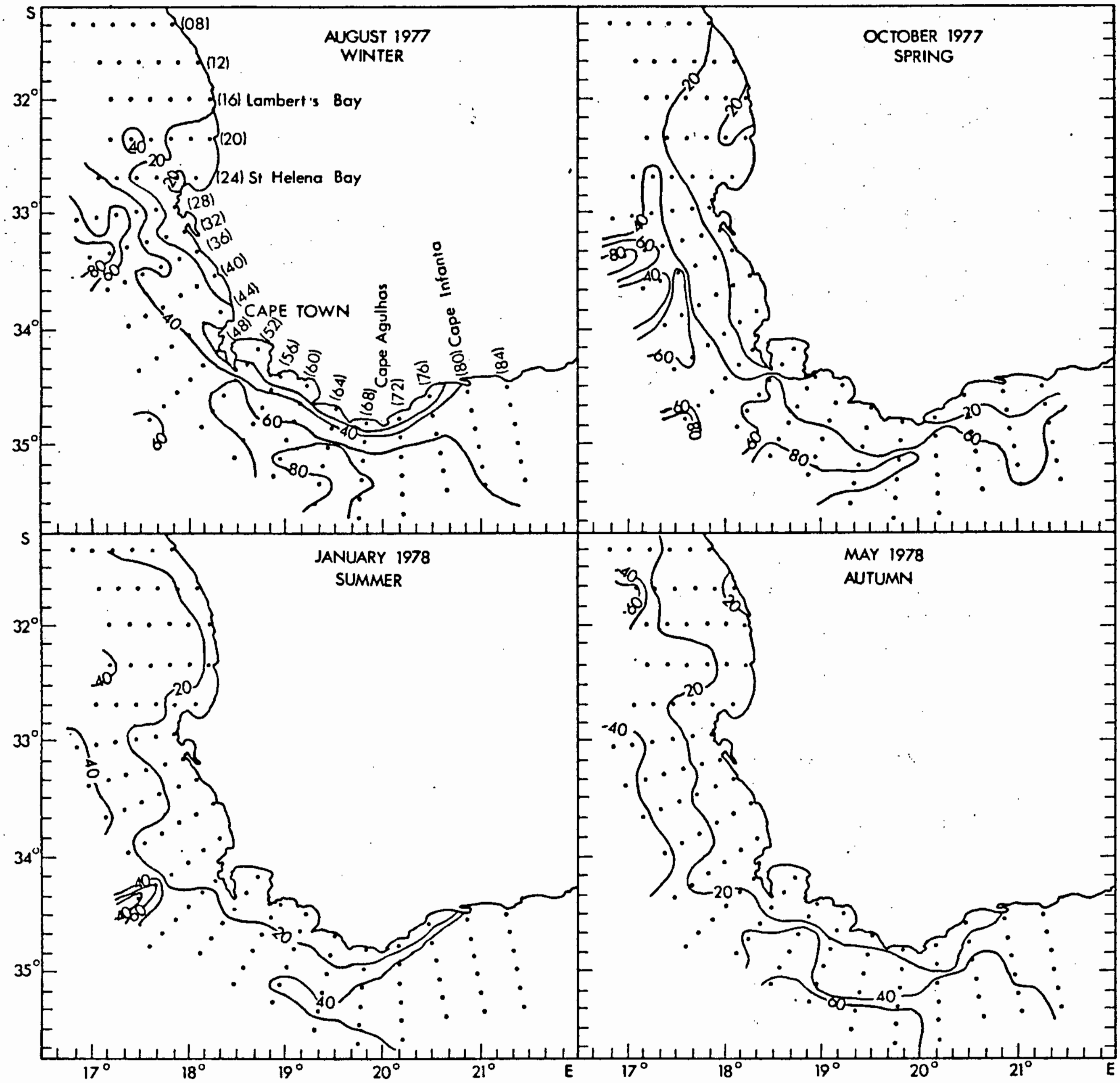

Fig. 2.2.5 Depth of the upper mixed layer (metres), based on temperature profiles obtained on board the ship during the surveys.

In October 1977 the turbulence index indicated only one major zone of potential vertical mixing, extending from Cape Columbine to Cape Point. Although conditions over the Agulhas Bank were relatively calm, the water column remained mixed down to more than 60m over a large portion of the area (Fig. 2.2.5). By comparison, in St Helena Bay there was intensification and shallowing of the thermocline. Deepening of the thermocline was found in association with both the Cape Canyon and the Cape Point Valley. The inner edge of the zone of turbulence along the west coast in October (Fig. 2.2.5) closely followed the thermal front which developed as a result of upwelling inshore and the incresed temperature of the water offshore (see Section 2.1). Outside the front turbulent mixing resulted in a deep upper mixed layer.

The index of turbulence in January 1978 showed that most of the Agulhas Bank area covered by the survey was calm (Fig. 2.2.4). As a result of reduced wind stress and the increased temperature of the surface layer, the water column was relatively stable. The area in the vicinity of Cape Point was turbulent while further north and in St Helena Bay the index was low at inshore stations but higher further offshore. Corresponding to the index of turbulence, there was a substantial shallowing of the depth of the upper mixed layer over the Agulhas Bank and most of the rest of the survey grid . The wind action offshore to the north of Cape Columbine did not appear to deepen the upper mixed layer to any significant extent except at the offshore station on line~~e~~ 44.

The strong westerly winds encountered in the eastern part of the survey grid in May 1978, representitive of autumn conditions, indicated the potential for turbulent mixing which, together with the cooling of the surface layer, would tend to disrupt the summer conditions of a highly stratified, stable water column over the Agulhas Bank. Although the 20m upper mixed layer depth contour occupied roughly the summer position, the depth of the upper mixed layer offshore of this contour deepened in response to increased wind mixing. In the vicinity of Cape Point conditions were comparatively calm while a high turbulence index was encountered offshore of St Helena Bay and Cape Columbine.

Ekman transport

The Ekman velocity vectors for August 1977 corresponding to the winter pattern of winds stress (Fig. 2.2.6) suggest that surface drift to the east of Cape Agulhas had an onshore component, whereas between Cape Agulhas and Cape Columbine the flow was offshore. Onshore Ekman drift in the vicinity of lines 64 to 68 and on line 84 corresponds to the penetration of warm water onto the Agulhas Bank (see Section 2.1). Ekman velocity vectors to the north of Cape Columbine were conducive to the formation of a cyclonic eddy in St Helena Bay to Lambert's Bay area with the onshore limb situated on lines 8 to 16.

In October 1977 Ekman transport was offshore between Cape Columbine and the Cape Peninsula where vigorous upwelling was encountered. To the north of Cape Columbine the flow diverged with the offshore Ekman vectors orientated to the north west and the weaker inshore vectors directed to the south east. This coincided with a similar divergence in the temperature front (see Section 2.1). During the survey onshore transport was encountered only in St Helena Bay and on lines 64 and 68 and there was a region of convergence between lines 72 and 76.

In January 1978 Ekman transport between Cape Point and Cape Columbine was largely longshore whereas north of line 16 (Lambert's Bay) the transport had an offshore component. Corresponding to the reduced wind stress, transport in the vicinity of Cape Columbine was negligable, and to the east of Cape Agulhas was largely onshore.

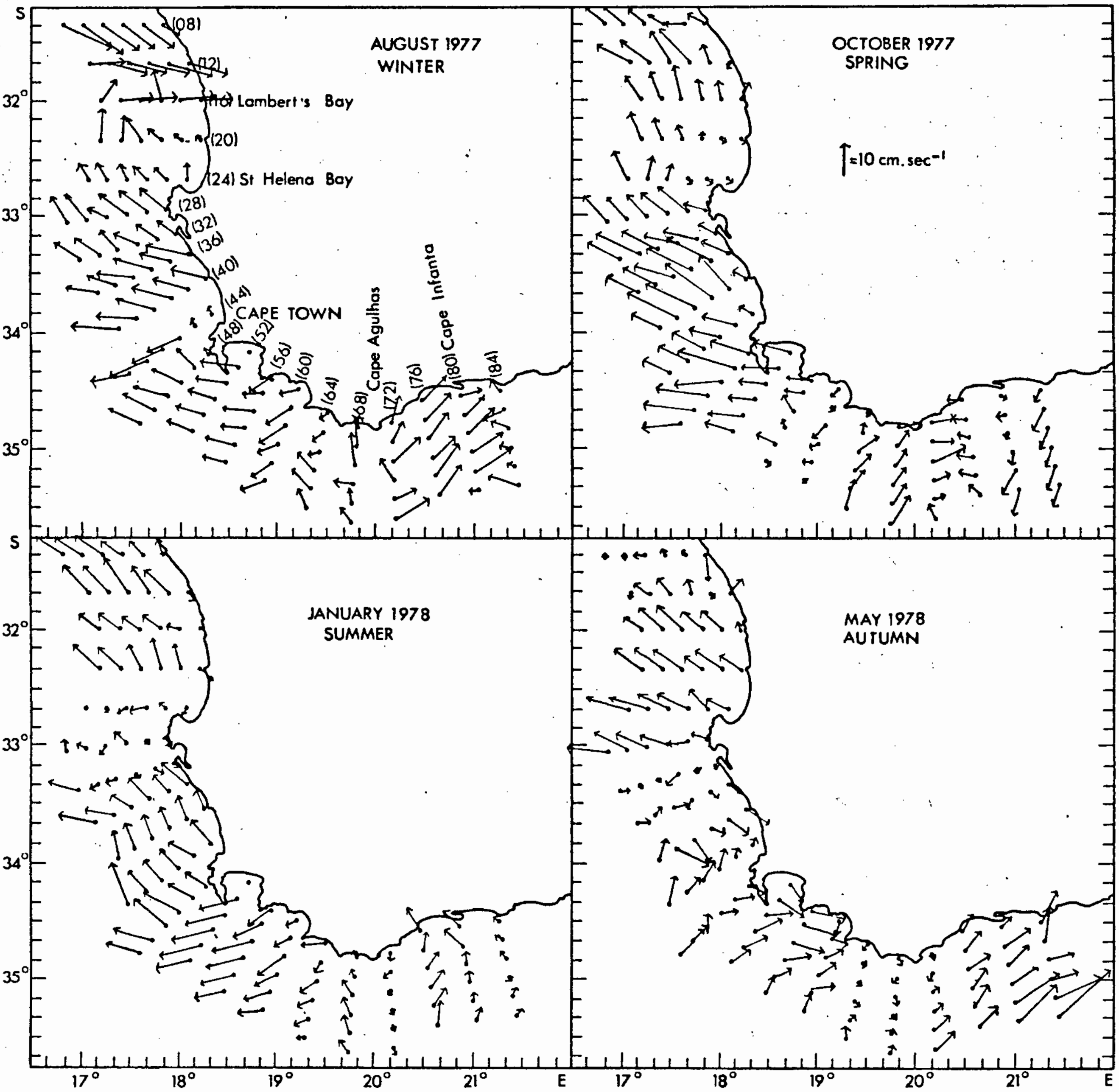

Fig. 2.2.6 Ekman velocity vectors (cm. sec^{-1}) calculated from the wind stress measurements made on board the ship during the surveys.

As a consequence of the wind stress, the Ekman drift during the May 1978 survey was offshore off Cape Columbine and further north, and partly onshore between lines 32 and 60. A divergence in flow occurred in the vicinity of Cape Agulhas with weak, partly offshore Ekman drift on lines 64 and 68 and relatively strong north easterly flow on lines 72 to 84.

Drift card trajectories

Drift card movements from about 27000 releases made during CELP are summarized in Table 2.2.2. The pattern of surface drift in August 1977 deduced from drift card returns (Fig. 2.2.7) confirms the wind stress and Ekman drift data in showing that there was a divergence in the flow pattern in the vicinity of Cape Agulhas. Cards released east of Cape Agulhas drifted eastwards as far as Mossel Bay (9 cards) and Plettenberg Bay (1 card) and onshore. From Table 2.2.2 and Fig. 2.2.7 it is evident that relatively large numbers of cards released on the western portion of the Agulhas Bank drifted around Cape Point (13% of all cards recovered), a number of which entered Table Bay where a cyclonic eddy can be deduced from the temperature structure along line 44 (Fig 2.2.8a). A proportion of the cards continued some distance up the west coast and 3 were recovered as far north as Port Nolloth. About 7% of the recoveries were from cards that drifted out of the Benguela Current system and into the South Atlantic gyre to be recovered in south America. These cards were released at stations between Cape Columbine and Cape Agulhas. This is in keeping with the offshore pattern of Ekman drift on the west coast. The fate of many of the cards released on the west coast is not clear, but it is suspected that a number of these cards also entered the South Atlantic gyre. The recoveries to the north of Lambert's Bay confirm the conclusion from Ekman drift patterns that flow was onshore in this region. One spectacular recovery was made just east of Mossel Bay from a card

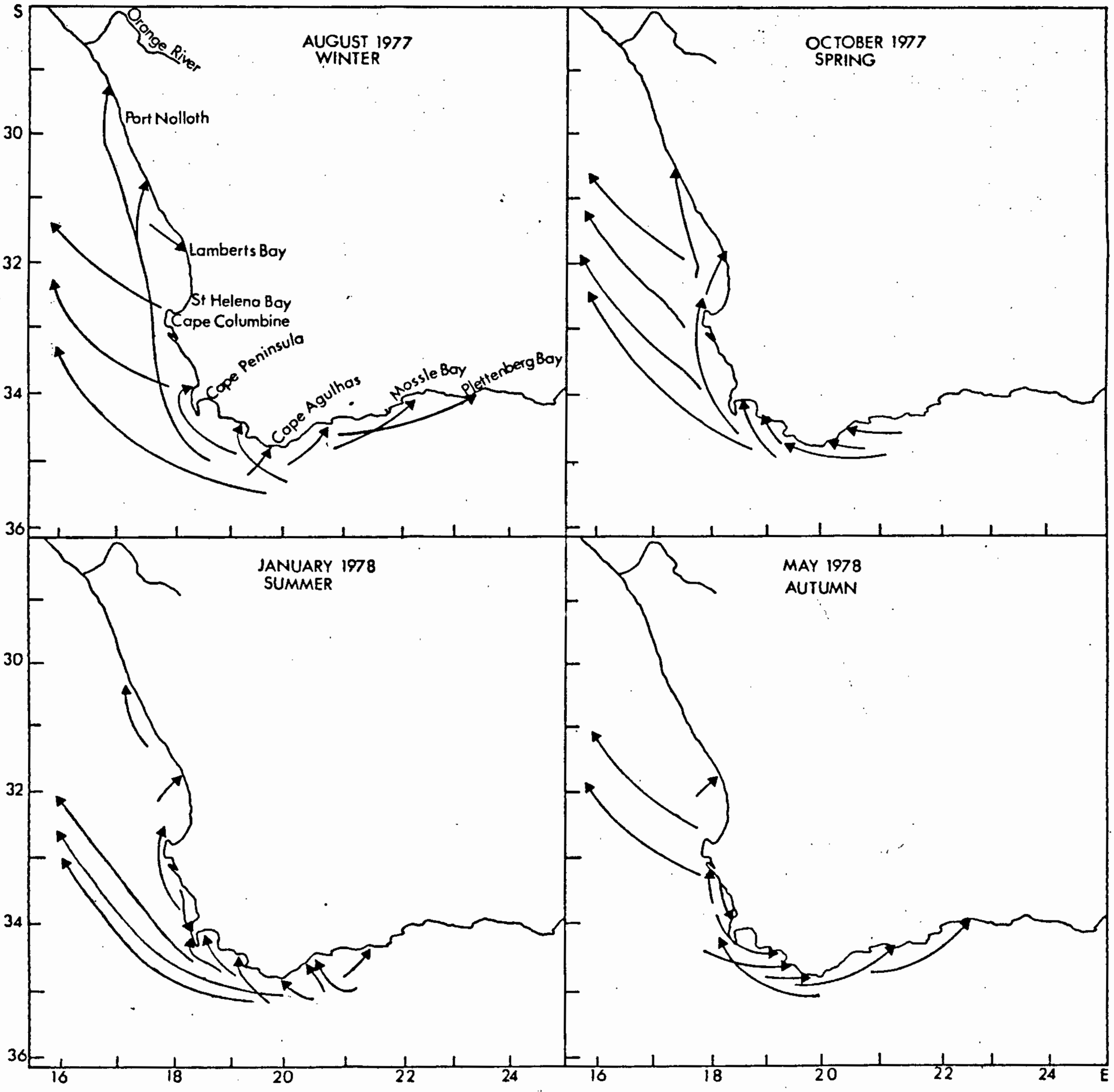

Fig. 2.2.7 A summary of drift card trajectories from releases of 20 cards per station over the CELP grid.

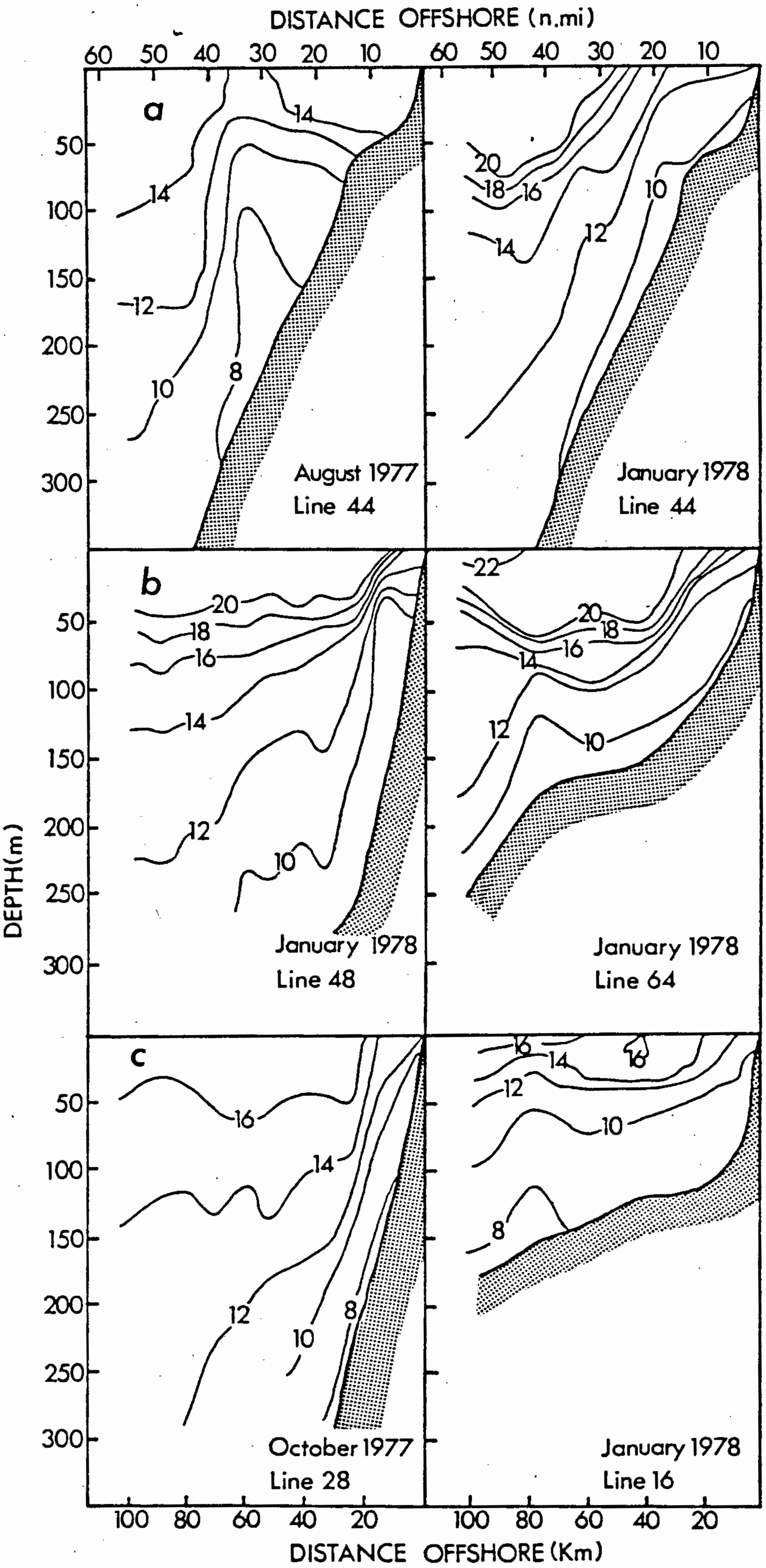

Fig. 2.2.8 (a) Temperature (°C) section along line 44 just north of Cape Town in August 1977 and again in January 1978 showing the change from downwelling to upwelling in the surface water. The August 1977 section is evidence of a cyclonic eddy in Table Bay. (b) Temperature (°C) section along line 48 off the Cape Peninsula in January 1978 showing a well developed front about 15Km from the coast, and a temperature section along line 64 just west of Cape Agulhas showing the south eastward extension of the front inshore and evidence of subsurface downwelling at about 50Km from the coast.

(c) Temperature (°C) section along line 28 at Cape Columbine in October 1977 showing a well developed thermal front, and along line 16 in January 1978 showing evidence of an eddy in St Helena Bay.

released inshore on line 8 to the north of Lambert's Bay. This drift was against the prevailing flow pattern and is indicative of an inshore counter current.

Table 2.2.2

Summary of drift card movements from about 27000 releases made at stations on the survey grid between August 1977 and August 1978.

Months	Aug	Sept	Oct	No/De	Jan	Feb	Mar	Apr	May	June	July	Aug
Season	Wi	Sp	Sp	Sp	Su	Su	Au	Au	Au	Wi	Wi	Wi
Releases	2400	2400	2400	2400	2400	2400	2400	2400	2400	2400	1240	2280
% Recovery	7	6	6	6	5	5	4	1	4	3	4	6
% Of recovered cards												
Entering the gyre	7	7	8	1	6	6	8	6	3	8	0	0
North past C. Pt. & C. Col.	5	4	8	1	4	1	5	0	0	7	0	1
N past C. Point	13	10	7	5	7	6	11	3	5	13	0	4
N past C. Columbine	6	8	7	1	7	3	6	6	1	8	4	1
S past C. Pt. & C. Col.	1	0	1	0	0	0	0	0	0	0	4	0
S past C. Point	1	1	1	0	0	0	0	0	10	3	7	4
S past C. Col.	1	0	1	0	0	0	0	0	0	0	4	1
Into St Helena Bay.	11	12	27	33	12	10	8	21	12	5	65	16
Onto C. Pt.-C. Col.	17	10	10	11	28	10	16	15	34	30	28	37
Onto E of C. Point	59	71	49	51	51	70	66	59	50	57	7	48
E past C. Agulhas	3	0	0	1	0	0	0	3	5	3	2	14
W past C. Agulhas	4	5	5	3	5	9	14	3	2	16	0	2

The recovery of drift cards released in October 1977 showed a predominant trend of westerly drift over the Agulhas Bank region and northerly drift along the west coast (Fig. 2.2.7). There was no trace of the divergence encountered in winter in the vicinity of Cape Agulhas and no cards drifted eastwards over the Agulhas Bank. A large percentage of the recoveries came from the vicinity of False Bay, Cape Agulhas and Lambert's Bay, where the Ekman velocity vectors were not strongly offshore. Drift cards released during the October 1977 survey gave the highest percentage of recoveries from the island of St Helena, Ihla de Trinadade and south America, corresponding to offshore Ekman drift on the west coast between Cape Columbine and Cape Point, although the loss of cards to the South Atlantic gyre is not only a spring phenomenon (Table 2.2.2).

The small number of recoveries of drift cards released offshore of the front during January 1978 suggests that these cards were probably lost from the Benguela Current system, although a number were transported up the west coast and presumably entrained in the geostrophic flow which can be deduced from the temperature section taken along lines 44 and 48 (Fig. 2.2.8a and b). Cards recovered at Ihla de Trinidade and south America accounted for 6% of the recoveries and came mostly from releases made on the Agulhas Bank south of the thermal front which was strongly developed between Cape Columbine and Cape Point, but weaker and close to the coast over the Agulhas Bank (Fig. 2.2.8b). The general summer flow as deduced from drift card trajectories was onshore east of Cape Agulhas, westwards and onshore between Cape Point and Cape Agulhas and longshore from south to north between Cape Point and Lambert's Bay (Fig. 2.2.7). There was some southerly movement inshore on the west coast in the lee of the Cape Peninsula. Flow around Cape Columbine and onshore in the vicinity of Lambert's Bay is indicative of a cyclonic eddy in this region, which is substantiated by the temperature section along line 16 (Fig. 2.2.8c). The reduction in the percentage of cards recovered in summer compared to spring suggests that in general, onshore flow was reduced (Table 2.2.2).

A decrease in the percentage of drift card recoveries in autumn compared to both spring and summer (Table 2.2.2) suggests increased transport out of the region at this time, although it may also be partially attributed to fewer people on the beaches. Most of the recoveries of cards released in May 1978 came from releases made at inshore stations, mainly south of Cape Columbine corresponding to onshore Ekman transport, and only three cards were recovered in south America (Fig. 2.2.7). Although the flow pattern was variable on the Agulhas Bank, there was a tendency towards eastward movement, particularly at inshore stations. One card was recovered as far east as Mossel Bay. This eastward drift is largely an autumn and winter phenomenon (Table 2.2.2).

2.2.4.2 Spatial pattern

The survey area can be divided into 4 regions on the basis of wind stress, Ekman drift and drift card recoveries: (i) The area between lines 8 to 24, including St Helena Bay, where drift close to the coast is predominantly onshore, and where there is normally evidence of a cyclonic eddy promoted by reduced wind stress or even wind reversal within St Helena Bay and further north as indicated by the wind stick diagram for station 6 on line 16 (Fig. 2.2.9). At offshore stations in this region, flow is frequently westwards and out of the system. (ii) The area between Cape Columbine and Cape Point, where wind stress is longshore from south to north over much of the year (e.g. station 6 on line 28, Fig 2.2.9), and where there may be substantial offshore Ekman drift leading to flow out of the coastal region, especially at stations some distance from the coast. Southward flow of surface water in the inshore region is a fairly common feature in the late autumn and early winter. This is an area of great turbulence, especially during winter and spring. Onshore flow along this part of the coast tends to be maximum in late autumn and winter when a cyclonic eddy may occur in the vicinity of Table Bay (Fig. 2.2.8a, line 44). At station 6 on line 28 off Cape Columbine, wind measured during the cruises was southerly (Fig. 2.2.9), whereas winds measured at station 6 on line 48 off the Cape Peninsula had more south easterly component. (iii) The area from Cape Point to Cape Agulhas, where flow is generally towards the west, often with an onshore component close to the coast, although in late autumn and winter flow may be eastwards. Flow from stations further offshore on the western edge of the Agulhas Bank may often be out of the system, although some drift cards released in this region were recovered considerable distances up the west coast. The wind measured at station 56-06 had a component from the east compared to more southerly winds between Cape Point and Cape Columbine. (iv) The area from Cape Agulhas to line 84 where flow is more consistently eastwards and onshore from autumn to spring and even occasionally in summer when the wind has a westerly component. An apparent divergence in the wind field at Cape Agulhas is indicated by the change in the orientation of the wind sticks at station 6 on lines 64 and 76 (Fig. 2.2.9). The change in wind direction from predominantly southerly winds at Cape Columbine to south easterly winds between Cape Point and Cape Agulhas and westerly winds east of Cape Agulhas indicates the importance of coastal topography in determining the pattern of the wind field in the southern Benguela Current region. Strong turbulence is a feature of the area east of Cape Agulhas in autumn and winter when westerly winds occur frequently.

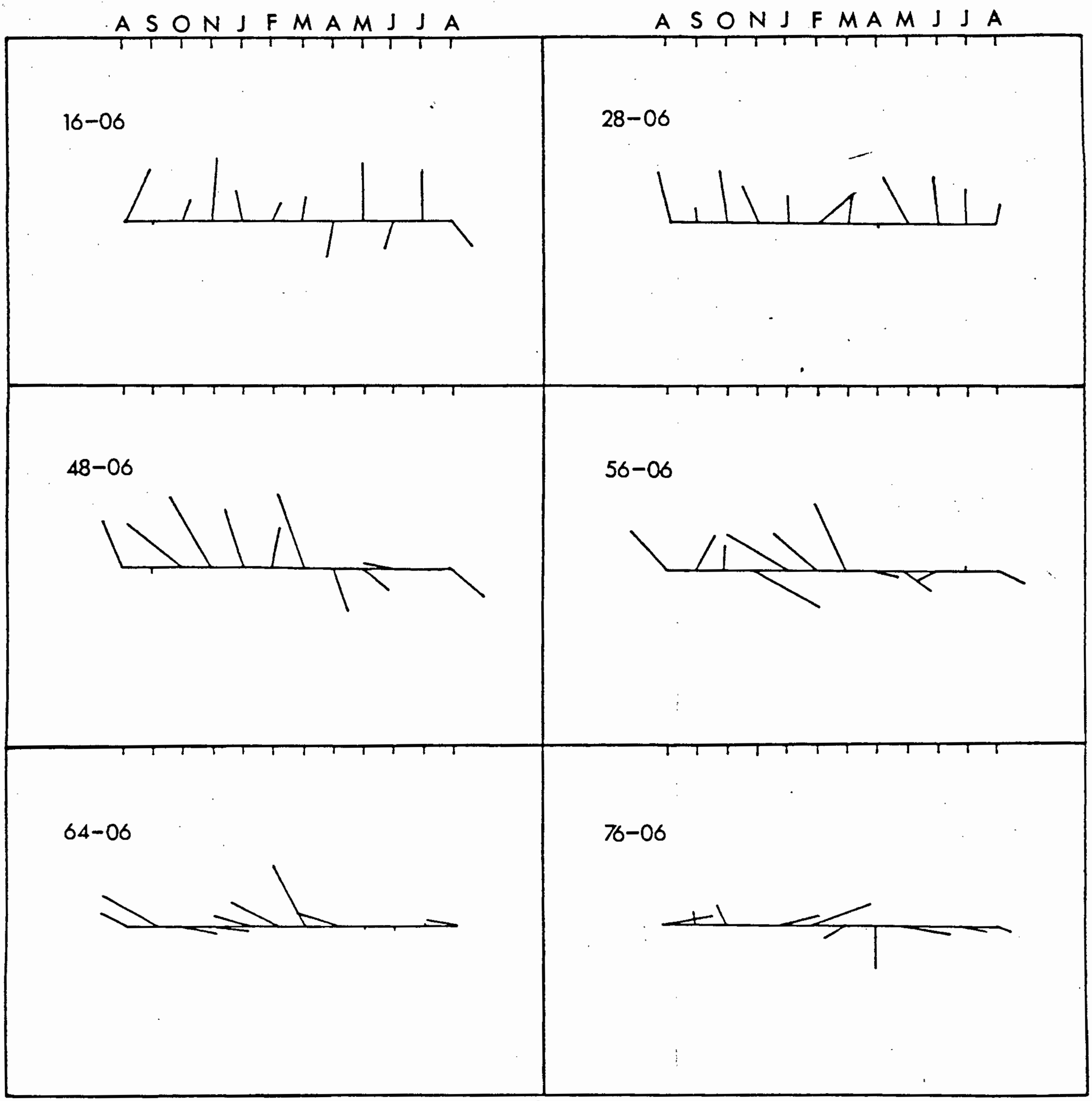

Fig. 2.2.9 Wind stick diagrams for August 1977 to July 1978 from wind measurements made at selected stations.

2.2.4 Discussion

Duncan and Nell (1969), Nelson and Hutchings (1983) and Shannon (1985) have produced generalized descriptions of the near surface circulation for the southern Benguela Current regiõn. In Fig. 2.2.10 an attempt is made to synthesize the results of the present study into a further generalized description based on the CELP data, emphasizing the seasonal component and dealing with transport out of the system. Future detailed descriptions of circulation over the whole water column are likely to result from the current meter work by Nelson and Holden (SFRI, in prep.), however in the mean time Fig. 2.2.10 may provide a useful basis for examining some of the mechanisms that may determine recruitment in neritic fish species in the southern Benguela region.

Although the orientations of the vectors are partly subjective, the flow pattern in Fig. 2.2.10 agrees in general with the descriptions given in the earlier studies. Flow deduced in this study suggests that the anticyclonic eddy off the Cape Peninsula and the inshore southward flow between Saldanha Bay and Table Bay illustrated in the diagrams of Nelson and Hutchings (1983) and Shannon (1985) may be better defined in winter with more direct northerly flow past the Cape Peninsula as far as Cape Columbine or beyond prevailing in summer. Shannon (1985) has identified an area of divergent flow off Cape Columbine which may be partly topographically induced, and which is associated with more northerly flow in spring and early summer, and more westward flow from late summer to winter. This is generally supported in the present study, although there is evidence that both the westward and northward components of flow are strong in spring and that the northward flow is accompanied by a cyclonic eddy into St Helena Bay which is most intense in summer (Fig. 2.2.10). The existence of the St Helena Bay eddy has been confirmed using radio tracked drifters (C. Holden, SFRI, pers.

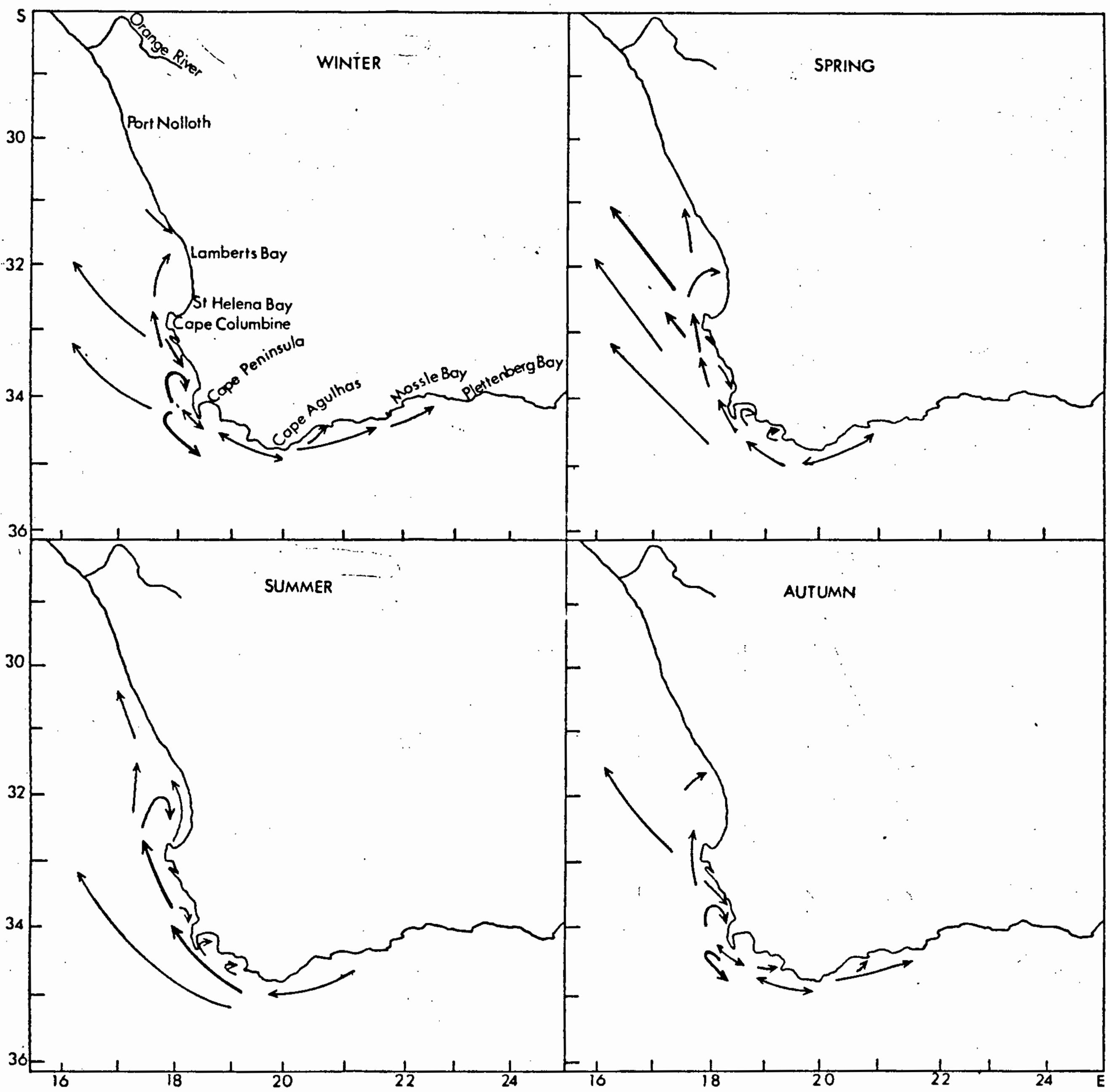

Fig 2.2.10 The generalized seasonal pattern of flow in the southern Benguela region deduced from winds stress measurements, Ekman velocity calculations, drift card trajectories and density gradients. The strength of flow is roughly proportional to the arrow thickness and double headed arrows indicate variable flow.

comm.). The temperature section along line 16 suggests that inshore of the eddy there may have been northward flow (Fig. 2.2.8c). Westward transport out of the system in summer appears to originate fairly far south on the Agulhas Bank.

Shannon and Chapman (1983), Schumann and Beekman (1984) and Shannon (1985) have suggested that a second area of divergence occurs just east of Cape Agulhas. This appears to coincide with the eastward limit of extensive offshore Ekman transport (see Section 2.1), although Schumann et al. (1982) have found upwelling associated with crenulated capes further east and upwelling was found in the vicinity of Plettenberg Bay in November 1984 and 1985. The existence of an area divergence near Cape Agulhas is supported by the analysis of surface Ekman velocity vectors (Fig. 2.2.6) and drift card trajectories (Fig. 2.2.7). It would appear to be weakest in summer when the incidence of westerly winds is lowest in the southern Benguela region (Andrews and Hutchings 1980), however the directional variation of wind throughout the year appears to be constrained by coastal topography along the whole southern Benguela region, with winds east of Cape Agulhas generally having a westerly component (Fig. 2.2.9). Although Hutchings and Nelson (1985) calculated the average wind stress curl for the year from the CELP data set and found a boundary between negative wind stress curl west of Cape Agulhas and positive curl to the east, the pattern in the individual months (not shown) is much more variable with zones of divergence and convergence shifting along the coast, probably as an artefact of temporal changes in wind~~s~~ stress during the non-synoptic coverage of the survey grid. However, in winter there was a relatively uniform area of divergence associated with Cape Agulhas which shifted west in spring and east in autumn and was reduced in summer.

Drift card returns indicated that the southern Benguela Current region has a relatively closed circulation longshore but has a major exit offshore. Only one drift card recovery was made north of the Orange River mouth, in the vicinity of Ludertiz, and no cards were recovered east of Port Elizabeth. Part of the reason for only one recovery from South West Africa/Namibia may be the low population density of the region and the fact that some areas are closed to the public because of diamond concessions, however the area east of Port Elizabeth is relatively densely populated. The lack of significant eastward drift confirms the results of Shelton and Kriel (1980) from releases made east of Cape Agulhas in spring.

While it has previously been suspected that there is some loss of water from the southern Benguela region into the South Atlantic gyre, based on the paths of satellite tracked drogues (e.g. Harris and Shannon 1979) and drift card recoveries (Stander et al. 1969), the relatively large number of south west Atlantic drift card recoveries in this study suggests that the loss of coastal water westwards is substantial. Nelson and Hutchings (1983) have described the path taken by a satellite tracked drogue which went northwards, veered away from the coast at latitude 24°S, and then passed through the gap in the Walvis Ridge. The recovery of drift cards on the Island of St. Helena from releases made within the CELP grid indicates that at least some of the cards recovered in the south west Atlantic may have followed a similar path to that of the drogue. The westward flow of shelf water out of the system may be inhibited by the thermal front which develops along the west coast in summer, as in January 1978 south west Atlantic recoveries came only from cards released south of the thermal front (Fig. 2.2.7). Relatively buoyant particles such as drift cards may behave differently from neutrally buoyant particles such as fish eggs and larvae. The neutrally buoyant particles may be more easily constrained by the front. At other times of the year, particularly in spring before an intense front has developed, but when Ekman transport has a westward component, the divergence at Cape Columbine may be a major exit point.

In a comparison of the four eastern boundary current systems, Parrish et al. (1983) suggested that avoidance of areas of turbulent mixing and offshore transport by spawning neritic fish species indicates that these processes have exerted important controls on reproductive success. Turbulent mixing is thought to disrupt the chlorophyll maximum layer within a stratified water column (Lasker 1975), whereas offshore transport is likely to carry the planktonic reproductive stages off the shelf and out of the neritic system (Parrish et al. 1981). In contrast, favourable transport could carry larvae to productive and oceanographically stable nursery grounds (Shelton and Hutchings 1982). Results from this study suggest that offshore Ekman transport may be particularly important in carrying eggs and larvae out of the southern Benguela Current region. Fish may avoid offshore transport by spawning inshore of the thermal front along the west coast in summer, or east of Cape Agulhas, or by spawning in autumn or winter when offshore Ekman transport is reduced. Reproductive products spawned in summer inshore of the front west of Cape Agulhas are likely to enter weak cyclonic eddys associated with Walker Bay and Table Bay (Harris 1978) or, more likely, be rapidly transported around Cape Point (Duncan and Nell 1969) and up the west coast in the geostrophic jet current (Bang and Andrews 1974, Shelton and Hutchings 1983) and enter the St Helena Bay Eddy (Fig. 2.2.10), or continue northwards, possibly as far as Luderitz which, as a major centre of upwelling (see Section 1.3), may interrupt further northward transport of plankton from the south. Duncan and Nell (1969) suggested that the southward flowing inshore counter currents, and in particular the cyclonic eddy measured by Duncan (1966) off the Cape Peninsula in July, could explain how fish eggs and larvae remain on the west coast instead of being transported out of the system in the general flow of the Agulhas Current. Eggs and larvae resulting from spawning east of Cape Agulhas, especially in winter or autumn, may drift inshore or eastwards as far as Port Elizabeth. In spring, eggs and larvae inshore of the front on the west coast may have a large probability of being carried into False Bay or Table Bay, whereas in winter and spring there may be an increased probability of being transported out of the system by way of the Columbine divergence.

Vigorous turbulence over the Agulhas Bank in winter, when the surface layer cools and the water column becomes less stable, results in substantial vertical mixing (Pugh 1982) and deepening of the upper mixed layer, and is likely to disrupt food layers, whereas the area within St Helena Bay has little turbulence throughout the year and may provide a perennially suitable feeding area for late stage larvae and juveniles, particularly if upwelling is associated with the eddy and if food particles and the larvae are retained in the bay by the cyclonic circulation. The increased depth of the upper mixed layer offshore of the 200m contour along the west coast, especially over the Cape Point Valley and the Cape Canyon may make this area less suitable for larval and juvenile feeding throughout the year.

2.2.5 Conclusion

Drift card returns indicate that the southern Benguela Current region has a relatively closed circulation longshore, but that there is a major loss of shelf water offshore, particularly in the vicinity of the Columbine divergence. The thermal front which develops along the west coast in summmer appears to present a barrier to the predominantly offshore Ekman transport of shelf water along the west coast, and it seems likely that planktonic particles inshore of the front have a high probability of being retained within the neritic environment by a number of cyclonic eddies associated with bays, in particular the St Helena Bay eddy. In general, the directional variation in the wind field is constrained by coastal topography, but a major divergence in the wind field and in the flow of surface water is associated with Cape Agulhas. The eastward flow east of Cape Agulhas is strongest in winter and autumn. The area between Cape Point and Cape Columbine is subject to strong turbulent action but the wind stress is reduced to some extent over the Agulhas Bank and particularly to the north in St Helena Bay, making these more favourable areas for the development of a stratified water column and associated plankton layers for larval feeding.

3 PATTERNS OF PLANKTON ABUNDANCE

3.1 SPATIAL AND TEMPORAL DISTRIBUTION OF CHLOROPHYLL IN SOUTHERN AFRICAN WATERS AS DEDUCED FROM SHIP AND SATELLITE MEASUREMENTS AND THEIR IMPLICATIONS FOR PELAGIC FISHERIES

L.V. SHANNON, L. HUTCHINGS*, G.W. BAILEY* AND P.A. SHELTON**

Information is presented on the distribution of chlorophyll *a* between the Cunene River (18°S), on the border of South West Africa (Namibia) and Angola, and East London (28°E) on the east coast of South Africa. Spectrophotometric measurements of samples collected during various research cruises and estimates from satellite measurements were used. The coast was divided into a number of oceanographic regions. Spatial and temporal variation of chlorophyll *a* in the waters off central-northern South West Africa, the Lüderitz region, the South-Western Cape and the Algoa region are discussed in some detail. There was a narrow coastal band of moderate to high chlorophyll *a* (3 to in excess of 10 mg·m^{-3}) at the surface between Cape Cross (22°S) and Möwe Point (*c.* 19°S) throughout most of the year, whereas in much of the area between 23 and 33°S concentrations reached maximum values in autumn. Along the South-Western Cape coast, high concentrations of chlorophyll *a* were observed in the St Helena Bay area up to 90 km off shore throughout the year, evenly distributed in the upper 30 m. A narrower band of high concentrations of chlorophyll *a* extended southwards to Cape Agulhas during summer when upwelling was most active. During late summer and autumn a subsurface maximum developed on the Agulhas Bank associated with the thermocline. Low to moderate concentrations were widespread over the entire coastal zone during winter, with strong mixing in the upper 50 — 100 m. A fairly consistent feature of the Algoa region was the presence of moderate concentrations of chlorophyll associated with a wedge-shaped zone of coastal and dynamic upwelling. The implications of the distribution of chlorophyll in time and space are discussed with respect to the distribution and migration of pelagic fish species, particularly anchovy.

Gegewens word aangebied omtrent die verspreiding van chlorofil *a* tussen die Kunenerivier (18°S), op die grens van Suidwes-Afrika (Namibië) en Angola, en Oos-Londen (28°O) aan die ooskus van Suid-Afrika. Spektrofotometriese metings van monsters wat in die loop van verskeie navorsingsvaarte versamel is, en ramings volgens satellietmetings is gebruik. Die kus is in 'n aantal oseanografiese streke verdeel. Variasies in ruimte en tyd van chlorofil *a* in sentrale-noordelike Suidwes-Afrikaanse waters, die Lüderitz-gebied, Suidwes-Kaapland en die Algoa-streek word taamlik uitvoerig bespreek. Daar was gedurende die grootste deel van die jaar 'n smal kusstrook van matige tot hoë chlorofil *a* (3 tot meer as 10 mg·m^{-3}) by die oppervlak tussen die Kruiskaap (22°S) en Möwepunt (*c.* 19°S), terwyl konsentrasies in 'n groot gedeelte van die gebied tussen 23 en 33°S in die herfs maksimale waardes bereik het. Langs die Suidwes-Kaapse Kus is hoë konsentrasies van chlorofil *a* die grootste deel van die jaar tot 90 km van die kus af in die gebied van St Helenabaai waargeneem — egalig in die boonste 30 m versprei. 'n Smaller strook van chlorofil-*a*-konsentrasies het suidwaarts tot by Kaap Agulhas gestrek in die somer toe opwelling die aktiefste was. Gedurende die nasomer en herfs het daar op die Agulhasbank 'n onderoppervlak-maksimum ontwikkel wat met die termoklien geassosieer was. Lae tot matige konsentrasies was gedurende die winter wyd oor die hele kussone versprei, met sterk vermenging in die boonste 50 — 100 m. 'n Redelik bestendige kenmerk van die Algoa-streek was die aanwesigheid van matige chlorofilkonsentrasies, met 'n wigvormige sone van kus- en dinamiese opwelling geassosieer. Die implikasies van die verspreiding van chlorofil in tyd en ruimte word bespreek ten opsigte van die verspreiding en migrasie van pelagiese visspesies, veral ansjovis.

The Benguela Current system on the west coast of southern Africa, which is bounded in the north near Cape Frio (18°S) by the interaction area with the south-flowing Angolan Current and in the south by the Agulhas retroflection area south of Cape Agulhas (35°S), is one of the world's four main coastal upwelling regimes. In sharp contrast, the East Coast is dominated by a major western boundary current, the Agulhas Current. The extent and the importance of these systems have been recognized for several decades and they have been described by Dietrich (1935), Clowes (1950), Hart and Currie (1960), Stander (1964), Shannon (1966), Bang (1973), De Decker (1973), Pearce (1977), Andrews and Hutchings (1980), Lutjeharms (1981), and Nelson and Hutchings (1983) amongst other.

Although several authors (De Jager 1957, Taylor 1964, Mitchell-Innes 1964, Nel 1968, Austin 1980, etc.) have discussed the distribution of phytoplankton around southern Africa, relatively little has been published on the macroscale and mesoscale distribution of chlorophyll *per se* in local waters. Andrews

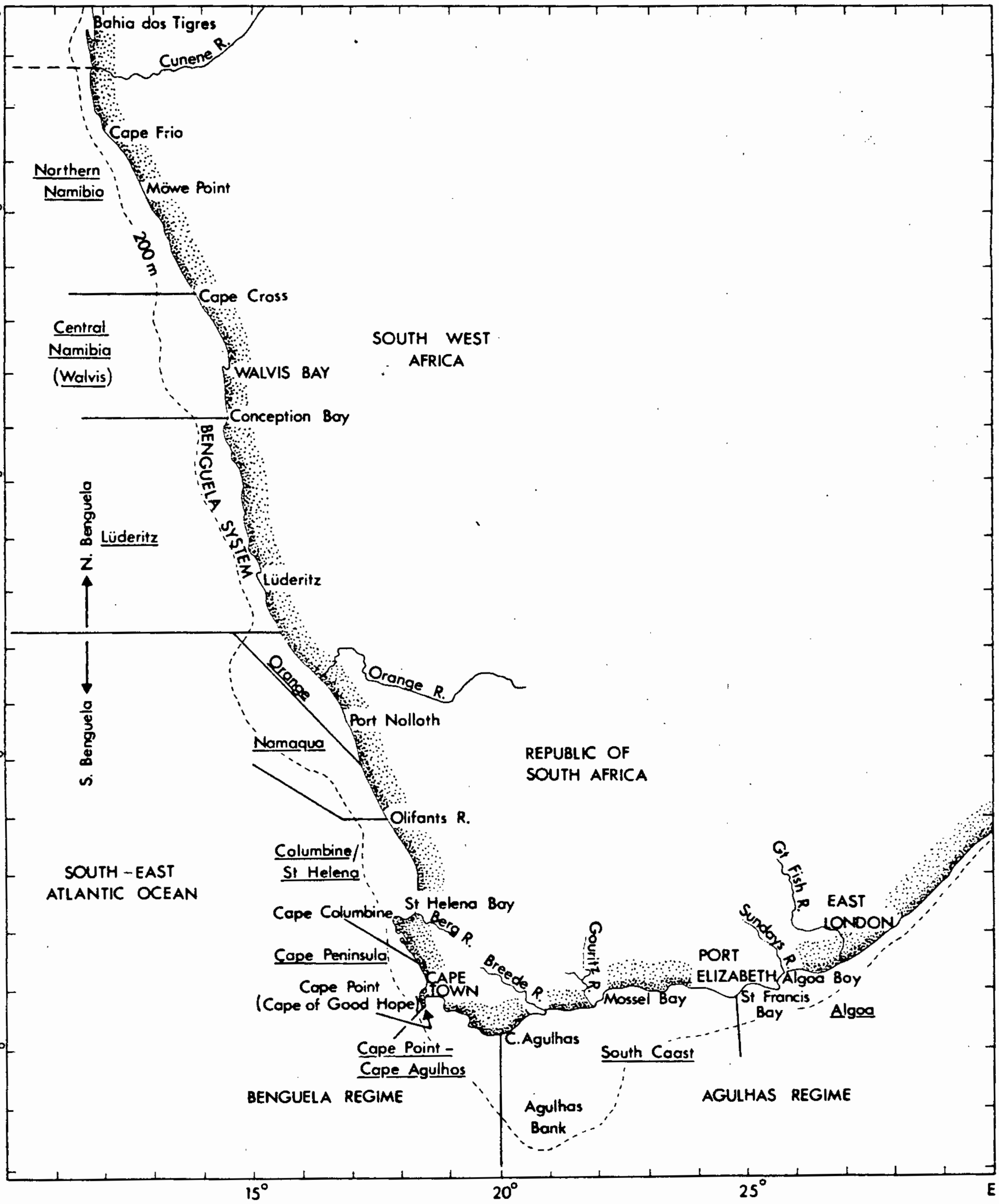

Fig. 1: The study area and the main oceanographic regions

and Hutchings (1980) described processes associated with the Cape Peninsula upwelling region and provided estimates of phytoplankton standing stock (chlorophyll *a*, nitrogen and carbon) and production along a monitoring line. More recent work by Barlow (1982a, b, c, 1983), Brown (1983), Hutchings *et al.* (1983) and Olivieri and Hutchings (1983) has provided a good understanding of the dynamics of plankton in response to upwelling events around the South-Western Cape, and the results of satellite measurements reported by Shannon *et al.* (1983) and Shannon *et al.* (in press) have provided a synoptic picture of the horizontal distribution of near-surface chlorophyll in the same area.

This report deals with the mesoscale and macroscale distribution of chlorophyll around southern Africa. It is based on extensive spectrophotometric measurements made on samples taken at sea during the 1970s off South West Africa (Namibia) and around the South-Western Cape, and on satellite measurements made between December 1978 and February 1980. The geographic area covered is illustrated in Figure 1.

METHODS

Analysis of chlorophyll *a* samples taken at sea

Discrete seawater samples were collected on a number of cruises by means of plastic N.I.O. bottles set at 10-m intervals in the upper 50 m. On some cruises the water column was sampled at more frequent intervals and/or to greater depths. After addition of 2 mℓ of $MgCO_3$, 1- or 2-ℓ aliquots were filtered through either 47/50-mm 0,8 μm glassfibre or 0,45-μm membrane filters. The filters were stored in the dark at -20°C over silica gel and analysed for chlorophyll *a* in the shore laboratory by the standard spectrophotometric method of SCOR/UNESCO Working Group 17 (1966). Chlorophyll *a* is expressed as a concentration in units of μg per litre and as a quantity in terms of integrated values of mg per m^2. Chlorophyll *a* is subsequently referred to in this paper as chlorophyll and is assumed to represent the biomass of phytoplankton (Andrews and Hutchings 1980).

Relatively few biological oceanographic measurements have been made between East London and Port Elizabeth, herein referred to as the Algoa region (excluding those made in estuaries or close inshore), although the area is thought to be important for pelagic fish species (Batchelor 1982).

During the period August 1977 through August 1978, chlorophyll measurements were made monthly as part of the Cape Egg and Larva Programme (CELP) at 120 stations (i.e. over 1 400 samples in total) off the South-Western Cape (Fig. 2). As voyages lasted 8 — 12 days they only represent quasi-synoptic distributions of chlorophyll.

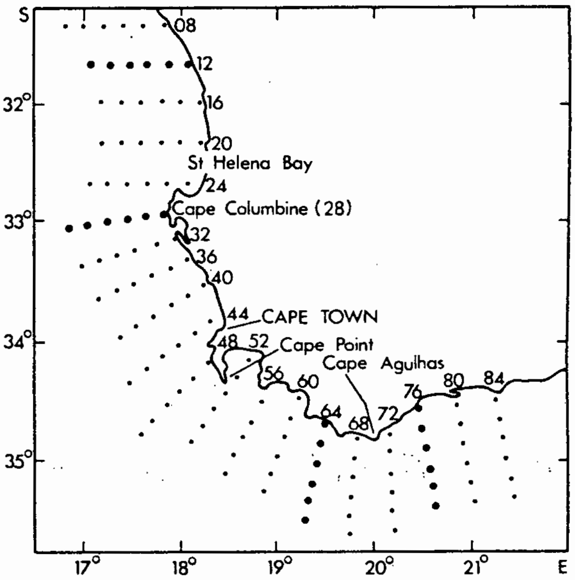

Fig. 2: The Cape Egg and Larva Programme (CELP) basic station grid, sampled monthly between August 1977 and August 1978 — the four lines selected for vertical sections (12, 28, 64 and 76) are shown with bold dots

Chlorophyll measurements were made in the upper 75 m during monthly cruises to South West Africa between 17 and 24°S from May 1971 to January 1972. Five quarterly cruises were undertaken between 24°30'S and 28°S between February 1976 and February 1977.

Satellite measurements

The estimation of near-surface chlorophyll concentrations from space was made with radiance data from the Coastal Zone Colour Scanner (CZCS) on the *Nimbus-7* satellite during the period November 1978 — February 1980. The CZCS is a six-channel scanning radiometer with four bands in the visible region of the spectrum at 443, 520, 550 and 670 nm, one in the near infra-red at 750 nm and one in the infra-red at 11,5 microns (Hovis *et al.* 1980). The satellite has a circular, sun-synchronous ascending

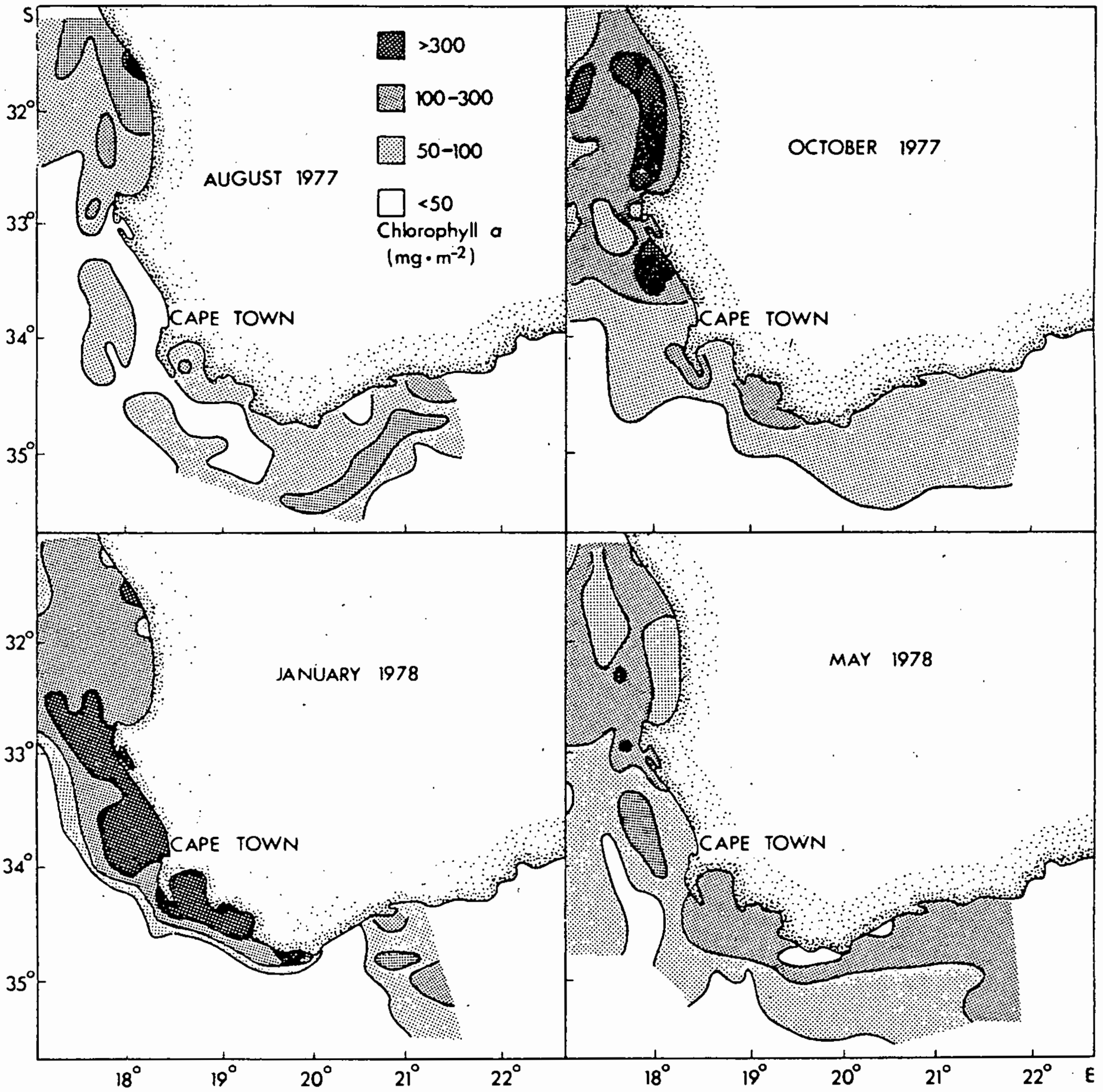

Fig. 3: Distribution of chlorophyll a integrated through the upper 50 m (mg·m^{-3}) in winter (August 1977), spring (October 1977), summer (January 1978) and autumn (May 1978) off the South-Western Cape

orbit with a swath width of 1 566 km, a substantial swath overlap, a spatial resolution of 0,825 km × 0,825 km and a repeat cycle of about six days. The chlorophyll concentrations can be calculated from the satellite-derived, subsurface upwelling radiances by means of algorithms such as that proposed by Clark (1981) and adapted for Cape waters by Walters (1983). Walters (op. cit.) and Shannon *et al.* (1983) showed that there was good correlation between the ship-measured and satellite-estimated chlorophyll in the Case I optical waters, as defined by Morel (1980), of the South-Western Cape ($r = 0{,}89$). In this report,

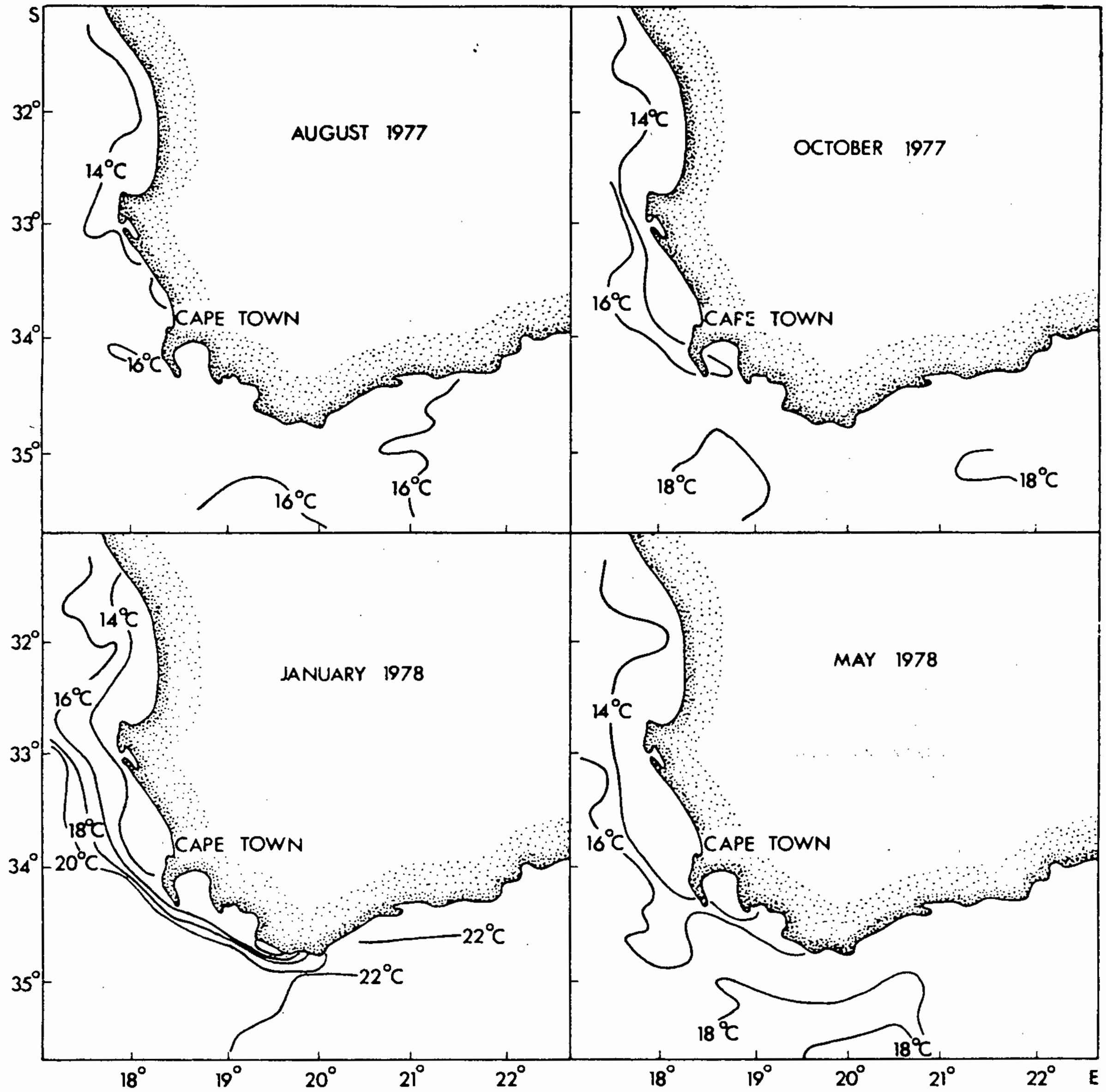

Fig. 4: Distribution of surface temperature (°C) for August 1977, October 1977, January 1978 and May 1978 off the South-Western Cape

charts of chlorophyll pigment produced by the National Aeronautics and Space Administration (NASA-level-2 product) were used, because these charts were readily available on a grey scale rather than in colour, and they covered a greater geographic range than those generated locally.

A comparison was made between 15 NASA-derived scenes of the South-Western Cape and corresponding chlorophyll charts produced by N.M. Walters (National Research Institute for Oceanology [CSIR]), and agreement with respect to structure (features) was found to be excellent. Chlorophyll concentrations compared well in all but three scenes (these three all reflecting winter — low sun elevation, high values of CZCS gain). Figure 10 (see later) illustrates the good agreement between the NASA-level-2 product and a chart produced by N.M. Walters for a single scene of the southern Benguela region on 19 February 1979. Further, chlorophyll charts generated by B. Sturm and G. Maracci and cited in Shannon *et al.* (in press) of two scenes of the Benguela system during February 1980 compared favourably with the NASA and Walters' products.

RESULTS FROM SAMPLES TAKEN AT SEA

Horizontal distribution of chlorophyll around the South-Western Cape

Four distributions of integrated chlorophyll in the upper 50 m have been selected to illustrate seasonal trends (Fig. 3). The surface temperature distributions for corresponding cruises are also shown (Fig. 4).

During winter (e.g. August 1977), upwelling was minimal along much of the South-Western Cape coast, except at the extreme north of the station grid. Chlorophyll levels were elevated north of St Helena Bay because of upwelling and in the east along a shallow ridge on the Agulhas Bank, where the water column had mixed to the bottom during the passage of a winter storm a few days prior to sampling. Elsewhere, low concentrations of chlorophyll were observed, as a deep layer of oceanic water invaded close inshore between Cape Agulhas and Cape Columbine. Similar distributions occurred during the following winter (June — August 1978), except that mixing was not strong enough to reach the bottom on the Agulhas Bank, and low concentrations of chlorophyll were observed everywhere south of Cape Columbine.

In spring, upwelling increased in frequency and winter mixing processes decreased in strength, allowing phytoplankton to develop in the upper layers both on the West Coast and on the Agulhas Bank. By October 1977, dense phytoplankton blooms were observed in cool, newly upwelled water inshore on the West Coast, while there was a general rise in concentrations of chlorophyll everywhere except off shore in the extreme south, as water stabilization increased.

As summer approached, frequent upwelling events created a narrow band of cool, chlorophyll-rich water along the whole West Coast as far south as Cape Agulhas. Off shore, sun-warming plus contributions of Agulhas Bank water raised surface temperatures to 19 — 21°C, creating a very strong thermal gradient, or front, on the outer boundary of the chlorophyll-rich belt. Very low concentrations of chlorophyll were found beyond this front, which was clearly identifiable from Cape Agulhas to Cape Columbine, where it moved off shore of the station grid. Moderate concentrations of chlorophyll were widespread in the northern coastal zone. Although marked fluctuations over a time-scale of 5 — 14 days do occur along the West Coast as upwelling-favourable winds pulse, similar distributions in temperature and chlorophyll were observed from November 1977 to April 1978.

During autumn the frequency and the intensity of upwelling decreased south of Cape Columbine, warming inshore waters and, as insolation was less, resulting in a decline in the frontal gradients. As the first severe winter storms deepened the upper mixed layer on the Agulhas Bank, moderate pigment concentrations (50 — 100 mg·m^{-2}) reappeared over a wide area. North of Cape Columbine, upwelling still persisted and moderate chlorophyll concentrations were maintained over the whole northern part, decreasing only in newly upwelled water inshore.

Vertical distribution of chlorophyll around the South-Western Cape

Vertical sections on two lines (12 and 28, Fig. 5) have been selected to display the vertical distribution of chlorophyll and temperature on broad (Line 12) and narrow (Line 28) Shelf configurations during summer (January 1978) and winter (August 1977) conditions on the West Coast. Two lines on the Agulhas Bank are also shown (Fig. 6), one on the western side where summer upwelling occurred (Line 64) and one on the eastern side (Line 76) where upwelling was seldom observed.

Line 12, which is representative of the CELP grid north of Cape Columbine, shows similar temperature and chlorophyll distributions in both summer and winter. However, in summer the upper mixed layer is shallower than in winter and chlorophyll concentrations are roughly doubled. As the upper mixed layer in winter was about twice as deep as in summer, integrated chlorophylls were similar. The belt of high phytoplankton was very broad, extending 70 — 100 km off shore, often to the edge of the grid, with highest concentrations inshore in the upwelling water.

The continental shelf off Cape Columbine (Line 28) is very narrow, and strong frontal features are often observed off this headland in summer (Nelson and Hutchings 1983). During winter well-mixed, chlorophyll-poor water intruded close inshore, with weak frontal gradients. A moderate maximum of subsurface chlorophyll occurred inshore. During summer a much stronger frontal gradient developed,

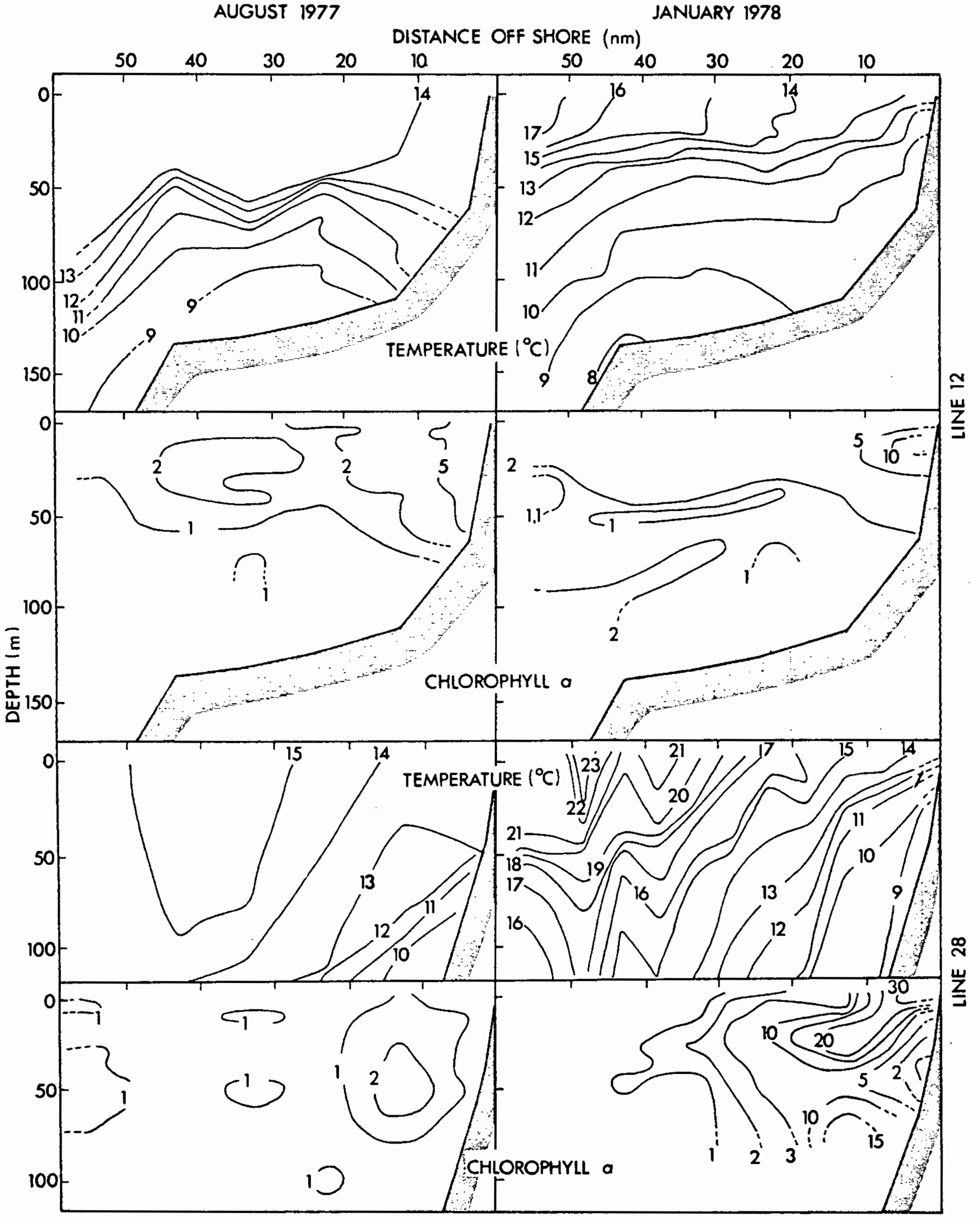

Fig. 5: Vertical sections of chlorophyll a (mg·m^{-3}) and temperature (°C) on Lines 12 and 28 in winter (August 1977) and summer (January 1978) showing narrow and wide shelf configurations on the West Coast

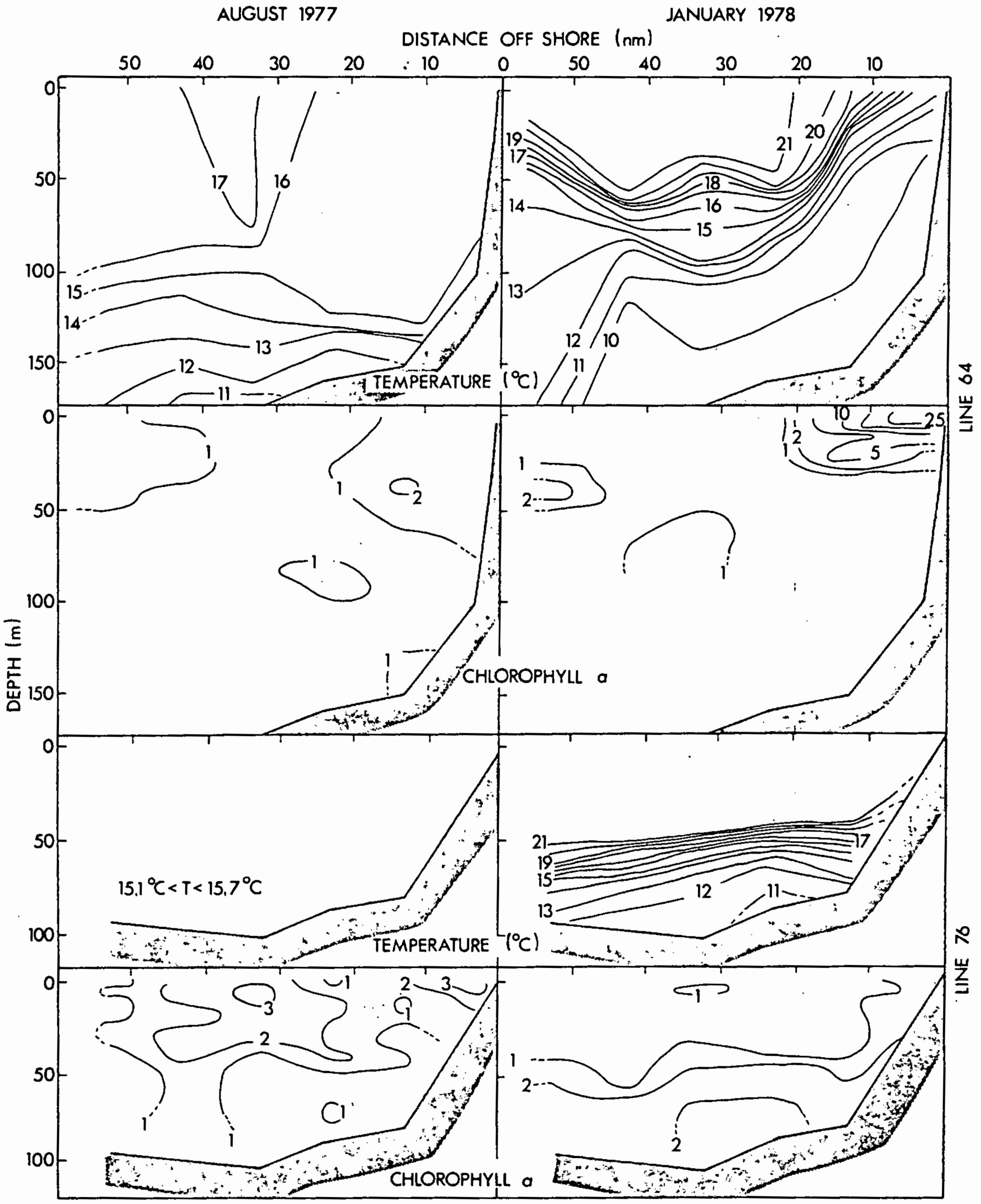

Fig. 6: Vertical sections of chlorophyll *a* (mg·m^{-3}) and temperature (°C) on Lines 64 and 76 in winter (August 1977) and summer (January 1978) on the Agulhas Bank

with very dense inshore chlorophyll concentrations, and this gradient followed the thermocline a short distance off shore before decreasing in strength rapidly in warm waters.

On the Agulhas Bank (Fig. 6) extreme variation between summer and winter conditions existed. On Line 64, deep mixing to about 100 m in winter did not allow phytoplankton to develop. Weak but significant stratification isolated sediment nutrients from the mixed layer. Close inshore, mixing through the whole water column allowed slightly enhanced chlorophyll concentrations to develop. By contrast, summer transects showed strong stratification off shore, with a narrow band of upwelling at the coast. This stratification began in September/October 1977 and remained widespread over the Agulhas Bank during summer and autumn. Only inshore were high chlorophyll concentrations observed. Moderate subsurface levels were associated with the thermocline.

On Line 76, further east, winter storms mixed the water column to the bottom, with less than 0,6°C variation over the transect. This would allow nutrients, which accumulated in bottom sediments, to enrich the entire water column, resulting in widespread increases in chlorophyll in the upper 40 m. Such response is likely to follow a particularly severe storm. During 1978, when the winter was considerably milder, stratification was not entirely destroyed, and no phytoplankton blooms were observed. During summer (January 1978), strong stratification occurred along the entire transect with enhanced chlorophyll concentrations limited to the thermocline at a depth of 50 — 70 m. The phytoplankton was probably maintained by a balance between light limitation and nutrient diffusion, and the rate of turnover was probably slow. Only in late autumn and early winter, when wind-induced mixing and cooling began to disrupt the stratification, did chlorophyll levels rise in the upper layers, in a manner similar to temperate autumn blooms.

Horizontal distribution of chlorophyll off South West Africa

Hart and Currie (1960), Stander (1964), Bailey (1979), Boyd (1983) and others have shown that upwelling off South West Africa is at a maximum during late winter and spring (August — October) and at a minimum (the quiescent phase) between January and March. Upwelling off South West Africa tends to precede that off the South-Western Cape by a few months.

For the area north of 24°S, three months, May and September 1971 and January 1972, have been selected as representative of an approaching upwelling season (i.e. an intermediate situation), maximum upwelling and quiescent conditions respectively. The corresponding distributions of sea surface temperature and surface chlorophyll for these months are given in Figure 7. Figure 7a (May 1971) illustrates the presence of an extended (wide) zone of moderate chlorophyll concentration (3 to >10 mg·m^{-3}) in the Walvis Bay region and a longshore coastal band of about 5 mg·m^{-3} chlorophyll extending north of Cape Cross, with a zone of high chlorophyll inshore near Dune Point. These zones corresponded to surface temperatures of 13 — 15°C (Fig. 8a). The upwelling situation is illustrated in Figures 7b and 8b. The recently upwelled water in the south was relatively poor in chlorophyll, as was expected. As in May, moderate concentrations corresponded with a longshore band of cool 12 — 14°C water. Low concentrations of chlorophyll were present in the warmer water 100 km off shore between 19 and 21°S and off Angola north of the Cunene River (typically 16 — 18°C). During January 1972, i.e. a quiescent period, apart from close inshore north of Cape Cross, temperatures over most of the region were about 20°C. Chlorophyll concentrations in excess of 3 mg·m^{-3} were confined to a narrow coastal zone, about 30 km wide. The high temperatures (21 — 22°C) inshore near Walvis Bay were the result of insolation, calm conditions or light northerly winds on the southern lines of the January 1972 cruise (Fig. 8c).

The general physical and chemical oceanography of the Lüderitz region, which is probably the major upwelling centre in the Benguela system, has been described by Bailey (1979). He identified November 1976 and February 1977 as characteristic of upwelling and quiescent phases respectively. The surface chlorophyll distributions during May and November 1976 and February 1977 are shown in Figure 9. High concentrations of chlorophyll (3 — 40 mg·m^{-3}) were characteristic of most of the region within 120 km of the coast during May 1976 (Fig. 9a), corresponding to water of less than 17°C. (Inshore temperatures were typically 12°C.) These values, which were typical of the upper 20 — 50 m mixed layer, when considered together with Figure 7a, suggest that during autumn the highest phytoplankton concentrations are south of about 23°S, an observation which will be commented upon in the next section. Low to moderate (< 5 mg·m^{-3}) concentrations of chlorophyll south of Lüderitz associated with strong southerly winds and active upwelling are shown in Figure 9b, high concentrations (10 — 25 mg·m^{-3}) being present further north. This distribution is in sharp contrast to that of February 1977 (Fig. 9c), when the high levels were present as a band (15 —30 mg·m^{-3}) centred about 30 km from the coast between Lüderitz and Easter Point, with relatively low values elsewhere.

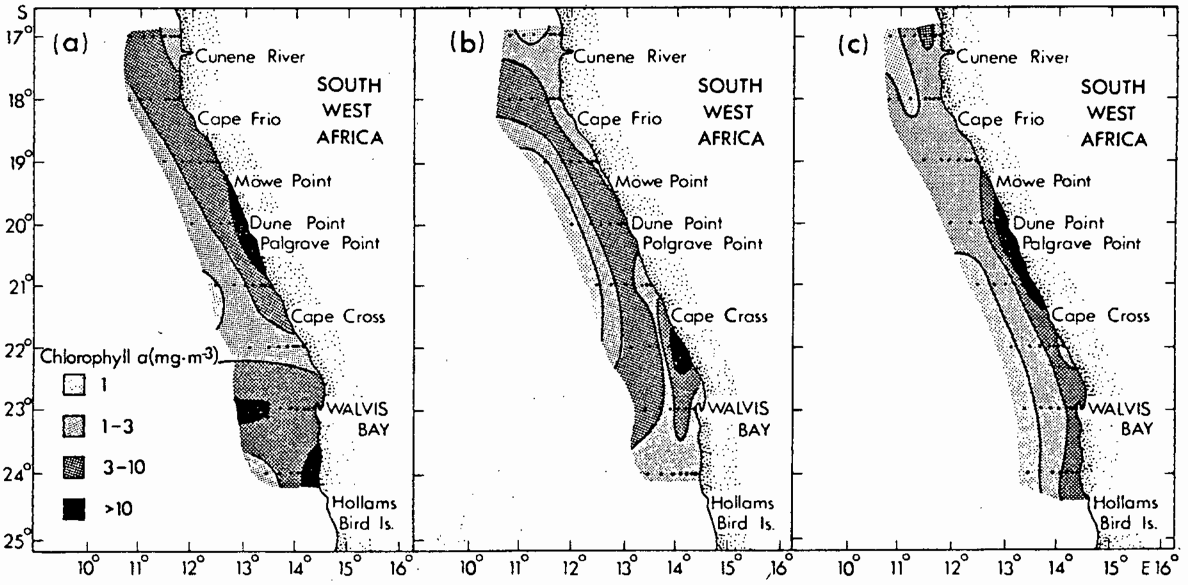

Fig. 7: Surface chlorophyll *a* (mg·m^{-3}) between 17 and 24°S during various phases (a) intermediate — May 1971, (b) upwelling — September 1971 and (c) quiescent — January 1972

Vertical distribution of chlorophyll off South West Africa

The vertical distribution of chlorophyll off South West Africa differs substantially from that in the extreme southern part of the Benguela system in that, although subsurface maxima occur (their frequencies of occurrence in the northern and southern South West African regions are given in Table I), the chlorophyll concentrations in these maxima are

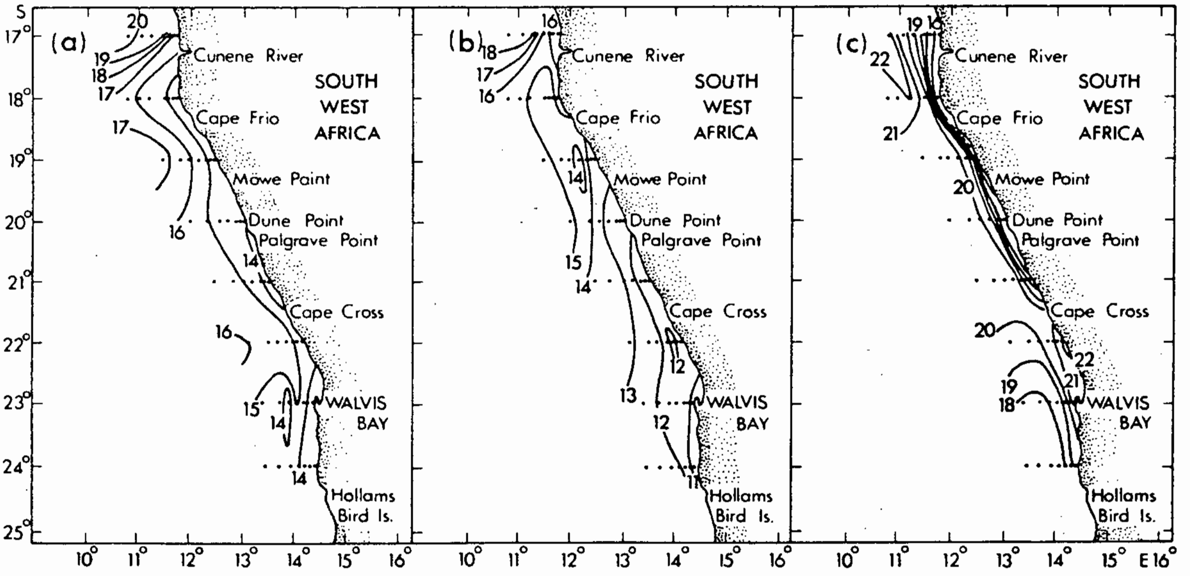

Fig. 8: Surface temperature (°C) between 17 and 24°S during various phases (a) intermediate — May 1971, (b) upwelling — September 1971 and (c) quiescent — January 1972

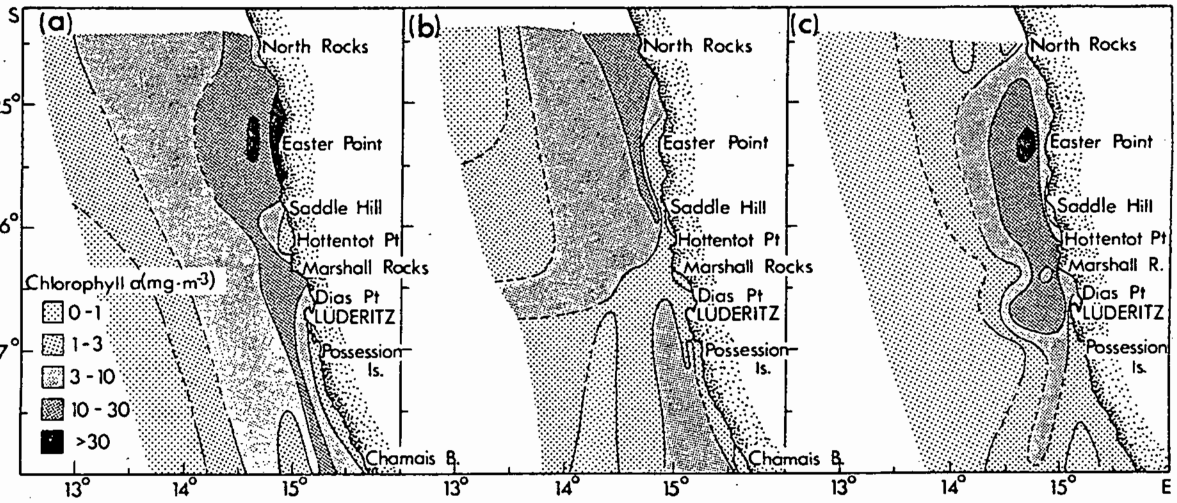

Fig. 9: Surface chlorophyll *a* (mg·m⁻³) in the Lüderitz region during various phases (a) intermediate — May 1976, (b) upwelling —November 1976 and (c) quiescent — February 1977 (based on Bailey 1979)

generally no more than double the surface value —often less than 20 per cent higher. Vertical gradients of chlorophyll appear to be closely related to the degree of stratification in the water column, and because the surface layer is well mixed during much of the year, the surface chlorophyll serves as a fair indicator of processes in the euphotic layer. This has favourable implications for the use of satellite imagery in the study of the chlorophyll distribution in this part of the Benguela system.

SATELLITE IMAGES IN RELATION TO SAMPLES TAKEN AT SEA

Macroscale structure

From the macroscale chlorophyll distribution determined from CZCS data, the Benguela system can be divided into a number of distinct regions which are related to bottom topography, orientation of the coast, orography and variation in intensity and extent of upwelling. These regions are illustrated in Figure 1 and are as follows:

(i) the region between Cape Agulhas and Cape Point, where a coastal zone of elevated surface chlorophyll concentrations exists during summer (see Fig. 13);
(ii) the Cape Peninsula upwelling area (Figs. 10 —14);
(iii) the Cape Columbine/St Helena Bay area (Figs. 10 — 14);
(iv) the Namaqua region (Figs. 10 — 13);
(v) the Orange Bight (Figs. 11 and 12 and also Fig. 3 of Shannon *et al.* in press);
(vi) the Lüderitz region (Figs. 11 and 12);
(vii) the central and northern South West African regions, extending northwards from Conception Bay (24°S), which can be divided into the Walvis region in the south (Fig. 12) and the narrow productive coastal zone between Cape Cross and Möwe Point.

The reasons for division of the Benguela system into these regions are set out in the discussion on macroscale features of chlorophyll distribution, width of continental shelf, upwelling centres and ocean currents later.

Reasonably cloud-free NASA-level-2 products giving the chlorophyll distribution around southern

Table I: Frequency of occurrence of chlorophyll maxima in the northern and southern South West African regions

Depth (m)	Frequency of occurrence (%)	
	Northern region	Southern region
0	39	26
5	(—)	29
10	28	22
20	21	11
30	8	6
50	3	5
75	1	(—)

(—) Samples were not taken at these depths

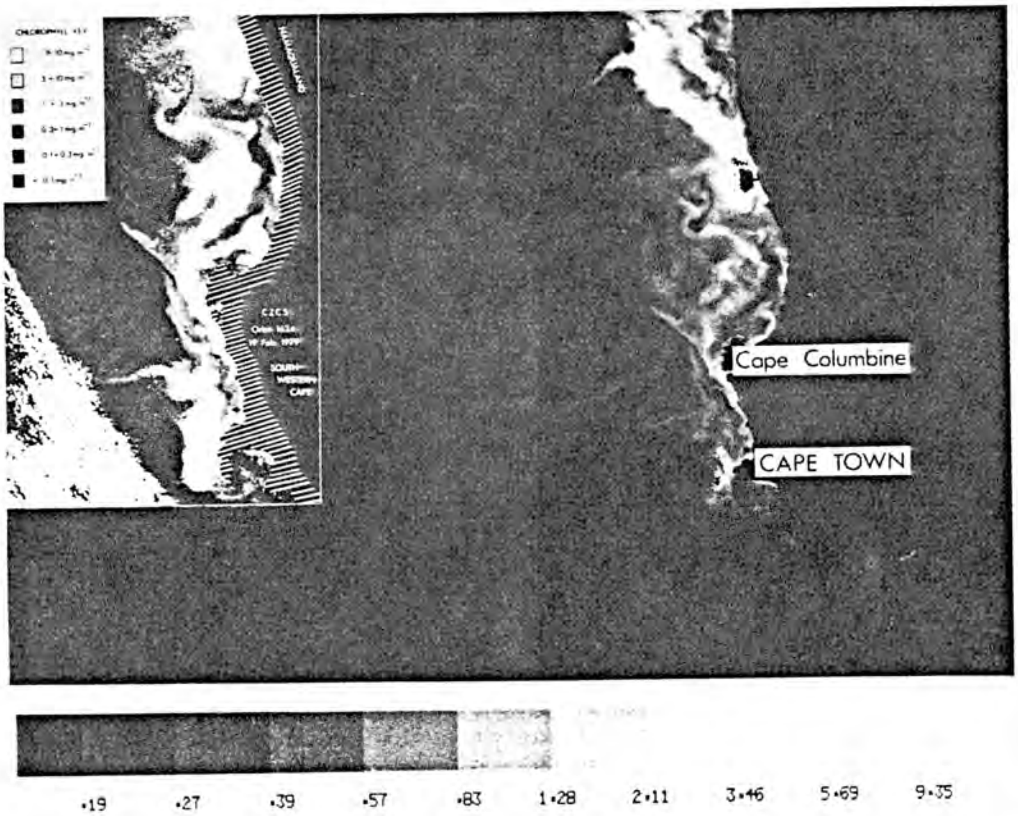

Fig. 10: A comparison between the NASA-derived pigment distribution and (inset) that generated by N.M. Walters for 19 February 1979 (after Shannon *et al.* 1983)

Africa were available for 24 days during the period December 1978 through April 1980, corresponding to CZCS Orbits 569 to 7 618. These 24 scenes form the basis of the discussion on the macroscale chlorophyll distribution and five of them are shown in Figures 10 — 14. It is possible to delineate the boundaries of the Benguela system with the use of these satellite images.

Southern and northern boundaries of the Benguela system — Andrews and Hutchings (1980) regarded the southern boundary of the Benguela system as Cape Point, whereas on the basis of several locally generated CZCS chlorophyll charts, mainly during summer, Shannon *et al.* (1983) proposed that Cape Agulhas seemed more appropriate. Inspection of all the available CZCS imagery indicates that the effective southern boundary of the zone of elevated chlorophyll levels of the Benguela system is in the region between Cape Point and Cape Agulhas (see Figs. 13 and 14). This boundary moves seasonally, with the dividing line between West and South Coast regions being more diffuse during autumn, winter and early spring (Figs. 11 and 12). This statement agrees with the view of Harris (1978), who considered that, from the evidence of currents in the area, the Benguela Current has a source as far east as Cape Agulhas in summer and further west in winter. Nelson and Hutchings' (1983) data on wind stress and Shannon and Chapman's (1983) assumed area of surface divergence south of Cape Agulhas point to the 21° E meridian as being the boundary between the Benguela and the Agulhas regimes.

CZCS imagery of the northern boundary of the Benguela system was not available, but from the work of Stander (1964) and others, and the chloro-

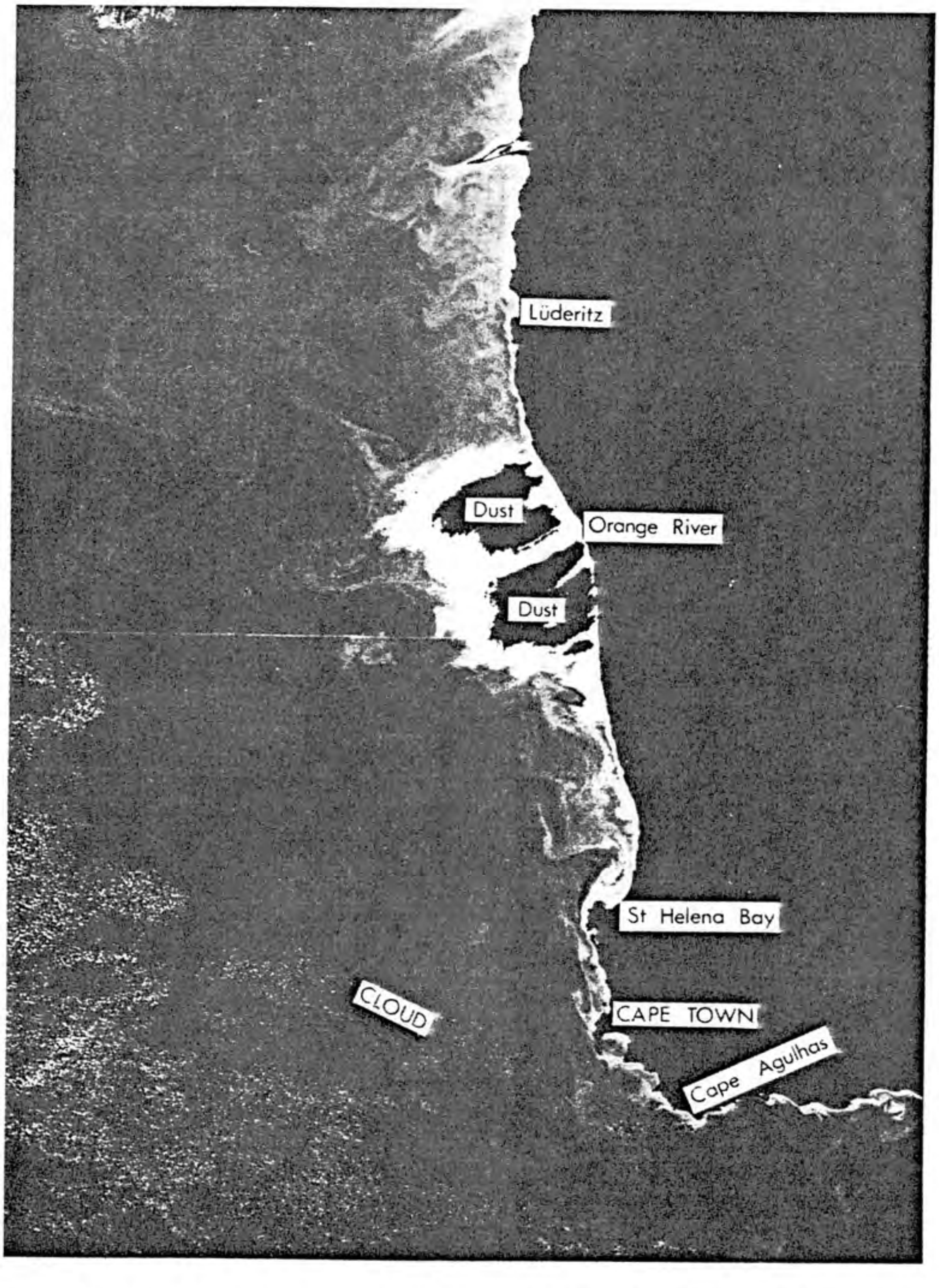

Fig. 11: Chlorophyll distribution between *c.* 23°30'S and 23°E on 9 May 1979 —note aeolean dust present

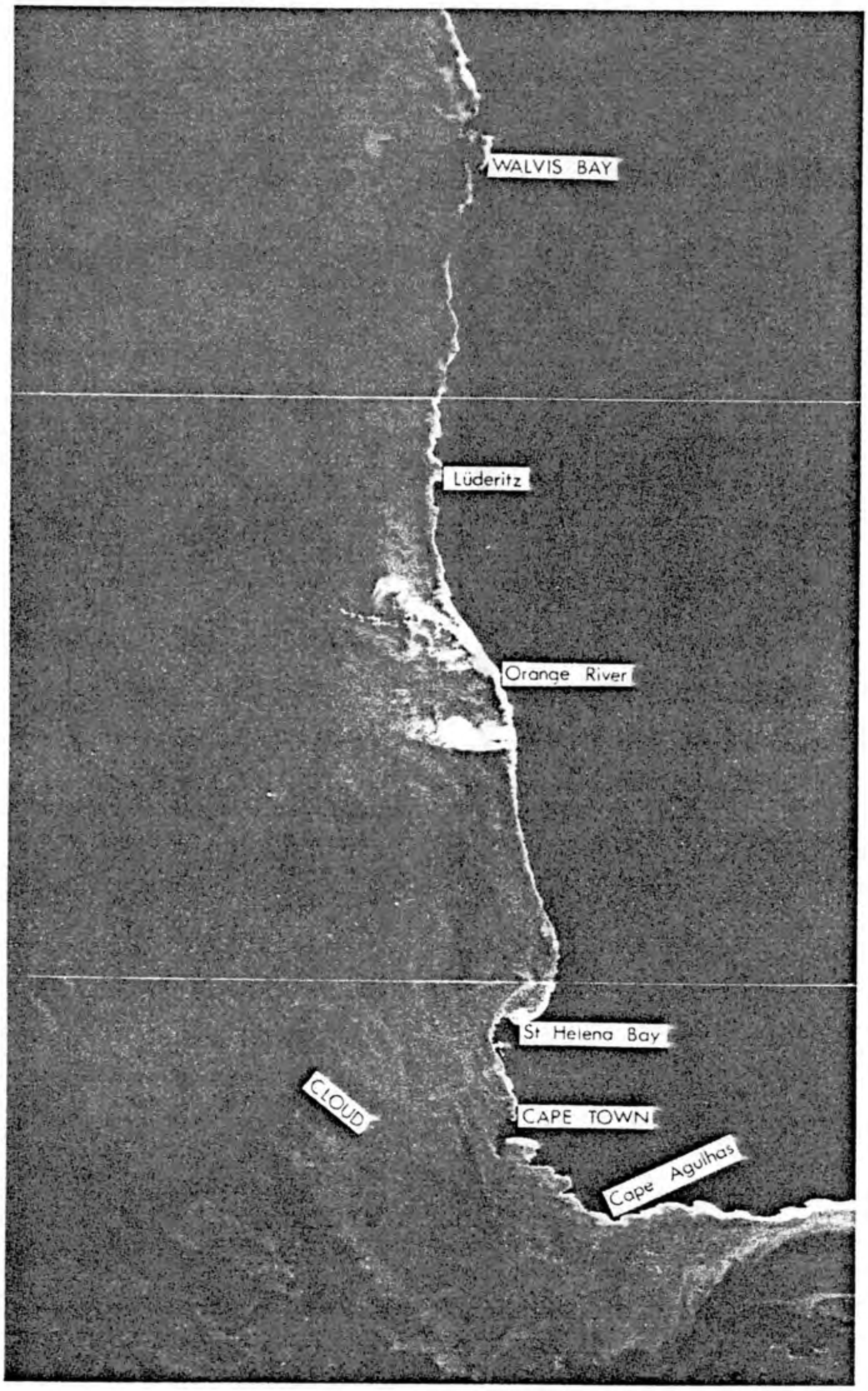

Fig. 12: Chlorophyll distribution between *c*. 21° S and 23° E on 3 September 1979

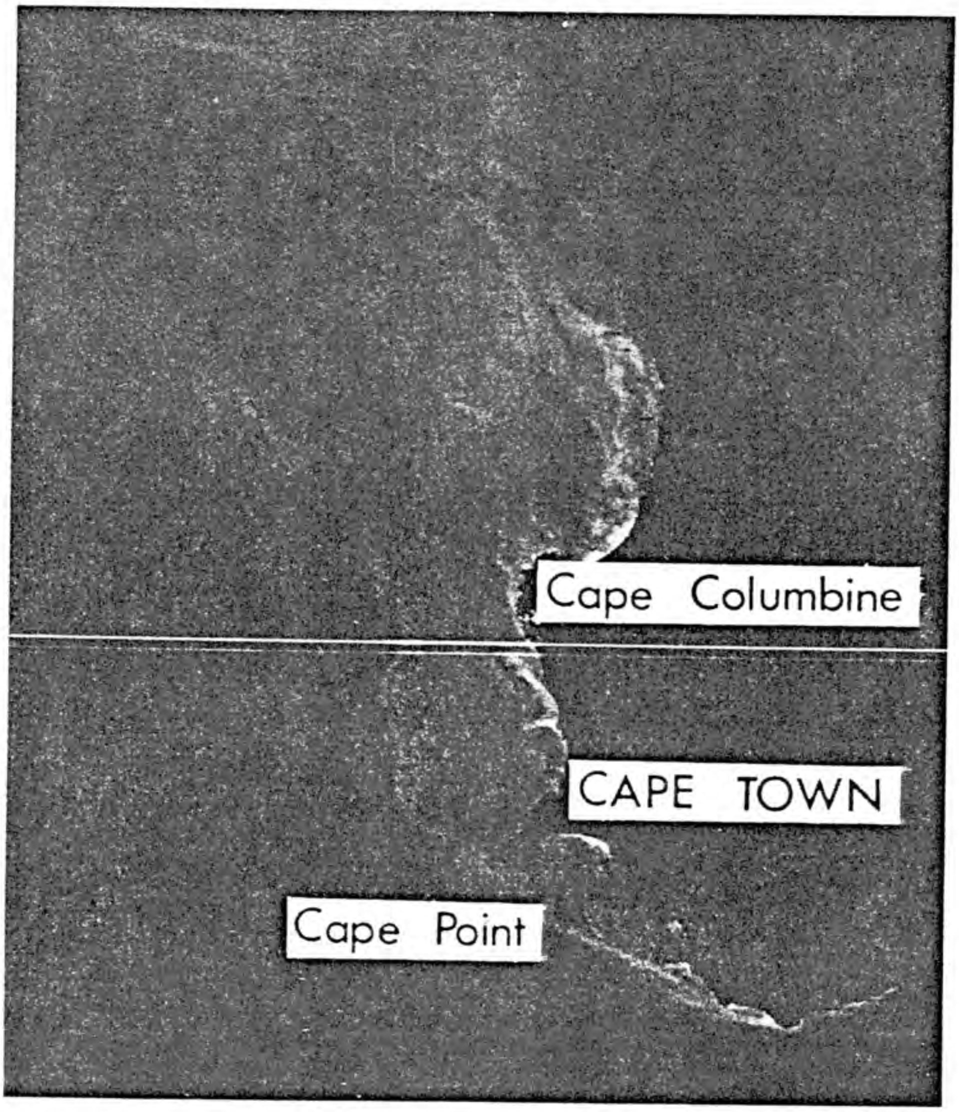

Fig. 13: Chlorophyll distribution around the South-Western Cape on 6 December 1978

phyll and temperature distribution charts of the area (see Figs. 7 and 8), it is evident the boundary lies between Cape Frio (18°S) and Bahia dos Tigres (17°S).

Off-shore boundary of the Benguela system — The near-surface chlorophyll concentrations in the productively active area of the Benguela system obtained from the CZCS imagery range typically from 1 $mg \cdot m^{-3}$ to in excess of 12 $mg \cdot m^{-3}$. The width of this area appears often to coincide with the width of the continental shelf, as indicated by the 200-m isobath in Figure 1, though it does fluctuate widely. The width of the Cape Peninsula area is characteristically 50 — 75 km (e.g. Figs. 10 — 14), and that of the Cape Columbine/St Helena Bay area 100 — 150 km, or approximately double the width of the former. However, west of the Orange River delta the colour

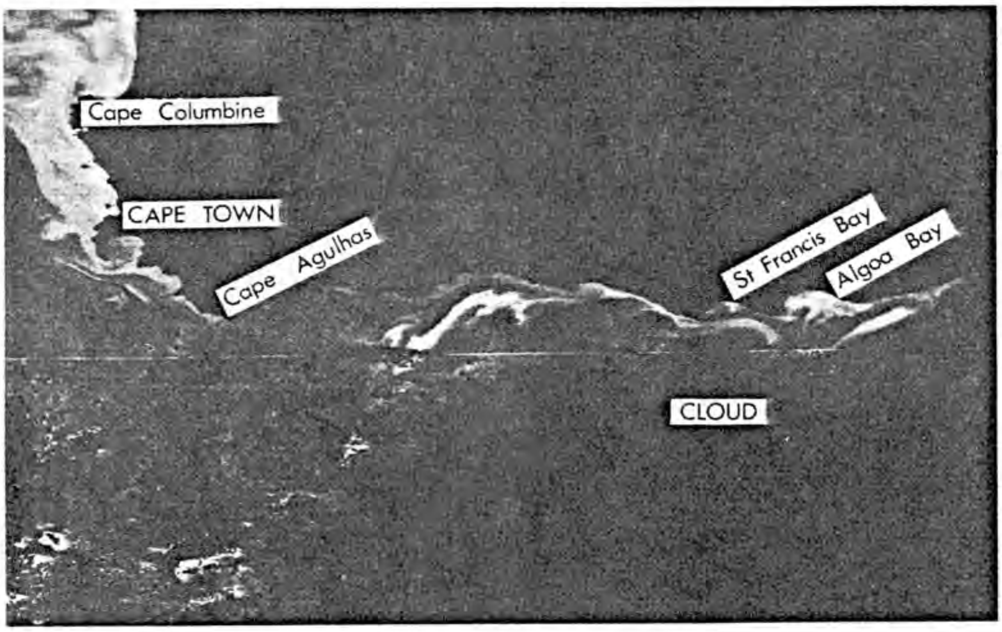

Fig. 14: Chlorophyll distribution around the South-Western Cape and along the South Coast on 13 February 1980

front lies typically 200 km off shore (Figs. 11, 12 and also Fig. 3 of Shannon *et al.* in press). Just south of Childs Bank and north of the Chamais Slump (31 and 28°S respectively), all available CZCS pigment charts indicate a reduced width of the productively active area to about 50 — 100 km (e.g. Figs. 10 — 13) in close agreement with the shelf bathymetry (Fig. 1). A third similar area appears to exist off Conception Bay (see Fig. 12). Including the Cape Peninsula — Cape Columbine region, the four "constricted" zones correspond to major upwelling centres.

The existence of the constricted zones is further supported by the temperature distributions given by Boyd and Cruickshank (1983) and Christensen (1980). Highest concentrations of chlorophyll would be expected downstream from these zones, which is apparently the case, viz. St Helena Bay, the broad shelf off the Orange River, the area north-west of Lüderitz and in the vicinity of Walvis Bay. The high levels of chlorophyll have been assumed by Bailey (in press) to reflect enhanced primary production resulting from the establishment of a semi-closed system on the "leeward" side of upwelling centres. The semi-closed system is thought to be sustained by preferential deposition of particulate organic matter, enhanced local recycling of nutrients and the establishment of a stable, nutrient-rich water column at these sites.

The South Coast and Algoa regions — In the area between Cape Agulhas and Cape St Francis (25°E), available CZCS imagery suggests low (typically 1 mg·m^{-3}), but variable, near-surface chlorophyll concentrations and elevated levels (5 mg·m^{-3}) sometimes present very close inshore or over the shelf in isolated bands (e.g. Figs. 14 and 15). Zones of very low chlorophyll (0,1 mg·m^{-3} — see Fig. 12) are often present over the Agulhas Bank, extending at times as far west as Cape Agulhas (Fig. 14). The oceanography of the Agulhas Bank region is not well documented or understood (Lutjeharms *et al.* 1981, Shannon and Chapman 1983), but relatively low and highly variable concentrations of chlorophyll could probably be anticipated for a wide shallow shelf where coastal upwelling is sporadic (Schumann *et al.* 1982). Subsurface chlorophyll maxima are, however, characteristic of the region during summer (see next section and also Crawford *et al.* 1980), and Shannon *et al.* (in press) have shown poor agreement between surface and deeper chlorophyll concentrations in the area.

The second region in the Agulhas regime, the Algoa region, is evident from the CZCS pigment charts and normally seems to extend between Cape

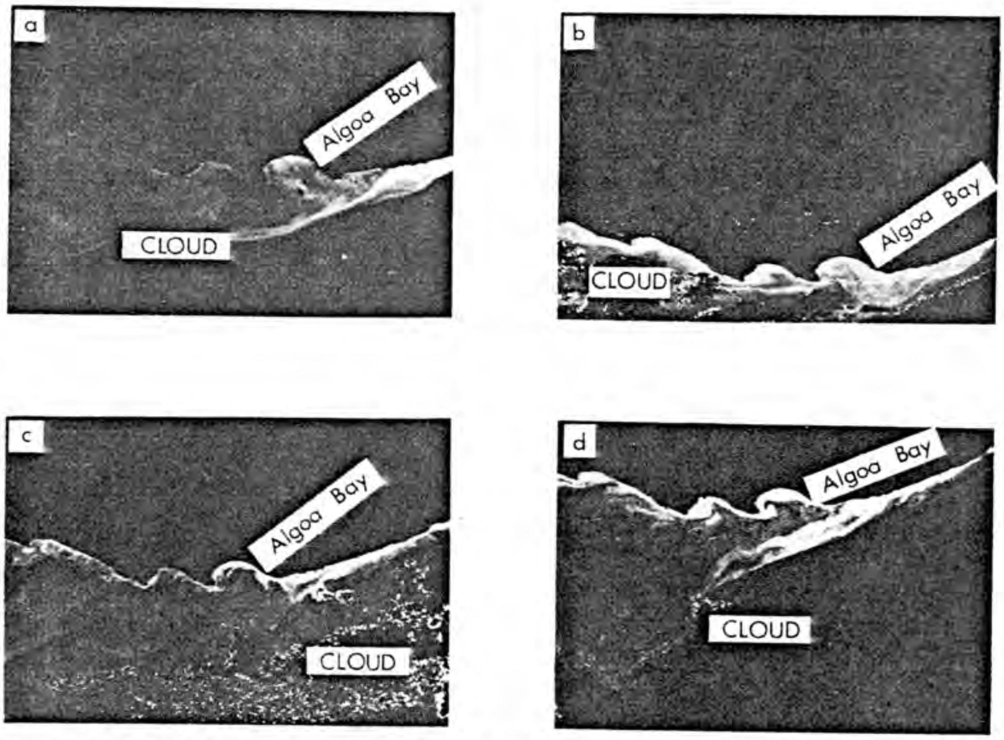

Fig. 15: Chlorophyll distribution in the Algoa region on (a) 15 January 1979, (b) 9 May 1979, (c) 31 May 1979, (d) 27 August 1979

St Francis and East London. It will be discussed in the next section.

Mesoscale features

Algoa region — Schumann *et al.* (1982) and Beckley (1983) have demonstrated that wind-induced coastal upwelling occurs intermittently along the South Coast, particularly off capes, and Gill and Schumann (1979) have discussed topographically induced changes in the structure of an inertial coastal jet as a mechanism for producing dynamic upwelling between Port Elizabeth and East London. Satellite infra-red thermal images in Lutjeharms (1981) and Schumann *et al.* (op. cit.) and sea surface temperature measurements by commercial vessels (South African Weather Bureau) show that a wedge of cold water is often present inshore of the Agulhas Current in the area where this current departs from the coast (Harris 1978), the tip of this wedge extending approximately to East London. (It should be noted that Harris found East London to be one of the windiest recording stations on the coast, with the prevailing winds being north-east, i.e. upwelling-favourable, and south-west.) Shannon *et al.* (in press) demonstrated that elevated concentrations of chlorophyll were evident in St Francis and Algoa Bays from a single CZCS scene on 13 February 1980. The extended NASA-derived pigment chart for this date is shown in Figure 14, and it indicates chlorophyll concentrations in Algoa Bay of 6 — 12 mg·m^{-3}.

The chlorophyll distribution in the region during four other relatively cloud-free CZCS scenes is given in Figure 15. A consistent feature of the Figures is the wedge-like zone of elevated chlorophyll (3 to >12 mg·m^{-3}), which corresponds closely with the endemic wedge of cooler, upwelled water. A note of caution must, however, be sounded about the inferred concentrations in view of the known input of fine sediments by rivers such as the Great Fish, an occurrence which distorts the inferred CZCS pigment concentrations during flood conditions (Walters and Neethling 1982). In fact, further east off Durban, these authors found that the coastal water corresponded to Class II optical type. This being the case, it is probable that the plume of high chlorophyll in Figure 15d is false in view of the heavy rains in the catchment area and consequent flood of the Great Fish River during the week preceding 27 August 1979. However, inspection of the 10-day mean sea surface temperature charts produced by the South African Weather Bureau for the periods encompassing the five CZCS scenes in Figures 14 and 15 indicates that the coastal water was consistently about 7°C colder than that 37 — 75 km off shore between East London and Port Elizabeth. Thus, although the chlorophyll concentrations indicated in the NASA-level-2 pigment charts may be partly in error as a result of the presence of suspended solids of terrigenous origin, the correspondence of the coastal zone of higher chlorophyll with that of the cooler water indicates that chlorophyll concentrations in the Algoa region are higher than in surrounding areas, and therefore that the region may be more productive than is generally appreciated.

South-Western Cape — The mesoscale distribution of chlorophyll around the South-Western Cape as determined from CZCS data has been discussed in some detail by Shannon *et al.* (1983) and Shannon *et al.* (in press). Their work has highlighted the spatial and temporal variability of chlorophyll in the region, particularly west of the Cape Peninsula, with the growth and decay of phytoplankton blooms responding to the pulsed nature of the upwelling. The enhanced chlorophyll concentrations (>12 $mg \cdot m^{-3}$), associated with blooms which develop in upwelling tongues off the Cape Peninsula and off Saldanha Bay/Cape Columbine are clearly evident in Figure 10, whereas in Figure 14 the chlorophyll-depleted zone corresponding to recently upwelled water is evident as a crescent-shaped feature near Cape Columbine. A characteristic of the summer distribution is the pronounced chlorophyll (colour) front — e.g. Figures 10, 13 and 14, which corresponds closely with the position of the thermal oceanic front. The close agreement between the CZCS chlorophyll distribution on 6 December 1978 and the sea surface temperature as measured by airborne radiation thermometry on 5 and 6 December is illustrated in Figures 13 and 16. A band of higher chlorophyll (3 —6 $mg \cdot m^{-3}$) can be seen extending from Cape Agulhas and around Cape Point. Its correspondence with the thermal front (16 — 18°C) west of the Cape Peninsula is clear.

The low concentrations of chlorophyll ($<0,2$ $mg \cdot m^{-3}$) immediately west of this front were confirmed by ship measurements in the area on 6 December 1978. The wind during the two weeks prior to this date was favourable for upwelling throughout the South-Western Cape (10 $m \cdot s^{-1}$ southerly at Cape Point, 5 $m \cdot s^{-1}$ south-westerly at Lambert's Bay and variable, but with a substantial easterly component, 0 — 14 $m \cdot s^{-1}$ at Cape Agulhas). However, on 4 and 5 December the wind was south-westerly, and this might have resulted in the intensification of the frontal gradients evident on 6 December. The meandering nature of the chlorophyll isolines off St Helena Bay (Figs. 10 — 13) is evident in all available CZCS scenes of the region and appears to be a semi-permanent feature associated with local surface currents. Spring and autumn CZCS images suggest that, whereas the near-surface chlorophyll concentrations around the SouthWestern Cape can be significant (0,5 — 6 $mg \cdot m^{-3}$), the distribution tends to be more uniform and fronts less pronounced (see Figs. 3 and 11). A characteristic feature of the South-Western Cape region is the mesoscale cyclonic eddies which seem to develop on the front (e.g. Figs. 10 and 11) following relaxation or reversal of the longshore wind. The significance of these eddies will be discussed later.

A combination of upwelling and temperate seasonal cycles are the major influences determining the

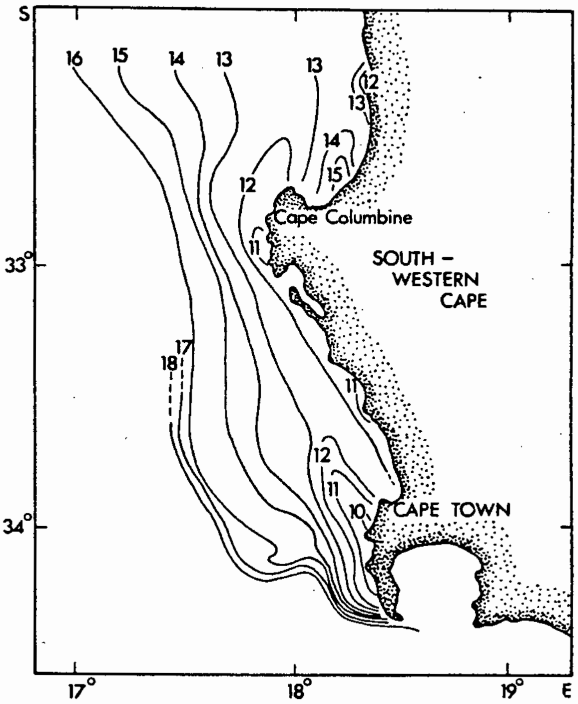

Fig. 16: Sea surface temperature on 5 and 6 December 1978 (from airborne radiation thermometry)

vertical and horizontal distribution of phytoplankton chlorophyll in the South-Western Cape. North of Cape Columbine the broad shelf and persistent upwelling create a wide chlorophyll-high zone with little seasonal variation. Where the shelf narrows off Cape Columbine and the Cape Peninsula, the plankton-rich zone narrows. South of Cape Columbine upwelling is seasonal, with maximum intensity during summer. During spring the chlorophyll-rich belt extends southwards to Cape Agulhas, where the orientation of the coast abruptly alters to one not favourable for upwelling. Rapid changes in the intensity and the frequency of south-easterly winds alter the hydrography and plankton distributions dramatically (Bang 1973, Bang and Andrews 1974, Andrews and Hutchings 1980), creating a highly variable mesoscale environment.

Mixing and stratification play important roles on the Agulhas Bank outside the coastal upwelling zone. In summer, sun-warming and the penetration of warm Agulhas Current water onto the Agulhas Bank create a strongly stratified water mass, with phytoplankton limited to subsurface maxima at the thermocline. In autumn, disruption and deepening of the thermocline results in moderate, but widespread, increases in chlorophyll in the upper layers, followed by decreases as very deep mixing persists over the Bank. Occasional blooms may develop if severe storms mix the entire water column to the sediment interface, releasing accumulated nutrients. During spring, mixing decreases, light levels increase and the upper layers stabilize, creating widespread, moderate blooms of phytoplankton. In this way a temperate seasonal cycle of phytoplankton is imposed on the Agulhas Bank.

South West Africa — In view of problems caused by cloud cover, and in particular fog, there are relatively few CZCS pigment charts available for the area north of the Orange River (Figs. 11 and 12). However, assuming successful correction for atmospheric contamination, satellite ocean-colour imagery could be used with confidence in this part of the Benguela system because of the absence of large subsurface chlorophyll maxima. Useful comparisons can be made between the chlorophyll observations made at sea and the distribution of phytoplankton.

Figures 7, 9, 11 and 12 show similarities to the microplankton (largely phytoplankton) distribution charts of Hart and Currie (1960 — pp. 225 and 231), which are summarized briefly as follows. During the quiescent and reduced upwelling phases, the maximum concentrations of phytoplankton appear to be south of 23°S within 80 — 120 km of the coast. (The shape of the 10 mg·m^{-3} contour in Figure 9c is very similar to the shape of the boundary of the high zone of microplankton during Hart and Currie's March 1950 survey.) Also, the high chlorophyll concentration within 60 km of the coast during the active upwelling phase (Fig. 9b) agrees with Hart and Currie's (1960) maximum microplankton zone. Further, there appears to exist a broad zone of low to moderate chlorophyll (1 — 3 mg·m^{-3}) at the approximate latitude of Walvis Bay during active upwelling. A consistent feature, which was not evident from Hart and Currie's data owing to station-line spacing but is evident from results presented here, is the narrow zone of high chlorophyll between Cape Cross and Möwe Point.

IMPLICATIONS FOR FISHERIES

Two major determinants of year-class strength in pelagic fish populations may be the availability of suitable feeding areas for first-feeding larvae and transport or dispersal of the eggs or larvae (Hjort 1926, Lasker 1975, Parrish *et al.* 1983). Whereas areas of enhanced chlorophyll may ensure adequate food for larvae, either in the form of naked dinoflagellates for the first-feeding larvae or the reproductive stages of zooplankton such as copepod nauplii for later-stage larvae and juveniles, upwelling may be associated with processes that are not directly beneficial to the planktonic stage. The off-shore Ekman transport during upwelling may carry eggs and larvae out of the system, and strong winds might dilute food patches through turbulent mixing within the water column (Lasker op. cit.).

Parrish *et al.* (1983) have suggested that pelagic fish avoid areas of off-shore transport and turbulent mixing for spawning, preferring waters downstream of the areas of maximum upwelling. This model is not entirely applicable to the anchovy *Engraulis capensis* in the southern Benguela region. In the South-Western Cape, spawning occurs at the same time as strongest upwelling (Fig. 17) and upstream of the major sites of upwelling, but in a region (Fig. 18a) where the orientation of the coastline does not facilitate Ekman transport during the prevailing summer south-east wind and where the shelf is wide. This region, the Agulhas Bank, has less persistent and lower chlorophyll concentrations than, for example, St Helena Bay. It would seem less likely to favour larval survival, although the subsurface chlorophyll maximum layer, which is resilient to turbulent mixing because of the stratified water column, may provide suitable feeding areas of limited size and duration. Anchovy may select this region for spawn-

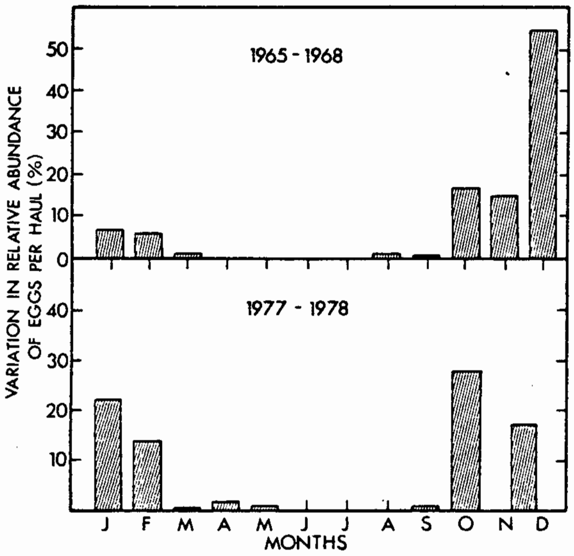

Fig. 17: Seasonal variation in relative abundance of anchovy *Engraulis capensis* eggs off the South-Western Cape for the periods 1965 — 1968 and 1977/78

ing because water near the surface is generally warmer than 14°C, the lower thermal limit for normal egg development in *Engraulis capensis* (King *et al.* 1978). Some four to five months after spawning, recruits to the fishery are most abundant in the vicinity of St Helena Bay (Crawford 1980), where it has been shown that the chlorophyll concentration is high.

Movement of the larvae from the warm-water southern spawning ground on the Agulhas Bank to the recruitment ground on the West Coast is thought to be facilitated by transport in a frontal jet current (Shelton and Hutchings 1982). The concentration of pre-recruit larvae (generally less than 20 mm long) is highest in the vicinity of the chlorophyll front between Cape Columbine and the Cape Peninsula (Fig. 18b). The moderate chlorophyll concentrations in the spawning area on 6 December 1978 (Fig. 13) and extending around Cape Point as a band along the thermal front (Fig. 16) agree with the general distribution of anchovy eggs and larvae (Figs. 18a, b). Mesoscale cyclonic eddies (Figs. 10, 11 and 14) associated with the front may be responsible for transporting larvae inshore to the recruitment ground. Concentration of larvae along the chlorophyll front indicates that this region of discontinuity may be more significant in determining the survival of larvae in the South-Western Cape than the vertical structure of chlorophyll in the water column.

The second concentration of anchovy larvae is separated from that in the west by a zone of divergence (Shannon and Chapman 1983, Nelson and Hutchings 1983), and it occurs in the bight from the Breede River mouth to Cape Barracouta near the eastern extremity of the grid (Fig. 18b). These larvae are presumably able to feed on smaller, local subsurface food concentrations which are not easily observable in the surface chlorophyll images. It is unlikely that they recruit to the West Coast fishery; they are more likely to end up on the East Coast, where seabirds in the Algoa Bay region prey on anchovy (Batchelor 1982). The existence of a potential food supply for these anchovy in the Algoa Bay region can be inferred from Figures 14 and 15.

Off South West Africa, upwelling is most intense in late winter and spring, with major centres off Lüderitz and between Cape Cross and Möwe Point. The inshore area from the Cunene River to Walvis Bay is most important for anchovy spawning during summer (Le Clus and Hewitson 1983), and it is associated with the semi-permanent zone of moderate chlorophyll concentrations. Larvae are most abundant in the northern part of this area, close to the discontinuity associated with the southward penetration of warm Angolan water. Anchovy larvae are uncommon between Lüderitz and Conception Bay. Recruitment from the north into the region of high chlorophyll near Walvis Bay is not well understood, but it may be facilitated by a cyclonic eddy which is thought to occur there (Nelson and Hutchings 1983). The high concentrations of chlorophyll during autumn south of Walvis Bay coincide with the appearance of large shoals of anchovy — the so-called anchovy run.

Whereas gross chlorophyll production in the Benguela system seems to exceed the requirements of the combined populations of pelagic fish species, food has not normally been considered to be limiting. However, the temporal and spatial scale at which food becomes available to fish may be important. Recent calculations by Shannon and Field (in preparation) suggest that, in the southern part of the South-Western Cape region, primary production may be limiting for pelagic fish. Shelton and Armstrong (1983) have found significant density-dependent responses in the pilchard *Sardinops ocellata*, which indicate that the population may have been limited by the carrying capacity of the system during years of peak biomass.

ACKNOWLEDGEMENTS

The authors wish to acknowledge with appreciation the following: Mr I. Kruger for chlorophyll data collected during the Cape Cross Programme; all those who participated in the cruises during which

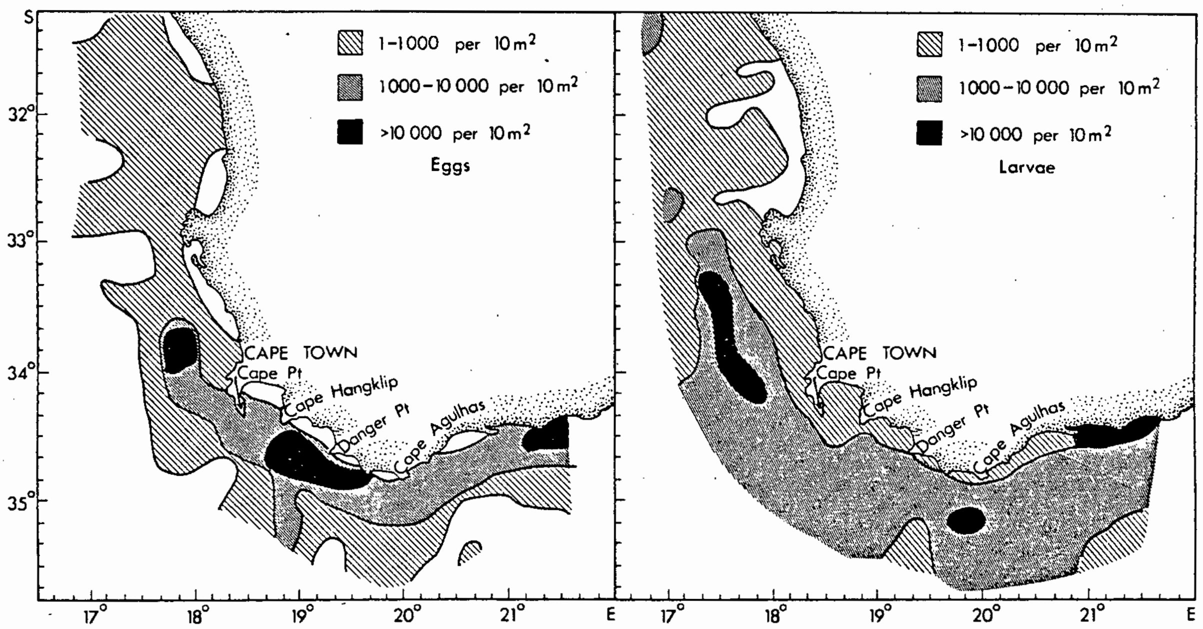

Fig. 18: Cumulative distribution of anchovy *Engraulis capensis* eggs and larvae off the South-Western Cape during 1977/78 (a) eggs (August 1977 — August 1978), (b) larvae (August 1977 — February 1978, April and June 1978)

chlorophyll data were collected; Mr G. Wehmeyer and Ms H. Sessions for spectrophotometric analysis of samples taken at sea; Mr N. M. Walters for the image used in Figure 10; Mr S.A. Mostert and Ms W. Hösch for the integrated chlorophyll values; Mr F.P. Anderson, Principal Investigator of the South African *Nimbus*-7 Programme, for making available the NASA-level-2 imagery; Messrs M.J. Swart and A.P. van Dalsen for the artwork. Prof. J.G. Field, of the University of Cape Town, and our colleagues Dr R.J.M. Crawford and Ms P.C. Brown made useful comments on the draft manuscript.

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3.2 Spatial and temporal patterns of microplankton from bottle samples and plankton displaced volumes from Bongo net hauls in the southern Benguela region

3.2.1 Introduction

The four eastern boundary current regions of the world compared by Wooster and Reid (1963) are major areas of upwelling (Cushing 1969) and are characterized by broad, slow, equatorward flow, high primary productivity and large pelagic fish stocks (Bakun and Parrish 1980). Ryther (1969) calculated that 50% of the world's fish catch comes from 0.1% of the ocean's area where coastal upwelling occurs. He considers that the high productivity of these areas can be attributed to the high levels of primary production and the short food chains that lead to clupeoids which are harvested in large amounts.

Phytoplankton and zooplankton production and abundance patterns in the vicinity of the Cape Peninsula upwelling plume of the southern Benguela Current system has been described by Hutchings (1979), Andrews and Hutchings (1980), Hutchings (1981), Hutchings et al. (1984) and Brown and Hutchings (1985), but larger scale descriptions of the pattern of abundance of plankton in the region, which are needed to extrapolate these mesoscale results, have been minimal. Recently the temporal and spatial distribution of chlorophyll has been described from data collected during the CELP surveys and from satellite measurements (Shannon et al. 1984c, see Section 3.1). In this section complimentary data on net plankton and microplankton collected during CELP are presented and discussed. Together, the chlorophyll-a, net plankton and microplankton abundance patterns allow the large scale interannual variability of potentially suitable grazing areas for different life stages of fish in the area to be examined.

Diet analysis of anchovy and pilchard off South West Africa/Namibia (King and Macleod 1976) indicated that, whereas juvenile anchovy and pilchard (< 8cm and <10cm respectively) feed mainly on zooplankton, phytoplankton contributed substantially, in terms of numbers, to the diet of larger anchovy and pilchard after the development of an efficient filtering mechanism. However, zooplankton dominates the diet of both adult and juvenile anchovy in the southern Benguela Current region (A.James, SFRI, pers. comm.), but it seems likely that clupeoids and other planktivorous fish in the region are capable of omnivory, and can switch to phytophagy when zooplankton is scarce. Omnivory has been recorded in the Californian anchovy (Smith and Eppley 1982).

For larval clupeoids Arthur (1976) and Hunter (1977) have shown that food particles have to be within a certain size range for first feeding (20-120 μm in width for anchovy). Particle concentrations in these size ranges in the sea (Beers and Stewart 1967, Sheldon and Parsons 1967, Sheldon et al. 1972, Arthur 1977) are on average an order of magnitude lower than the roughly 1000 particles per litre required to support clupeoid larval growth in the laboratory (O'Connell and Raymond 1970, Lasker et al. 1970). This has led to investigations of small scale patchiness of larval food in the sea and the ability of larvae to locate and remain in a patch (Hunter 1972, 1977, Owen 1980). Results have shown that larvae may depend on the existence of food particle patches on scales of considerably less than 10m and 1 week (Vlymen 1977). Owen (1980) has concluded that patchiness of plankton particles frequently results from patterned circulation such as eddies and fronts, suggesting that these may be important in determining feeding areas for larvae.

3.2.2 Methods

Plankton displaced volumes were calculated from the amount of plankton retained by a double oblique haul of a Bongo sampler with a mouth opening of 57cm, fitted with 300 µm mesh net, flowmeters, as well as a bathykymograph or bathythermograph to determine depth. Samples consisted mostly of zooplankton, but chain forming diatoms were also retained to some extent by the mesh. Tows were carried out down to 100m where the depth of water permitted, otherwise the net was sent down to 5m off the bottom. The total displaced volume of the plankton was measured on shore before removing fish eggs and larvae for further analysis. No corrections were made for day-night differences. In the double oblique tow of the Bongo sampler through the water column, the concentration of plankton will be influenced by the depth of the tow in relation to the depth of the plankton layer. Recent sampling of zooplankton with open and closing nets indicates that zooplankton biomass i~~f~~s greatest in the upper mixed layer in the southern Benguela Current region (L. Hutchings, SFRI, pers. comm.), which may lead to an under-estimate of the concentration in tows at deep water stations where the depth of the tow may have exdeeded the depth of the mixed layer by a considerable amount. The mean tow depth over the CELP grid is shown in Fig. 3.2.1 and the depth of the upper mixed layer in selected months is shown in Section 2.2, Fig. 2.2.5. In order to reduce potential sources of bias in comparing inshore and offshore samples, plankton displaced volume was standardized to the amount under 10^2 of sea surface area by means of the formula

Volume per 10m2 = volume in net * (10 * depth of tow / volume of water filtered)

This is the same formula recommended by Smith and Richardson (1977) for standardizing ichthyoplankton collected by the Bongo sampler.

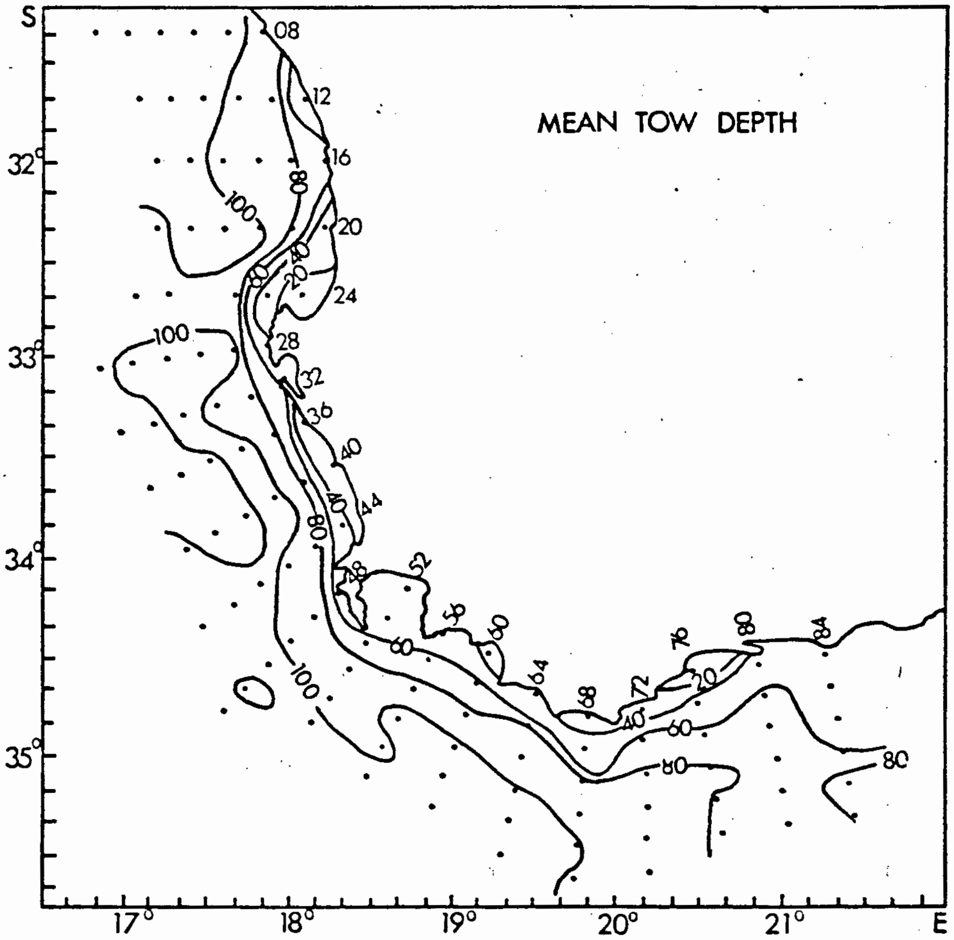


Fig. 3.2.1 The mean depth of plankton tows made with the Bongo sampler at CELP stations sampled between August 1977 and August 1978.

Microplankton was sampled by casts of 5 litre water bottles down to a maximum depth of 75m. Up to 5 samples were collected at each station, from the surface and at 4 other depths which depended on the temperature profile. An attempt was made to obtain samples from just above, within and below the thermocline. The 37 to 100 µm fraction was filtered off from 2 litres of the sample at sea and preserved in 200ml of 4% buffered formalin. On land samples were poured into a volumetric funnel and the particles were allowed to sediment for 90 minutes. From the concentrated sample 10ml was decanted into "Z" trays and particles were counted under a dissecting microscope at a magnification of 20X. Although all particles were enumerated only "esculent" (nutritious to fish larvae, Sharp 1980) particles such as copepod eggs, nauplii and copepodite stages and dinoflagellates were plotted for analysis. Items such as diatoms, although often very abundant, were considered to be non-esculent and were ignored in the analysis. Recent re-evaluation of this technique has shown that substantial numbers of the smaller particles were retained in the funnel tap and microplankton numbers have thus been under-estimated (D. Armstrong, SFRI, pers. comm.)

3.2.3 Results

Plankton volumes

Mean plankton displaced volumes from the Bongo net hauls were greatest in the inshore area from the Cape Peninsula (line 48) northwards (Fig. 3.2.2), but particularly just north of the Cape Peninsula and Cape Columbine, the sites of major upwelling plumes (see Section 2.1). East of the Cape Peninsula, over the Agulhas Bank, plankton displaced volumes were generally smaller.

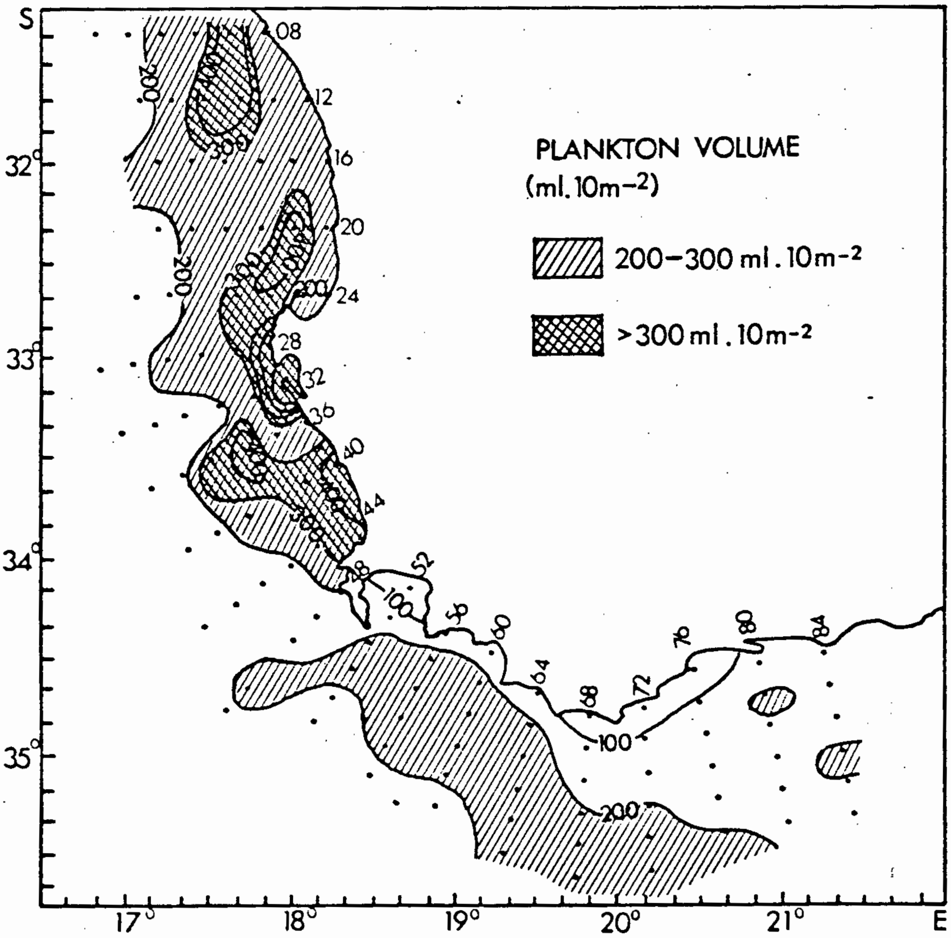


Fig. 3.2.2 The mean pattern of abundance of plankton volumes collected from the double oblique tows with Bongo net fitted with a 300 um mesh net.

Within the average pattern of abundance of plankton considerable seasonal variability was encountered (Fig. 3.2.3). Plankton displaced volumes were most consistently enhanced downstream of the Cape Columbine upwelling centre, in the vicinity of St Helena Bay. In winter, large plankton displaced volumes, dominated by euphausiids, were virtually restricted to the area from Cape Columbine north (line 28). This area corresponds to a region of reduced temperature and salinity (see Section 2.1, Figs. 2.1.2 and 2.1.3), suggesting that the enhanced plankton standing stock was related to winter upwelling. Over the Agulhas Bank, plankton volumes were almost uniformly small.

In spring (e.g. October) there was a substantial increase in the plankton standing stock, presumably as a result of increased upwelling activity (see Section 2.1, Fig. 2.1.2), and large concentrations of plankton, comprising mostly small copepods, amphipods and chain forming diatoms, were encountered over most of the survey grid. Large plankton volumes found in the vicinity of St Helena Bay consisting mostly of chaetognaths, juvenile stomatopods, small copepods, chain forming diatoms and amphipods. Gelatinous plankton dominated at offshore stations further south where large plankton volumes were recorded. In general, the elevated plankton volumes inshore on the west coast occurred within the area where the upper mixed layer was less than 20m in depth (see Section 2.2, Fig 2.2.5). The band of reduced displaced volumes of plankton associated with the area off the Cape Peninsula partly overlapped an area of vigorous turbulent mixing and offshore Ekman transport encountered during the cruise (Figs. 2.2.4 and 2.2.6) and it is likely that this diluted the plankton concentration.

In summer (e.g. January) there was a remarkable restriction of large displaced volumes to Table Bay, just north of the Cape Peninsula upwelling centre, and in St Helena Bay, north of the Cape Columbine upwelling centre. The broken line in the

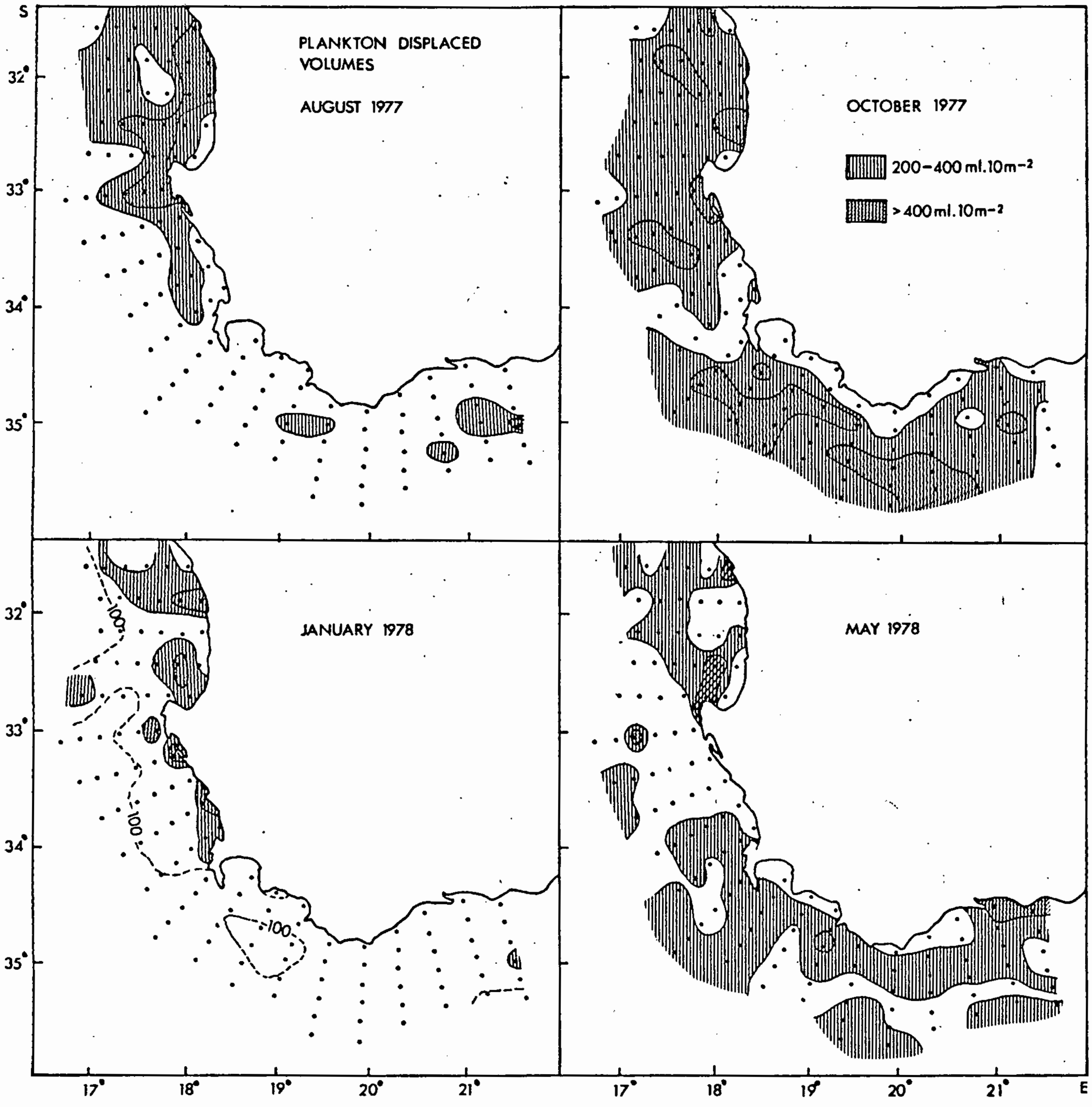


Fig. 3.2.3 The seasonal pattern of plankton volumes over the CELP survey grid.

January 1978 figure indicates the position of the $100ml.10m^{-2}$ displaced volume isoline. Comparison with Fig. 2.1.2 in Section 2.1 shows that the elevated plankton standing stocks were restricted to the inshore area by the presence of warm water offshore. Off Cape Columbine, in association with the Columbine divergence (see Section 2.1), plankton concentrations of more than $100ml.10m^{-2}$ were found to the offshore limit of the grid. At the inshore stations where large plankton displaced volumes were sampled, the plankton was dominated by small copepods, amphipods and chain forming diatoms, although euphausiids and chaetognaths were also present.

In autumn (e.g. May) the area where elevated plankton displaced volumes were sampled expanded substantially, corresponding to a relaxation of the front and an increased influence of cool, recently upwelled water over the survey area. However, there were a number of areas where small values were encountered, for example just south of Cape Columbine. In this particular area strong turbulent mixing was encountered during the cruise (see Section 2.2, Fig. 2.2.4). Deepening of the upper mixed layer (Fig. 2.2.5), and an intrusion of water with a surface temperature of 18°C (see Section 2.1, Fig. 2.1.2) over the Agulhas Bank in May 1978 may have been part of the cause for reduced volumes of plankton over part of this area. Although copepods and chain forming diatoms still dominated the plankton, euphausiids were also common.

Microplankton

Despite the underestimate in numbers of microplankton in samples using the sedimentation technique, comparisons with results from experiments using the reverse filtration technique were significantly correlated, ($r^2 = 0.556$, n=23), supporting the use of the present data in a semi-quantitative manner (L. Hutchings, SFRI, pers. comm.). The average peak microplankton concentrations at each station for the 12 CELP surveys conducted between August 1977 and August 1978 (Fig. 3.2.4) has been calculated as an index of where large concentrations of microplankton most frequently occurred during the survey. Large values of microplankton (> 50 particles per litre) were most frequently associated with the area to the north of line 36, inshore on line 40 (Bok Point), the inshore area between Cape Point and Cape Agulhas, and, to a lesser extent, the eastern periphery of the grid. There is similarity in the pattern of abundance of microplankton from bottle samples and plankton sampled with the Bongo net. North of Cape Columbine (line 28) microplankton was most abundant in a band extending into the middle of St Helena Bay, following the inner shelf break and the average postion of the upwelling front (see Section 2.1). Large concentration of microplankton were also found in other sheltered areas in the vicinity of Saldanha Bay (line 32), in the lee of the Cape Peninsula on line 40, and between Cape Point and Cape Agulhas, mainly False Bay (line 52) and Walker Bay (lines 56 and 60). South of Cape Columbine the concentration of microplankton was small away from the coast.

The seasonal microplankton abundance patterns were very variable (Fig 3.2.5). In winter the very small concentrations of microplankton sampled were dominated by crustacean eggs, copepod eggs, nauplii and copepodid stages. In spring elevated concentrations of particles were more widely distributed, and areas with more than 50 particles per litre were sampled over the eastern portion of the grid, in the vicinity of Walker Bay and False Bay (lines 52 to 60), and in the vicinity of Lambert's Bay. Where large values were recorded the microplankton tended to be dominated by dinoflagellates. The patch of microplankton off Lambert's Bay appeared to occur in association with the cyclonic eddy generally found in the area (see Section 2.2). The scarcity of microplankton just north of the Cape Peninsula corresponded quite closely to the similar band of reduced net plankton

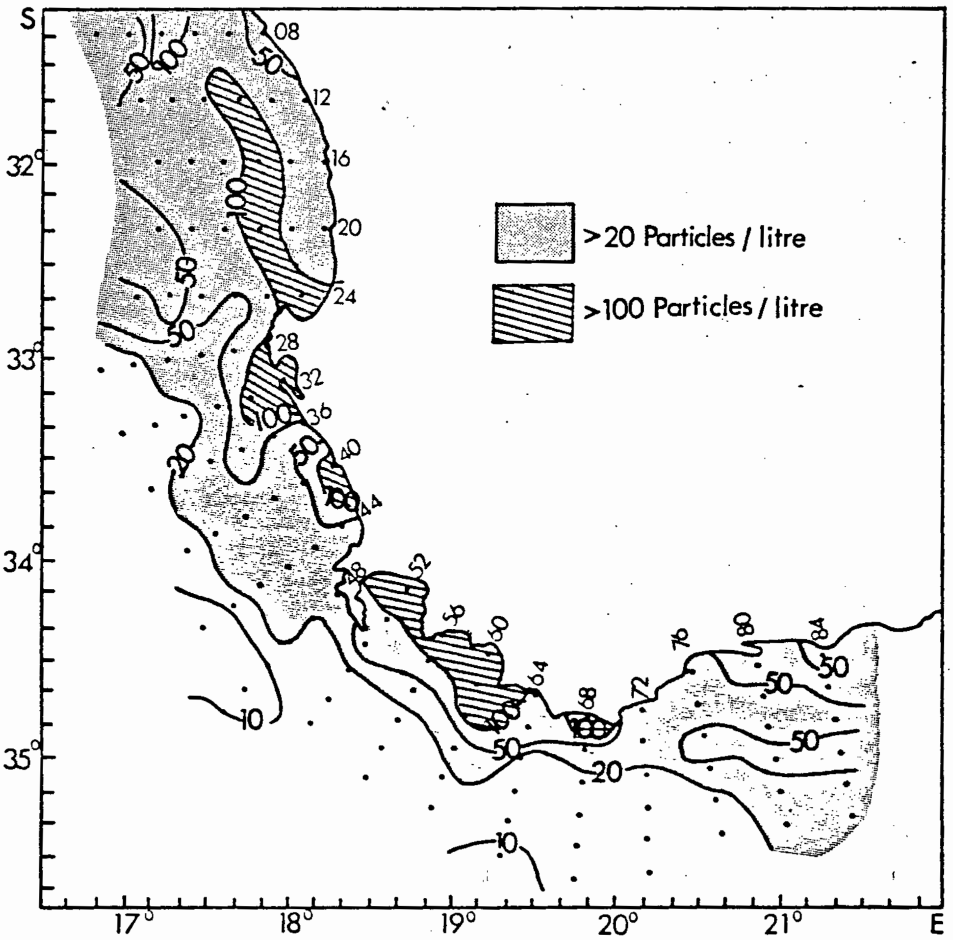


Fig. 3.2.4 The mean pattern of the maximum concentration of microplankton particles between 37 and 100 µm, filtered from bottle samples collected at 5 depths at CELP stations between August 1977 and August 1978.

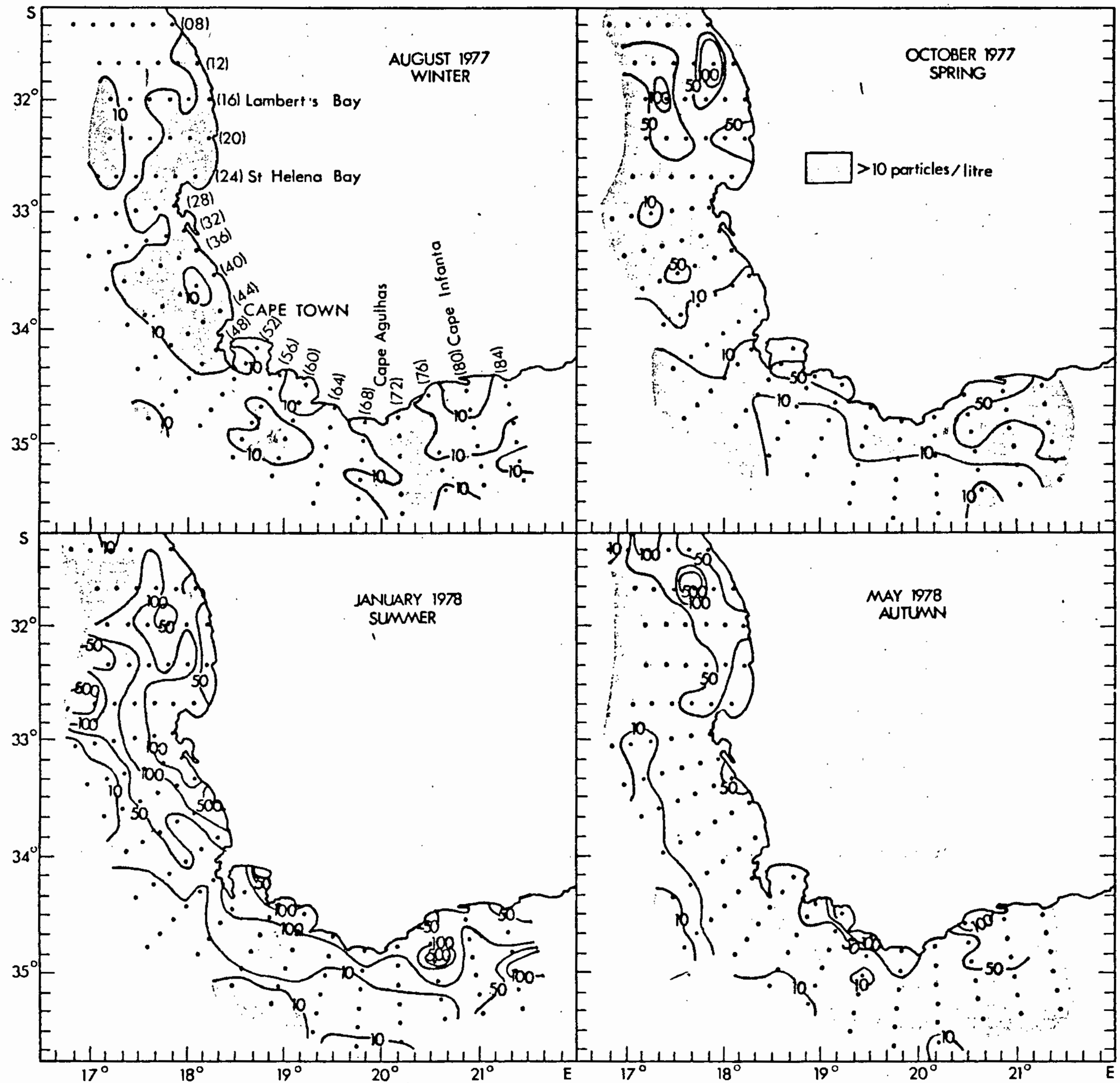


Fig. 3.2.5 The seasonal pattern of microplankton maxima over the CELP survey grid.

concentration (Fig. 3.2.3), and may also have been caused by vigorous turbulent mixing (see Section 2.2, Fig. 2.2.4). The area with less than 10 particles per litre over the Agulhas Bank corresponded to water where the upper mixed layer was more than 60m deep (see Section 2.2, Fig. 2.2.5).

The abundance of microplankton particles increased over summer and in January concentrations of more than 100 particles per litre were widespread over the survey grid (Fig. 3.2.5). The largest count was 575 particles per litre found at the outermost station on line 24, just north of where the front diverged offshore in the vicinity of Cape Columbine. The microplankton at this station consisted almost entirely of dinoflagellates. Even larger concentrations were encountered in February 1978 (not shown) when a lull in upwelling coincided with the cruise. During this survey 723 particles per litre were encountered at Cape Columbine and 741 particles per litre were found just off Walker Bay, near Danger Point on line 60. In March 1978 (not shown), 966 particles per litre were recorded off Saldanha Bay just inside a strong front at the head of the upwelling plume extending off the Cape Peninsula, and 3 379 particles, mostly dinoflagellates, were encountered at the station inside Walker Bay. In March only small levels of microplankton were found offshore of the front. In January 1978 the correspondence between microplankton and suface temperature was not as good as in March 1978, however reduced concentrations of microplankton at offshore stations between lines 36 and 72 corresponded to water warmer than 21°C (Fig 2.1.2).

In autumn (May) the number of stations at which large concentrations of microplankton were encountered decreased. A patch of water with more than 500 particles per litre, mostly dinoflagellates and copepod nauplii, was situated in the vicinity of Lambert's Bay. Elevated concentrations were also encountered between Cape HangKlip (line 56) and Cape Agulhas and in the vicinity of Cape Infanta east of line 76. At these stations dinoflagellates again dominated the microplankton.

Although the abundance of microplankton through the water column was generally very variable, it was patterned by the strong front on the west coast in summer, particulary where elements of the front formed the St Helena Bay eddy (Fig. 3.2.6), and by the intense thermocline that developed over the Agulhas Bank at the same time of the year (Fig. 3.2.7). In both instances the elevated microplankton concentrations were largely due to blooms of dinoflagellates.

Chlorophyll

The seasonal pattern of abundance of chlorophyll-a sampled during the CELP surveys has been described by Shannon et al. (1984c) in Section 3.1. For comparison with the physical environment and other components of the plankton, the chlorophyll-a data is summarized into mean integrated values in Fig. 3.2.8. The overall pattern is similar to that found for plankton displaced volume and microplankton concentration with elevated values inshore along the west coast as far as Cape Agulhas, extending offshore north of Cape Columbine. Large mean values were associated with the St Helena Bay area and in the vicinity of False Bay (inshore stations on lines 52 and 56). Chlorophyll-a concentrations were reduced at offshore stations from line 28 south, corresponding approximately to the area where the sounding exceeded 200m and corresponding closely to the area with a mean SST of more than 17°C (see Section 2.1, Fig. 2.1.1). The Agulhas Bank area, with the exception of the inshore stations west of Cape Agulhas, generally had low levels of integrated chlorophyll-a. However, chlorophyll-a sections show enhanced concentrations within the seasonal thermocline (Crawford et al. 1980, Shannon et al. 1984c).

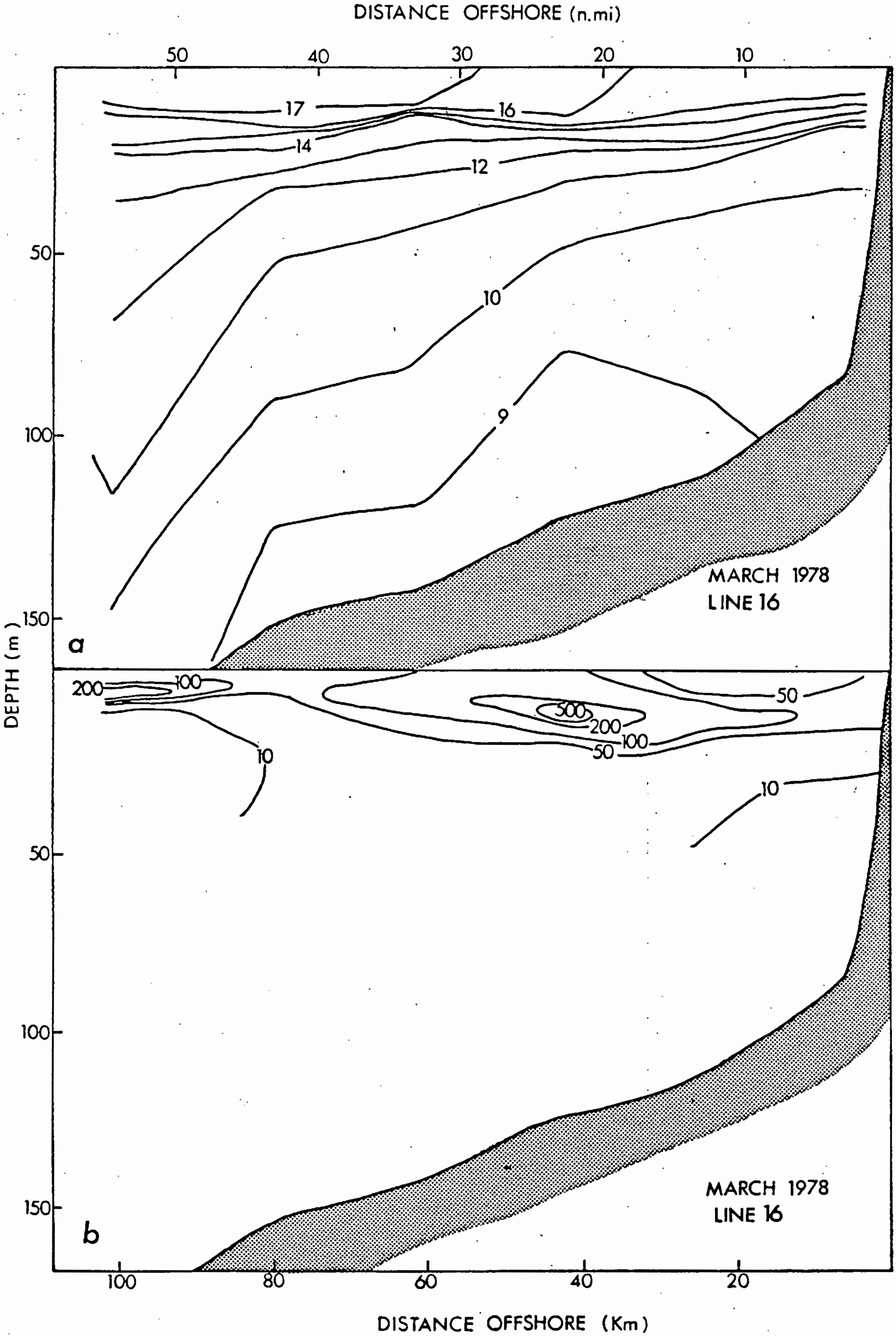


Fig. 3.2.6 A vertical section along line 16 in St Helena Bay, the site of a semi-permanent eddy, in March 1978 showing (a) temperature (°C) and (b) microplankton concentration (particles per litre).

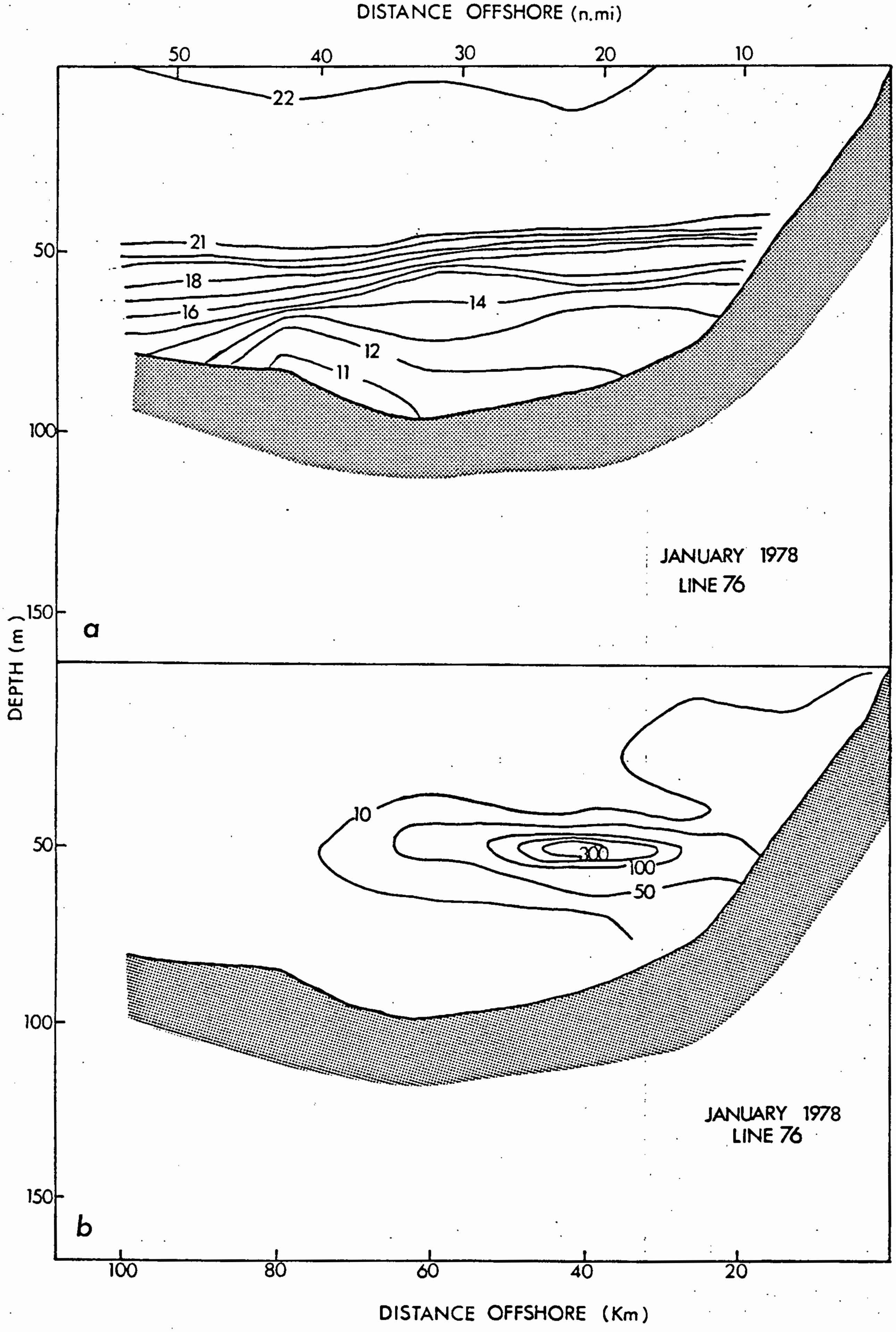


Fig. 3.2.7 A vertical section along line 76 over the Agulhas Bank in January 1978 showing (a) a strong thermocline (°C) centered at about 50 m and (b) microplankton concentration (particles per litre) with elevated values at approximately the same depth

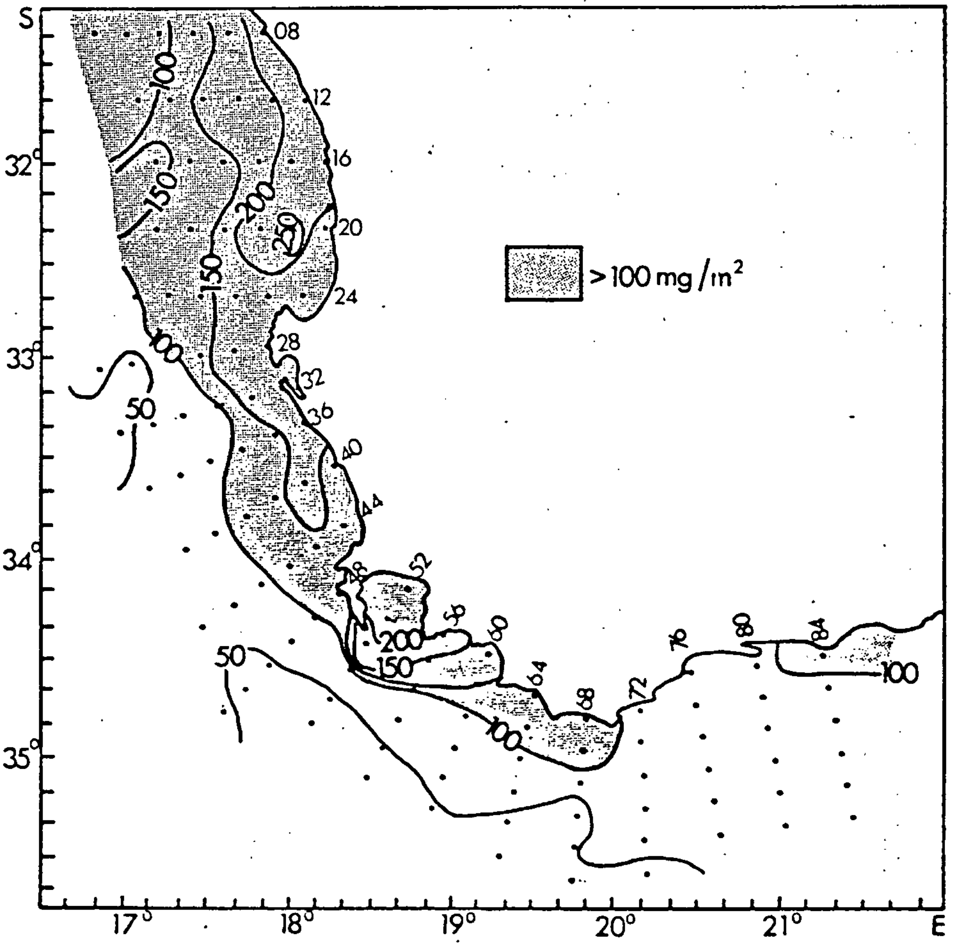


Fig. 3.2.8 The mean pattern of abundance of chlorophyll-a values integrated down to 75m sampled at CELP stations between August 1977 and August 1978.

Comparison of temporal variability

The temporal variability of net plankton, microplankton maxima and integrated chlorophyll-a are compared in terms of monthly mean values and coeffecients of variation (CV) for the whole CELP survey grid in Fig. 3.2.9. In general, chlorophyll-a and microplankton displayed a seasonal increase in abudance over summer, whereas plankton displaced volume showed no apparent seasonal variability. No CV was calculated for microplankton because only the maximum value in each profile was used to calculate the mean. The CV's for chlorophyll and plankton displaced volume estimates tended to be greater over the summer period, indicating less uniform abundance patterns at this time. The small mean plankton displaced volume recorded in the November/December 1977 survey had a small CV. Quiescent upwelling allowed the front to advance shorewards and temperatures of 15°C to 18°C occurred at inshore stations on the west coast, diluting plankton concentrations associated with inshore stations inside the front in October 1977. In January 1978 the small mean plankton volume was associated with a strong front and active upwelling and had a high CV. Plankton was concentrated close to the coast by the front (Fig. 3.2.3), giving rise to the patchy distribution as indicated by the high CV.

3.2.4 Discussion

In general there is good agreement in the abundance patterns of the various components of the plankton sampled during CELP. Although values tended to increase seasonally over summer, the pattern of abundance was least uniform over the survey grid at this time as a result of the patterning introduced by the the strong temperature front which dominated conditions on the west coast during summer (see Section 2.1). Offshore of the front plankton concentrations were

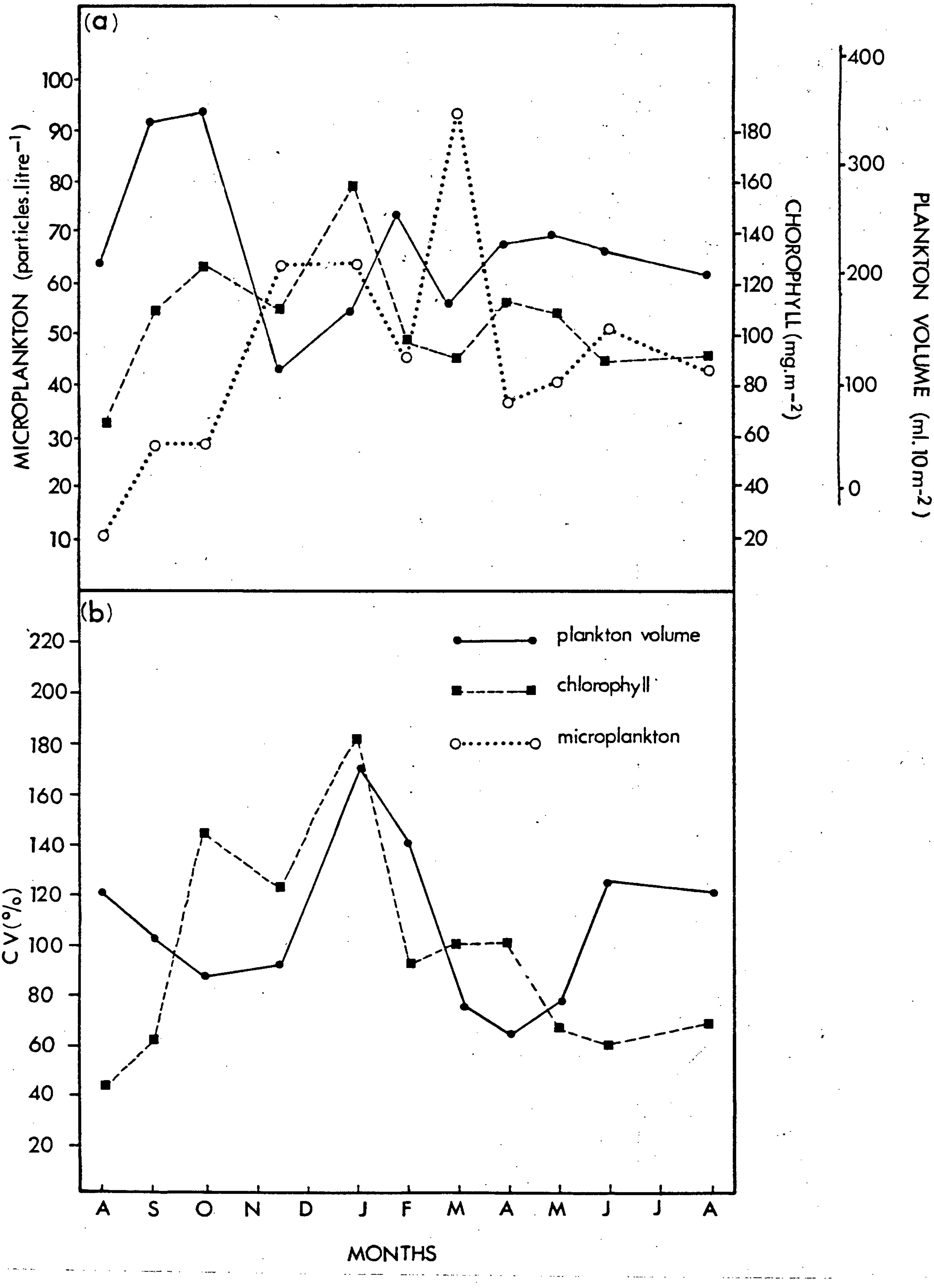


Fig. 3.2.9 (a) Monthly changes in the mean net plankton, integrated chlorophyll-a and maximum microplankton concentrations over the CELP survey grid between August 1977 and August 1978. (b) The percentage coefficient of variation (CV) for the monthly mean integrated chlorophyll-a and net plankton values.

small. Pillar (1980), in an examination of night-time Bongo net samples taken during CELP, also found a summer increase in the abundance of copepods on the west coast whereas the abundance of euphausiids remained relatively constant.

The seasonal influence of the temperature front introduced a marked onshore-offshore pattern in the abundance of plankton, as indicated by the elevated CV's at this time of the year. Concentrations in summer tended to be very small offshore of the front. Although the wind stress in summer is predominantly upwelling favourable in the southern Benguela Current region, reversals occur two to five times each month, allowing warm water to advance towards the coast. Because of the narrowness of the shelf, particularly between Cape Columbine and the Cape Peninsula, the front approaches close to the coast and plankton is consequently concentrated in the coastal zone, or in a subsurface layer associated with the thermocline if the warm layer meets the coast. Hutchings et al. (1984) found that during the summer of 1982/83 when upwelling was reduced by about one third of the twenty year mean, the area of enhanced primary productivity was reduced to 60% of that which occurs during normal summer conditions, restricting the area suitable for fish feeding. Off the Oregon coast, very high standing stocks of zooplankton only occured within 25Km of the coast in the zone of most frequent upwelling (Peterson et.al. 1979).

Unpublished data from vertical hauls with a N70V net made on the west coast showed little change in plankton volume in an inshore-offshore direction, but considerable change in species composition (Hutchings 1979). Hutchings (1979) and Andrews and Hutchings (1980) found that zooplankton standing stocks were irregularly distributed along a line of stations which bisected the upwelling plume off the Cape Peninsula. During summer they found that maximum values occured 40 to 100Km offshore (eg. 90Km from the coast in December 1979) and minimum values 20 to 50Km offshore, whereas in winter highest standing stocks were closest to the coast with very low values offshore. Variability within the plume therefore differs from the average large scale pattern over the southern Benguela region, as determined from the CELP surveys.

At Cape Columbine the front regularly diverges offshore following the outer shelf break (see Section 2.1 and Shannon 1985). This offshore divergence corresponds to the extension of moderate levels of plankton right out to the offshore limit of the grid. Drift card returns indicate that the divergence at Cape Columbine may be a major exit out of the system (see Section 2.2) and may therefore constitute an important leak of plankton-rich water from the near-shore zone. Just north of the divergence, temperature structure and surface drift indicate a mesoscale cyclonic eddy into St Helena Bay (see Sections 2.1 and 2.2), presenting an alternative route for planktonic material produced at the Cape Peninsula and Cape Columbine upwelling sites. Large concentrations of net plankton, microplankton and chlorophyll-a frequently encountered in the St Helena Bay to Lambert's Bay area during the CELP surveys may thus result from the accumulation of plankton production carried downstream in the geostrophic flow from the centres of upwelling, but may also be supplemented by local production resulting from domeing of nutrient rich water in the core of the eddy (Hutchings 1981). In a detailed study of the plankton on line 16 of the CELP grid, Hopson (1983) presented evidence suggesting that the eddy in St Helena Bay may physically aggregate phytoplankton. She found a consistently large phytoplankton biomass in the area. Pillar (1986) found that the biomass of copepods and euphausiids, which dominated the zooplankton collected by the Bongo sampler during CELP, tended to be greatest north of Cape Columbine and to increase inshore. Conditions which would cause the weakening of the eddy and the flushing of the St Helena Bay to Lambert's Bay area would disrupt the dense concentrations of plankton which accumulate when the eddy is present, causing a decrease in food for larvae, and hence in larval survival rates.

East of Cape Point, over the broad Agulhas Bank, the seasonal formation of a strong thermocline is the dominant physical process (see Section 2.1), and considerable vertical patchiness of microplankton, as well as phytoplankton measured by chlorophyll-a abundance (Crawford et al. 1980, Shannon et al. 1984c) appears to be typical from late spring to early autumn. The cold water that moves along the bottom onto the Agulhas Bank in summer, and upwelling in the vicinity of Plettenberg Bay, may be important in sustaining Agulhas Bank plankton production.

The importance of patterned circulation such as eddies in concentrating particles has been emphasized by Owen (1980, 1981) and the eddy in St Helena Bay may play a similar role to the Southern California Bight Eddy which is associated with increased plankton concentrations and forms an area of enhanced suitability for larval feeding (Owen 1980). Lasker (1975) found that in the Southern California Bight, anchovy larvae are dependent on the inshore environment for an above threshold number of nutritious particles and that offshore areas were particularly sparse in the kinds and sizes of particles needed for first feeding larvae. Sette and Ahlstrom (1948) found that sardine eggs and larvae appeared to be concentrated in the Southern California Eddy. Smaller eddies in Walker Bay, False Bay and Table Bay (see Section 2.2) may be the cause for occasionally large plankton concentrations associated with these areas.

Lasker (1975, 1978, 1981) has found strong evidence that food for first feeding larval anchovy off California becomes limiting when storms or strong upwelling occur and dilute food aggregations. Based on the results of Lasker's work, Parrish et al. (1983) have suggested that wind generated turbulent mixing may be an important determinant of larval survival in other eastern boundary current regions of the world. The strong thermocline that develops at about 50m over the Agulhas Bank in summer as a result of cold water on the bottom and sun warmed and Agulhas Bank Mixed Water above is particularly stable. Pugh (1982) has calculated that wind speeds greater than $20 m.sec^{-1}$ would be required for its erosion. Wind speeds of this strength were not encountered over the Agulhas Bank during the CELP survey and data in Parrish et al. (1983) indicate that winds more frequently approach this speed in winter. At this time of the year the water column is less stable due to cooling of the surface layer and the retraction of the cool bottom layer off the shelf, and mixing can occur down to at least 75m (Pugh 1982). The thermocline layer may therefore form a relatively stable source of food for larvae, and perhaps for spawning fish as well, during the summer and autumn period.

3.2.5 Conclusion

From the descriptive analysis of the CELP plankton data it is evident that the dynamics of the front, together with the St Helena Bay eddy on the west coast and the seasonal thermocline over the Agulhas Bank, are important in determining the distribution and patchiness of plankton food for fish larvae, juveniles and adults in the southern Benguela region. Plankton production may be lost from the neritic environment via the divergence off Cape Columbine. The variability associated with the area between Cape Point and Cape Columbine, particularly in summer, as a result of changes in strength of upwelling at the Capes and the dynamic nature of the temperature front, probably makes this area unsuitable in terms of a predictable food supply for the various life history stages of fish. In contrast plankton associated with the thermocline on the Agulhas Bank or concentrated in the St Helena Bay eddy may be a more predictable source of food for fish larvae. In winter, although the area over which moderate levels of plankton occurs expands considerably, patterning by fronts, eddies and thermoclines is reduced and concentrations of particles suitable for early stage larvae are likely to be scarce.

4. PATTERNS OF FISH EGG AND LARVAL ABUNDANCE

4.1 Introduction

Pattern in the abundance of fish eggs and larvae in the plankton may result from non-random spawning behaviour by the adults, patterned circulation such as eddies, fronts and thermoclines, or non-random mortality eating "holes" in the pattern of abundance of eggs spawned randomly. Non-random spawning is to be expected as a result of natural selection within an environment which has been shown to have considerable temporal and spatial variablity (see Sections 2 and 3). Subsequent diffusion and mortality of the planktonic stages will be largely the result of the space and time "choices" made by the spawners. Populations in which adults school will impart patchiness to the initial egg abundance which will resemble that of the spawning school (Smith 1973). For fish populations which require schooling in the post-planktonic stages, larval patchiness will contribute to survival by facilitating visual contacts necessary for school formation (Hewitt 1981). Such populations should exhibit spawning adaptations which will limit dispersal from the patchiness imparted by the spawners. In contrast, populations in which the post-planktonic stages have a comparatively uniform pattern of abundance, might display spawning adaptations which reduce subsequent patch formation, and therefore reduce intraspecific competition for a limited resource. In instances where the post-planktonic stages are not very mobile, dispersal would facilitate the colonization of new or depopulated areas. If density dependent processes controlling population growth operate in the early life history stages through such mechanisims as intraspecific competition or cannibalism (Ricker 1975), then strong density-dependence is likely to be associated with those species in which the planktonic stages are patchily distributed. For example, rapid dispersion after spawning leading to a more uniform distribution would reduce cannibalism on the eggs. By examining the observed effects of the processes causing pattern in ichthyoplankton it may be possible, by inductive reasoning, to infer the general causes and to consider how anomalies in the causative mechanisms may affect recruitment.

In the southern Benguela region the eggs and larvae of a number of species of fish have been described (Gilchrist 1903, 1904, 1916, Gilchrist and Hunter 1919, Matthews and De Jager 1951, Davies 1954, De Jager 1955, Haigh 1972a, 1972b, Louw and O'Toole 1977, King et al. 1977, 1978, Brownell 1979). In comparison, there is little information available on the patterns of abundance of the ichthyoplankton. This is despite the fact that an intensive 20-year survey was undertaken by the Sea Fisheries Research Institute on a more or less monthly basis over a substantial grid of stations between 1950 and 1969, expressly to sample the egg and larval stages of the pilchard Sardinops ocellata, and later the anchovy Engraulis capensis.

The results from this survey have only been superficially dealt with in the literature (Davies 1954, Anders 1965 and Crawford 1980) although Anders (unpublished charts, SFRI) produced monthly and seasonal average charts of the pattern of abundance of pilchard eggs (1950 - 1969) and anchovy eggs (1964 - 1969) from surface tows. The samples were collected mainly with a 1m diameter net although a 70cm net was also used at some inshore stations on occasion. The net was towed for 10 minutes and it sampled the top 0 to 5m of the water column. No flowmeters were used. Initially the sampler was fitted with 900 um mesh but from April 1964 300 µm mesh was used to capture the smaller anchovy eggs. In addition to the surface tows, oblique tows from 150m or shallower were conducted at each station with the 1m or 70cm diameter nets. Samples from these tows were not analysed immediately but Loeb (unpublished MS), under contract to the National Marine Fisheries Service, Southwest Fisheries Center, USA, recently examined some samples from the collection for comparison with those taken in other eastern boundary current systems. She considered the surface tows to be of little value.

In addition to the 1950 to 1969 survey, there have been a number of studies of short duration covering limited portions of the southern Benguela region and the area further east. Anders (1975) reported on pilchard and anchovy spawning on the east coast, Baird (1977) described the pattern of abundance of mackerel Scomber japonicus eggs and larvae in the vicinity of Cape Columbine, Hutchings (1979), Shelton and Hutchings (1982) and Shelton (1984) described the distribution of anchovy eggs, particularly in the vicinity of the Cape Peninsula, and Olivar (1984, 1985) reported on the occurrence of the eggs and larvae of a number of species at 26 stations sampled in the southern Benguela region between June and July 1983 and a further 41 stations sampled in January 1984. Some preliminary results from the CELP survey are given in Davies et al. (1981) while Shelton and Davies (1979) and Prosch and Shelton (1983) published preliminary reports on the pattern of abundance of lightfish Maurolicus muelleri and lanternfish Lampanyctodes hectoris eggs collected during the CELP survey.

In this section the patterns of abundance of the ichthyoplankton of commercially important, abundant or distinctive species collected during the 12 month CELP survey of about 1 400 stations are described. For most of the species considered, this represents the first comprehensive description for the southern Benguela region throughout the year. The emphasis throughout is on the development of generalizations which will simplify the search for causative mechanisms in Section 5.

4.2 Methods

At each of the 120 CELP stations a double-oblique tow with a Bongo sampler was made down to about 100m, or 5m from the bottom if the water depth was shallower. The Bongo sampler used was modified from that of Pogsay et al. (1968) and is described in King and Robertson (1973). The unit was towed at 2 knots behind the vessel and the winch speed was maintained at about 1m.sec-1 during the vetch and at 0.5m.sec^{-1} during the heave. Winch speed had to be estimated from the readings on a meter clock and the depth of the sampler from the approximate angle of the wire. When sufficient wire had been let out the unit was allowed to stabilize at depth for 30 seconds before being retrieved. A calibrated mechanical flowmeter in the mouth of each net was used to measure the volume of water filtered and the maximum depth of the tow was obtained from a bathythermograph attached to the cable just above the Bongo sampler. The standard haul factor for each tow was calculated using the method described by Kramer et al. (1972) and Smith and Richardson (1977). A typical tow lasted about 12 minutes. Nets were washed using a fine spray and samples were preserved in 5% buffered formalin. Although samples from both units were preserved, only the sample retained by the unit fitted with 300 μm mesh net was sorted, whereas the samples from the 500 μm mesh net were preserved for future analysis.

In the laboratory all fish eggs and larvae were removed from the sample collected by the 300 μm net and identified to the lowest possible taxonomic category. Some fairly common species and a number of the rarer species were difficult to identify in a consistent fashion and this is indicated in the results. Some of the taxonomic groupings represent more than one species.

In November 1983, November 1984 and November 1985 a more extensive area was sampled for anchovy eggs by means of a vertical tows with a CalVET net (Smith et al. 1985) from 200m or 5m off the bottom to determine the spawner biomass of anchovy using the egg production method (Lasker 1985).

Distribution and pattern

Following Pielou (1977) the term "distribution" is used to refer to the statistical distribution of a variate independent of spatial pattern. If every plankton sample taken during CELP had an equal chance of capturing a particular component of the ichthyoplankton then the variance would have been approximately equal to the mean and the variate would follow a Poisson distribution. However, comparisons of expected and observed distributions have shown the wide applicability of the negative binomial distribition to biological data (Bliss and Fisher 1953) in which the variance is significantly larger than the mean.

Indices of pattern

The pattern of abundance of the ichthyoplankton collected during CELP was examined statistically by means of a number of indices discussed in detail in Hewitt (1982). Indices describing pattern intensity can fall into two categories - those that are sensitive to population density and those that are not. Of those that are density dependent, the variance/mean ratio (1) is the simplest and has been used as an index of ichthyoplankton distribution by Loeb et al. (1983a) for samples collected in the California Current:

$$\text{Index} = V/m \quad \text{...(1)}$$

Where V = sample variance

m = sample mean

For large sample sizes the expected value of the index is equal to 1 for individuals randomly distributed, less than 1 for uniform or under-dispersed patterns and greater than 1 for aggregated or over-dispersed patterns (Hewitt 1981). Significant departures from a random distribution were tested for by calculating the index of dispersion:

$$ID = (xj-\bar{x})2 / \bar{x} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2)$$

Where ID = the index of dispersion

xj = the variate

$\bar{x}$ = the mean of all the xj's

The sum is approximately distributed as a χ^2 variate with n-1 degrees of freedom (Pielou 1977). The probability of obtaining a value of the index from a random distribution at the appropriate degrees of freedom was obtained from a χ^2 table.

As a second index of density dependent pattern, the index of mean crowding was calculated (Lloyd 1967):

$$\overset{*}{m} = m+(V/m)-1 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (3)$$

Where $\overset{*}{m}$ = index of mean crowding

m = sample mean

V = sample variance

The index , $\overset{*}{m}$, is defined as mean number per individual of other individuals in the sample.

A density independent measure of pattern is useful because it allows a comparision to be made between populations irrespective of their levels of abundance (Hewitt 1981, 1982), although sample size and the station grid configuration should remain constant.

To determine pattern independent of abundance, Lloyd's patchiness index (Lloyd 1967) was calculated:

$$C = \overset{*}{m}/m = 1+(V-m)/m2 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(4)$$

Where C = Lloyd's patchiness index

$\overset{*}{m}$ = index of mean crowding

m = sample mean

V = sample variance

If the sample distribution of the variate can be described by the negative binomial distribution then the maximum likelihood estimate of K, $\hat{k}$ (Bliss and Fisher 1953) may be a usefull index of contagion (Smith and Richardson 1977, Hewitt 1982):

$$\hat{k} = m^2/(V-m) \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(5)$$

Where $\hat{k}$ = the maximum likelihood estimate of K of the negative binomial distribution or the index of contagion

m = sample mean

V = sample variance

Multispecies pattern

Pattern from the multispecies data from months selected as representitive of the seasons was examined using the approach of Field et al. (1982). This involves the search for patterns amongst biological variables followed by an attempt to interpret these in terms of the environment. Species selected for the analysis are indicated by a "+" symbol in Tables 4.1 and 4.2. Samples were arranged into groups with similar species using the Bray-Curtis measure of similarity on "root-root" transformed values (Field et al. 1982).

$$_{jk} = \frac{\sum_{i=1}^{s} |Y_{ij} - Y_{ik}|}{\sum_{i=1}^{s} (Y_{ij} + Y_{ik})} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(6)$$

Where $_{jk}$ = the dissimilarity measure between the jth and kth samples summed over all s species

Y_{ij} = the score for the ith species in the jth sample

Y_{ik} = the score for the ith species in the kth sample

The similarity measure is $S_{jk} = 1-\delta_{jk}$

The analysis was performed on 60 species which were selected because they were most abundant in the 4 months chosen to represent the seasons. Eggs and larvae of the same species were treated as independent items in the analysis. The similarity matrix was transformed into a dendrogram using group average sorting (Field et al. 1982). Where about 10 or more samples formed a distinct cluster in the dendrogram at a similarity level of above an arbitrary value of 50%, indicating similar species composition, the group was allocated a letter and the positions of samples within the group were plotted on the survey grid using the letter and then examined for coherent pattern. Inverse analysis was performed on the standardized species data, with rare species omitted, using the Bray-Curtis measure as advocated by Field et al. (1982). Only species groups formed above an arbitrary value of 30% similarity level were considered further. Selected species data based on larvae collected in the four months representitive of the seasons, were pooled and the overall species associations examined. The similarity matrix was summarised both by classification into a dendrogram, and by ordination using multi-dimensional scaling (Field et al. 1982).

4.3 Results

Total abundance

The monthly mean number of larvae per 10m^2 over the CELP survey grid between August 1977 and August 1978 (Fig. 4.1) varied by an order of magnitude being abundant in spring and summer (August 1977 - February 1978) and less abundant in autumn and winter (March 1978 - June 1978). The abundance in August 1978, although nearly double that of June 1978, was smaller than the August 1977 value. The mean abundance of larvae over the CELP grid between August 1977 and August 1878 (Fig. 4.2) had a coherent pattern with the greatest abundance (>2000 larvae per 10m^2) occuring roughly over the shelf break (approximately the 200m contour, see Fig. 2.3.1) and between the 100m and 200m contours over the western portion of the Agulhas Bank.

Species diversity

The larval diversity (total number of species per month) within the CELP grid decreased by a factor of 2 from a peak in October 1977 to a trough in March 1978 (Fig. 4.3). The small diversity between February and May 1978 overlaps with the reduced abundance of larvae encountered between March and June resulting in a significant positive relationship between diversity and larval abundance ($r=0.735$, $n=12$, $p<0.01$, Fig. 4.4).

The greatest diversity of larvae was found at offshore stations between line 20 in the north to line 72 in the east (Fig. 4.5). Larval diversity decreased from offshore to inshore and the smallest diversity of larvae was found at inshore stations to the north of Lambert's Bay (line 16), in St Helena Bay (lines 20 and 24), False Bay (line 52), Walker Bay (lines 56 and 60) and at the inshore station on

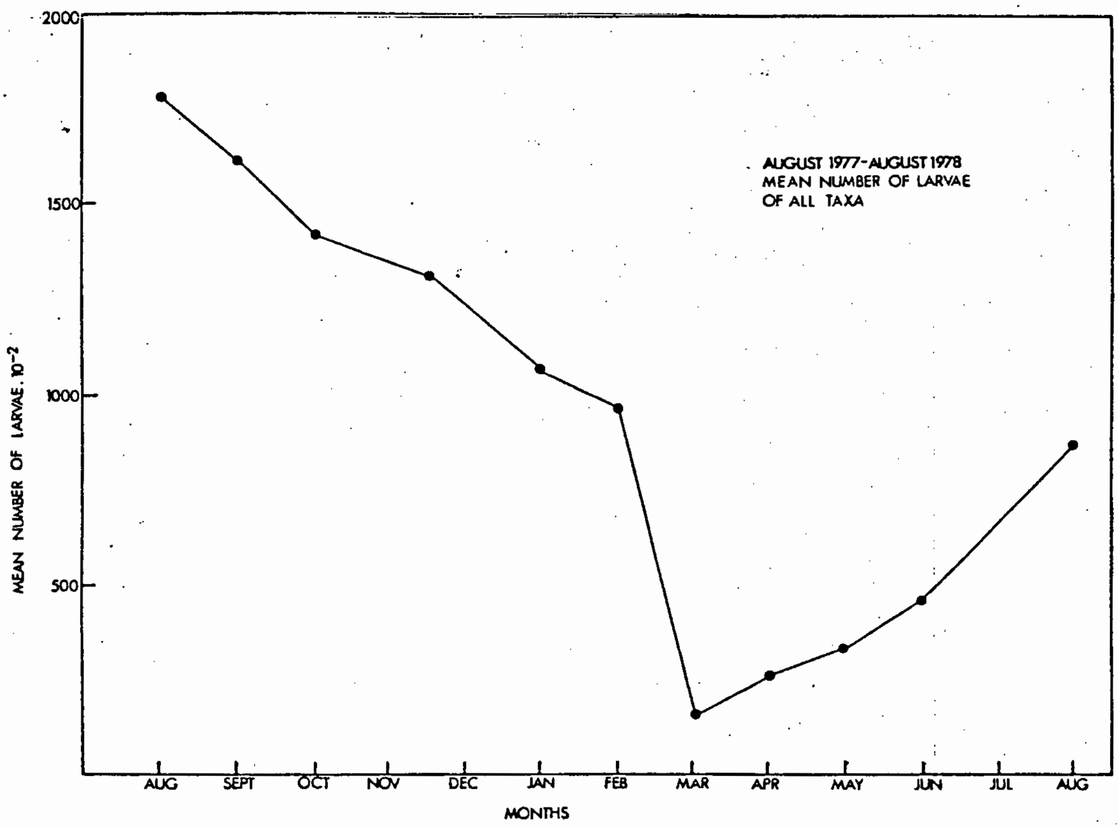


Fig. 4.1 Monthly mean number of fish larvae per 10m2 over the CELP survey grid between August 1977 and August 1978.

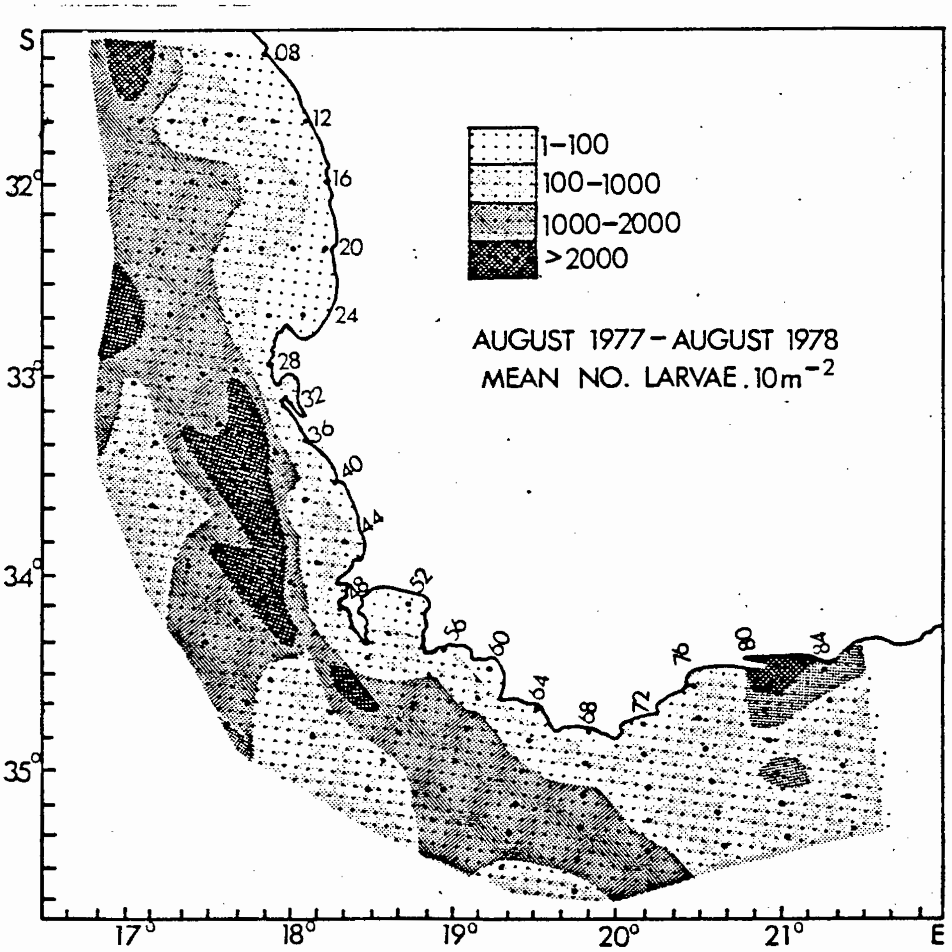


Fig. 4.2 Mean pattern of abundance of fish larvae per 10m2 over the CELP survey grid between August 1977 and August 1978.

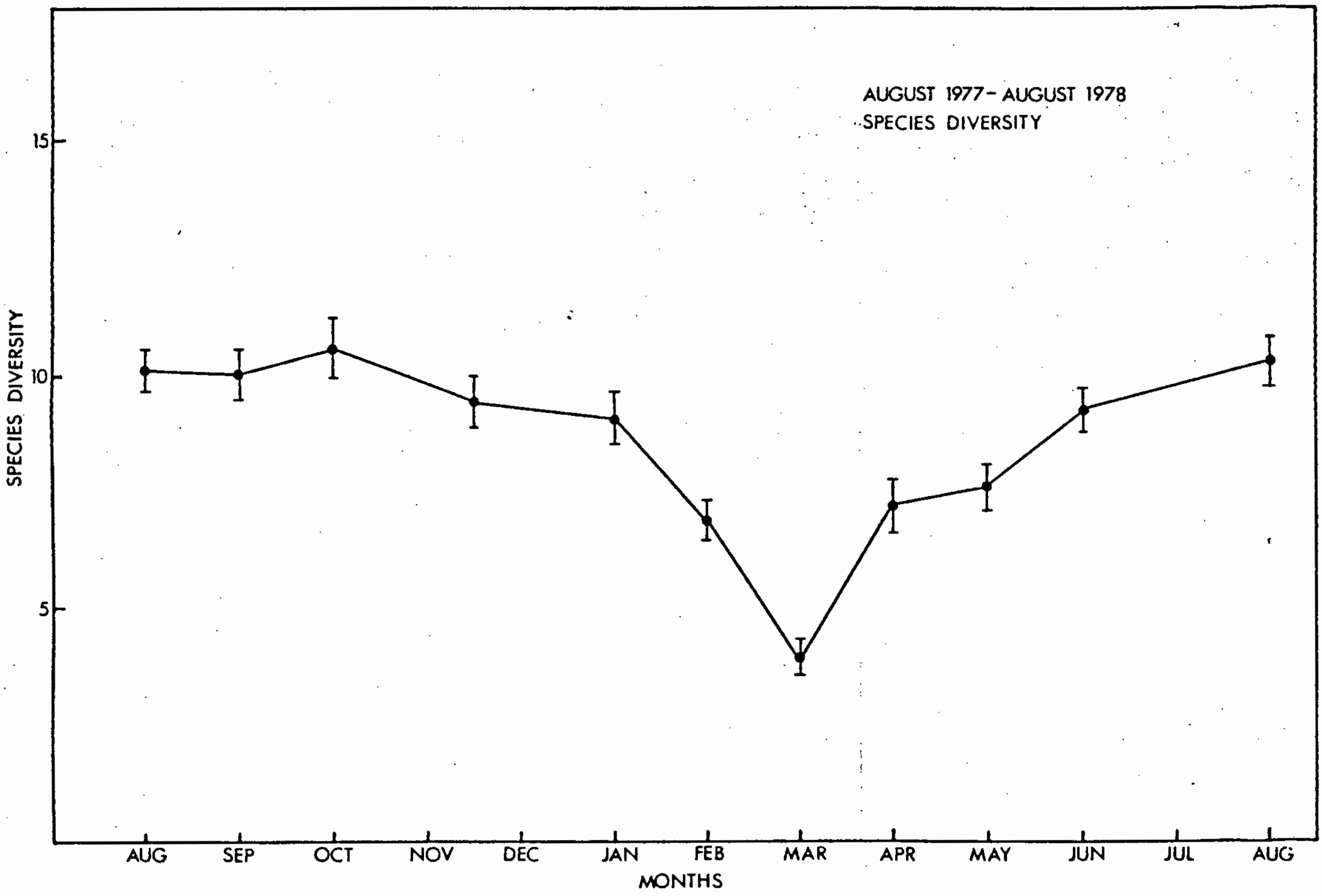


Fig. 4.3 Fish larval diversity (number of species per tow) over the CELP survey grid between August 1977 and August 1978. Error bars equal one SE either side of the mean.

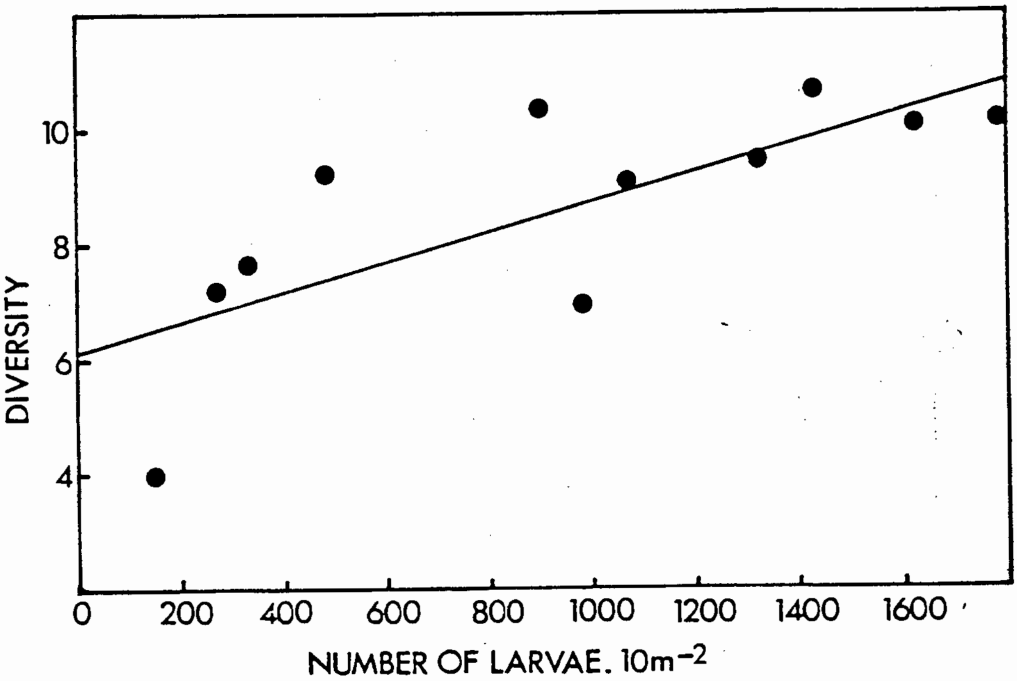


Fig. 4.4 Relationship between diversity and number of larvae per $10m^2$.

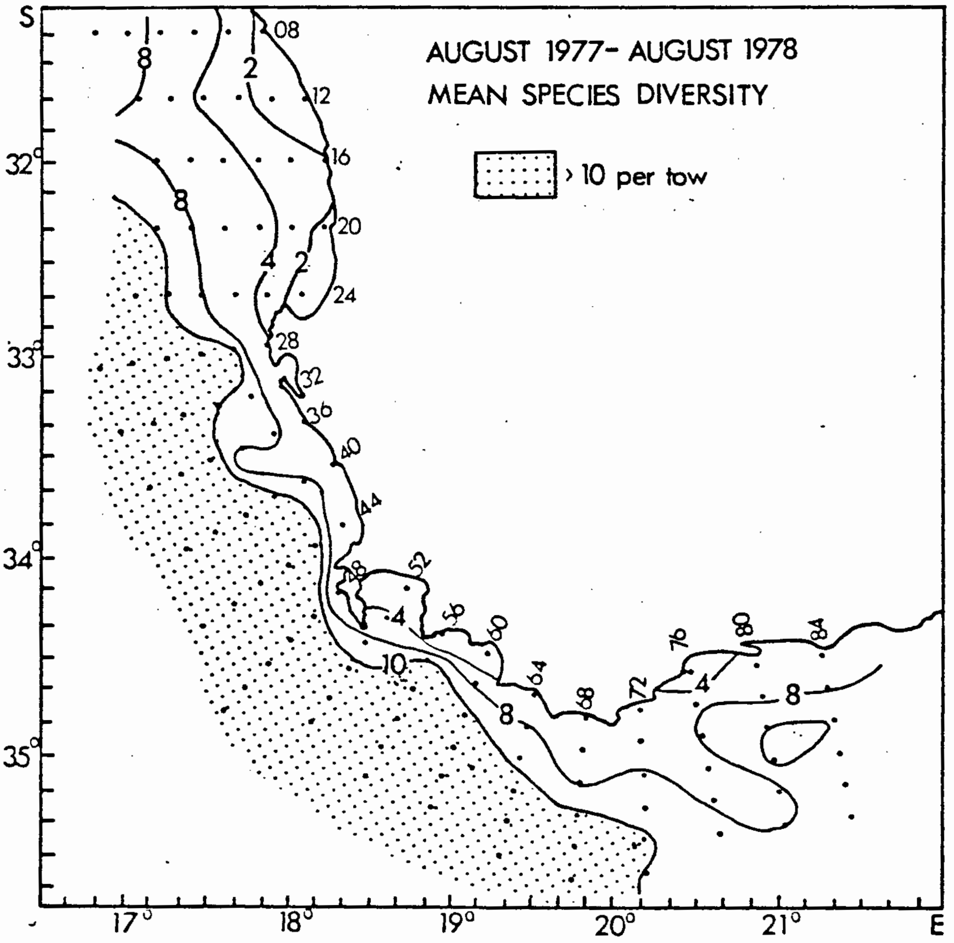


Fig. 4.5 Mean species diversity (number of species per tow) over the CELP survey grid between August 1977 and August 1978.

line 76, just west of Cape Infanta. The small diversity corresponds to areas of reduced abundance of larvae, but may also be partly a function of water depth and the number of mixing water types, since isolines of diversity correspond fairly closely with isolines of mean tow depth over the survey grid (see Section 3.2, Fig. 3.2.1).

Rank order of abundance

The species assemblage within the CELP survey grid between August 1977 and August 1978 was dominated by 9 taxa which together comprised 96% of all identifiable larvae sampled (Table 4.1). The identified larvae (larvae allocated to a taxon or type category) comprized more than 90% of all larvae collected during the survey. The 9 taxa, with the exception of the dragonet Paracallionymus costatus and the lightfish Maurolicus muelleri, are all species of considerable commercial importance. Although anchovy Engraulis capensis was the most abundant larval taxon, comprising 29.3% of all larvae sampled, anchovy eggs accounted for only 18.1% of all identified eggs and were less abundant in the survey grid than those of lightfish (34.5%) and the round herring Etrumeus whiteheadi (27.5%) (Table 4.2). Similarly, the larvae of the lanternfish Lampanyctodes hectoris ranked second (28.6%), whereas the eggs of this species only ranked fifth (6.7%). Although the eggs of the lightfish were most abundant in the survey grid (34.5%), the larvae ranked fifth (7.6%). The identification of eggs in the samples was hampered by the paucity of distinctive features exhibited by a number of species.

Table 4.1

The rank order of abundance and percentage contribution of larval taxa collected within the CELP survey grid between August 1977 and August 1978. Reference numbers were assigned sequentially during sorting. Ease of identification is indicated by e=easy, a=average and h=hard; +=those categories selected for cluster analysis.

Rank	%	Taxon	Ref.	Family	Ident.
1	29.3	Engraulis capensis	1	Engraulidae	a+
2	28.6	Lampanyctodes hectoris	10	Myctophidae	a+
3	14.0	Etrumeus whiteheadi	3	Clupeidae	a+
4	7.8	Paracallionymus costatus	7	Callionymidae	e+
5	7.6	Maurolicus muelleri	8	Sternoptychidae	e+
6	3.7	Sardinops ocellata	2	Clupeidae	a+
7	2.5	Trachurus trachurus	4	Carangidae	e+
8	1.3	Merluccius spp.	5	Merlucciidae	e+
9	0.7	Thyrsites atun	23	Gempylidae	e+
10	0.5	Cynoglossus capensis	9	Cynoglossidae	e+
11		Helicolenus dactylopterus	14	Scorpaenidae	e+
12		?Serranid	36	?Serranidae	e+
13		Lepidopus caudatus	28	Lepidopidae	e+
14		Sebastes capensis	15	Scorpaenidae	a+
15		Symbolophorus ?boops	20	Myctophidae	a+
16		Genypterus capensis	16	Ophidiidae	e+
17		Hygophum ?brunni	24	Myctophidae	a+
18		Type 27	27	Gadidae	e+
19		Chelidonichthys capensis	12	Triglidae	e+
20		Type 62	62	Scienadae	h+
21		Type 82	82	Gobiidae	h+
22		Arnoglossus capensis	65	Bothidae	e+
23		All leptocephali	54	Various	e
24		Gaidropsaurus capensis	13	Gadidae	e+
25		?Seriola lalandi	79	Carangidae	a+
26		Type 64	64	Carangidae	e+
27		Scomber japonicus	6	Scombridae	a+
28		Vinciguerria sp.	69	Sternoptychidae	e+
29		Lampanyctus sp.	25	Myctophidae	a+
30		Sufflogobius bibarbatus	11	Gobiidae	a+
31		Blenniid	17	Blenniidae	a+
32		Type 22	22	Macrouridae	a+
33		Protomyctophum sp.	63	Myctophidae	a+
34		Cyclothone sp.	51	Sternoptychidae	e+
35		Type 26	26	Carangidae	a+
36		Type 56	56	Gobiesocidae	a
37		Type 31	31	Carapidae	e+

Table 4.1 (contd.)

Rank	%	Taxon	Ref.	Family	Ident.
38		Austroglossus pectoralis	44	Soliedae	e+
39		Diogenichthus ?atlanticus	42	Myctophidae	a+
40		Lampanyctus sp.	52	Myctophidae	e
41		Type 102	102	?Myctophidae	h+
42		Scopelosaurus ?ahlstromi	66	Scopelarchidae	e+
43		Chorisochismus dentex	77	Gobiesocidae	a+
44		Idiacanthus sp	30	Idiacanthidae	e+
45		Type 32	32	?Clupeidae	h
46		Congiopodus spinifer	37	Congiopodidae	e+
47		Lophius upsicephalus	18	Lophiidae	e+
48		Chiasmodon ?niger	73	Chiasmodontidae	e+
49		Type 96	96	Mugilidae	h
50		Type 53	53	?Scombridae	h
51		Type 71	71	Scorpaenidae	a
52		Type 61	61	Paralepididae	e+
53		?Chauliodus sloani	68	Chauliodontidae	e+
54		Paralepis ?lestidium	40	Paralepididae	e
55		Scomberesox saurus	88	Scomberesocidae	e+
56		Type 85	85	Scombridae	h
57		Type 99	99	Myctophidae	h
58		Type 57	57	?Triglidae	h
59		Type 89	89	Scorpaenidae	a
60		Coccotropsis gymnoderma	58	Scorpaenidae	e+
61		Type 45	45	Callionymidae	a
62		Type 74	74	Carapidae	e
63		Type 86	86	Bothidae	e
64		Type 41	41	Syngnathidae	e
65		Lampanyctus sp.	67	Myctophidae	h
66		Caranx sp.	60	Carangidae	a
67		Type 84	84	Scombridae	h
68		Synodontid synodus	70	Synodontidae	e
69		Melanostomias sp.	43	Melanostomiatidae	e
70		Melamphaes sp.	75	Melamphaeidae	a+
71		Type 76	76	Paralepididae	a
72		Type 97	97	Labridae	h
73		Benthalbella sp.	78	Scopelarchidae	a+
74		Type 34	34		h
75		Type 80	80		h
76		Zeus faber	87	Zeidae	a
77		Type 100	100		h
78		Bregmaceros macclellandi	101	Bregmacerotidae	a
79		Tetraodontid	104	Tetraodontidae	e
80		Melanphaeid	59	Melamphaeidae	h
81		Type 81	81		h
82		Regalecus glesne	98	Regalicidae	a+

A number of species have round eggs with a diameter of about 1mm, a smooth chorion, a narrow perivitteline space and an oil globule with a diameter of about

0.2mm. Tests for hake <u>Merluccius spp.</u> eggs described by Porebski (1975) did not prove useful on a routine basis and the reliability with which these eggs were separated was poor unless they were abundant and co-occured with large numbers of newly hatched hake larvae. The rank order of hake eggs (Table 4.2) may therefore underestimate the abundance of this taxon in the samples.

Table 4.2

The rank order of abundance and percentage contribution of identifiable or separable egg taxa collected within the CELP survey grid between August 1977 and August 1978. Ease of identification is indicated by e=easy, a=average and h=hard; +=those taxa selected for cluster analysis.

Rank	%	Taxon	Ref.	Family	Ident.
1	34.5	Maurolicus muelleri	29	Sternoptichidae	e+
2	27.5	Etrumeus whiteheadi	21	Clupeidae	e+
3	18.1	Engraulis capensis	38	Engraulidae	e+
4	8.9	Paracallionymus costatus	90	Callionymidae	a+
5	6.7	Lampanyctodes hectoris	33	Myctophidae	e+
6	2.8	Sardinops ocellata	19	Clupeidae	e+
7	0.6	Thyrsites atun	91	Gempylidae	h
8		Lepidopus caudatus	92	Lepidopidae	e+
9		Trachurus trachurus	48	Carangidae	a+
10		Type 47	47		e
11		Scomberesox saurus	93	Scombresocidae	e+
12		Scomber japonicus	50	Scobridae	h
13		Type 94	94		a
14		Merluccius spp.	49	Merlucciidae	h
15		?Cynoglossus capensis	55	Cynoglossidae	a
16		Type 95	95		a

Patterns of abundance of individual species

Anchovy

Of the identified ichthyoplankton collected during CELP, anchovy Engraulis capensis accounted for 29.3% of the larvae and 18.1% of the eggs (Tables 4.1 and 4.2). A distinct spawning season existed with the greatest abundance of eggs and larvae recorded from October 1977 to February 1978 (spring/summer) and the least in August 1977 and from March 1978 to August 1978 (autumn/winter, Fig. 4.6). While eggs were most abundant in the plankton tows in October, larvae peaked in abundance in samples collected during the November/December cruise.

The mean abundance of anchovy eggs over the survey grid between August 1977 and August 1978 (Fig. 4.7) had a coherent pattern with maximum abundance south and east of line 40, extending over the Agulhas Bank, and a narrow ribbon-like zone of more than 100 eggs.10m^{-2} extending up the west coast and fanning out to the north of Cape Columbine. Anchovy eggs were not encountered inshore on the west coast. Eggs were found at the offshore limit of the grid on lines 12 and 16 on the west coast and on a number of lines that crossed the Agulhas Bank.

Anchovy larvae were more widespread than the eggs (Fig. 4.7) with mean numbers in excess of 1 000.10m^{-2} occurring to the edge of the grid on a number of lines south of Cape Columbine and north of the Cape Peninsula (line 48) on the west coast. The abundance of larvae was reduced to the north of Cape Columbine and at inshore stations on the west coast. The main areas of maximum larval abundance occurred between Cape Columbine and Cape Point (lines 28 to 48) at about 60km from the coast, as well as closer inshore near the eastern limit of the survey grid.

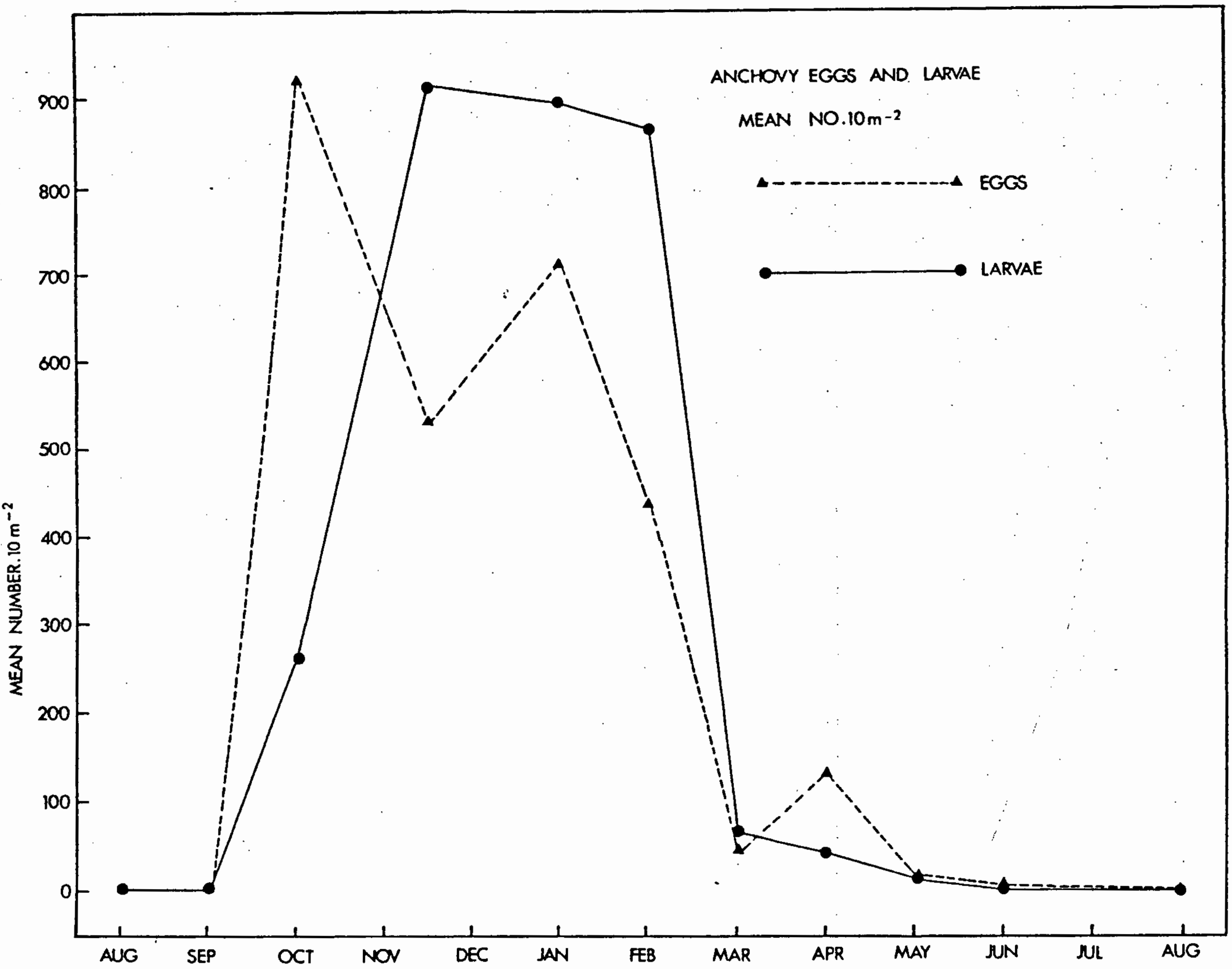


Fig. 4.6 Mean number of anchovy eggs and larvae per $10m^2$ over the CELP survey grid between August 1977 and August 1978

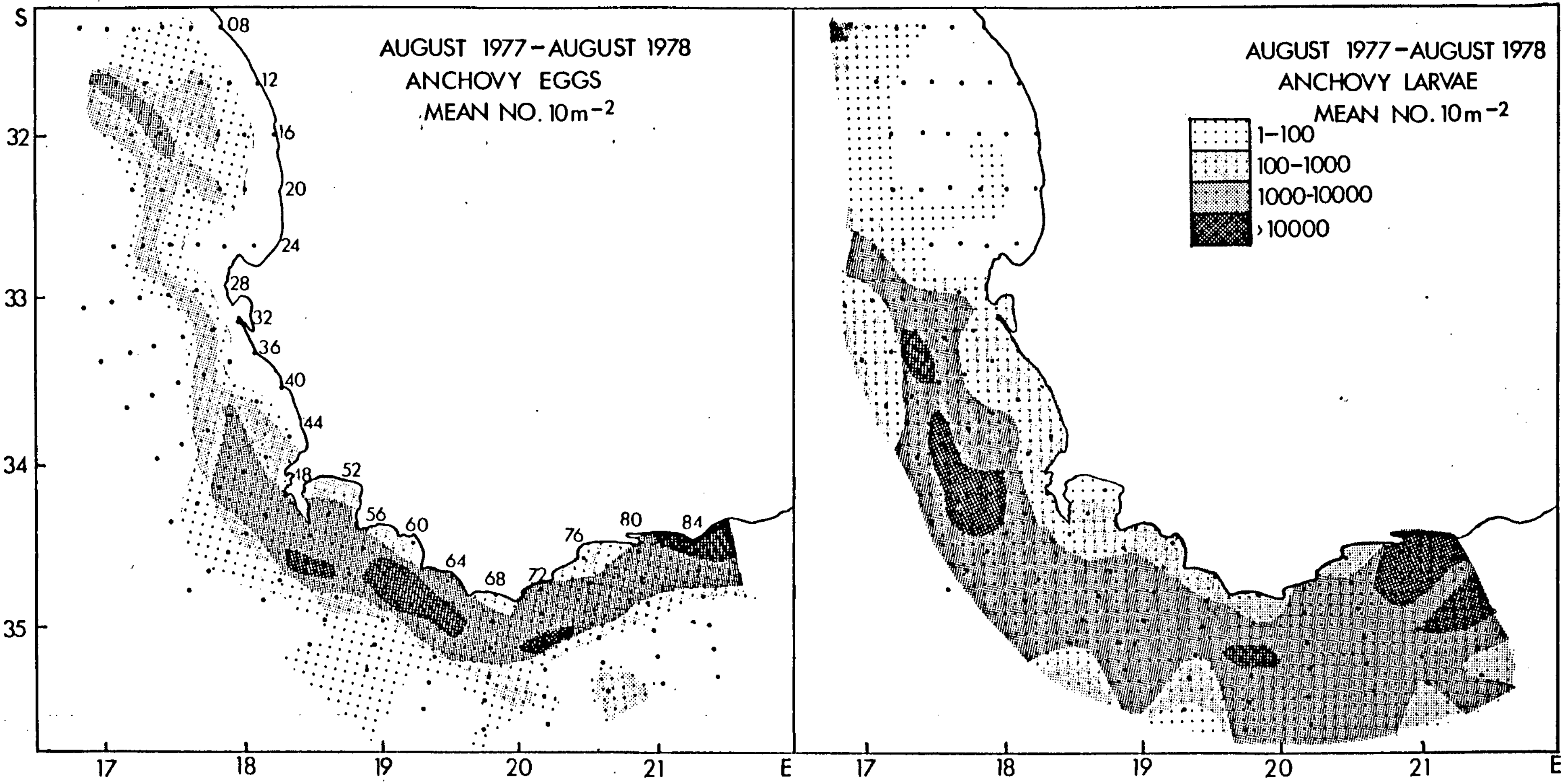


Fig. 4.7 Mean abundance of anchovy eggs and larvae per $10m^2$ over the CELP survey grid between August 1977 and August 1978.

Comparison of the pattern of abundance of anchovy eggs during the peak of the spawning season in four November surveys (Fig. 4.8) shows some degree of similarity. In November 1977 anchovy eggs were most abundant some distance from the coast from line 40 south to Cape Agulhas. The abundance decreased inshore and offshore and no eggs were found north of line 24. In November 1978 greater densities of eggs were sampled and an area with an egg abundance exceeding 1000 eggs.10m^{-2} extended to the offshore limit of the survey grid off Cape Agulhas and further east, In other respects the pattern was similar to 1977. In November 1981 only the eastern half of the survey grid was sampled. A large area with an egg density of more than 1 000.10m^{-2} was found to extend to the offshore limit of the survey grid on lines 56 and 60 as well as on line 80. In November 1982 the pattern of abundance was very similar to November 1978, although greater egg densities were encountered over a larger area.

The larger survey grid sampled in November 1983, November 1984 and November 1985 using the CalVET net gave information on the pattern of anchovy egg and larval abundance further offshore on the Agulhas Bank and further east. In November 1983 the pattern was similar to that observed in earlier surveys although eggs were rare at inshore stations (Fig. 4.9). A narrow band of eggs extended from the Agulhas Bank up the west coast as far as Cape Columbine. Eggs were found out to the edge of the Agulhas Bank and further east than the area previously sampled. The abundance pattern of anchovy larvae in November 1983 was similar to that of the eggs although larvae were abundant on the west coast to the north of Cape Point (Fig. 4.10). In November 1984 egg densities in excess of 10 000.10m^{-2} covered a larger portion of the survey grid (Fig. 4.11). No eggs were collected north of Cape Town and eggs were more abundant in the vicinity of Port Elizabeth than they were in 1983. A break in the pattern of

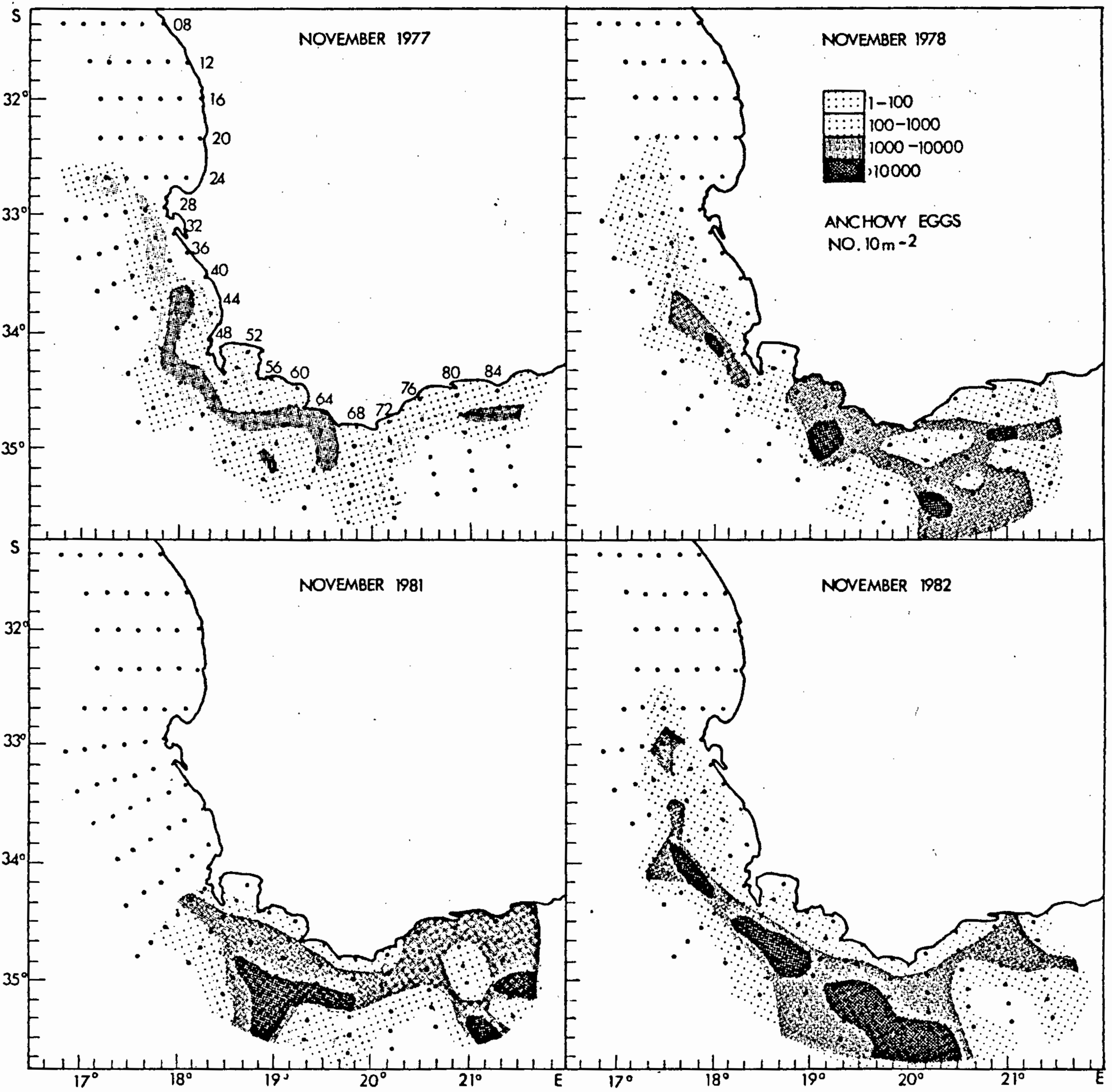


Fig. 4.8 A comparison of the pattern of abundance of anchovy eggs over the CELP survey grid during peak spawning over four years.

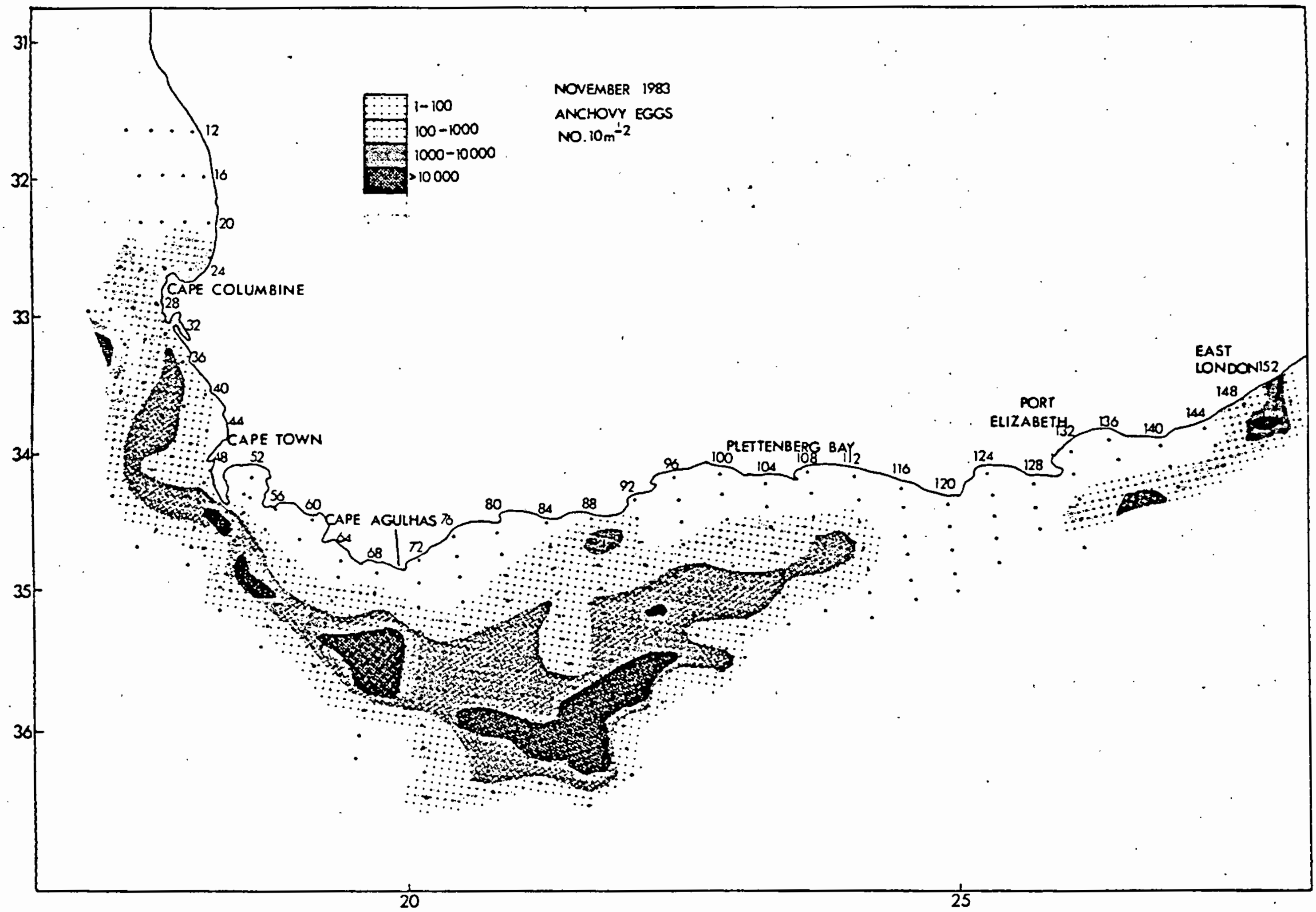


Fig. 4.9 Pattern of abundance of anchovy eggs over the Extended CELP survey grid in November 1983.

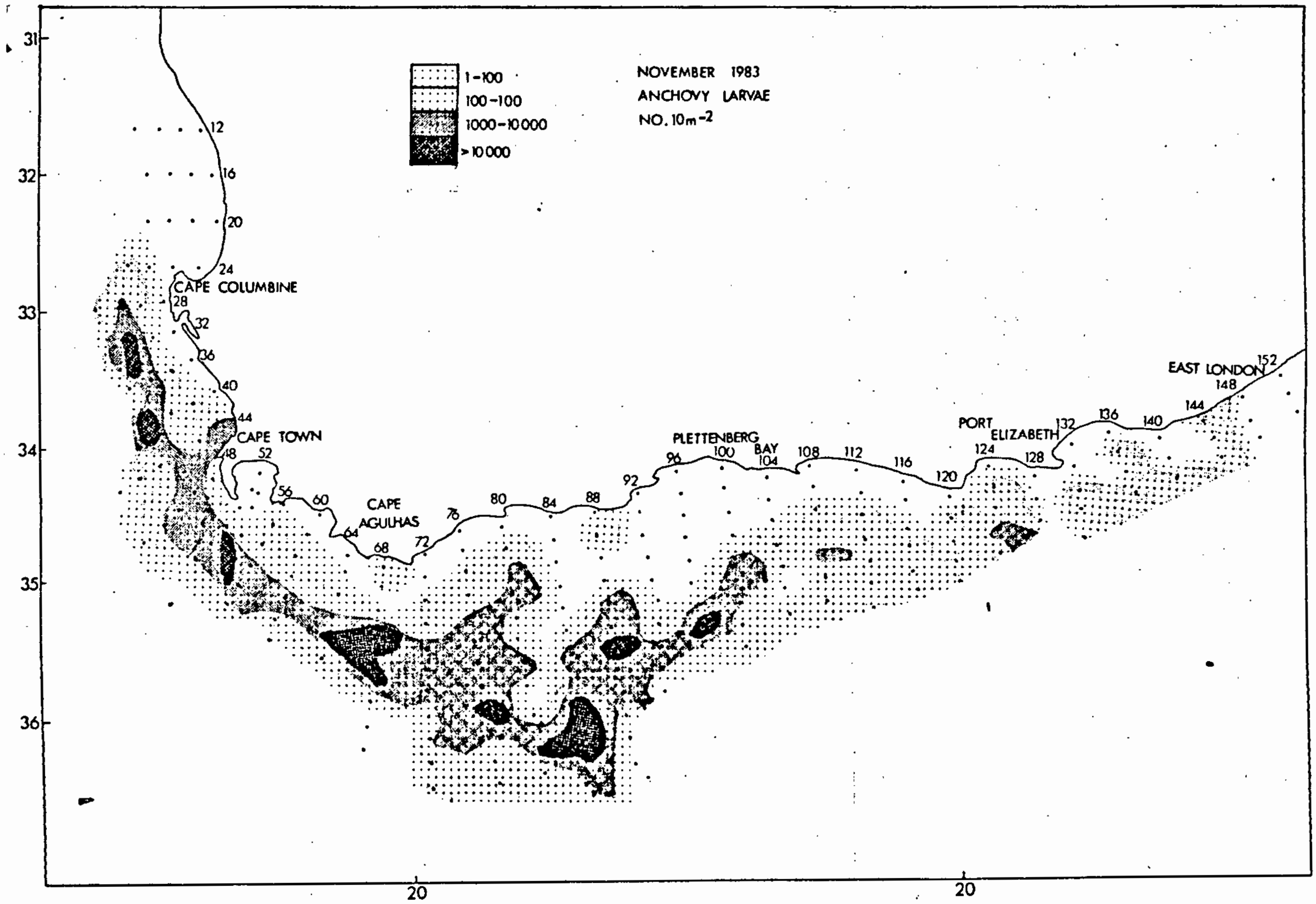


Fig. 4.10 Pattern of abundance of anchovy larvae over the Extended CELP survey grid in November 1983.

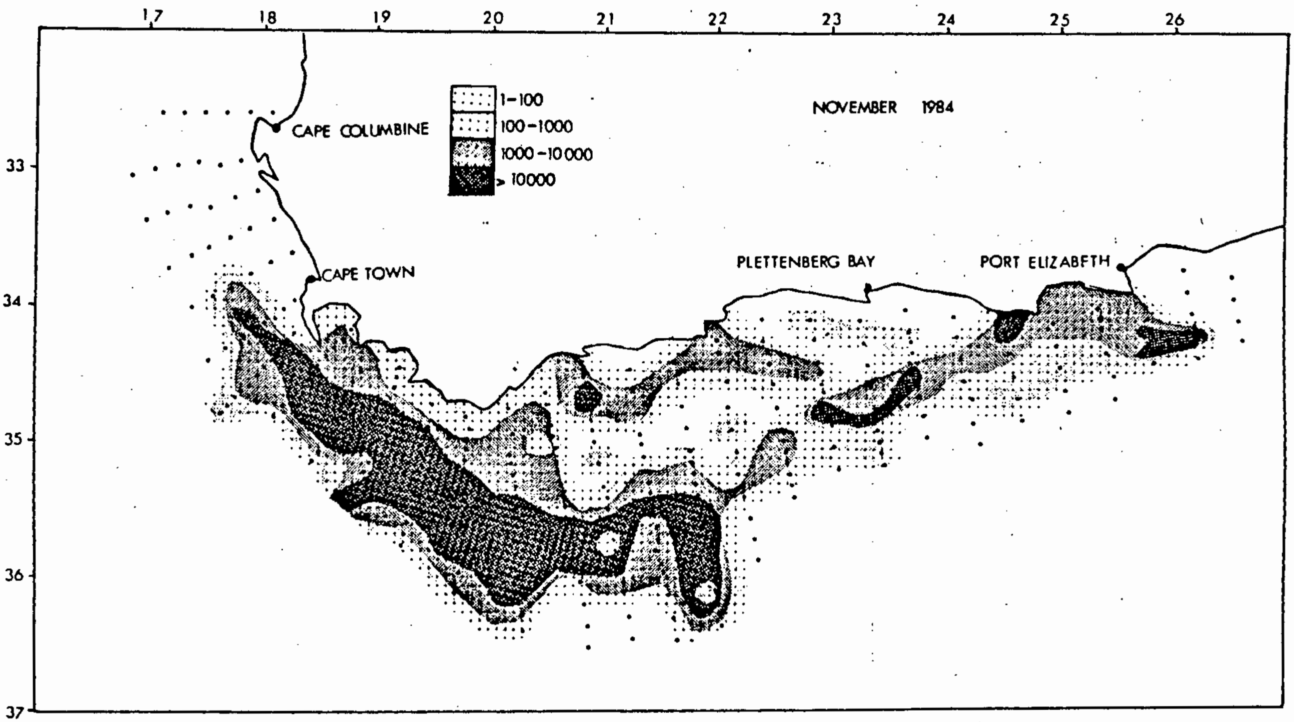


Fig. 4.11 Pattern of abundance of anchovy eggs over the Extended CELP survey grid in November 1984.

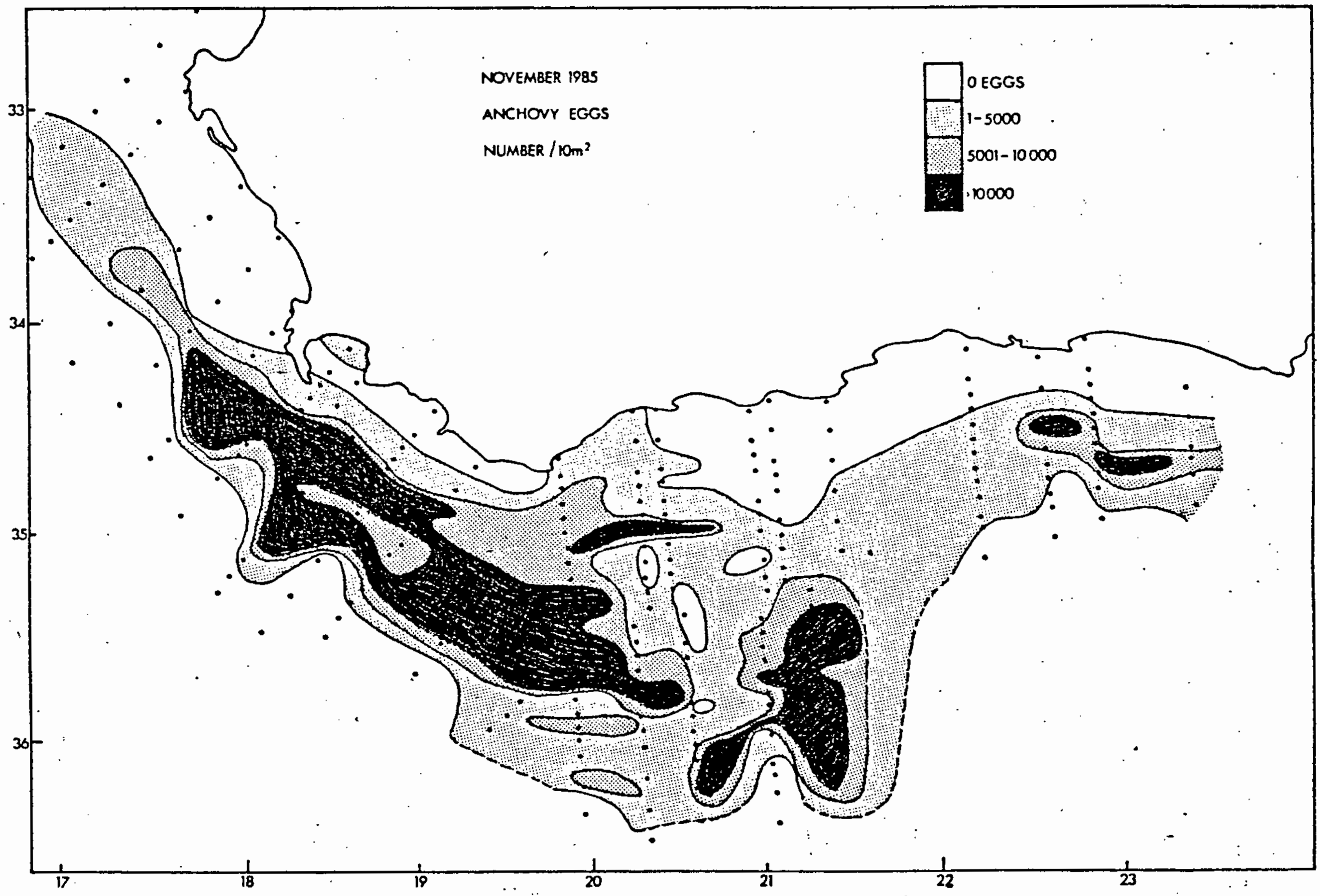


Fig. 4.12 Pattern of abundance of anchovy eggs over the Stratified Random survey grid in November 1985.

abundance occurred just west of Plettenberg Bay. The pattern of egg abundance in 1985 (Fig. 4.12) was very similar to that found in the previous two surveys.

Lanternfish

Lanternfish Lampanyctodes hectoris larvae were the second most abundant larval taxon and accounted for 28.6% of all identified larvae. The eggs were less abundant and only ranked fifth, accounting for 6.7% of the identified eggs. Like the anchovy, lanternfish had a distinct spawning season (Fig. 4.13), although this occurred out of phase with that of the anchovy. Eggs and larvae were most abundant from August to October 1977 and in June and August 1978 (winter/spring) and virtually no eggs or larvae were sampled between November and May. The mean egg abundance was greatest off Cape Columbine (lines 20 to 36) and the Cape Peninsula (lines 44 to 56), in the vicinity of undersea canyons (see Section 2.3), as well as in the extreme north of the survey grid (Fig. 4.14). Eggs were not encountered at inshore stations, except at Cape Columbine (line 28), or over the Agulhas Bank east of line 64. Lanternfish larvae were more widespread than the eggs but were not abundant at inshore stations and over the eastern portion of the Agulhas Bank. Larvae were moderately abundant ($>100.10m^{-2}$) along the whole offshore area as far south as line 64, just west of Cape Agulhas. Concentrations of more than 1 000 larvae.$10m^{-2}$ tended to occur offshore on the west coast with the density decreasing towards the coast.

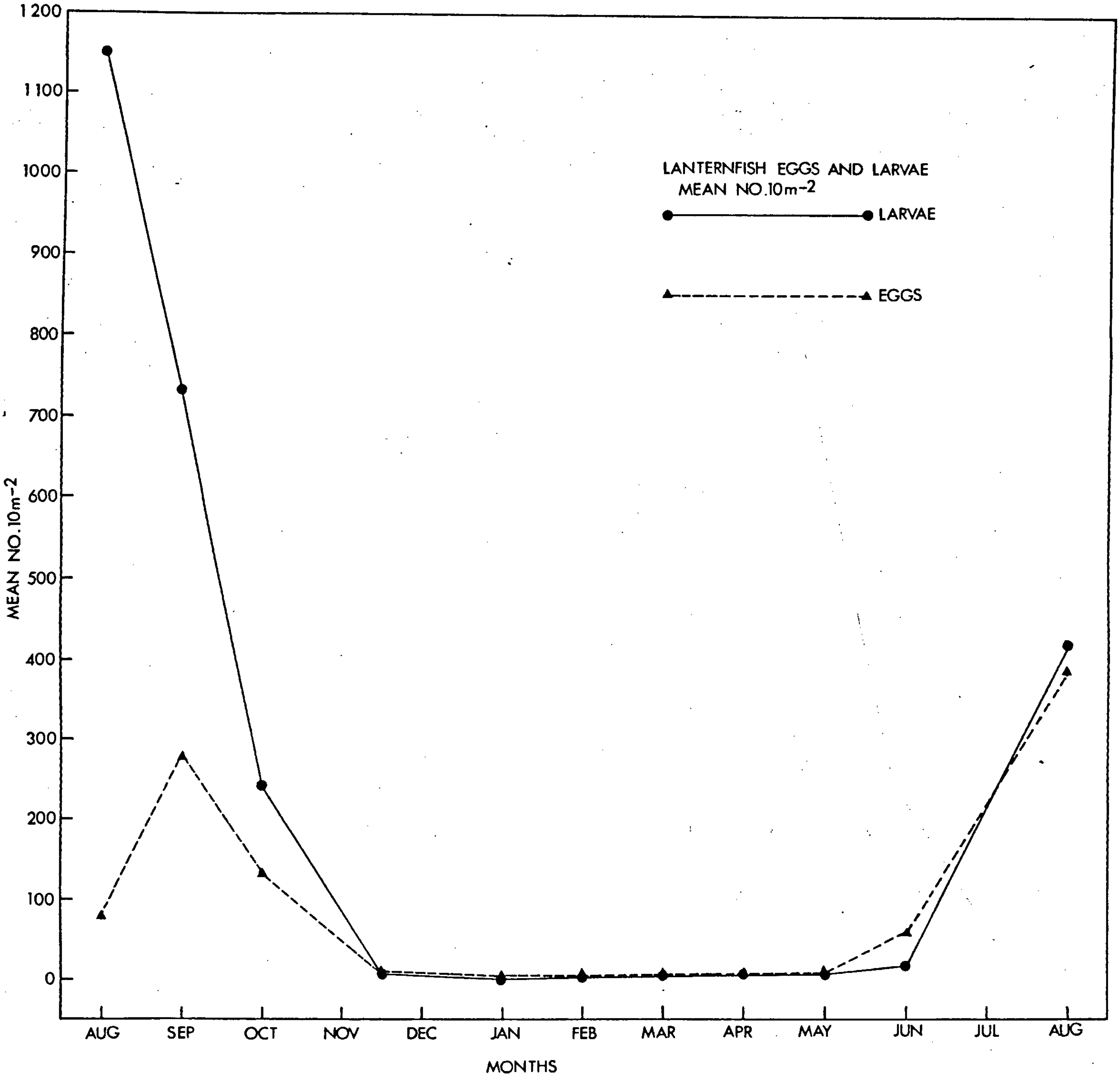


Fig. 4.13 Mean number of lanternfish eggs and larvae per $10m^2$ over the CELP survey grid between August 1977 and August 1978.

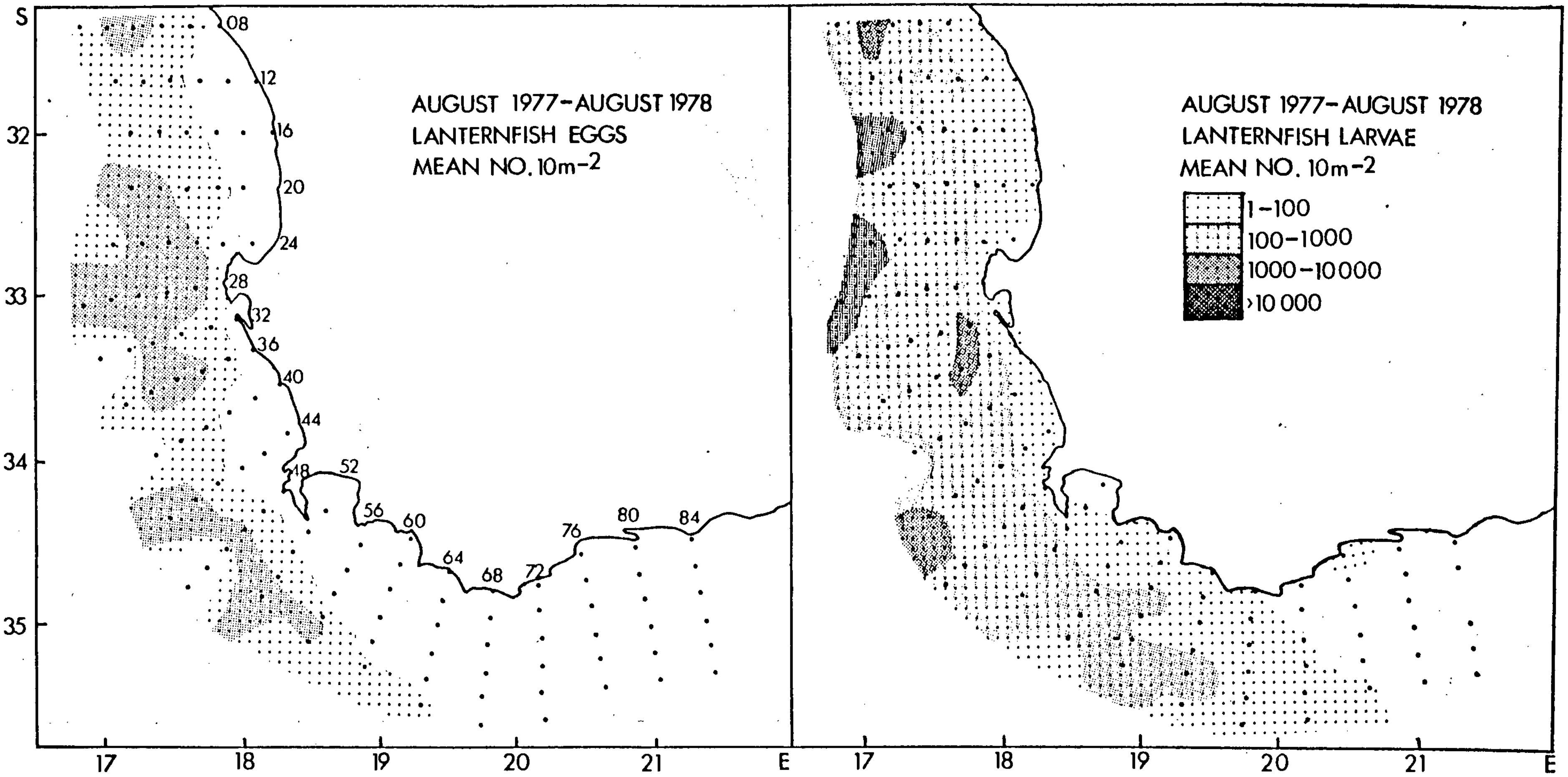


Fig. 4.14 Mean pattern of abundance of lanternfish eggs and larvae over the CELP survey grid between August 1977 and August 1978.

Roundherring

Roundherring Etrumeus whiteheadi larvae ranked third and the eggs ranked second, consisting of, respectively, 14.0% and 27.5% off the identified eggs and larvae collected in the survey. The spawning season was well defined but more protracted than those of the anchovy and lanternfish (Fig. 4.15), and some roundherring eggs and larvae were present in the samples in all months. The abundance was least from November 1977 to April 1978 (summer/autumn) and greatest in August, September and October 1978 (late winter/spring). The mean egg abundance from samples collected during the 12 cruises had a coherent pattern (Fig. 4.16) with reduced concentrations of eggs at inshore stations as well as at offshore stations between Cape Columbine and due south of Cape Point (lines 28 to 56). The main area of greater egg abundance extended east of Cape Point along the western edge of the Agulhas Bank to the offshore limit of the survey grid. This pattern was also clearly apparent in the data for most of the individual months of the survey (not shown). A second patch of abundant roundherring eggs occurred offshore to the north of Cape Columbine. Roundherring larvae had a similar pattern of abundance to the eggs although densities were generally smaller.

Dragonet

The larvae of the dragonet Paracallionymus costatus ranked fourth and accounted for 7.8% of all identified larvae. The egg stage of this species also ranked fourth but were not consistently identified. Dragonet larvae were present throughout the year in small densities with no clearly defined spawning season, although larvae were least abundant in February and March 1978 and most abundant in June to August 1978 (Fig. 4.17). Dragonet eggs were found in small densities over the

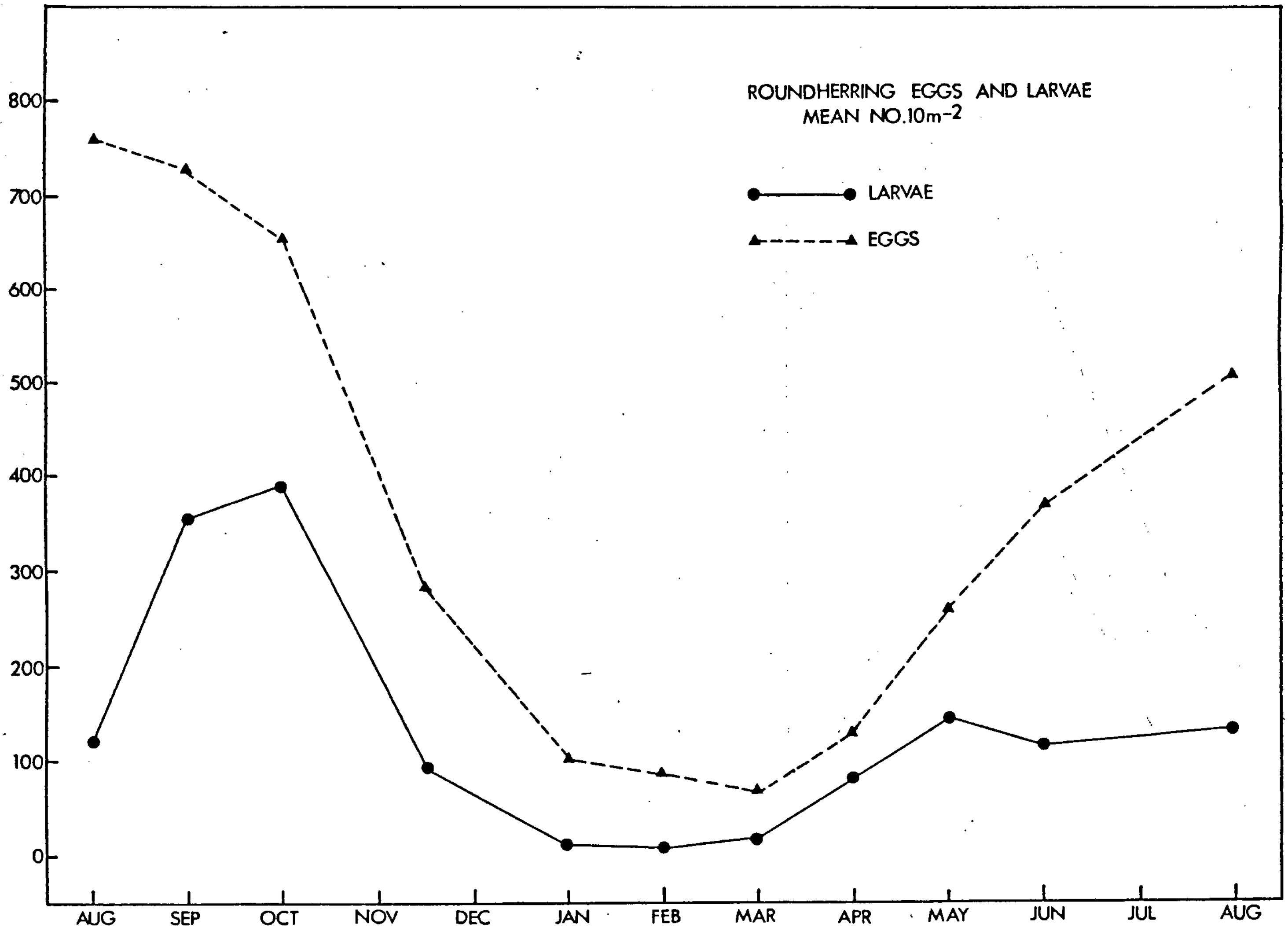


Fig. 4.15 Mean number of round herring eggs and larvae per 10m2 over the CELP survey grid between August 1977 and August 1978.

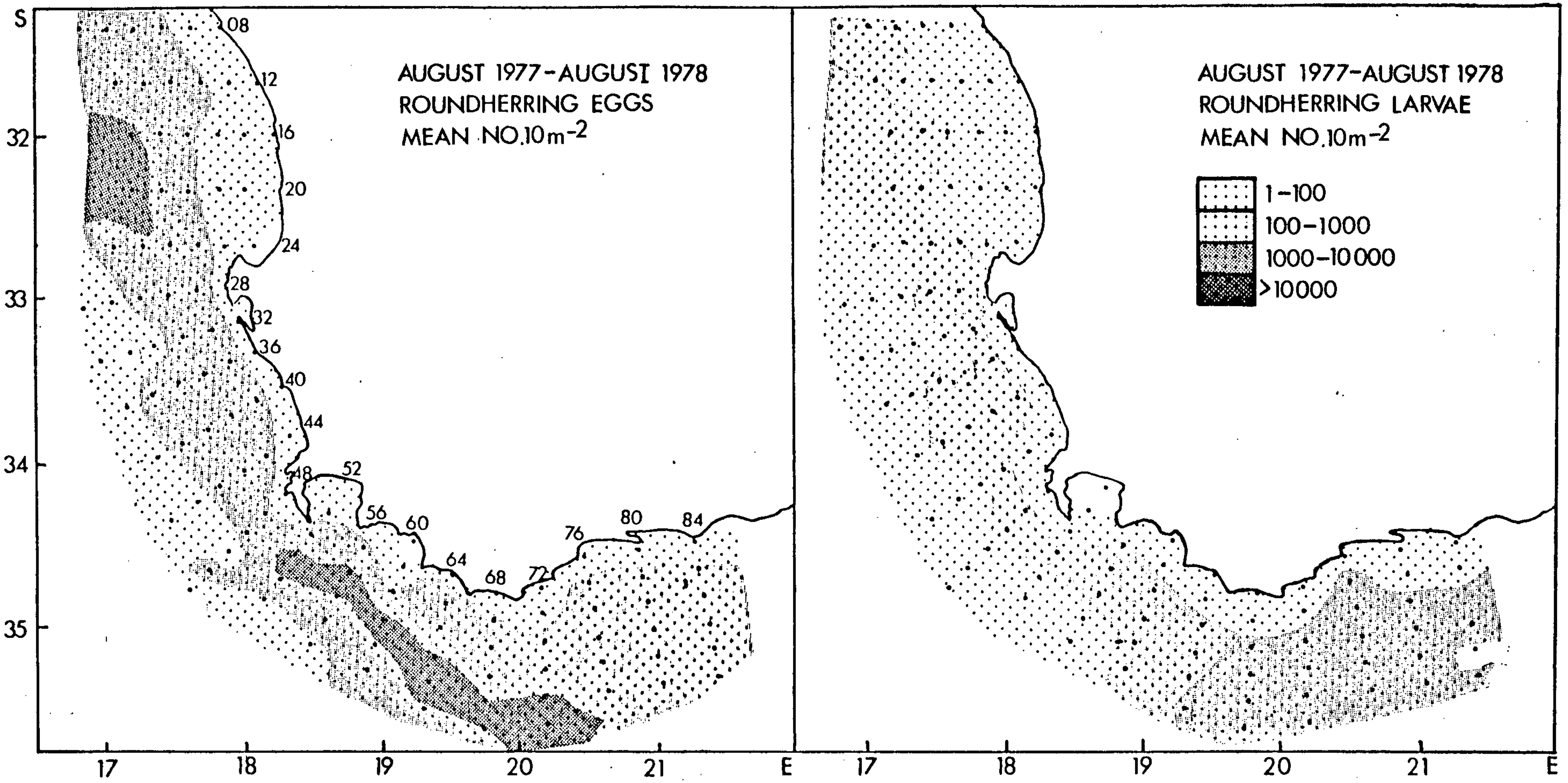


Fig. 4.16 Mean pattern of abundance of round herring eggs and larvae over the CELP survey grid between August 1977 and August 1978.

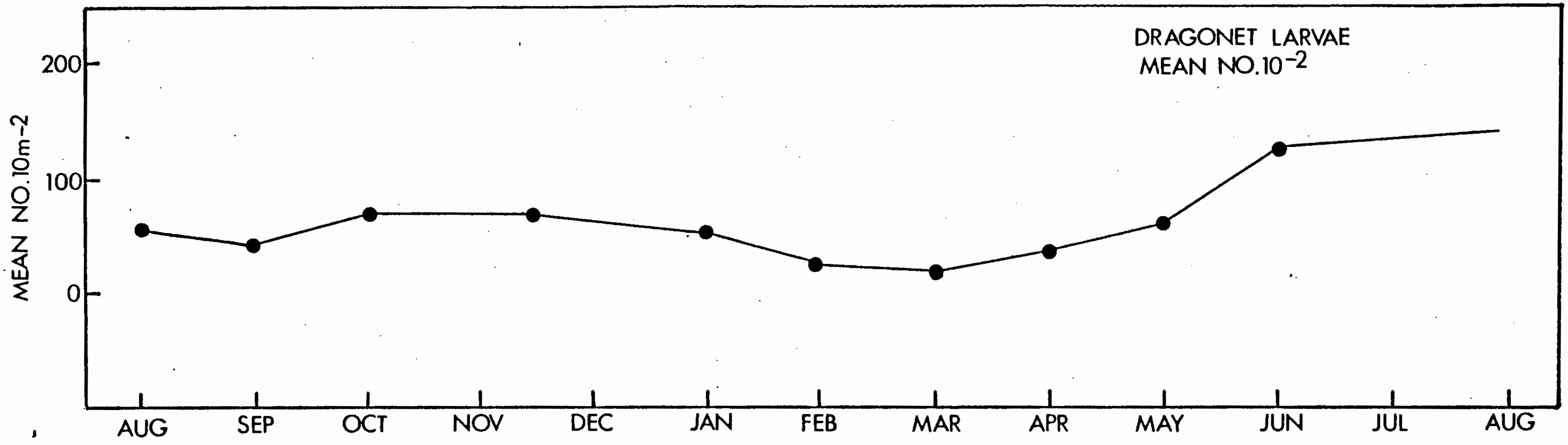


Fig. 4.17 Mean number of dragonet larvae per 10m^2 over the CELP survey grid between August 1977 and August 1978.

whole survey grid (Fig. 4.18) and, although not too much reliance should be placed on the pattern because of difficulties in identification, were most abundant in a band betweeen Cape Columbine and the Cape Peninsula and in an area to the north of Cape Columbine. Dragonet larvae were also widespread at small densities throughout the survey grid with a large area of more than 100 larve.10m^{-2} extending north of the Cape Peninsula and a smaller area offshore of Cape Agulhas.

Lightfish

Lightfish Maurolicus muelleri eggs ranked first amongst the eggs and comprised 34.5% of all identified eggs whereas the larvae ranked fifth and comprised only 7.6% of the identified larvae. Although lightfish eggs and larvae were present throughout the survey (Fig. 4.19), the abundance of eggs was least from February to May 1978 (late summer/autumn) and greatest from August 1977 to January 1978 (spring/summer). Lightfish eggs were abundant in a band running longshore from Cape Columbine south to line 64 (Fig. 4.20). Few eggs were found inshore on the west coast and eggs were absent over the Agulhas Bank east of Cape Agulhas (line 68). Lightfish larvae were also absent over the eastern portion of the Agulhas Bank. An area with a mean abundance of more than 100 larvae.10m^{-2} extended from the Cape Peninsula north betwen 20 and 120km from the coast. Two smaller patches with a mean abundance of more than 100 larvae.10m^{-2} were found between Cape Point and Cape Agulhas.

Pilchard

Pilchard Sardinops ocellata larvae ranked sixth amongst the larvae in the samples and accounted for 3.7% of all identified larvae. The eggs also ranked sixth and

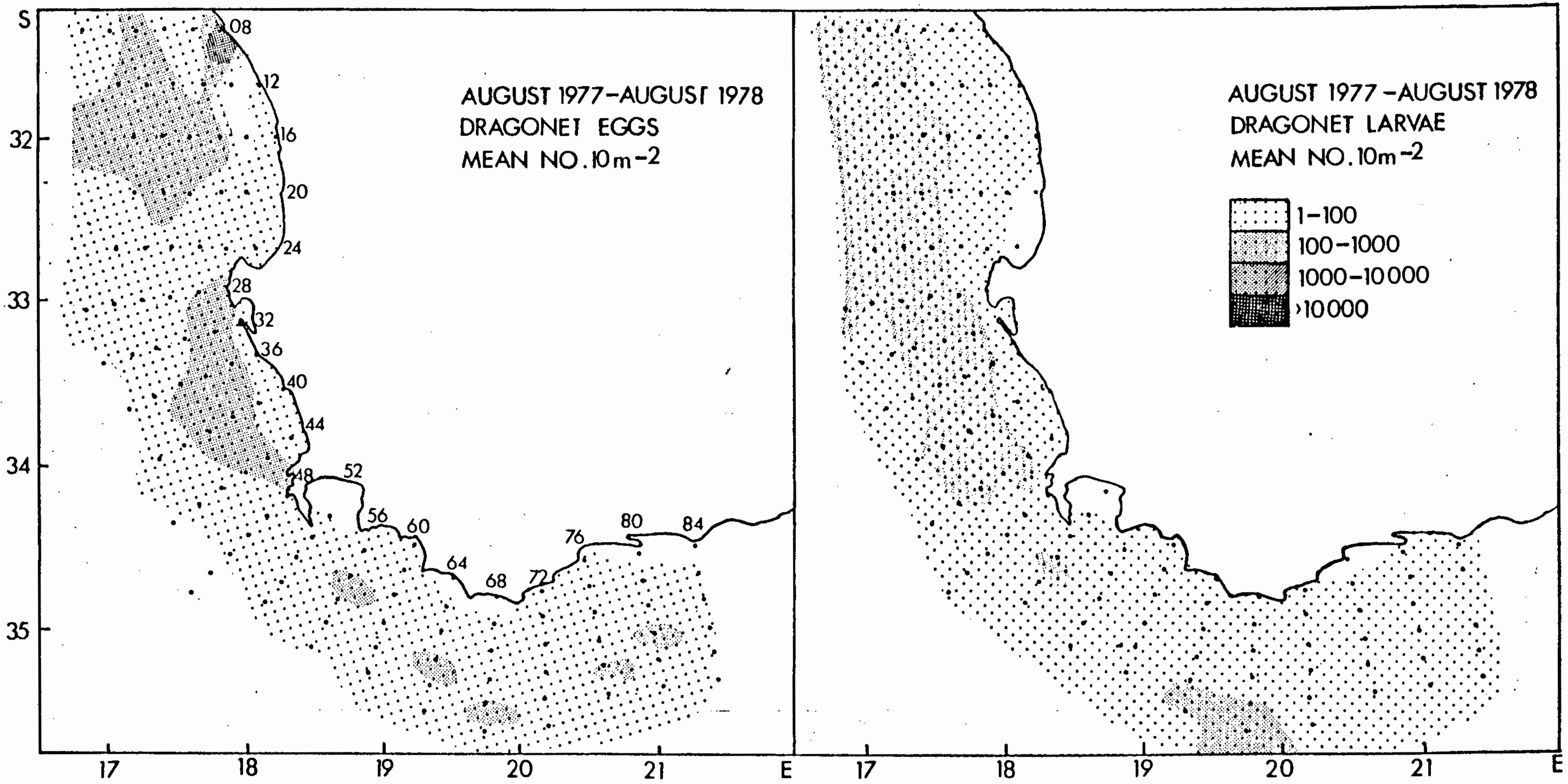


Fig. 4.18 Mean pattern of abundance of dragonet eggs and larvae over the CELP survey grid between August 1977 and August 1978.

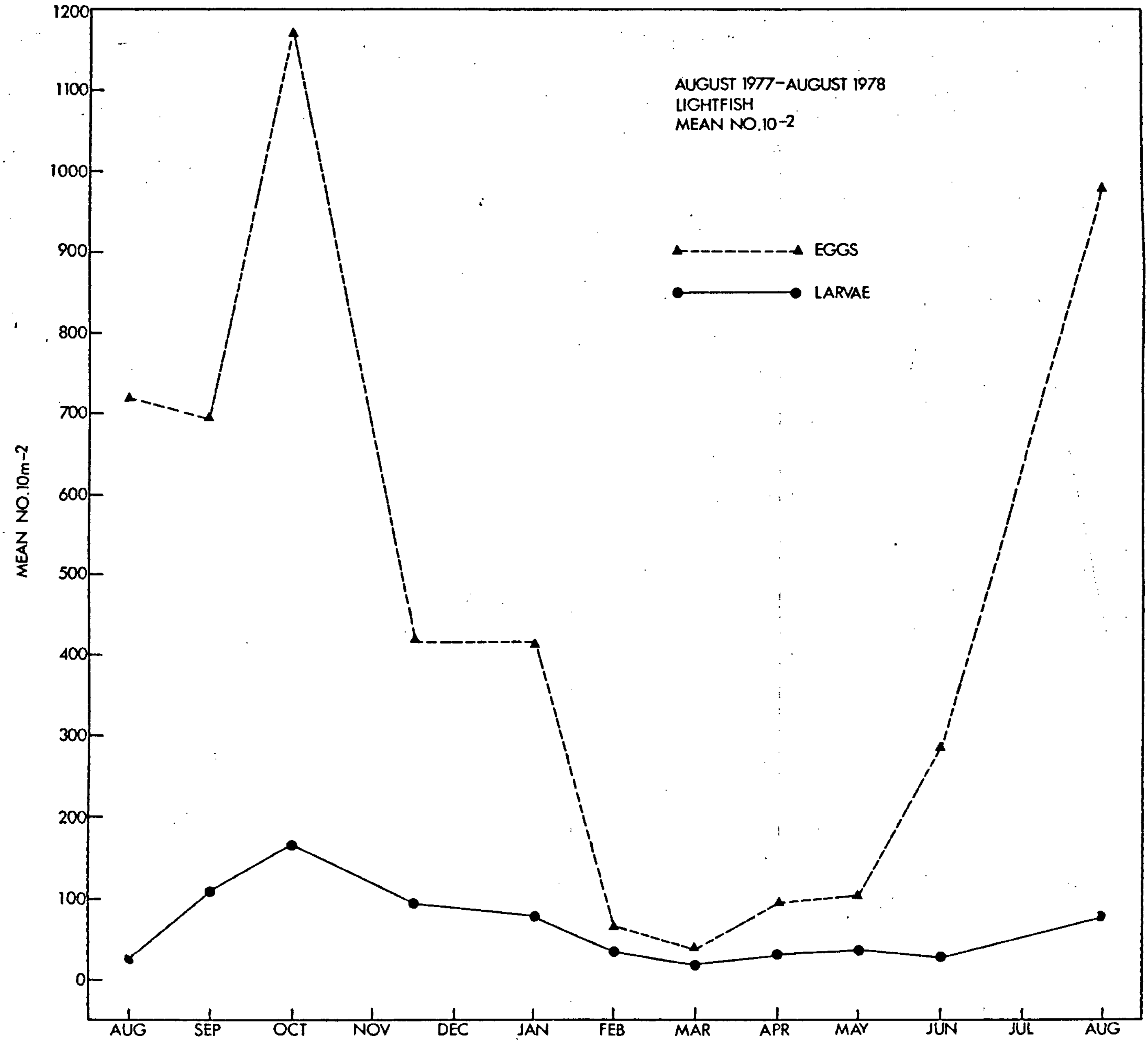


Fig. 4.19 Mean number of lightfish eggs and larvae per $10m^2$ over the CELP survey grid between August 1977 and August 1978.

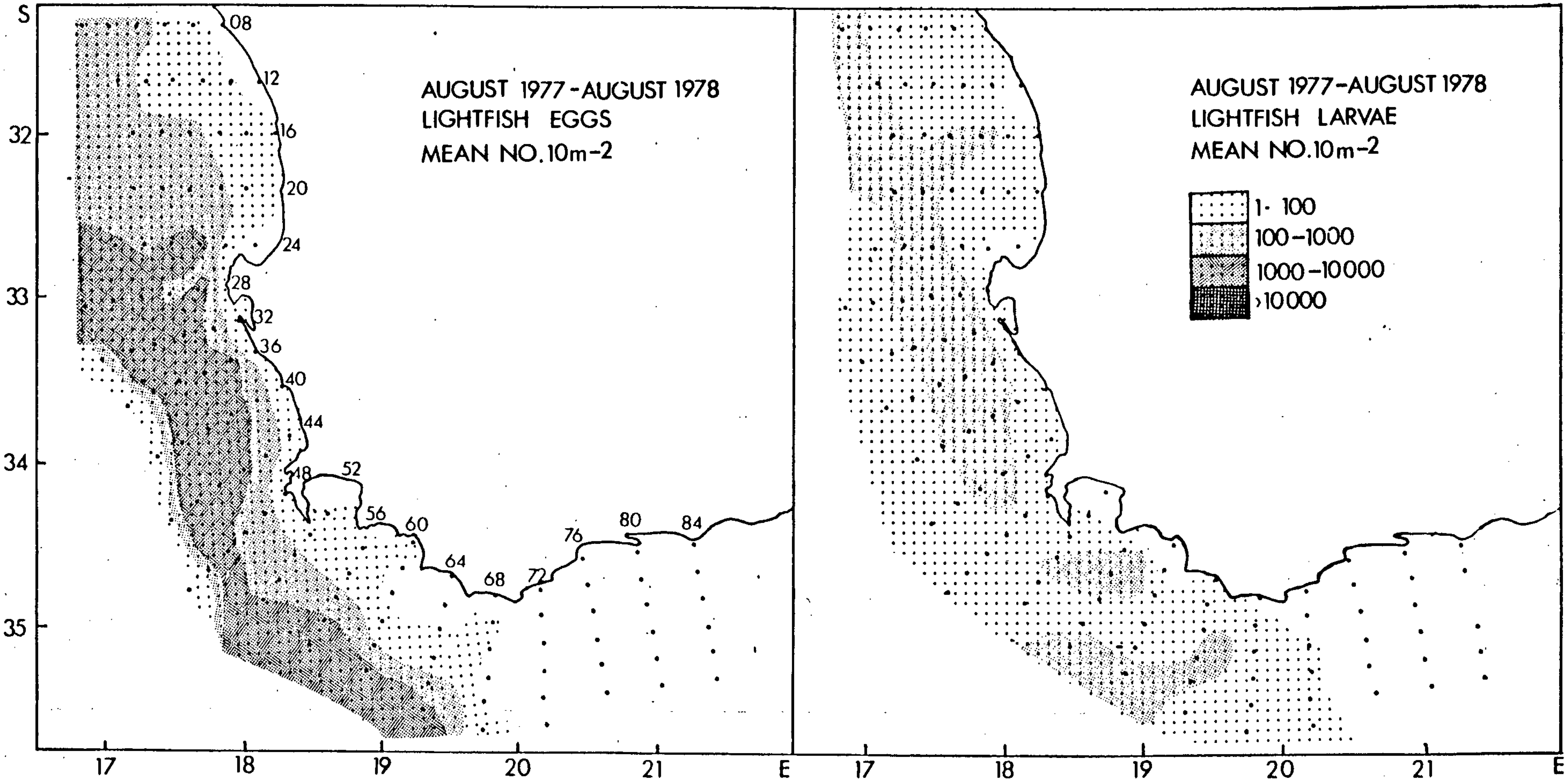


Fig. 4.20 Mean pattern of abundance of lightfish eggs and larvae over the CELP survey grid between August 1977 and August 1978.

comprised 2.8% of the identified eggs. Pilchard eggs and larvae were present in each month of the survey without a clearly defined peak (Fig. 4.21). Both the egg and larval stages were at a maximum abundance in August 1978 although the abundance of eggs and larvae was small in August 1977. The abundance of eggs in the plankton appeared to be raised from October 1977 to January 1978 and again in July and August 1978. Pilchard eggs were widespread over the survey grid but did not occur at inshore stations north of line 44 or at offshore stations between line 32 and line 56 (Fig. 4.22). Pilchard larvae were also widespread although the mean abundance was reduced in St Helena Bay (line 24) and the inshore area to the north. Mean concentrations of more than 100 larvae.10m^{-2} occurred off the Cape Peninsula (line 44) and on the Agulhas Bank (lines 64 to 72).

Horse mackerel

Horse mackerel Trachurus trachurus larvae ranked seventh comprising 2.5% of the identified larvae and the eggs ranked ninth. However, the eggs were not identified in a consistent manner, particularly when they were rare in the samples. Horse mackerel larvae were most abundant in the samples during winter/spring (Fig. 4.23). Horse mackerel larve were found over most of the survey grid in small densities (Fig. 4.24). Numbers were particularly small at inshore stations north of line 24 as well as in False Bay (line 52), Walker Bay (line 60) and in the vicinity of Cape Infanta (lines 72 to 80).

Hake

Hake Merluccius paradoxus and Merluccius capensis larvae together ranked eighth in abundance amongst the larvae and accounted for 1.3% of all identified larvae. Hake eggs were not consistently enumerated. Larvae were most abundant in

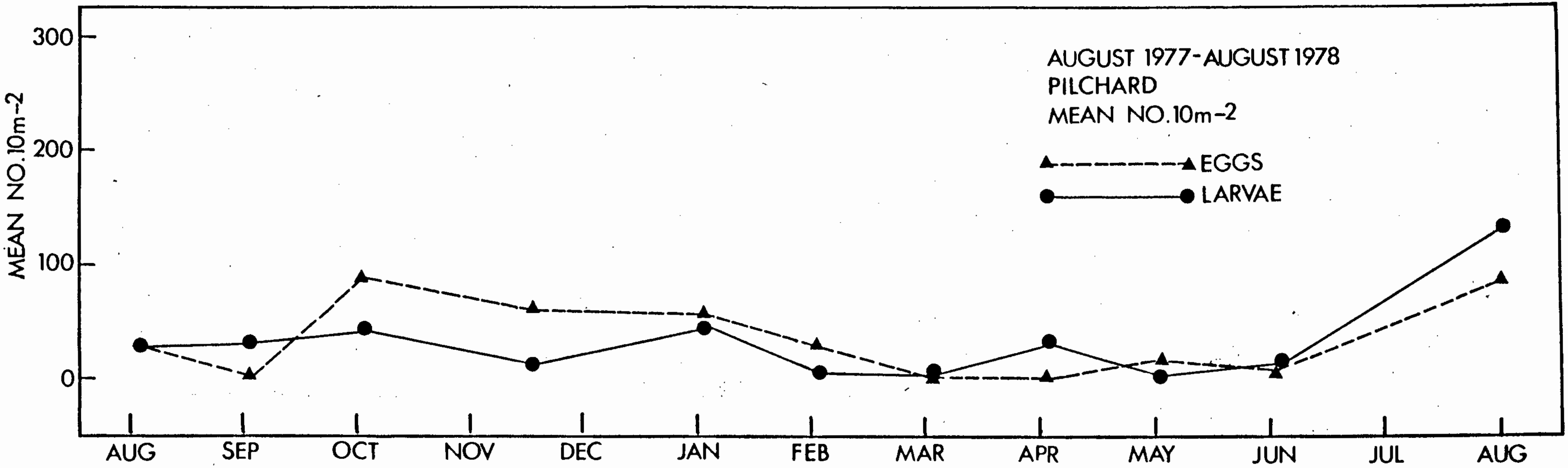


Fig. 4.21 Mean number of pilchard eggs and larvae per $10m^2$ over the CELP survey grid between August 1977 and August 1978.

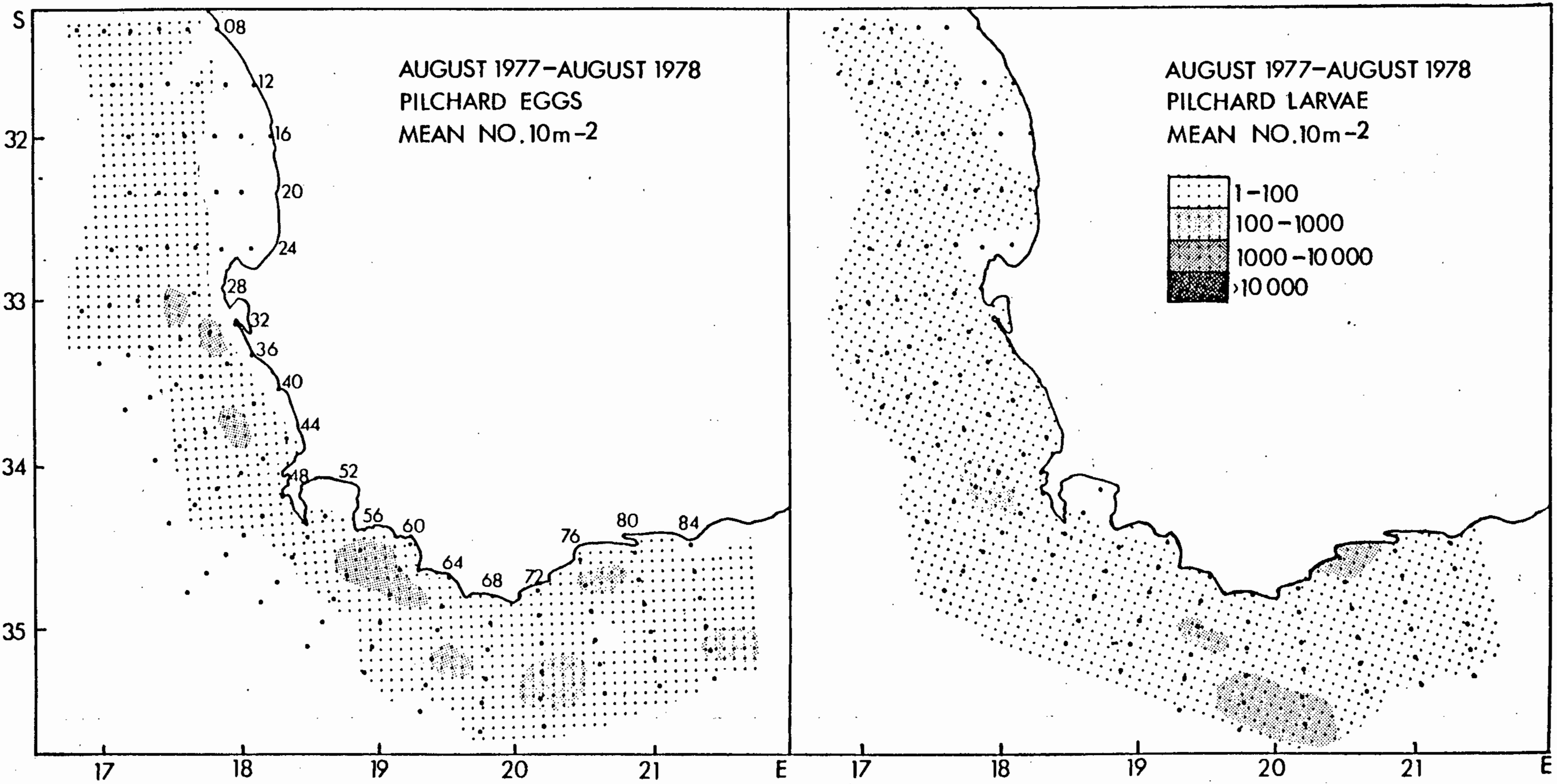


Fig. 4.22 Mean pattern of abundance of pilchard eggs and larvae over the CELP survey grid between August 1977 and August 1978.

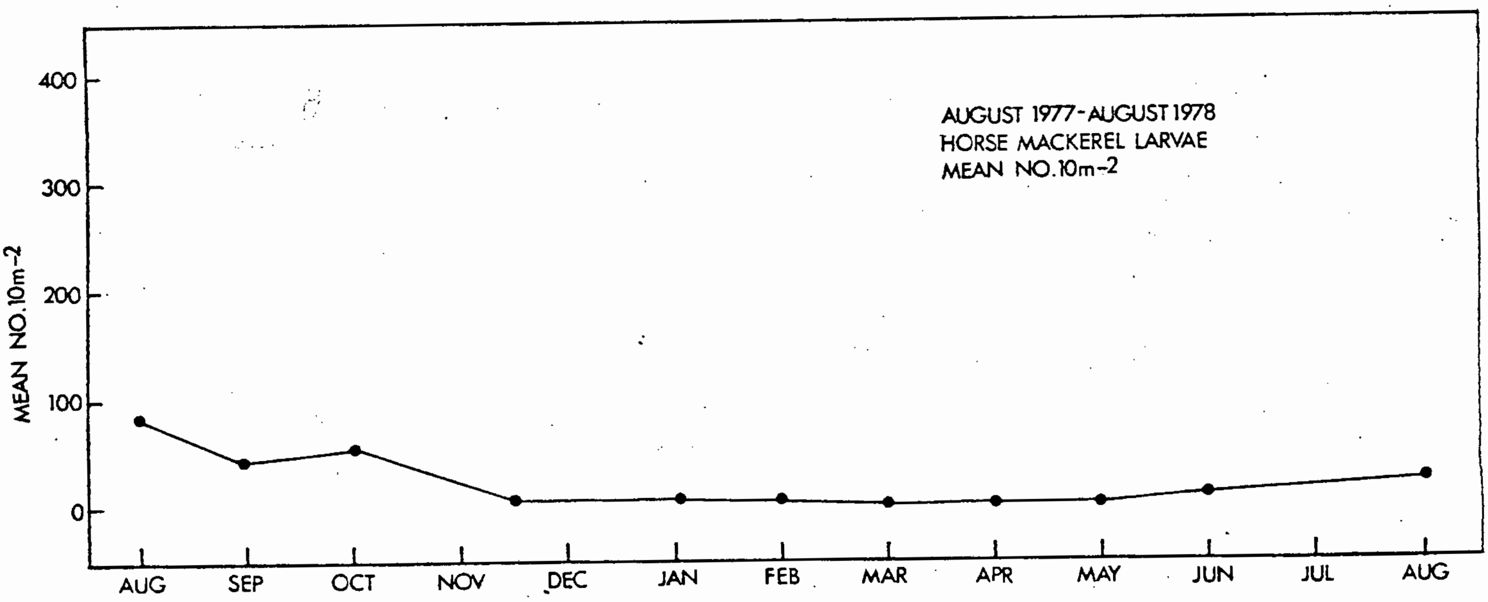


Fig. 4.23 Mean number of horse mackerel larvae per $10m^2$ over the CELP survey grid between August 1977 and August 1978.

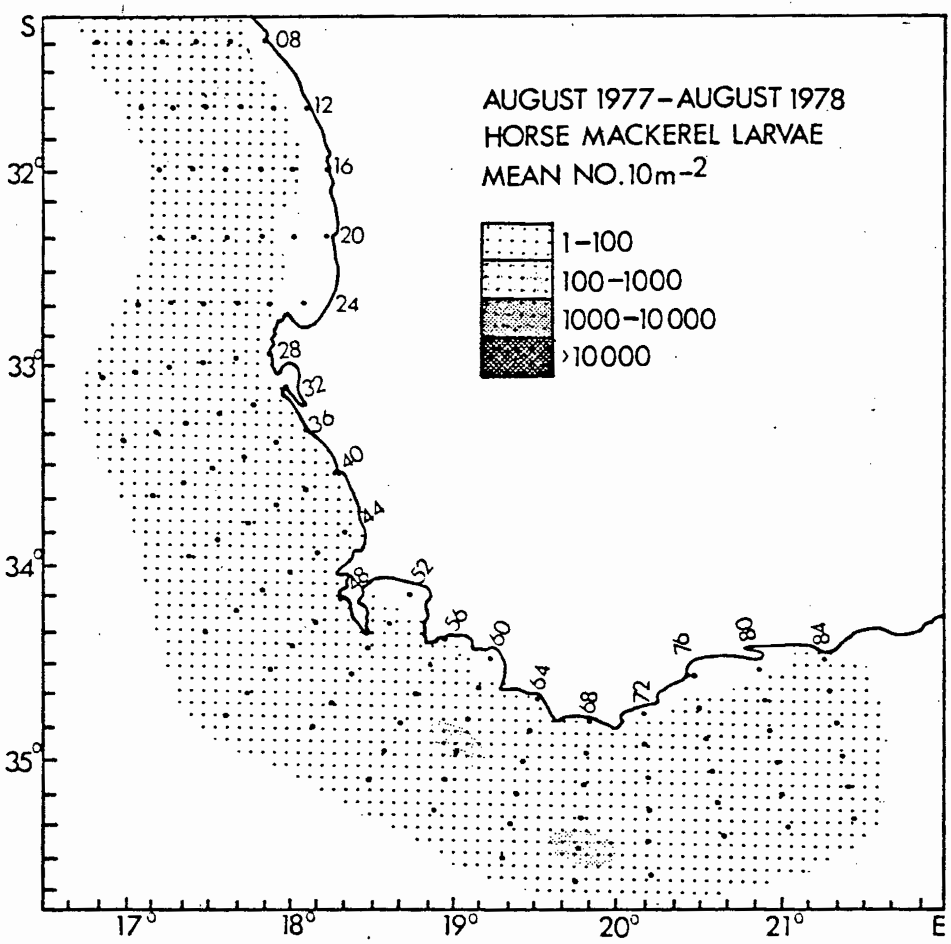


Fig. 4.24 Mean pattern of abundance of horse mackerel larvae over the CELP survey grid between August 1977 and August 1978.

August and September 1977 and from May to August 1978 (winter), although they were present in all months (Fig. 4.25). In July 1978, when only the west coast stations were sampled, the mean abundance of hake larvae was comparable to June 1978. Hake larvae were found over the whole survey grid except for inshore stations to the north of Cape Columbine, in Table Bay (line 44), False Bay (line 52), and Walker Bay (line 60), and at inshore stations just east of Cape Agulhas (Fig. 4.26).

Snoek

Snoek <u>Thyrsites atun</u> larvae ranked ninth and comprised 0.7% of the identified larvae collected during CELP. The eggs were relatively easy to identify once the embryo formed the characteristic pigment pattern, but they were not consistently enumerated in the samples. Snoek larvae were most abundant in the survey grid in August and September 1977, June and August 1978 (winter/spring, Fig. 4.27). Although only the western half of the survey grid was sampled in July 1978, a mean abundance of 13 larvae.$10m^{-2}$ was found. Snoek larvae were absent in January and February 1978 and were only present in small densities in November/December 1977, March, April and May 1978. Larvae were widespread over the survey grid (Fig. 4.28) but were rarely found at inshore stations and were scarce within 40km of the coast north of Cape Columbine and east of Cape Agulhas.

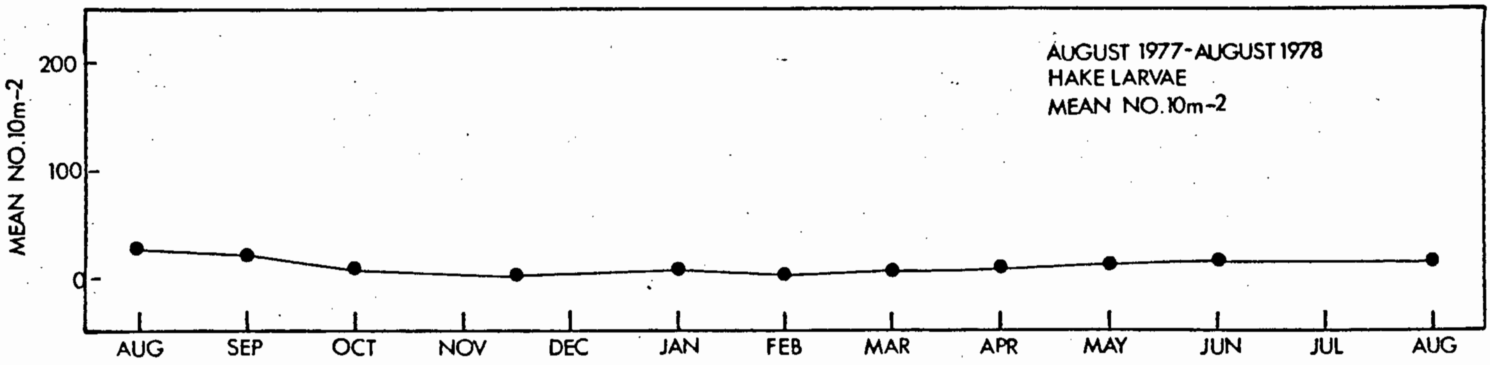


Fig. 4.25 Mean number of hake larvae per 10m^2 over the CELP survey grid between August 1977 and August 1978.

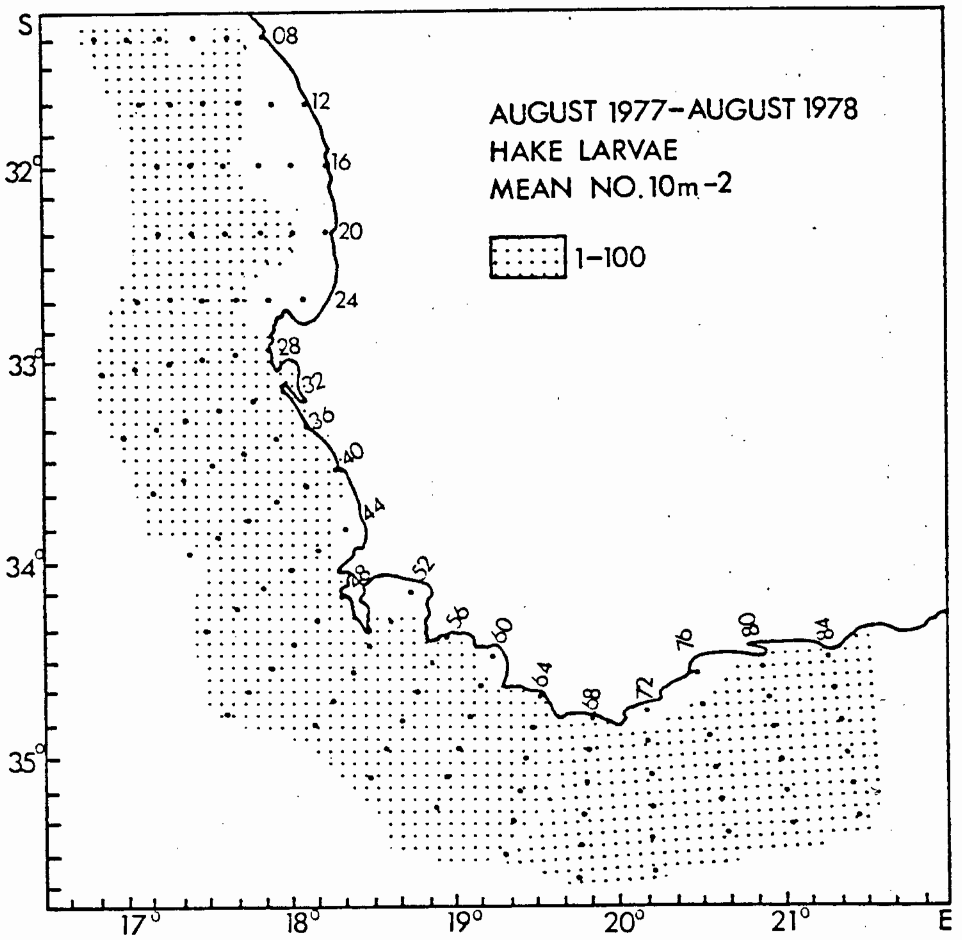


Fig. 4.26 Mean pattern of abundance of hake larvae over the CELP survey grid between August 1977 and August 1978.

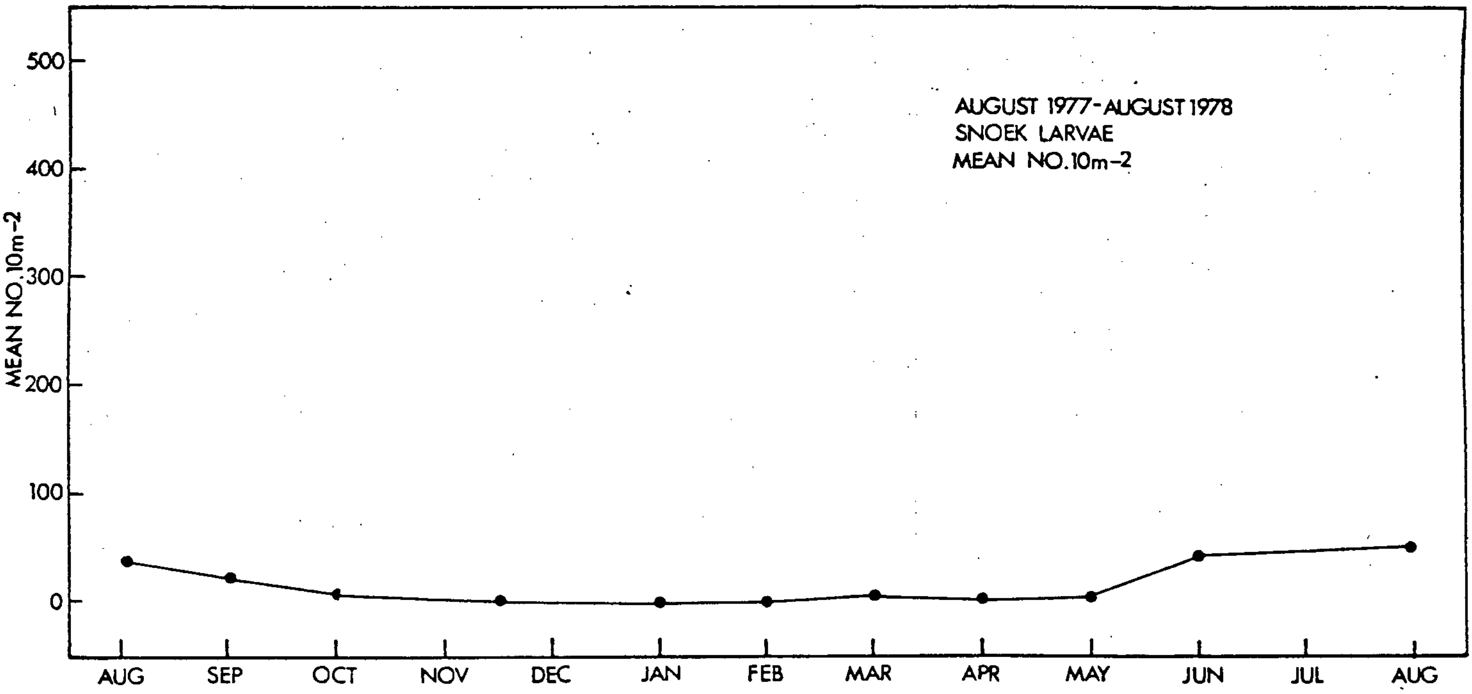


Fig. 4.27 Mean number of snoek larvae per $10m^2$ over the CELP grid between August 1977 and August 1978.

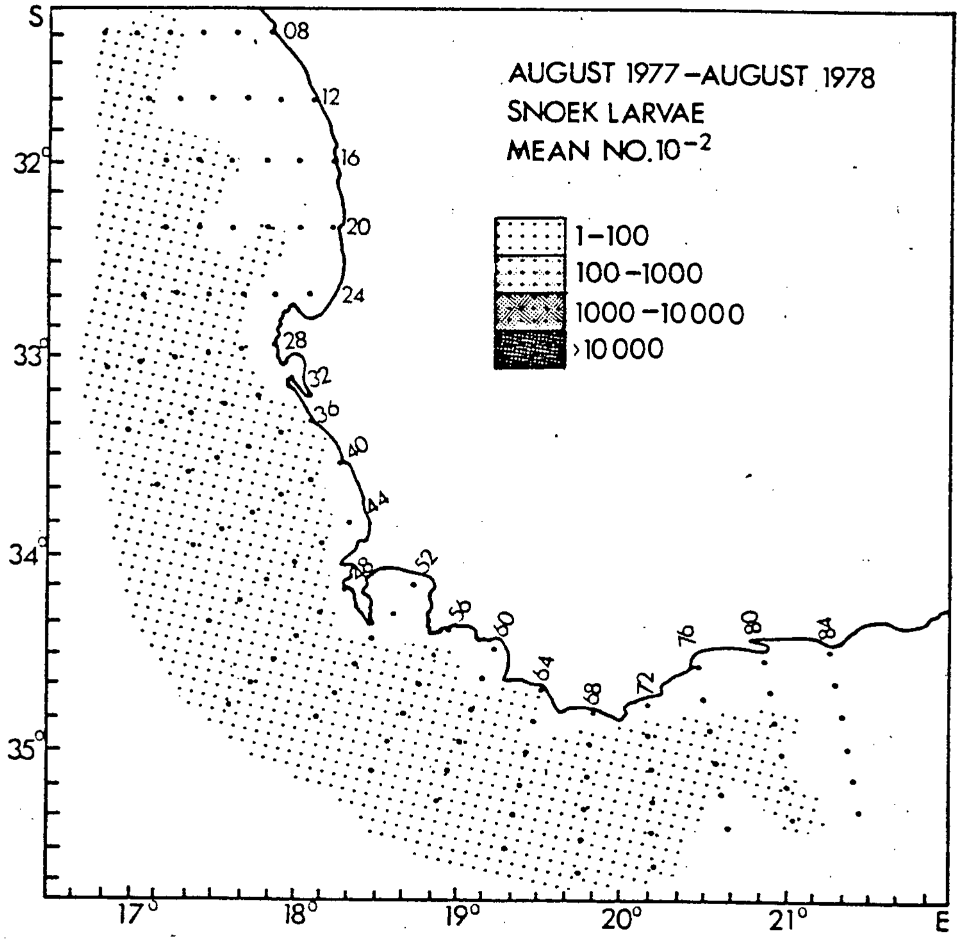


Fig. 4.28 The mean pattern of abundance of snoek larvae over the CELP survey grid between August 1977 and August 1978.

Quantification of pattern

In Table 4.3 statistics are given quantifying the monthly pattern of abundance of the nine most abundant taxa sampled over the CELP survey grid between August 1977 and August 1978. It was assumed on the basis of the large variance to mean ratios that all components of the ichthyoplankton in all months followed the negative bionomial distribution. The index of dispersion for individual components of the ichthyoplankton in each month differed significantly ($p<0.05$) from that which would be expected from a random distribution.

Table 4.3

Quantitative description of pattern in each month of the CELP survey for the 9 most abundant categories in the ichthyoplankton

Taxon	Month/year	Total	Pos	Mean	SD	V/M	Patch	Crowding	$\hat{k}$
Anchovy eggs	Aug 77	119	0						
	Sep 77	120	7	3.1	14.2	66.0	22.2	68.1	0.05
	Oct 77	115	27	930.0	6972.3	52269.9	57.2	53199.0	0.02
	Nov/Dec 77	119	57	539.8	1608.5	4792.5	9.9	5331.3	0.11
	Jan 78	110	38	714.0	3750.0	19694.0	28.6	20407.0	0.04
	Feb 78	119	35	439.2	1855.9	7841.6	18.9	8279.9	0.06
	Mar 78	120	19	43.0	248.7	1439.4	34.5	1481.3	0.03
	Apr 78	114	12	132.4	1247.6	11758.0	89.8	11889.5	0.01
	May 78	120	6	21.4	136.9	873.8	41.7	894.2	0.02
	Jun 78	120	5	4.1	34.0	284.1	70.8	287.2	0.01
	Jul 78	61	0						
	Aug 78	110	0						
Anchovy larvae	Aug 77	119	10	1.2	5.6	25.2	20.7	25.5	0.05
	Sep 77	120	14	1.1	4.2	15.2	13.4	15.3	0.07
	Oct 77	115	34	264.1	2154.6	17577.4	67.6	17840.5	0.02
	Nov/Dec 77	119	84	914.1	2172.3	5162.4	6.6	6075.5	0.18
	Jan 78	110	86	893.7	1793.1	3597.5	5.0	4490.2	0.25
	Feb 78	119	97	865.7	2837.8	9302.3	11.7	10167.0	0.09
	Mar 77	120	53	67.0	237.1	839.4	13.5	905.4	0.08
	Apr 78	114	53	40.3	179.6	800.5	20.9	839.8	0.05
	May 78	120	47	11.0	43.1	169.4	16.4	179.3	0.07
	Jun 78	120	12	0.7	2.7	9.8	13.3	9.6	0.07
	Jul 78	61	0						
	Aug 78	110	9	0.4	2.2	12.0	28.6	11.4	0.04

Table 4.3 (contd.)

Taxon	Month/year	Total	Pos	Mean	SD	V/M	Patch	Crowding	$\hat{K}$
Lanternfish eggs	Aug 77	119	4	78.2	656.7	5513.8	71.5	5591.0	0.01
	Sep 77	120	21	288.2	1274.0	5632.8	20.5	5920.0	0.05
	Oct 77	115	20	131.7	612.4	2847.1	22.6	2977.8	0.05
	Nov/Dec 77	119	11	10.7	75.1	526.0	50.0	535.7	0.02
	Jan 78	110	3	0.4	2.5	17.0	45.6	16.4	0.03
	Feb 78	119	1	<0.1	0.4	3.9	89.6	2.9	-
	Mar 78	120	8	0.4	2.3	12.3	28.0	11.7	0.03
	Apr 78	114	7	2.3	11.2	54.6	24.1	55.9	0.04
	May 78	120	19	1.8	7.1	27.9	15.7	28.7	0.07
	Jun 78	120	18	57.4	294.5	1509.7	27.3	1566.1	0.04
	Jul 78	61	23	187.4	640.9	2192.2	12.7	2378.6	0.09
	Aug 78	110	35	382.1	1419.9	5277.0	14.8	5658.1	0.07
Lanternfish larvae	Aug 77	119	89	1153.0	3139.3	8547.2	8.4	9699.2	0.13
	Sep 77	120	78	730.2	2278.0	7106.8	10.7	7836.0	0.10
	Oct 77	115	70	244.4	583.0	1390.6	6.7	1634.0	0.18
	Nov/Dec 77	119	31	11.4	29.9	78.7	7.8	89.0	0.15
	Jan 78	110	3	0.2	1.2	8.5	45.1	7.7	0.03
	Feb 77	119	7	1.2	6.8	38.8	32.9	39.0	0.03
	Mar 78	120	14	1.9	7.6	30.1	16.0	31.0	0.06
	Apr 78	114	12	1.6	6.0	22.2	14.1	22.8	0.07
	May 78	120	45	4.6	9.5	19.6	5.0	23.2	0.25
	Jun 78	120	51	19.2	63.4	209.9	11.9	228.0	0.09
	Jul 78	61	51	701.8	1397.2	2781.5	5.0	3482.3	0.28
	Aug 78	110	87	412.9	695.3	1171.0	3.8	1582.9	0.35
Roundherring eggs	Aug 77	119	89	761.8	1269.3	2114.9	3.8	2875.7	0.36
	Sep 77	120	78	729.0	1384.1	2627.9	4.6	3355.9	0.28
	Oct 77	115	78	651.9	1428.3	3129.3	5.8	3780.2	0.21
	Nov/Dec 77	119	75	287.8	792.4	2181.9	8.6	2468.7	0.13
	Jan 78	110	43	102.5	304.1	901.9	9.8	1003.5	0.11
	Feb 78	119	62	89.8	242.2	653.1	8.3	741.9	0.14
	Mar 78	120	49	73.0	239.5	786.0	11.8	857.9	0.09
	Apr 78	114	62	180.4	426.2	1007.0	6.6	1186.3	0.18
	May 78	120	76	256.1	542.9	1150.8	5.5	1406.0	0.22
	Jun 78	120	82	378.6	766.4	1551.4	5.1	1929.0	0.24
	Jul 78	61	36	422.6	836.7	1656.5	4.9	2078.1	0.26
	Aug 78	110	83	503.8	1100.0	2401.1	5.8	2903.8	0.21

Table 4.3 (contd.)

Taxon	Month/year	Total	Pos	Mean	SD	V/M	Patch	Crowding	$\hat{k}$
Roundherring larvae	Aug 77	119	102	124.5	204.5	335.7	3.7	459.2	0.37
	Sep 77	120	97	354.3	624.4	1100.6	4.1	1453.9	0.32
	Oct 77	115	90	393.8	871.1	1927.2	5.9	2320.0	0.28
	Nov/Dec 77	119	67	97.7	283.4	821.7	9.4	918.5	0.12
	Jan 78	110	70	13.1	32.5	80.6	7.1	92.7	0.16
	Feb 78	119	44	8.6	21.4	53.6	7.1	61.1	0.16
	Mar 78	120	36	21.8	98.1	441.9	21.2	462.7	0.05
	Apr 78	114	68	85.8	211.0	519.2	7.0	604.0	0.17
	May 78	120	100	146.2	260.3	463.2	4.2	608.4	0.32
	Jun 78	120	102	119.4	206.0	355.6	4.0	474.0	0.34
	Jul 78	61	50	110.1	221.5	445.6	5.0	554.7	0.25
	Aug 78	110	93	130.4	210.9	341.0	3.6	470.4	0.38
Lightfish eggs	Aug 77	119	65	716.0	1595.8	3556.4	6.0	4271.4	0.20
	Sep 77	120	61	692.5	1669.6	4025.2	6.8	4716.7	0.17
	Oct 77	115	63	1181.1	2488.5	5243.1	5.4	6423.3	0.23
	Nov/Dec 77	119	60	419.3	899.1	1927.9	5.6	2346.2	0.22
	Jan 78	110	48	416.3	1173.0	3305.1	8.9	3720.4	0.13
	Feb 78	119	39	69.9	256.3	939.5	14.4	1008.5	0.07
	Mar 78	120	38	40.2	139.5	484.0	13.0	523.2	0.08
	Apr 78	114	37	97.6	258.6	685.4	8.0	781.9	0.14
	May 78	120	43	106.9	384.1	1380.1	13.9	1486.0	0.08
	Jun 78	120	51	335.9	1167.0	4054.9	13.1	4389.7	0.08
	Jul 78	61	40	590.5	1373.1	3192.8	6.4	3782.3	0.18
	Aug 78	110	65	985.5	2104.5	4494.0	5.6	5478.5	0.22
Lightfish larvae	Aug 77	119	58	25.6	52.6	108.1	5.2	132.7	0.24
	Sep 77	120	71	108.4	260.8	627.6	6.8	734.9	0.17
	Oct 77	115	69	169.2	366.5	793.6	5.7	961.8	0.21
	Nov/Dec 77	119	70	92.3	186.1	375.2	5.1	466.5	0.25
	Jan 78	110	49	80.0	237.4	704.9	9.8	783.9	0.11
	Feb 78	119	48	38.6	137.8	492.5	13.7	530.0	0.08
	Mar 78	120	45	22.5	64.1	182.5	9.1	204.0	0.12
	Apr 78	114	53	33.3	66.7	133.8	5.0	166.1	0.25
	May 78	120	56	39.0	81.3	169.5	5.3	207.5	0.23
	Jun 78	120	67	27.7	62.5	141.2	6.1	167.9	0.20
	Jul 78	61	33	145.0	825.2	4697.2	33.4	4841.2	0.03
	Aug 78	110	73	75.0	187.6	469.1	7.2	543.1	0.16

Table 4.3 (contd.)

Taxon	Month/year	Total	Pos	Mean	SD	V/M	Patch	Crowding	$\hat{k}$
Dragonet larvae	Aug 77	119	76	51.5	103.0	205.7	5.0	256.3	0.25
	Sep 77	120	73	49.4	99.8	205.7	5.0	249.8	0.25
	Oct 77	115	70	72.4	131.5	238.7	4.3	310.1	0.30
	Nov/Dec 77	119	82	72.5	189.6	495.8	7.8	567.3	0.15
	Jan 78	110	72	51.7	118.2	269.9	6.2	320.6	0.19
	Feb 78	119	81	25.7	55.7	120.7	5.7	145.4	0.21
	Mar 78	120	52	24.7	82.2	273.7	12.0	297.4	0.09
	Apr 78	114	78	38.2	143.6	539.2	15.1	576.5	0.07
	May 78	120	86	66.9	104.1	162.0	3.4	227.8	0.42
	Jun 78	120	101	125.4	183.6	268.8	3.1	393.2	0.47
	Jul 78	61	51	178.2	289.5	470.3	3.6	647.4	0.38
	Aug 78	110	86	144.1	241.5	404.9	3.8	548.0	0.36
Pilchard eggs	Aug 77	119	26	36.1	129.2	462.2	13.8	497.3	0.08
	Sep 77	120	16	7.6	35.0	160.0	21.8	166.6	0.05
	Oct 77	115	32	89.6	394.0	1731.3	20.3	1819.1	0.05
	Nov/Dec 77	119	40	61.2	244.3	975.1	16.9	1035.3	0.06
	Jan 78	110	23	57.3	404.2	2849.8	50.7	2906.1	0.02
	Feb 78	119	20	33.8	222.2	1459.1	44.1	1492.0	0.02
	Mar 78	120	12	4.0	32.9	271.0	68.6	274.0	0.01
	Apr 78	114	12	4.4	20.3	93.0	21.8	96.4	0.05
	May 78	120	15	15.6	81.8	429.6	28.6	444.2	0.04
	Jun 78	120	20	6.1	29.2	139.3	23.6	144.4	0.04
	Jul 78	61	14	62.0	401.8	2605.4	43.0	2666.4	0.02
	Aug 78	110	28	88.3	557.8	3523.4	40.9	3610.8	0.03
Pilchard larvae	Aug 77	119	52	26.3	104.7	416.4	16.8	441.7	0.06
	Sep 77	120	72	36.8	79.8	172.7	5.7	208.5	0.21
	Oct 77	115	47	46.4	219.1	1035.7	23.3	1081.1	0.04
	Nov/Dec 77	119	47	14.1	33.9	81.5	6.7	94.6	0.18
	Jan 78	110	38	47.1	264.9	1490.1	32.6	1536.2	0.03
	Feb 78	119	28	8.1	30.8	117.2	15.3	124.3	0.07
	Mar 78	120	11	1.5	6.8	31.9	22.2	32.4	0.05
	Apr 78	114	37	34.3	218.6	1394.4	41.7	1427.7	0.02
	May 78	120	48	8.3	29.8	107.6	13.9	114.9	0.08
	Jun 78	120	62	10.5	26.1	65.4	7.2	74.9	0.16
	Jul 78	61	24	34.2	88.1	226.9	7.6	260.1	0.15
	Aug 78	110	43	6.6	15.7	37.8	6.6	43.4	0.18

Table 4.3 (contd.)

Taxon	Month/year	Total	Pos	Mean	SD	V/M	Patch	Crowding	$\hat{k}$
Horsemackerel larvae	Aug 77	119	87	84.3	174.5	360.8	5.3	444.2	0.23
	Sep 77	120	73	49.3	84.2	143.5	3.9	191.8	0.35
	Oct 77	115	51	52.7	116.2	256.0	5.8	307.8	0.21
	Nov/Dec 77	119	44	6.5	17.2	45.5	7.9	51.0	0.15
	Jan 78	110	29	3.3	9.7	28.9	9.5	31.1	0.12
	Feb 78	119	36	3.5	11.1	35.6	10.9	38.1	0.10
	Mar 78	120	4	0.2	1.5	9.6	37.2	8.9	0.02
	Apr 78	114	33	6.5	20.3	63.4	10.6	68.9	0.10
	May 78	120	34	5.4	19.5	70.6	13.9	75.0	0.08
	Jun 78	120	62	9.7	16.7	28.8	3.9	37.5	0.35
	Jul 78	61	13	24.4	128.9	679.2	28.7	702.6	0.04
	Aug 78	110	51	23.3	67.9	197.9	9.5	220.2	0.12
Hake larvae	Aug 77	119	79	26.1	38.1	55.8	3.1	80.9	0.48
	Sep 77	120	58	21.2	46.1	100.3	5.7	120.4	0.21
	Oct 77	115	51	9.8	16.9	29.2	3.9	38.0	0.35
	Nov/Dec 77	119	38	3.6	7.9	17.4	5.5	20.0	0.22
	Jan 78	110	38	6.5	18.7	54.2	9.2	59.6	0.12
	Feb 78	119	30	4.0	11.1	31.0	8.6	33.9	0.13
	Mar 78	120	30	7.0	21.1	64.7	10.1	70.7	0.11
	Apr 78	114	45	7.5	20.1	54.4	8.2	60.8	0.14
	May 78	120	51	12.4	36.4	106.6	9.5	118.1	0.12
	Jun 78	120	78	13.4	17.7	23.4	2.7	35.8	0.60
	Jul 78	61	30	14.3	29.6	61.2	5.2	74.5	0.24
	Aug 78	110	65	12.2	18.8	28.8	3.2	40.1	0.44
Snoek larvae	Aug 77	119	50	34.1	158.6	739.1	22.7	772.2	0.05
	Sep 77	120	45	22.0	59.0	158.2	8.1	179.2	0.14
	Oct 77	115	29	3.5	7.4	16.0	5.3	18.4	0.24
	Nov/Dec 77	119	8	0.7	2.8	11.8	16.7	11.5	0.07
	Jan 78	100	0						
	Feb 78	119	0						
	Mar 78	120	3	0.3	2.3	20.0	74.4	19.3	0.02
	Apr 78	114	1	<0.1	.5	5.1	92.5	4.1	-
	MAy 78	120	7	0.4	1.5	6.8	17.4	6.1	0.09
	Jun 78	120	50	4.9	9.2	17.2	4.3	21.1	0.38
	Jul 78	61	20	13.5	37.6	104.6	8.7	117.1	0.13
	Aug 78	110	45	5.8	10.7	19.7	4.3	24.5	0.31

A comparison of the pattern of abundance associated with egg and larval stage of the most abundant taxa is possible using the mean index of patchiness which is independent of abundance. Mean patchiness indices calculated from the data for individual months are shown in Table 4.4.

Table 4.4

Mean patchiness indices of the egg and larval stages of the most abundant taxa in the CELP survey ranked in order of increasing patchiness (see Table 4.3 for monthly values).

Category	Mean	SD	n
Hake larvae	6.25	2.74	12
Dragonet larvae	6.26	3.72	12
Roundherring eggs	6.72	2.40	12
Roundherring larvae	6.86	4.87	12
Lightfish eggs	8.93	3.61	12
Lightfish larvae	9.37	8.00	12
Horse mackerel larvae	12.26	10.31	12
Lanternfish larvae	13.95	12.54	12
Pilchard larvae	16.63	11.51	12
Anchovy larvae	19.79	17.18	11
Snoek larvae	25.44	31.50	10
Pilchard eggs	32.84	16.55	12
Lanternfish eggs	35.19	24.32	12
Anchovy eggs	41.49	26.32	9

Anchovy eggs and lanternfish eggs were the most patchy and were about a factor of 2 more patchy than their larval stages. Pilchard eggs were also more patchy than the larval stage whereas lightfish and lanternfish larvae were more patchy than their egg stages. Dragonet and hake larvae were the least patchily distributed.

Analysis of variance was used to test the null hypothesis that the sample means of patchiness for the various categories were not significantly different. The null hypothesis was rejected ($F=5.25$, d.f.=13.148, 2-tailed $p<0.001$). Since a significant F value resulted from the analysis of variance, the Newman-Keuls multiple range test was applied to examine differences between all possible pairs of means (Zar 1974). The results showed that anchovy eggs were significantly more patchy than any other category ($p<0.05$) including anchovy larvae. In addition pilchard eggs and lanternfish eggs were significantly more patchy than a number of other categories of the ichthyoplankton.

Table 4.5

The mean patchiness indices ($\overset{*}{m}/m$) for the egg and larvae of species ranked in Table 4.4 are compared using the Newman-Keuls multiple range test. Significant differences are indicated by * for $p<0.05$ and ** for $p<0.01$.

Category	1	2	3	4	5	6	7	8	9	10	12	13	14
1 Hake larvae													
2 Dragonet larvae													
3 Roundherring eggs													
4 Roundherring larvae													
5 Lightfish eggs													
6 Lightfish larvae													
7 Horsemackerel larvae													
8 Lanternfish larvae													
9 Pilchard larvae													
10 Anchovy larvae													
11 Snoek larvae													
12 Pilchard eggs	*	*	*	*	*	*							
13 Lanternfish eggs	**	**	**	**	*	*							
14 Anchovy eggs	**	**	**	**	**	**	*	*	*	*	*	*	

Least squares regressions of the index of mean crowding ($\overset{*}{m}$) against mean density (m) for the monthly measurements during CELP are plotted in Fig. 4.29. Iwao (1977, in Hewitt 1982) designated the slope as the density contagious coefficient such that when the slope equals 1 the distribution is random, >1 when the distribution is contagious and <1 when the distribution is regular. The slope of all 14 categories of fish eggs and larvae under consideration was found to be >1. The anchovy and pilchard egg regressions gave the steepest slopes whereas the slopes for the larval stages of these two species were less steep. Conversely, the regression for the larval stage of the lightfish had a steeper slope than that for the egg stage. Roundherring eggs and larvae and hake and dragonet larvae had the least contagious distribution as indicated by the slopes of the regression lines for these components of the ichthyoplankton. In general,

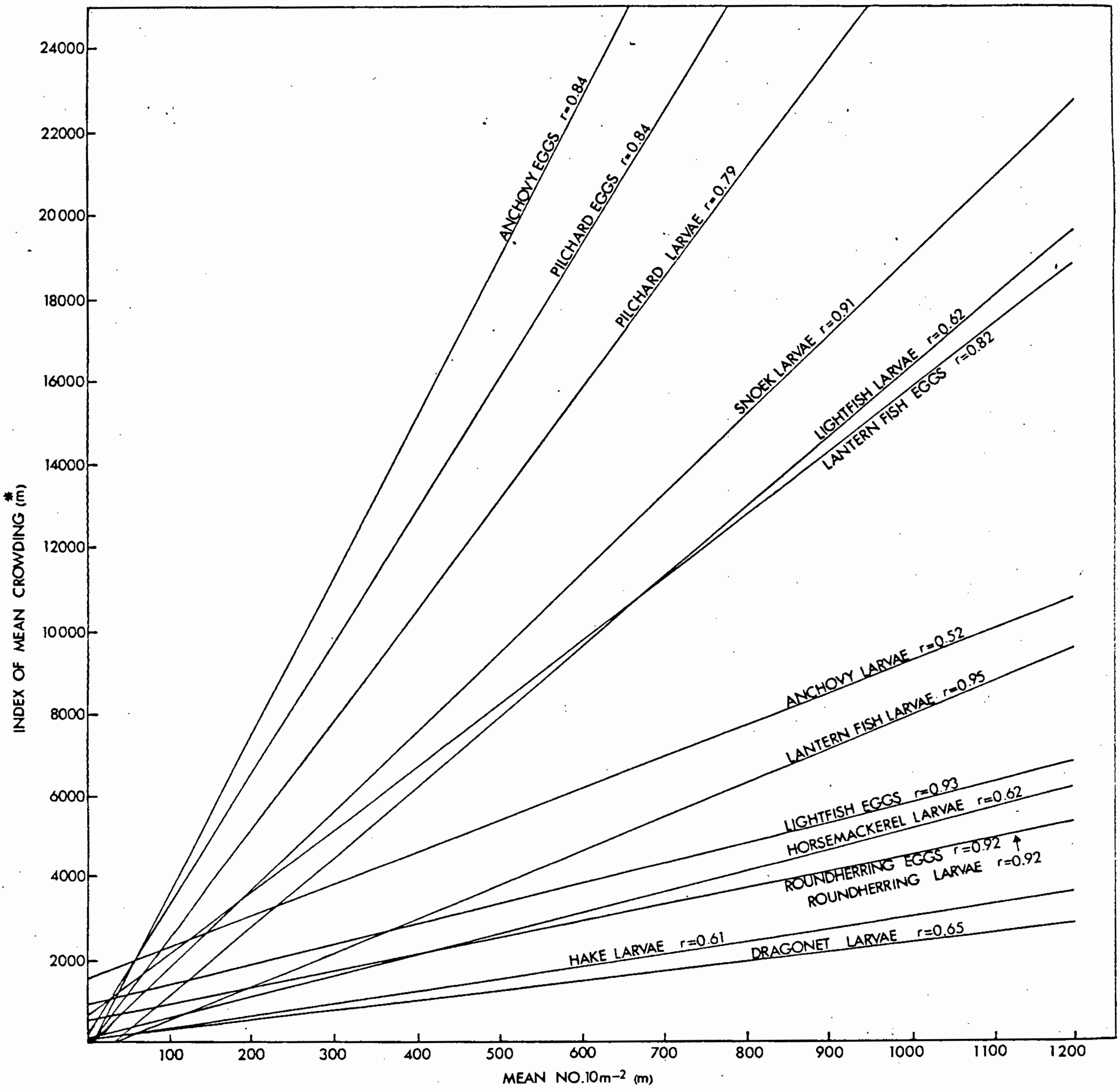


Fig. 4.29 Least squares regressions of the index of mean crowding ($\overset{*}{m}$) against mean density (m). Regression lines are extrapolated considerably beyond the range of data in most instances for clarity. The regression lines for roundherring eggs and larvae have approximately the same slope and intercept.

the order of the categories with regard to decreasing slope is similar to the order with regard to decreasing patchiness in Table 4.4.

Classification of samples

In Fig. 4.30 simplified dendrograms indicating station affinities are shown, based on the root-root transformed abundance of the eggs and/or larvae of 60 species for 120 stations, for the selected months of August 1977, October 1977, January 1978 and May 1978 representing the four seasons. The positions of stations belonging to the groups are plotted on the survey grid in Fig. 4.31. Five groups of stations with fairly consistent species composition and geographic location could be identified. Group A extended from the western portion of the Agulhas Bank up the west coast at an intermediate distance from the shore along the grid lines. Common members of this group were the eggs and larvae of the round herring Etrumeus whiteheadi, dragonet Paracallionymus costatus eggs and larvae, lightfish Maurolicus muelleri eggs and larvae, lanternfish Lampanyctodes hectoris eggs and larvae, hake Merluccius spp. larvae, and in August and October 1977, Helecolenus dactylopterus larvae. Group B occurred over the Agulhas Bank and in October 1977 and May 1978 extended inshore of Group A up the west coast. Common members of this group included pilchard Sardinops ocellata eggs and larvae, anchovy Engraulis capensis eggs and larvae, horse mackerel Trachurus trachurus larvae, and in August and October 1977, the larvae of the gurnard, Trigla capensis. Groups C occurred over the eastern portion of the grid. Common members of this group were pilchard and anchovy eggs and larvae, and the larvae of the flatfish Trulla capensis. Group D could not be recognized from the data collected in August 1977. In the other months stations clustered in this group occurred inshore of stations in the A and B groups to the north of Cape Town, particularly in association with the areas off the Cape Peninsula and Cape

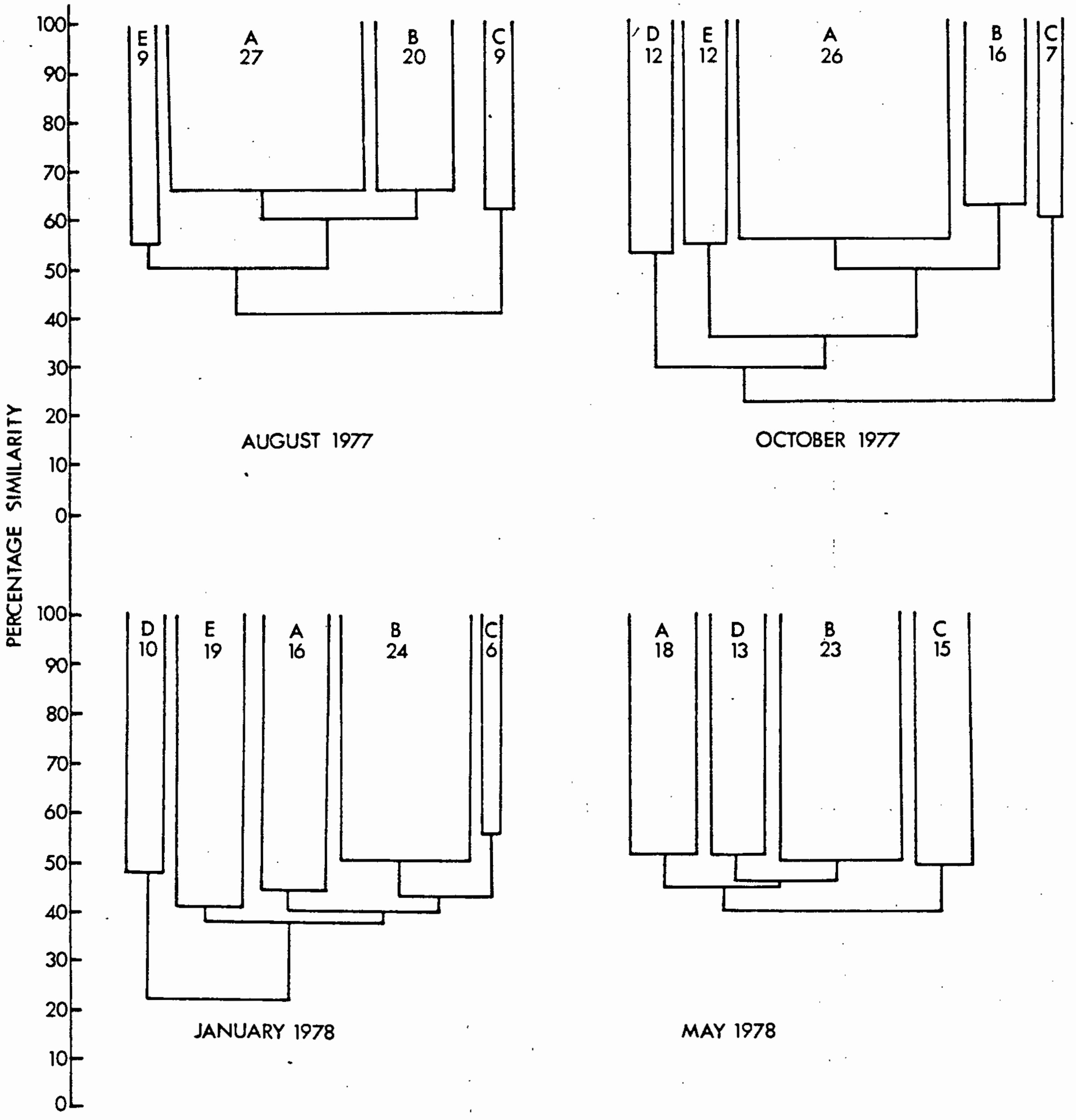


Fig. 4.30 Classification of stations using the Bray Curtis measure of similarity. Assemblages that appear to be similar in the 4 months are identified as A - E, with the values below indicating the number of stations within each assemblage.

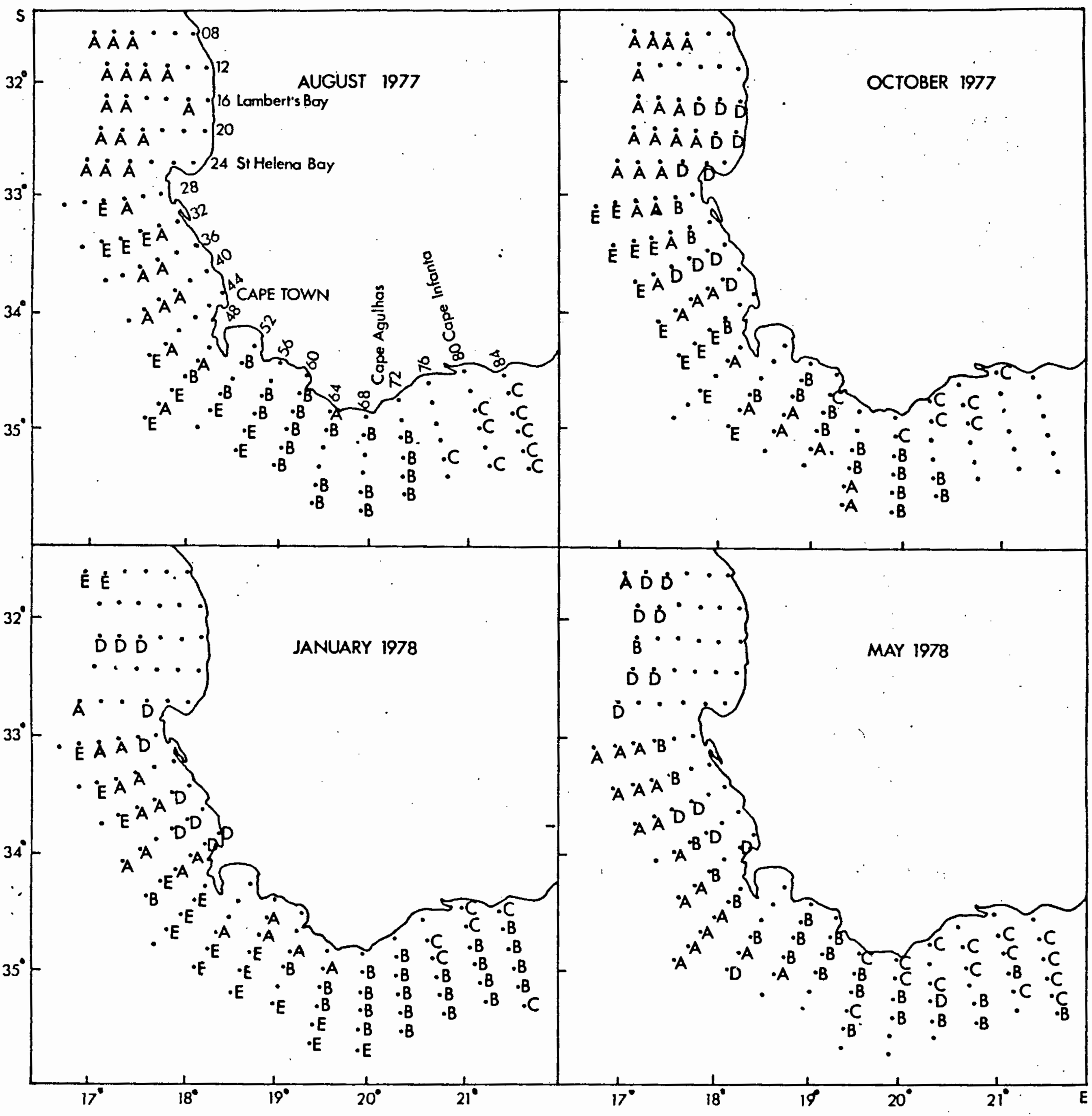


Fig. 4.31 Geographical location of each station belonging to assemblages A - E shown in Fig. 4.30.

Columbine. Common members of Group D included the larvae of Sebastes capensis in October 1977 and January 1978, lightfish eggs and larvae and dragonet eggs and larvae. Stations belonging to group E occurred in the offshore part of the grid between Cape Columbine and Cape Agulhas, offshore of stations belonging to group A. However, in 1978 group A extended to the offshore limit of the grid between Cape Columbine and Cape Point. Common members of Group E included roundherring and lightfish larvae, lanternfish eggs and larvae, saury Scomberesox saurus eggs and larvae, and the larvae of Hygophum ?brunni, Symbolophorus ?boops and Vinciguerria sp.

Although station groups A-E formed distinct clusters in the dendrograms, there was considerable overlap in terms of species composition, as indicated by the similarity levels linking the designated groups (Fig. 4.30). In August and October 1977 groups A and B were linked the most closely, at similarity levels of about 60% and 50% respectively. In January 1978 groups B and C had a number of species in common whereas in May groups D and B had the highest similarity. In all these instances groups with the highest degree of similarity were located close together on the survey grid.

Classification of species

The species associations defined by inverse analysis showed that above the arbitrary 30% similarity level, Trachurus larvae, Etrumeus eggs and/or larvae, and Merluccius larvae formed a group in August 1977, October 1977 and May 1978 (Fig. 4.32a-d). Additional members of this group included Paracallionymus larvae in October 1977 and Genypterus larvae in May 1978. Maurolicus eggs, Lampanyctodes, Helecolenus and Hygophum larvae formed a group in August 1977 and October 1977, with Symbolphorus larvae an additional member of this group in October 1977. Maourolicus larvae were associated with Paracallionymus larvae in

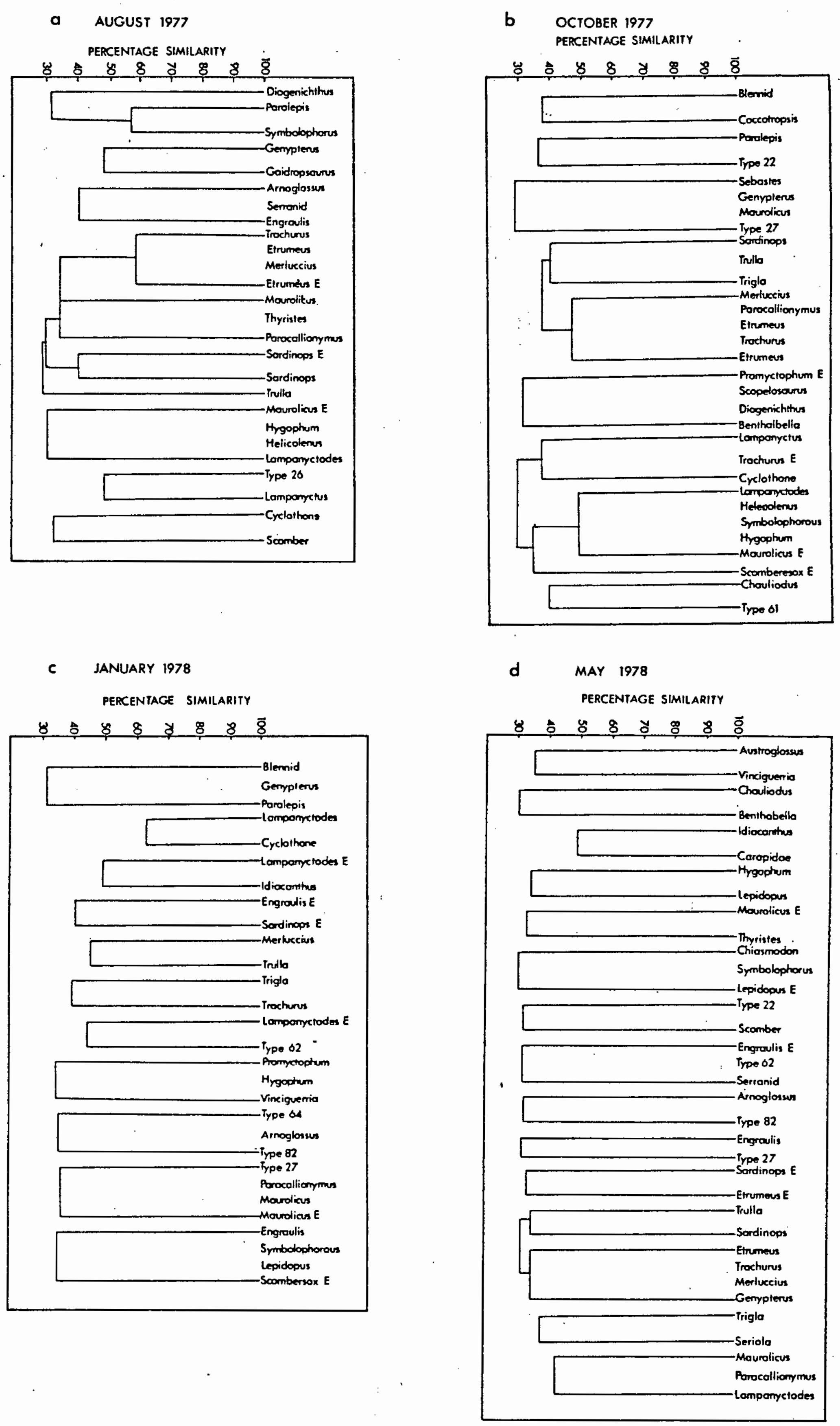


Fig. 4.32 Classification of species using the Bray Curtis measure of similarity for (a) August 1977, (b) October 1977, (c) January 1978, and (d) May 1978.

August 1977, January 1978 and May 1978. In May 1978 Lampanyctodes larvae were found in association with Maurolicus larvae and Paracallionymus larvae whereas in January 1978 Lampanyctodes larvae were associated with Cyclothone larvae at about the 65% confidence level. In January 1978 Engraulis eggs and Sardinops eggs were associated at about the 40% level, and in August 1978 Sardinops eggs and larvae were associated at about the same level of similarity. In October 1977 Sardinops larvae were associated with those of the sand sole Trulla and the gurnard Trigla and again in May 1978 Sardinops larvae were associated with Trulla larvae. There was apparently no repeated association between Engraulis larvae and the eggs and larvae of other species in the months selected for analysis above the 30% similarity level. However, in August 1977 Engraulis larvae were grouped with those of the Arnoglossus larvae and in October 1978 with Austroglossus larvae, both flatfish species, but at a low level of similarity. Larvae of deep water species formed groups including Protomyctophum, Scopelosaurus, Diogenichthus and Benthabella in October 1977, Protomyctophum, Hygophum and Vincinguerria in January 1978 and Diogenichthus, Paralepis and Symbolophorus in August 1977.

Species associations from larval data pooled for the four months representive of the seasons, are summarised by classification into a dendrogram in Fig. 4.33 and by ordination in Fig. 4.34. In the dendrogram Etrumeus, Trachurus, Merluccius and Cynoglossus formed a group and Maurolicus and Paracallionymus were associated. Engraulis, Sebastes and Thyrsites were not closely linked to other species. The results form the ordination were similar. Etrumeus, Trachurus, Merluccius and Paracallionymus formed a group of psuedo-demersal and neritic species, and was quite closely associated with the neritic/epipelagic Sardinops and and the neritic/demersal Cynoglossus. Helecolenus, Sebastes ,Thyrsites and Engraulis showed no association with each other or with other species.

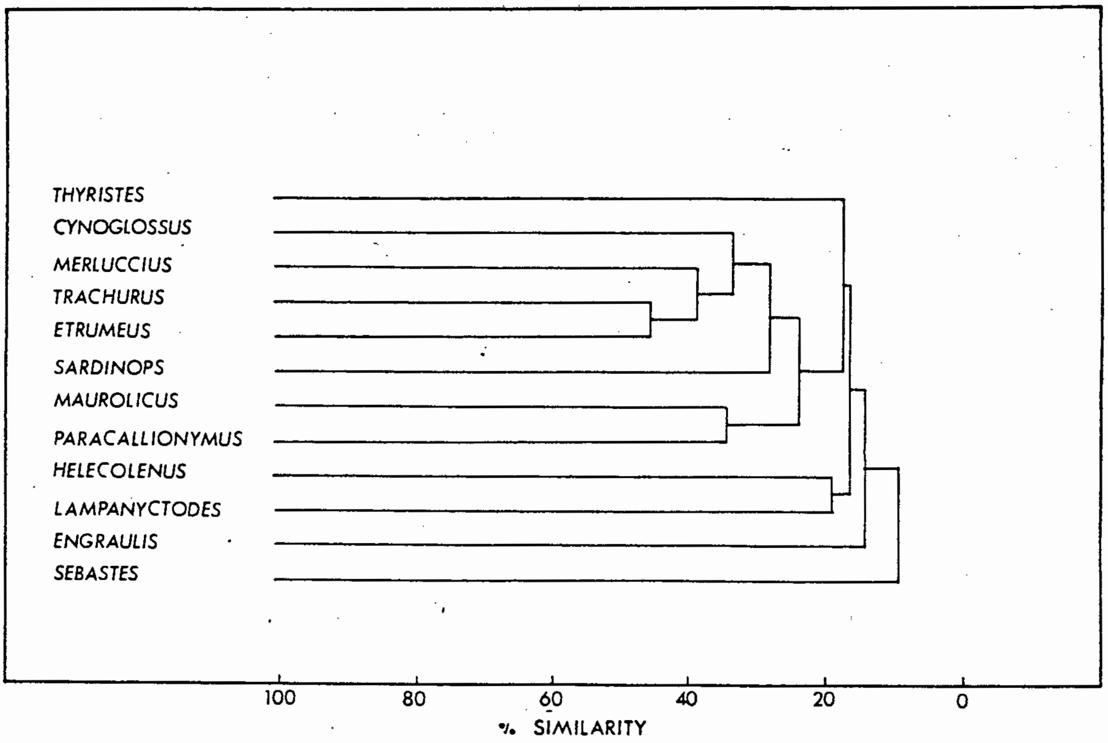


Fig. 4.33 Classification of the pooled selected larval species data for the month of August 1977, October 1977, January 1978 and May 1978, representing the seasons.

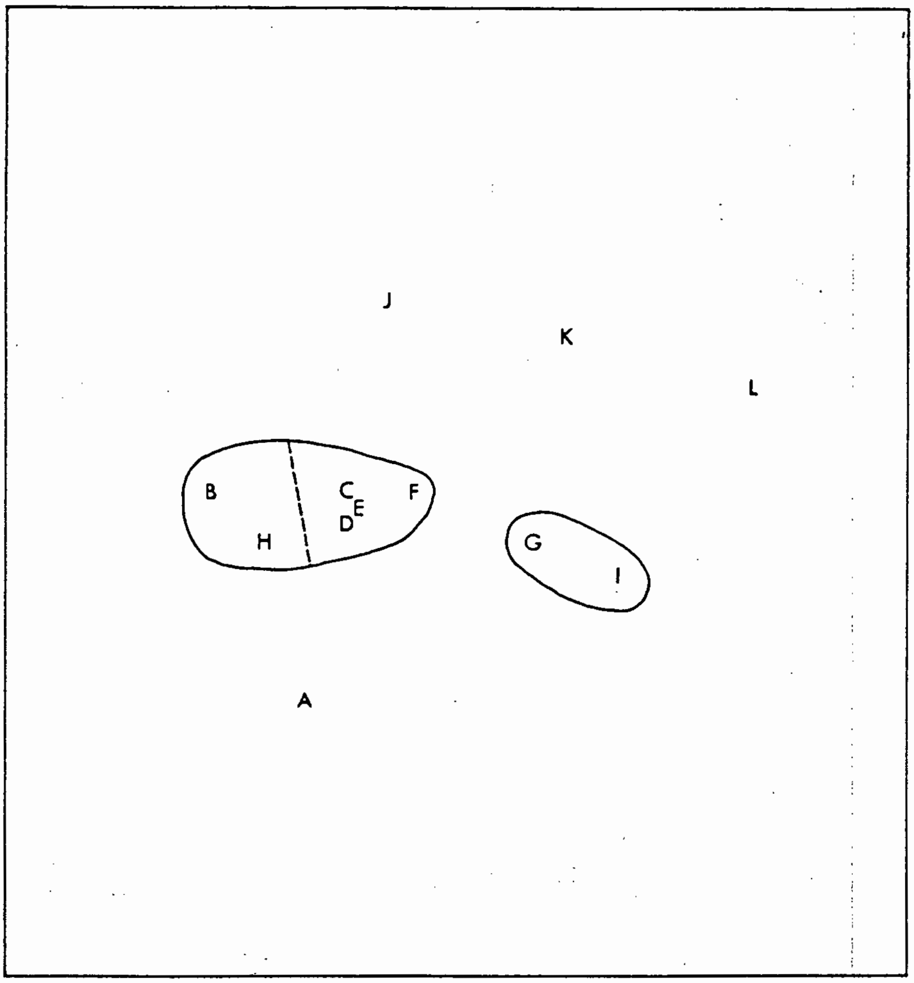


Fig. 4.34 Ordination of the pooled selected larval species data for the four months representing the seasons. A-Engraulis, B-Sardinops, C-Etrumeus, D-Trachurus, E-Merluccius, F-Paracallionymus, G-Maurolicus, H-Cynoglossus, I-Lampanyctodes, J-Helecolenus, K-Sebastes and L-Thyrsites. The groupings are discussed in the text.

Maurolicus and Lampanyctodes, both midwater/shelf slope species formed a group.

Two factor analysis of variance without replication was used to compare the monthly abundance patterns of anchovy, pilchard, lanternfish, hake and dragonet larvae. There was no significant difference, either between months or species. A similar test on the egg data, excluding hake and dragonet for which reliable counts of egg abundance were not obtained, gave a significant difference between species ($F=3.76$, d.f.= 3/33. 2-tailed $p<0.05$), but differences between individual species or months were shown to be not significant at the $p<0.05$ level using the Schéffe's multiple comparison test.

4.4 Discussion

Fish egg and early larval stages are temporary members of the plankton (meroplankton), and their temporal and spatial pattern of abundance is largely determined by the spawning strategy of the nektonic adults. In most instances the distribution of the eggs and early larvals stages were not uniform, suggesting that adults are selecting specific space and time windows for spawning in order to maximize surivival through to recruitment into the spawner population, and are therefore adapted, through natural selection, to the determinism perceived in the environment. If persistent anomalies in the environment occur, there will be a mismatch between the favourable environmental window and the ichthyoplankton pattern, which may result in large and abrupt changes in year class strength. Similarities and differences in the abundance pattern in the early stages of different species, and comparison of these patterns with those found in other similar systems, may lead to an understanding of which deterministic components of the environment species are adapted to.

Species dominance in comparison with the northern Benguela Current and the California Current

Bakun and Parrish (1980) pointed out a number of similarities between the four major eastern boundary current regions, including the neritic fish communities, and suggested that processes occurring in these systems may be direct analogs. The ichthyoplankton in the California Current is probably better studied than elsewhere. A comparison of the dominant species in the ichthyoplankton in the southern Benguela region in 1977/78 and in the California Current surveyed by the CalCOFI grid in 1975 (Loeb et al. 1983b), which, together with the data for the northern Benguela Current, shows a number of differences (Table 4.7), which may point to dissimilarities in processes occurring in the three systems. The data for the northern Benguela region is the mean from the data reproted in O'Toole (1977), and shows that even within the Benguela Current there are important regional differences in the ichthyoplankton.

Table 4.7

A comparison of species dominance in the southern Benguela region, the northern Benguela region and the California Current.

Taxon	Southern Benguela 1977/78		Northern Benguela 1972/74		California Current 1975	
	Rank	%	Rank	%	Rank	%
Anchovy	1	29.3	3	8.8	1	58.9
Pilchard (sardine)	6	3.7	2	10.4	26	0.1
Roundherring	3	14.0	-	+	12	<0.1
Hake	8	1.3	6	2.1	2	14.5
Horse mackerel	7	2.5	5	3.9	7	2.0
Lightfish	5	7.6	7	1.4	-	-
Dragonet	4	7.8	-	-	-	-
Snoek	9	0.7	-	+	-	-
Lanternfish	2	28.6	4	6.3	-	-
Scomber	27	<0.1	-	-	11	<0.1
Sebastes	14	0.4	-	-	3	3.1
Triphoturus	-	-	-	-	4	2.8
Citharichthys	-	-	-	-	5	2.8
Vinciguerria	28	0.4	-	-	6	2.2
Leuroglossus	-	-	-	-	8	1.5
Stenobrachius	-	-	-	-	9	1.4
Bathylagus	-	-	-	-	11	0.4
Sufflogobius	-	-	1	62.8	-	-
Dicologlossus	-	-	8	1.2	-	-
Austroglossus	-	-	9	0.8	-	-

Although anchovy larvae were dominant in the ichthyoplankton in both the southern Benguela region and in the California Current, hake comprised a much larger percentage of the CalCOFI ichthyoplankton samples. Roundherring were more abundant in the southern Benguela region and lightfish, dragonet and snoek were not represented in the California Current. Pilchard larvae were much less dominant in the California Current whereas *Sebastes*, *Trichopturus*, Citharichthys, Vinciguerria, Leuroglossus and Stenobrachius were either only found in the California Current or constituted a more important fraction of the ichthyoplankton than in the southern Benguela region. The dominance amongst Myctophids by Lampanyctodes hectoris in the southern Benguela region contrasts with a more equal contribution by a number of Myctophid species in the California Current. In the California Current anchovy and hake together comprise 73% of the ichthyoplankton with a large number of other species contributing small percentages. In contrast, in the southern Benguela region three species: anchovy, lanternfish and roundherring contribute 71% of the ichthyoplankton, and the dragonet and lightfish together contributed a further 15% indicating a greater degree of co-dominance. In the northern Benguela region the ichthyoplankton was dominated by the goby Sufflogobius bibarbatus, with anchovy, lanternfish, pilchard and horse mackerel larvae also making significant contributions. In comparison with the southern Benguela region, lightfish and roundherring were apparently less abundant and the dragonet absent.

Changes in species dominance

The ichthyoplankton in the survey grid in 1977/78 was dominated by nine taxa. Loeb (unpublished MS) selected the months of November to March (late spring to early autumn) to examine the ichthyoplankton dominance in the southern Benguela region in 1954/55, 1962/63, 1965/64, 1966/67 and 1977/78. With the exception of snoek and lanternfish, the dominant species in the region have remained similar, although the rank order has varied (Table 4.6). Loeb (unpublished MS) found few snoek and lanternfish larvae in the samples and grouped the latter with other Myctophids. Anchovy larvae were dominant in the samples in each year, including the early years before the collapse of the pilchard resource which occurred in the early 1960's (Crawford et al. 1983). The largest contribution by anchovy larvae was in 1977/78. Pilchard larvae were at least a factor of 5 less abundant than anchovy larvae in the samples from selected months and years. In part this may be due to the slight mismatch between pilchard spawning and the months selected by Loeb (November-March, upublished MS) for comparison. Pilchard eggs were common in the plankton from September to February (Crawford et al. 1980).

Table 4.6

Changes in the percentage contribution by taxa to the larval component of the ichthyoplankton present in the spring/summer months of November to March in the southern Benguela, between selected years (from Loeb, unpublished MS).

Taxon	1954/55	1962/63	1964/65	1966/67	1977/78
Engraulis (anchovy)	66.2	42.3	52.0	44.5	71.4
Sardinops (pilchard)	4.5	8.1	2.0	7.3	1.9
Etrumeus (roundherring)	3.3	3.9	2.0	3.4	3.9
Merluccius (hake)	0.9	3.8	1.6	1.6	0.6
Trachurus (horse mackerel)	1.4	4.8	2.7	2.1	7.6
Maurolicus (lightfish)	1.8	7.0	9.6	4.6	6.2
Paracallionymus (dragonet)	6.8	12.6	5.1	14.1	4.6
Flatfish	1.1	2.2	1.6	1.7	0.6
Scorpaenids	2.1	1.2	1.1	0.6	0.4
Myctophids	2.9	3.8	5.9	5.1	0.8
Unid. Clupeoids	4.7	3.7	6.1	6.9	-
Others	4.5	6.5	10.3	8.2	1.9

Roundherring larvae comprised a similar percentage of the ichthyoplankton in all years but lightfish larvae were more abundant after 1954/55. Dragonet larvae constituted a siginificant percentage of the ichthyoplankton and ranked second, after anchovy, in 1954/55, 1962/63 and 1966/67 but only fourth in the November-March period in 1977-78. Horse mackerel larvae ranked second in 1977/78 and comprised 7.6% of the November-March ichthyoplankton whereas the percentage contribution in earlier years was much less. This is inconsistent with recruitment trends estimated by Virtual Population Analysis which suggest that since 1970 recruitment has never exceeded 10% of the 1947 maximum (Crawford et al. 1983), and may be a result of the use of a bridle in front of the net in the tows made before 1977, which could have caused increased avoidance of the more mobile larval forms such as Trachurus (V. Loeb, in litt.). The reduced contribution by hake to the ichthyoplankton in 1977/78 is consistent with the decrease in spawner biomass over the early 1970's (Payne et al. 1984). The small percentage contribution by hake larvae in 1954/55 may be partially attributed to the fact that the survey grid was limited to a small part of the west coast prior to 1961. The contribution by lightfish was smaller in 1954/55 than in any of the other years selected for comparison, but, as with the hake, this may also be partly a result of the configuration of the survey grid in the 1950's.

In general, the species composition in the plankton samples from the southern Benguela region over late spring to early autumn period has remained fairly constant, despite apparent large decreases in the spawner populations of a number of commerically exploited species (Crawford et al. 1983), changes in the sampling grid and the switch to the Bongo sampler for CELP in 1977.

Seasonality in spawning

The seasonality in the abundance and diversity of larvae (Figs. 4.1 and 4.3) shows that the late summer, autumn and early winter period (February to July) is generally less favoured by spawners than the late winter, spring and early summer months (August to January). Both abundance and diversity of larvae were at a minimum in March whereas maximum larval abundance was reached in August 1977 and maximum diversity in October. Loeb et al. (1983a) and O'Toole (1977) found similar large seasonal abundance fluctuations in larvae in the Californian Current system and the northern Benguela region. The observation that diversity and abundance are significantly correlated suggests that the favourable period for spawning is shared by a number of species within the system, rather than dominated by only one or two species.

Within this general pattern of abundance, spawning by individual species appears to occur either in (i) spring-summer (September-February), such as in the anchovy (Fig. 4.6), and, to some extent the pilchard (Fig. 4.21), particularly before the collapse in the early 1960's (Crawford 1981); (ii) winter-spring (August-November), such as in the lanternfish (Fig. 4.13), roundherring (Fig. 4.15) and the lightfish (Fig. 4.19); or (iii) throughout the year, as in the hake (Fig. 4.25) and the dragonet (Fig. 4.17). These three temporal strategies correspond to epipelagic/neritic, midwater/shelf slope and psuedo-demersal/neritic (on the bottom over the shelf during the day but rising into midwater at night) modes of existence in the adults, and suggests that environmental conditions determining spawing adaptions are very different in these three habitats.

Spatial pattern

Two important aspects of spatial pattern in fish eggs and larvae are the geographical location of areas of abundance and the statistical description of the pattern within these areas. The fact that fairly consistent species-specific geographical locations of great abundance were found in the southern Benguela region indicates that the spawning location has been selected with respect to deterministic features of the environment. With respect to the statistical description of pattern, social behaviour to reduce predation, enhance reproductive activities or increase the efficiency of movement and population regulation is often considered to be the cause of patchiness in animals (Hewitt 1981). In planktonic organisms capable of only limited movement and displaying little social behaviour, pattern is more likely to be due to adaptive spawing behaviour by the adults and the result of patterned cirulation such as eddies, fronts and thermoclines, or to be caused by differential mortality. Hewitt (1982) has suggested that the study of the statistical properties of spatial pattern may facilitate inferences regarding reproductive strategy. Both the geographic and statistical aspects of the spatial pattern of ichthyoplankton in the southern Benguela region and other areas are considered below.

In the California Current Loeb et al. (1983a) found that the maximum mean abundance of larvae occurred inshore and the maximum diversity offshore. In the northern Benguela region, O'Toole (1977) found that off the northern part of Namibia maximum spawning tended to occur offshore whereas further south spawning was more abundant close to the coast. In contrast, in the southern Benguela region the maximum mean abundance of larvae occurred at an intermediate distance from the coast in the vicinity of the shelf break (roughly the 200m bottom contour) on the west coast north of Cape Point, and between the 100m and 200m contours over the western portion of the Agulhas Bank (see Section 1.1, Fig. 1.1 for bottom topography). Both abundance and diversity were reduced east of Cape Agulhas over the shallow Agulhas Bank area, and offshore changes in abundance and diversity were not as marked as on the west coast. The occurrence of the maximum mean diversity of larvae at offshore stations where the water depth was greater than 100m (Fig. 4.5) is similar to the pattern found off California. The diverse larval assemblage over deep water where the mean abundance was less than maximum, is a result of the increased occurrence of the larvae of deep water forms which were seldom abundant in the CELP samples. A similar conclusion was reached by Loeb et al. (1983a) with respect to the increase in diversity offshore in the California Current. De Decker (1984) found the greatest diversity of copepods offshore on the west coast of South Africa. The occurrence of the maximum abundance at an intermediate distance from the coast appears to be a significant difference between the southern Benguela region and the other two regions considered, and possible causes are considered in the next section.

Underlying the mean abundance pattern, there were considerable differences between species, althought at least 3 general forms can be distinguished:

(i) Anchovy, roundherring, and to a lesser extent, pilchard, eggs and larvae were most abundant between the 100 and 200m bottom contours over the western part of the Agulhas Bank and along the west coast as a narrower ribbon associated with the shelf break (300-500m), widening north of Cape Columbine where the shelf broadens (Figs. 4.7, 4.16 and 4.22). The anchovy egg production cruises in November 1983-1985 showed that anchovy eggs and larvae were fairly widespread over the outer portion of the Agulhas Bank east of Plettenberg Bay (Figs. 4.9-12). Anders (1975) recorded anchovy and pilchard eggs as far east as 33°E and 30°E respectively, but it seems that egg abundance is reduced east of Algoa Bay. Before the pilchard collapse in 1962-64, the pattern of abundance of pilchard eggs was very similar to that of the anchovy, but they were particularly abundant offshore of Cape Columbine (Anders, unpublished charts, SFRI) corresponding to the area where the older age classes of pilchard were located prior to the stock decline in the early 1960's (Crawford 1980).

(ii) In contrast to the pattern of abundance displayed by the anchovy and roundherring, the ichthyoplankton stages of the lanternfish and lightfish were uncommon over the Agulhas Bank, except for the western perimeter, but were abundant offshore over the shelf along much of the west coast (Figs 4.14 and 4.20). Lightfish eggs tended to be associated with stations over the slope region rather than at the outermost stations of the grid on the west coast. In the Canary Current system and in New Zealand waters, the planktonic stages of light fish have also been found to be most abundant over the slope (Blackburn and Nellen 1976, Robertson 1976). Lanternfish eggs tended to be most abundant over deep water, especially in the vicinity of the canyons off Cape Columbine and Cape Point. The abundance of lanternfish larvae tended to increase offshore.

(iii) Dragonet, horse mackerel, hake and snoek larvae were widespread over the survey grid, with the exception of some inshore stations, particularly in the vicinity of St Helena Bay (Figs 4.18, 4.24, 4.26, and 4.28).

With the exception of roundherring, horse mackerel and snoek, these egg abundance patterns correspond to epipelagic/neritic, midwater/slope and psuedo-demersal neritic habitat preferences of the adults. In the northern Benguela Current region, despite the simpler coastal topography, generalizations appear more difficult to make with regard to the patterns of abundance described in the literature (e.g. O'Toole 1973, 1978, King 1977, Ahlstrom et al. 1976, Le Clus 1984, Olivar 1985). It appears that in this system the onshore-offshore pattern is complicated by the Luderitz upwelling centre in the south and the influence of Angolan Current water in the north which sets up considerable longshore patterning. Nevertheless, abundance of lanternfish larvae was maximum offshore (Ahlstrom et al. 1976) and the goby tended to be maximum inshore (O'Toole 1978). Off the Oregon coast in the northern part of the California Current, Richardson (et al. 1980) found that a coastal and offshore assemblages were always present, separated by transitional stations, with the boundary parallel to the shelf break.

A comparison of the statistical description of pattern using the pooled sample data should be exercised with caution.(P. Smith, Southwest Fisheries Center, in litt.). Pooled samples of fish eggs contain more than one day's spawning, and the samples of larvae span several weeks production, so that comparison between species with different egg and larval development rates, and with different levels of catchability of larvae with respect to the plankton sampler, will obscure real differences in pattern intensity. Since there is no simple way to account for this effect without determining age-specific abundance patterns, interpretation of the data is restricted to gross differences in multi-age components of the ichthyoplankton.

The eggs of the epipelagic species, anchovy and pilchard reached mean crowding values which were an order of magnitude more than the egg or larval stages of any other taxa. In addition the eggs of anchovy were significantly more patchy than the eggs or larvae of any other taxa and were also significantly more patchy than anchovy larvae. Although lanternfish eggs were the next most patchy they were not significantly more patchy than pilchard eggs. Pilchard eggs were, however, significantly more patchy than the eggs of roundherring and lightfish as well as the larvae of dragonet, hake, roundherring, and lightfish. The pattern of abundance of anchovy and pilchard eggs suggests that the survival of reproductive products of epipelagic fish is enhanced by crowding and aggregation, which is a result of the large batch fecundity (M. Armstrong, SFRI, pers comm., Le Clus 1979, Hunter and Goldberg 1980) and the fact that the spawning area is distinct and the spawning season abbreviated, particularly in the case of the anchovy. The result that anchovy larvae of potentially different ages are found in close association suggests that the advantages conferred with respect to shoal formation outweigh the disadvantages of intraspecific competition and cannibalism. The small gape of anchovy larvae compared with, for example hake, indicates that considerable age differences would be required for cannibalism to take place (C. Brownell, University of Cape Town, pers comm.).

As a result of diffuse shoaling behaviour and reduced fecundity (Gjosaeter and Kawaguchi 1980), the eggs of the midwater/slope lightfish and roundherring were less crowded and less patchy than the ichthyoplankton stages of the epipelagic species. In both species the larval stages were more patchy than the eggs. Increased patchiness and crowding in lightfish and roundherring from the egg to larval stage may be a result of physical processes or non-random mortality and contrasts with the less patchy and less crowded pattern of abundance found in the larval epipelagic species compared with their egg stage. In contrast to lightfish and roundherring, the eggs of lanternfish were very patchy and the larvae substantially less so. The difference in the pattern of abundance of lanternfish eggs may be associated with the relatively abrupt spawning season as well as the offshore nature of the spawning ground, which only partly intersected the CELP survey grid in the vicinity of the underwater canyons off Cape Columbine and Cape Point. In general, the dispersed pattern of abundance of the ichthyoplankton stages of midwater/slope species is compatible with the dispersed nature of the adults and points to a substantially different life history strategy to that employed by epipelagic species.

The lack of a clear temporal peak and the widespread spatial distribution of the psuedo-demersal/neritic hake and dragonet larvae found during the CELP survey confirms that spawning in these two species is widespread in both time and space. Hake and dragonet had the smallest index of mean patchiness and crowding out of the most abundant taxa sampled during CELP. Dragonet are not caught commercially in the South East Atlantic, but Smith (1965) describes members of the Family Callionymidae as being small fish which display sexual dimorphism and live on the bottom of most seas, extending out to deep water. Most members of the family off South Africa appear to be Indian Ocean forms, with the exception of *Paracallionymus costatus* which Smith (1965) records as endemic to the St Helena Bay to Durban area between about 40 and 500m. Although not much is known about *P. costatus* it is clearly a species associated with the bottom over the shelf and the similarity in its pattern of abundance to that found in the hake is evident in the CELP data, suggesting that the spawning strategy in the two species is similar. The very dispersed nature of the ichthyoplankton stages of these two species suggests a very different life history strategy compared to either epipelagic/neritic or midwater/slope species.

Multispecies pattern

Pielou (1977) has suggested that the factors controlling and determining pattern are likely to affect many species rather than just one, and that much may be learned by investigating the way in which species are associated with one another. It has become common practice to classify multispecies ichthyoplankton data sets into similar sample and species groups to assist in the interpretation of pattern and causality (e.g. Loeb et al. 1983c, Richardson et al. 1980, Olivar 1985). Generally some consistent patterns have been found, but since in most cases samples are from oblique tows through the water column which give no information on vertical structure, interpretation requires caution. Research on vertical patterns of abundance is therefore a priority. In addition, since ichthyoplankton are only temporary members of the plankton, caution needs to be taken in using what is essentially a tool for looking at community structure. Species associations found in one month will not necessarily occur in a later month when the adults of one of the species is no longer spawning. Within these constraints it is necessary to examine only broad generalizations regarding multispecies pattern.

The 5 sample groups apparent in the CELP data set were fairly persistent throughout the survey but changes in species composition were evident. This points to some persistent causative environmental factors, an aspect which is examined further in Section 5. In broad terms, Group A represents a transitional group of stations separating the inshore Group D from the offshore Group E (Fig 4.31). Groups B and C were associated with the western and eastern Agulhas Bank respectively, with group B extending up the west coast inshore of Group A in some of the months. The three categories formulated above on the basis of adult life styles - epipelagic/neritic, midwater/slope, and psuedo-demersal/neritic, do not fit neatly into the 5 sample groups, but Group A comprised mostly midwater species and species associated with the shelf bottom, Groups B and C epipelagic species, Group D midwater and species associated with the bottom, and Group E midwater species. The problem of interpreting samples integrated over depth is apparent in the species composition of Group E, which included the eggs and larvae of the epipelagic oceanic saury _Scomberesox saurus_ (Dudley et al. 1985), midwater species which have adults which frequent the shelf slope, such as the lightfish and lanternfish, and species in which the adults are probably associated with deeper water offshore of the CELP grid, _Hygophum_, _Symbolophorus_ and _Vinciguerria_. The eggs and larvae of the saury almost certainly were restricted to the top few metres of the water column, whereas the eggs and larvae of the lightfish (Shelton 1979) and the lanternfish probably occurred in or just below the thermocline. The larvae of the deeper water mesopelagic species may have been associated with less stratified water near the bottom of the 100m tow. In samples from the North Pacific Central Gyre, Loeb

(1979) found that two species of Hygophum occurred between 25 and 225 metres, a species of Symbolophorus was most abundant at 50 to 75 metres, and Vinciguerria occurred most consistently between 25 and 75 metres. Ahlstrom (1959) recorded Vinciguerria as being distributed in the upper mixed layer in the Califorina Current region.

In their analysis of fish larvae off the coast of Oregon in the nothern California Current system, Richardson et al. (1980) classified samples into coastal, transitional and offshore assemblages which were present in each of six surveys. They found that the transition from coastal to offshore assemblages roughly paralleled the shelf break. This result is similar to that found off the west coast in the southern Benguela system where Group A is a transitional group with Group D inshore and Group E offshore. The close affinity between Group A and Group B in August 1977, October 1977 and January 1978 (Fig 4.30) is in accord with the idea that ichthyoplankton from the western part of the Agulhas Bank may be transported up the west coast in a frontal jet (Shelton and Hutchings 1982). In the spring and summer Group D was shown to be considerably different in species composition and abundance from the other groups in the classification. A possible indicator species of this group is Sebastes capensis, which, together with a number of members of the Class Chrondrichthyes, dominates the inshore benthic community on the west coast (B. Rose and A. Payne, SFRI, pers. comm.). Group C on the Agulhas Bank, was, with the exception of January 1978, fairly dissimilar from Group B which was also associated with the Agulhas Bank, despite the fact that the species composition in the two groups was similar. The dissimilarity may best be explained by the apparent abundance of larvae of species such as anchovy associated with inshore stations in the eastern part of the survey grid (Fig. 4.2). The larvae of the flatfish Cynoglossus capensis were also fairly commonly found in samples in Group C, forming a possible indicator species.

Analysis of species associations have been performed on samples collected in eastern boundary current regions by Richardson et al. (1980) using similar methods to this study, by Loeb et al. (1983c) using the methods of Fager (1957,1963) and by Olivar (1985) using a correlation matrix. Although the species compositions of the samples from the southern California Current region (Loeb et al. 1983b), the northern Benguela region (Olivar 1985) and this study are similar in many respects, the species composition off the coast of Oregon (Richardson et al. 1980) is very different. In the Californian study data from a number of surveys were used in a single analysis. In the analyses in the Benguela system some species groups showed persistence but in general the associations reveal changing affinities over the months, reflecting different patterns of seasonality in spawning amongst species. There is little correspondence in the lumped or separate groupings from the three areas. For example, in the southern Benguela region, *Trachurus*, *Merluccius* and *Etrumeus* formed a group in 3 of the 4 months, with associations with *Paracallionymus* in one of the months and *Genypterus* in another month. Similar associations do not occur in the other regions, although *Merluccius* and *Trachurus* were grouped together in one of the three surveys off the northern Benguela region. *Engraulis* larvae, which were abundant in all 3 regions, were not strongly or persistently associated with any other genera in the southern Benguela region. In the northern Benguela region, *Engraulis* was associated with *Trachurus* larvae and in the southern California Current region with *Merluccius*, *Stenobrachius* and *Leuroglossus*. *Lampanyctodes* larvae, the next most abundant component after anchovy in the southern Benguela region, formed a group with *Maurolicus* eggs, *Helecolenus* larvae and *Hygophum* larvae in two of the months. In the northern Benguela region *Lampanyctodes* larvae were associated with the larvae of Maurolicus in two of the surveys. These two genera were not included in the Californian analysis. The grouping of the larvae of deep water forms in three of the four months in the southern Benguela region included the genera Diogenichthys, Symbolophorus and Vinciguerria. These three genera, together with Bathylagus and Ceratoscopelus, formed a major group off California.

The analysis of species associations in the pooled data for the four months representitive of the seasons partly supported the grouping of species into psuedo-demersal/neritic, midwater/slope, and epipelagic/neritic, but did not show much association between the two epipelagic species anchovy and pilchard.

4.5 Conclusion

The ichthyoplankton in the southern Benguela region was strongly patterned with respect to both time and space indicating that spawning strategies are adapted to predictable environmental features. The maximum abundance occurred in the vicinity of the shelf break on the west coast, and between the 150m and 200m contours over the western portion of the Agulhas Bank. Diversity increased offshore on the west coast and was low over the Agulhas Bank. The seasonality in the abundance and diversity of larvae showed that the late summer, autumn and early winter period (February - July) was generally less favoured by spawners than the late winter, spring and early summer months (August - January). The ichthyoplankton was dominated by 9 taxa which together constituted 95.5% of the ichthyoplankton. The dominants included species of major commercial importance as well as several species which are not exploited and whose abundance in the system may not previously have been recognised.

Adults generating the ichthyoplankton were classified as epipelagic/neritic, midwater/slope or psuedo-demersal/neritic depending on adult habits. These three groups appeared to impart different temporal and spatial patterns of abundance to the eggs and larvae in the plankton, however, although analysis of variance showed differences between the temporal abundance of eggs in anchovy, pilchard, lanternfish and lightfish, the individual species were not significantly different. Examples of species from the three habitats are, respectively, anchovy, lanternfish and hake. Anchovy spawned in spring and summer (September - February), lanternfish in winter and spring (August - November) and hake throughout the year. Anchovy eggs and larvae were most abundant between the 100m and 200m contours over the western portion of the Agulhas Bank and along the west coast as a narrower ribbon associated with the shelf break, widening north of Cape Columbine where the shelf break is less steep and further offshore. Lanternfish eggs and larvae were uncommon over the Agulhas Bank but were abundant offshore of the shelf break, especially in the vicinity of the canyons off Cape Point and Cape Columbine. Hake larvae were widespread but were absent at most inshore stations. The statistical analysis of pattern showed that the ichthyoplankton of epipelagic species tended to be most patchy, that of midwater species less patchy and that of psuedo-demersal species least patchy. Anchovy eggs were significantly more patchy than the eggs or larvae of any other species and pilchard eggs were significantly more patchy than the eggs and larvae of a number of psuedo-demersal and mid-water species. Lanternfish eggs were suprisingly patchy compared to other mid-water species, but this may have more to do with incomplete coverage of the spawning area than a spawning strategy adaptation.

The classification of samples showed the persistent occurrence of an inshore, transitional, and offshore assemblages of stations on the west coast and the presence of two assemblages over the Agulhas Bank. The assemblage over the western portion of the Bank extended up the west coast inshore of the transitional assemblage in some months. Species associations were less clear and persistent, reflecting the temporary nature of the ichthyoplankton in the plankton which is influenced by adult spawing season preferences. Nevertheless, some groups reccurred indicating similar spawning and larval requirements. The species associations in the pooled data for the four months selected as representitive of the seasons only partly reflected habitat groupings of epipelagic/neritic, psuedo-demersal/neritic and mid-water/shelf slope. An analysis of the similarity matrix for this data using ordination showed that hake and dragonet larvae had similar abundance patterns although they were also closely associated with species, the adults of which occupy other habitats, and that lanternfish and ~~and~~ lightfish had similar abundance patterns.

Despite large decreases in the spawner populations of a number of commercially exploited populations, the species dominance in the ichthyoplankton has remained fairly constant since the 1950's. Differences in species dominance and patterns of abundance in the northern and southern Benguela Current and the California Current, suggest that different causative environmental factors and/or behavioural responses are found in each of the three regions.

5 ICHTHYOPLANKTON ABUNDANCE PATTERNS IN RELATION TO THE ENVIRONMENT

5.1 Introduction

The southern Benguela region is characterized by considerable temporal pattern at the scale of seasons and spatial pattern at the scale of 10's to 100's of Kilometers, in terms of the physical environment, the plankton in general (See Sections 2 and 3), and some of the neritic and shelf slope fish populations (e.g. Crawford 1980). It is therefore not surprising to find that spawning and the abundance of the eggs and larvae of a number of fish species are also strongly patterned in time and space (see Section 4). It was more unexpected to find that some species such as hake and dragonet spawned fairly uniformly in time and space. In either case, the observed pattern of spawning and subsequent egg and larval abundance must reflect the individual species adaptation to ensure maximum survival of progeny. Although each species must, by definition, be uniquely adapted to its environment, three general temporal and spatial patterns of spawning were identified in Section 4 which appear to hold for groups of species. These correspond to epipelagic/neritic, mid-water/slope, and psuedo-demersal/neritic adult habits, and are typified by, respectively, anchovy, lanternfish and hake.

Since the temporal and spatial pattern of spawning in these three species are so different, it can be assumed that they have resolved different environmental problems in ensuring progeny survival. Bakun (1985) has suggested that the observed results of natural selection in terms of geographical and seasonal aspects of reproductive strategies may point the way to processes determining recruitment. For example Parrish et al. (1983) have convincingly shown that anchovy and sardines in the major eastern boundary current systems have spawning areas and seasons that minimise wind-induced turbulent mixing and offshore Ekman transport. An apparent anomaly with respect to the Peruvian anchoveta is satisfactorily resolved by Bakun (1985). Thus, according to the arguement of Bakun (1985), turbulent mixing and offshore transport may be important determinants of recruitment strength, and therefore worthy of intensive sampling or monitoring, either in order to predict year class strength, or to understand mechanisms leading to poor early stage survival. The classic field study of the effect of turbulence was made by Lasker (1975), who found that a chlorophyll maximum layer present in the Los Angeles Bight, which provided particles of a suitable size and density for first feeding anchovy larvae, was destroyed by storm induced mixing.

An alternative argument, not addressed by Bakun (1985) is that fish species may be adapted, not only to the mean environmental conditions, but also to the expected probability distribution of the environmental variable, or some measure of this distribution such as the variance, as well as to the probable time period for which anomalies persist and the time interval between the occurences of the anomaly. The response of a fish population to a particular occurrence, such as the disruption of the chlorophyll maximum layer recorded by Lasker (1975), will depend on the life history strategy the species has developed to cope with the expected nature of the variability in its habitat, and it is only those anomalies to which it is not adapted (e.g. widespread and prolonged disruption of food layers by turbulence in the case of anchovy?) which will elicit a measurable response in the population, and are therefore worth monitoring. As an example of this approach, Shelton et al. (1985) have suggested that neritic species such as anchovy are probably adapted to upwelling variability, but that population size may be affected by prolonged and severe periods of warming and cooling.

Similarities in the pattern of the environment and the abundance of fish eggs and larvae may therefore only be useful as a first step in selecting, from the set of all possible environmental variables, the appropriate environmental variables worth investigating further. As a second step it is necessary to determine the variance, period and spatial extent of the variability to which the species is adapted, in order to determine whether a particular anomaly in the environment is likely to cause an anomaly in the fish population. The first step is given further consideration in this section. Solving the second step empirically is only possible with lengthy time series of accurate measurements of relevant environmental variables and fish year class strength. As a possible alternative, mechanistic or cause and effect solutions would, in most instances, require large scale and prolonged sampling of the environment and early stage survival, beyond the capacity of most research institutions. Some preliminary ideas regarding the kind of variability likely to be worth sampling with respect to different species, which has a bearing on both the empirical and mechanistic approaches, are explored in Section 6 using simulation modelling.

5.2 Methods

The mean total abundance of larvae of all species, mean diversity and mean abundance of the eggs and larvae of three species, anchovy, lanternfish and hake, representing, respectively, adults with epipelagic/neritic, mid-water/slope and psuedo-demersal/neritic habits described in Section 4, were examined in combination with features of the physical environment described in Section 2 and components of the plankton described in Section 3. The aim was to attempt to elucidate broad temporal and spatial similarity in patterns, and thereby determine potentially important environmental variables for future sampling and analysis, rather than attempt to determine statistically rigorous dependence at the 95% confidence level, which would be inappropiate given the few degrees of freedom and the probable non-linearity of the functional response between fish egg and larval abundance patterns and environmental variables. Where natural logarithms of the number of eggs or larvae have been used, this was calculated as

$$Y = \log_e(x+1)$$

5.3 Results and Discussion

Temporal patterns

Temporal patterns in the ichthyoplankton and the environment can be looked for at a variety of time scales, but given the the lack of synopticity and the time interval between resampling, it was considered advisable to focus attention on differences between the seasons rather than at the weekly scale at which upwelling events occur in the system (Andrews and Hutchings 1980). Although each season was sampled more than once, there is still the limitation that only one seasonal cycle was covered. Although 1977/78 was not associated with a major anomaly, Shannon et al. (1984a) do indicate that the sea temperature in 1978 was somewhat cooler than average and that there was a negative atmospheric pressure gradient anomaly. Figure 7 in McLain et al. (1985) is more informative in that it indicates that the survey took place at the end of a warm period that extended from 1971 to mid-1979 and that April, May and June 1978 were somewhat cooler than the previous few years, but warmer than in the following cool period which occurred from 1979 to the beginning of 1984. Therefore, while being aware of the longer term patterning shown in McLain et al. (1985), there does not appear to be any reason why 1977/78 should not be taken to be representative of seasonal changes.

The mean total abundance of larvae of all species and the mean species diversity in each of the 12 months of CELP are plotted against mean sea surface temperature (SST), mean volume of plankton collected by the 300 um mesh Bongo unit, mean chlorophyll-a concentration integrated down to 75m, and the mean maximum microplankton (particles 37 to 100μm in diameter) concentration in the water column (Fig. 5.1). The seasonal summer increase in mean SST to a peak in February 1978, caused by the advection of warm water of oceanic and Agulhas Current origins towards the coast and increased solar heating, coincided with a an increase in upwelling activity inshore, caused by the seasonal increase in the incidence of upwelling-favourable SE winds as shown in Andrews and Hutchings (1980). This resulted in the development of a strong temperature front along the west coast and the western portion of the Agulhas Bank (see Section 2.1). The summer increase in SST and the development of the front was associated with an increase in the abundance of microplankton and a decrease in the abundance and diversity of fish larvae over the CELP grid, but was preceded by a spring increase in chlorophyll-a abundance. Although changes in plankton displaced volumes did not follow the SST pattern, the coefficient of variation of the abundance measurements of plankton displaced volume and chlorophyll-a concentration increased over summer (see Section 3.2, Fig. 3.2.9) as a result of a less uniform pattern of abundance caused by the strong temperature front. This is demonstrated by a plot of chlorophyll-a concentration against SST in October 1977 (Fig. 5.2) when the outer edge of the front was demarcated by the 16°C isotherm. Phase diagrams of the mean abundance and diversity of larvae against mean SST clearly show the strong seasonality found within the ichthyoplankton in general (Fig. 5.3). It would clearly be inappropriate to fit simple regressions to these non-stationary seasonal relationships.

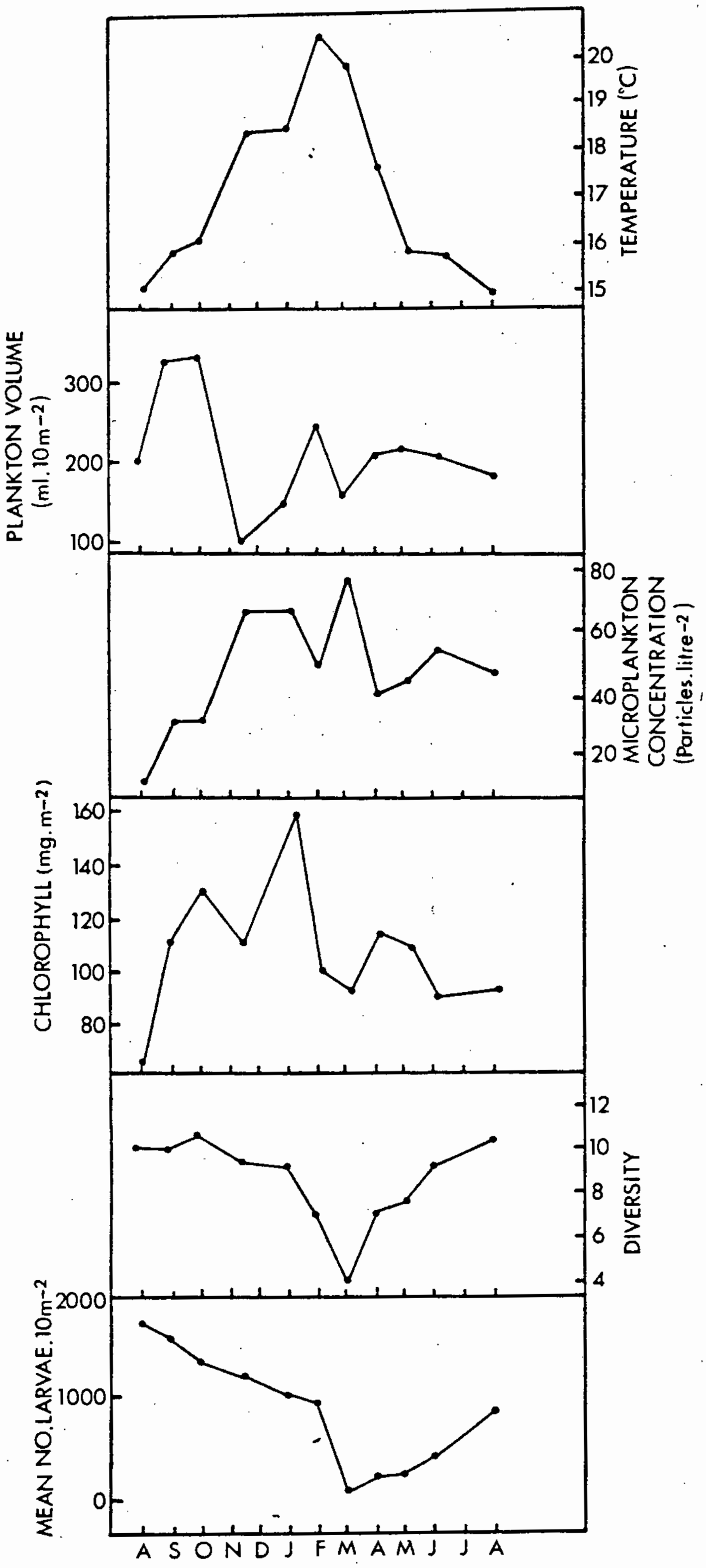


Fig. 5.1 Mean total number and diversity of larvae of all species between August 1977 and August 1978 over the CELP survey grid, plotted together with mean sea surface temperature (SST), mean plankton displaced volume sampled with the 300 micron Bongo unit, mean microplankton concentration (mean of the maximum value recorded at each station) and mean chlorophyll-a concentration integrated down to 75m.

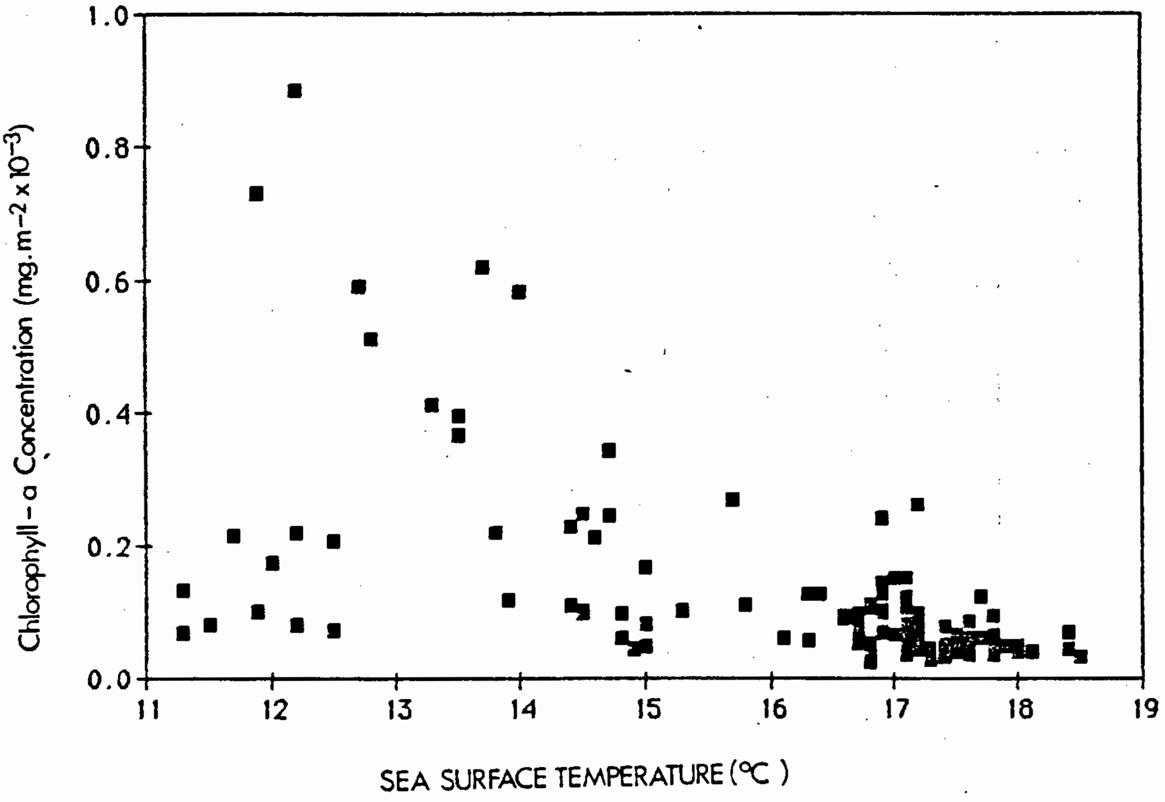
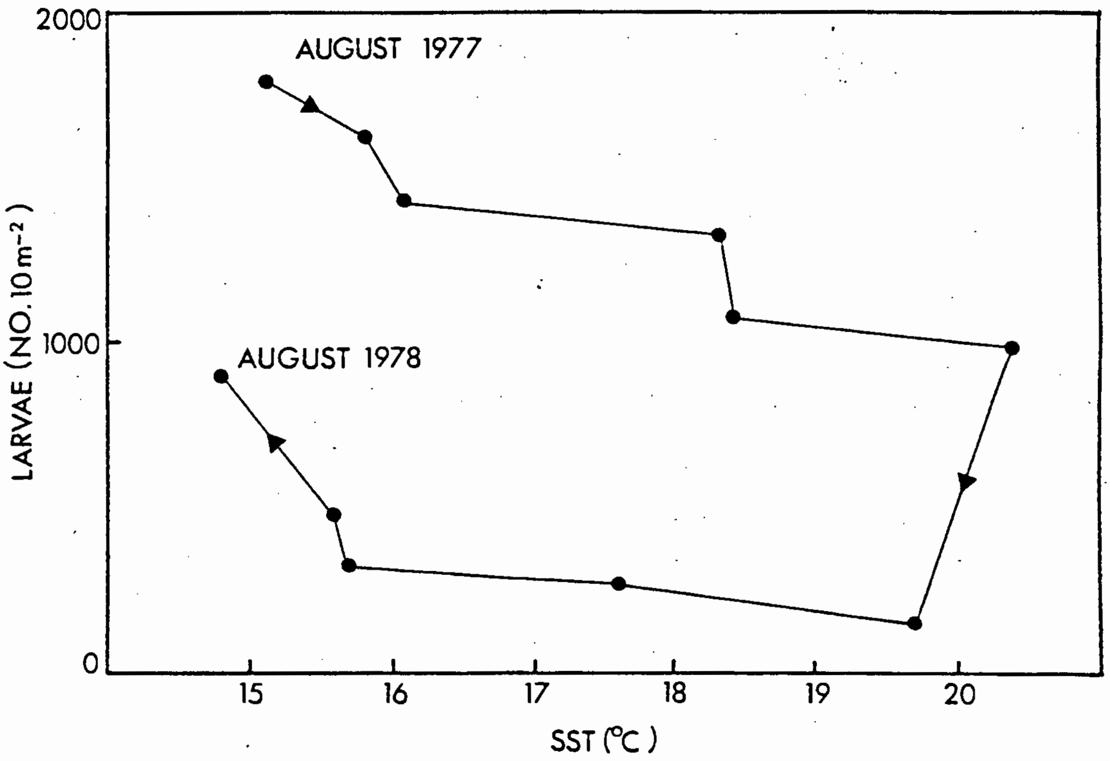


Fig. 5.2 Chlorophyll-a concentration plotted against SST from samples over the CELP grid of stations for October 1977 demonstrating the low concentrations of chlorophyll-a offshore of the front. The outer edge of the front corresponded to a SST of 16°C.



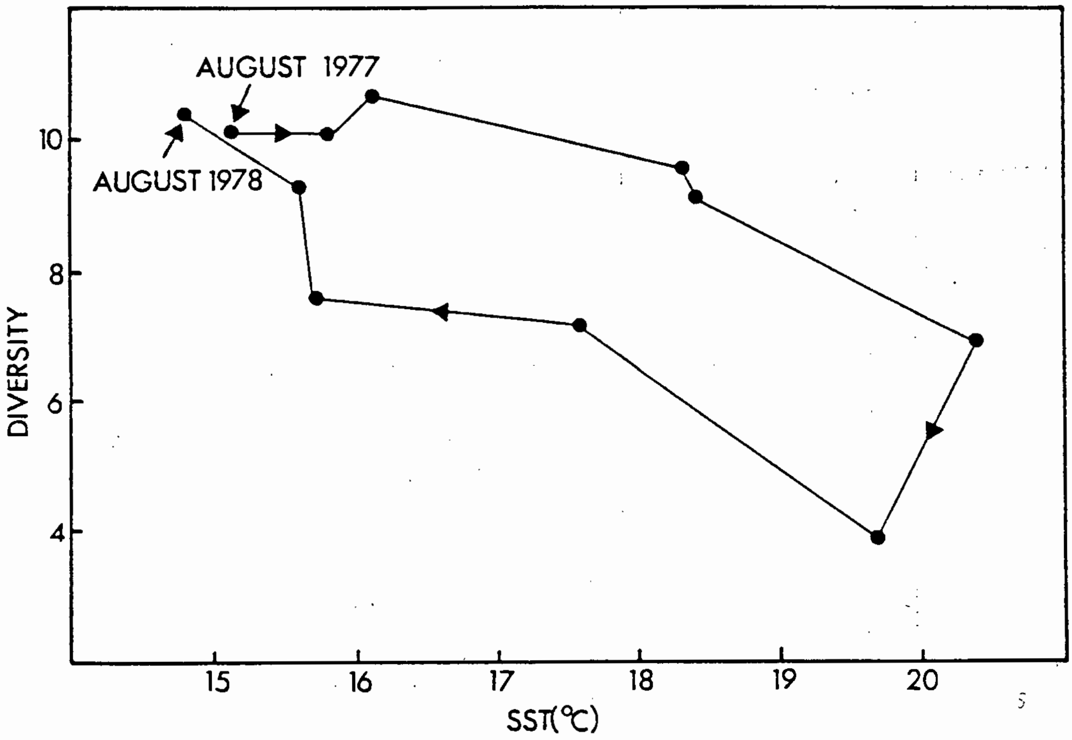


Fig. 5.3 Phase diagrams of the mean total number of larvae and mean diversity plotted against mean SST over the CELP grid of stations between August 1977 and August 1978.

The temporal pattern of anchovy and lanternfish egg abundance in relation to SST and the abundance of the various components of the plankton is shown in Fig. 5.4. Substantially different spawning seasons were displayed by anchovy and lanternfish, which, based on the number of larvae in the plankton samples, were co-dominants in the system. Anchovy eggs were most abundant in the plankton in spring and summer and lanternfish eggs were most abundant in winter and spring, giving rise to a positive relationship between anchovy eggs and mean SST ($r=0.70$, $n=10$, $p<0.02$) and a negative relationship between lanternfish eggs and mean SST ($r=0.80$, $n=10$, $p<0.01$). Although hake eggs were not consistently identified in the CELP samples, Botha (1986) recorded a November/December spawning peak in both species and a February/March peak in mainly Merluccius paradoxus based on a study of the gonads. However, he also records that spawning took place throughout the year. The monthly abundance of hake larvae in the plankton samples collected during CELP did not indicate any seasonality in spawning. While it cannot be concluded that anchovy and lanternfish spawning is adapted to sea temperature, per se, the seasonality in spawning in these two species does indicate adaptation to some component of the environment that is seasonally patterned, whereas hake spawning would appear to be only slightly adapted to seasonality, if at all.

The abundance of anchovy eggs in the plankton increased with increasing chlorophyll-a concentration, preceding the summer increase in SST, and the abundance remained high until the SST started to decrease rapidly after February. Microplankton abundance tended to be high during anchovy spawning months whereas plankton displaced volume varied independently of anchovy egg abundance. In general, all measured components of the plankton had a low mean abundance during the time of the year when lanternfish eggs were abundant in the plankton. However, as pointed out above and shown in Section 3.2, Fig. 3.2.9,

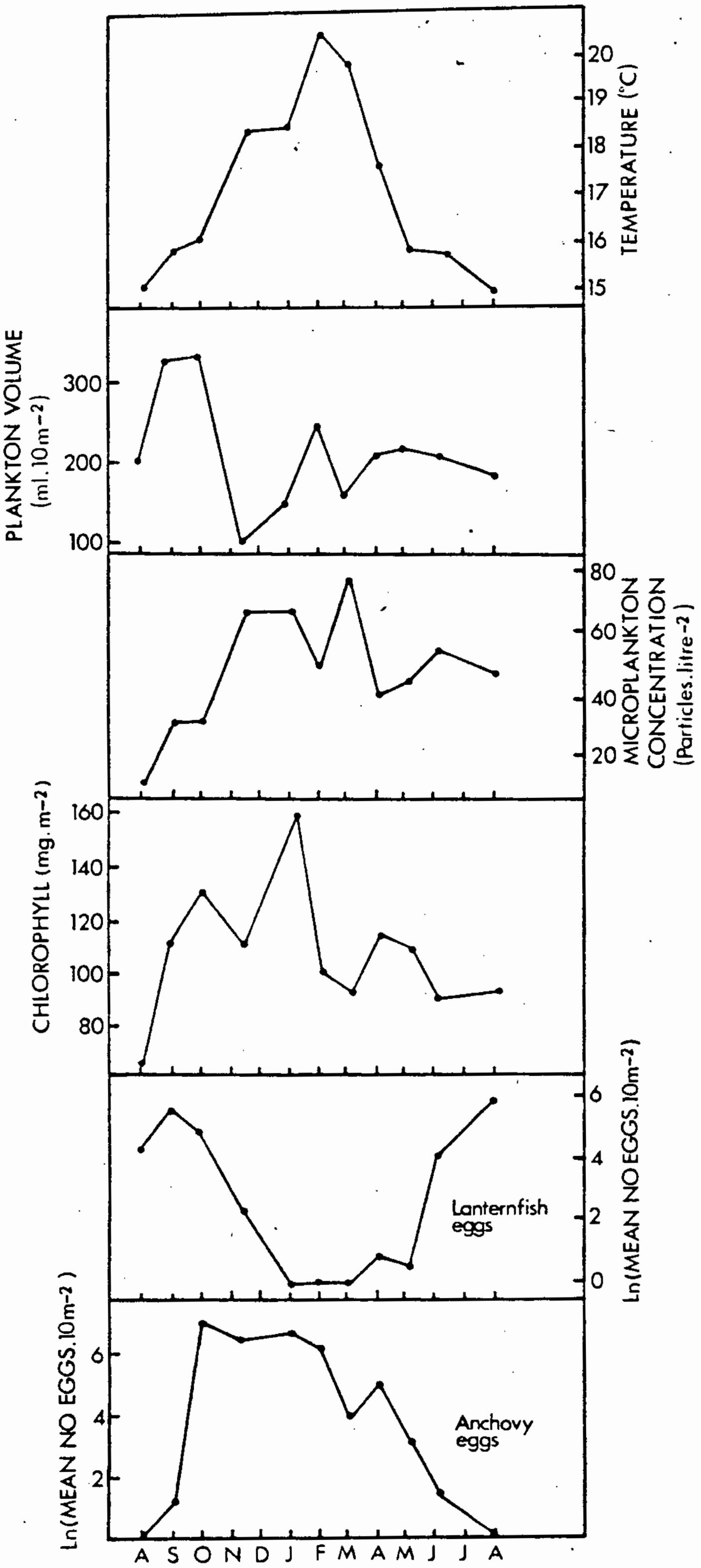


Fig. 5.4 Natural logarithm of the mean number of anchovy and lanternfish eggs sampled over the CELP grid between August 1977 and August 1978 showing the difference in spawning season, plotted together with SST and the abundance of various components of the plankton.

plankton, as measured by displaced volume and chlorophyll-a concentration, was more uniformly distributed over the CELP grid in winter. This was a result of the weakening of the temperature front which allowed the area covered by cool, productive water to expand towards the offshore limit of the survey grid. This may have increased the food supply to lanternfish spawners and early stage larvae, since spawning in this species takes place in the vicinity of the shelf slope. However the gelatinous fraction of the plankton tends to be greater in winter (L. Hutchings, SFRI, pers. comm.).

The temporal pattern of abundance of anchovy, lanternfish and hake larvae in relation to the other components of the plankton and SST is shown in Fig. 5.5. Chlorophyll-a and microplankton concentrations were on the increase at the start of the anchovy spawning season with the result that anchovy larvae were abundant during months of enhanced concentrations of potential food particles. This suggests that the availability of food particles suitable for larval feeding may be important in determining the spawning season in this species. This is in line with the "match/mismatch hypothesis" of Cushing (1978), who proposed that the temporal overlap between the production of fish larvae and that of their food will vary with the magnitude of the resulting year class, and that the population will be adapted to maximise the amount of overlap.

The volume of plankton retained by the 300 µm Bongo sampler, representing larger components of the zooplankton such as euphausiids, copepods and chaetognaths, and chain forming diatoms, showed a spring peak in 1977, which may have been important in supplying the energy needs for subsequent spawning by adult anchovy. Since some of these larger zooplankters represent potential predators on anchovy larvae, the small plankton volume in some of the months of elevated anchovy larvae abundance, may have favoured surival of the larvae. In

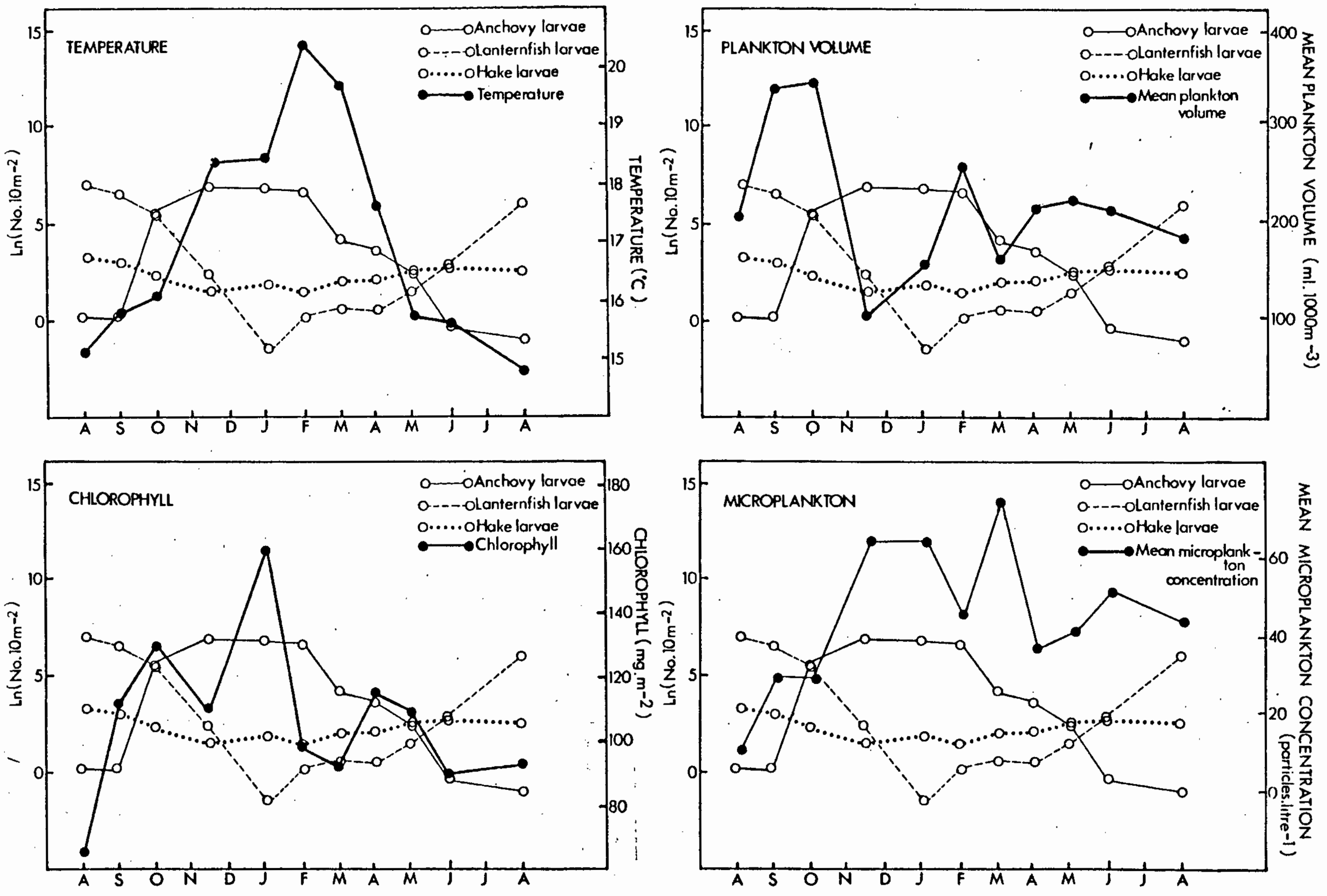


Fig. 5.5 Natural logarithm of the mean number of anchovy, lanternfish and hake larve plotted against mean SST, plankton volume, chlrophyll-a concentration and microplankton concentration over the CELP grid between August 1977 and August 1978.

reviewing the role of zooplankton predators on fish larvae Hunter (1981) concluded that yolksac lavae are vulnerable to a variety of predators, such as copepods, euphausiids and chaetognaths, whereas larger larvae could be preyed upon by large species of Chaetognatha, Siphonophora, Chrondrophora, Medusa and Ctenophora, although no detailed studies of these larger potential predators have been made in the Benguela Current system.

The concentration of food particles within the area inshore of the front and in the thermocline that developed over the Agulhas Bank (see Sections 3.1 and 3.2), may have formed important feeding areas for both anchovy spawners and the larvae. Lasker (1975), Lasker and Zweifel (1978), and Owen (1980) stress the importance of such physical processes in providing suitable feeding areas for anchovy larvae in the California Current. The reduced physical patterning of the system in winter, caused by the retraction of warm water off the shelf, the decrease in upwelling activity and the resultant disappearance of the front along the west coast as far south as Cape Agulhas, and the mixing of the less stable water column by storms, and therefore the disruption of the thermocline over most of the Agulhas Bank, resulted in a more uniform but less abundant standing stock of plankton (Fig. 5.5). Although this appeared to be a highly unsuitable time for anchovy to spawn, lanternfish spawning occurred predominantly in winter with the result that larvae were most abundant in the plankton in winter and spring. As suggested above, the survival of lanternfish larvae may have been enhanced by the more widespread abundance of potential food particles at this time. The lack of seasonality in the abundance of hake larvae in the plankton, with the result that hake larvae were equally abundant at all SST, chlorophyll and microplankton values is evidence that the hake habitat is less strongly influenced by seasonality than that of the anchovy and lanternfish.

From a study of the spawning strategies of a number of fish species off the east coast of north America, Sherman et al. (1984) found that peak spawning in some species was in synchrony with increasing abundance levels of planktonic prey, and thus fitted the Cushing (1978) match/mismatch hypothesis, whereas others, notably the silver hake Merluccius bilinearis and a number of other hakes, displayed ubiquitous spawning. They interpreted a ubiquitous spawning strategy as an r-selected trait evolved to ensure that at least some of the larvae will encounter favourable conditions for growth and survival. They suggested that by maintaining relatively high densities of eggs in the plankton over a wide temporal and spatial range, fish displaying a ubiquitous spawning strategy would be able to respond rapidly to favourable conditions. Although not stated by the authors, this presupposes that no time of the year or area of the habitat is predictably better than any other time or area. In general the anchovy displays a greater degree of r-selection, but indulges in seasonal spawning within a limited area of its habitat. An alternative explanation for ubiquitous spawning in hake may be that it is to reduce intraspecific interaction, such as competition between similar sized larvae, or cannibalism between different sized larvae. Intraspecific interaction would be minimized by uniform temporal and spatial larval distribution patterns. This is in line with the arguments of Lambert (1984) who concluded that because herring larvae have a greater capacity for intraspecific competition than capelin, the larvae of herring have greater temporal and spatial spacing.

In addition to, or as an alternative to being adapted to maximize the availability of food to the larvae, the time of spawning in anchovy and lanternfish may be adapted to patterns of circulation. The spring/summer spawning season of the anchovy is also the time of maximum S and SE wind, and consequently the time of greatest potential offshore Ekman transport on the west coast (see Section 2.2).

However, the loss of drift cards from the system, as indicated by recoveries from the Island of St Helena, Ihla de Trinadade and south America, suggests that offshore transport was substantial throughout the year, as may be expected from the predominantly southerly wind stress (see Section 2.2). The formation of the temperature front along the west coast and the western portion of the Agulhas Bank in summer may serve to limit the loss of inshore components of the plankton, as indicated by the relatively greater number of recoveries of drift cards released inshore of the front in January 1978. There is also evidence that anchovy are adapted to make use of the jet current associated with the front for longshore transport of eggs and larvae from the spawning ground on the Agulhas Bank to the recruitment ground on the west coast (Shelton and Hutchings 1982). The St Helena Bay eddy appeared to be most intense in summer (see Section 2.2) and may play an important role in entraining larvae within the inshore area in this region where plankton standing stocks are greater than average, and where anchovy recruitment appears to be centered (Crawford 1980). For fish such as lanternfish, which spawn offshore, and hake which recruit inshore, the reduced offshore Ekman transport in winter may favour larval survival at this time of the year. Bailey (1981) found that year class strength in the Pacific hake Merluccius productus and offshore Ekman transport at the time of spawning were negatively correlated. In both lanternfish and hake, eggs and larvae are likely to be most abundant some distance below the sea surface, probably beneath the upper mixed layer, and may therefore be subject to reduced offshore transport or even onshore transport during south easterly winds.

Spatial patterns

Spatial pattern in the abundance of fish eggs and larvae may reflect adaptive choice of spawning area by the adults, the effect of patterned circulation such as eddies, fronts and thermoclines on the planktonic stages, or the result of differential egg and larval mortality. Since the egg stage in most of the neritic species in the Benguela System appears to be brief - typically less than 4 days (C. Brownell, SFRI, pers. comm.), egg abundance patterns are likely to closely reflect the choice of spawning area by the adult. In comparison, the pattern of abundance of the larval stage is more likely to be the result of transport, diffusion and differential mortality.

The mean total abundance of larvae between August 1977 and August 1978 is compared with the bottom topography, mean SST, mean plankton volume, mean chlorophyll-a concentration and mean microplankton concentration in Figs. 5.6-10. From Fig. 5.6 it is clear that larvae were most abundant over the shelf edge and were not abundant where the water depth was greater than 500m, or in the area inshore of the 200m contour, except over the western portion of the Agulhas Bank where larvae were abundant between the 100m and 300m contours. The small area where a mean of more than 1000 larvae per $10m^2$ occurred at inshore stations at the eastern limit of the survey grid cannot be related directly to any topographical feature. The mean sea surface temperature pattern (Fig. 5.7) shows that larvae were most abundant within the temperature front between 15°C and 17°C, which coincided with the shelf break north of Cape Point (line 48). The mean temperature pattern east of Cape Point shows that warm water derived from Agulhas Current and the South Atlantic Surface Water penetrated fairly close inshore over the Agulhas Bank as a result of the reduced amount of coastal upwelling activity in this area (see Section 2.1). This caused the weakening of the front east of Cape Point, whereas on the west coast the presence of warm water outside the upwelling zone served to intensify the front (see Section 2.1). The association between the mean position of the front and the shelf break on the west coast is well documented (Bang and Andrews 1974).

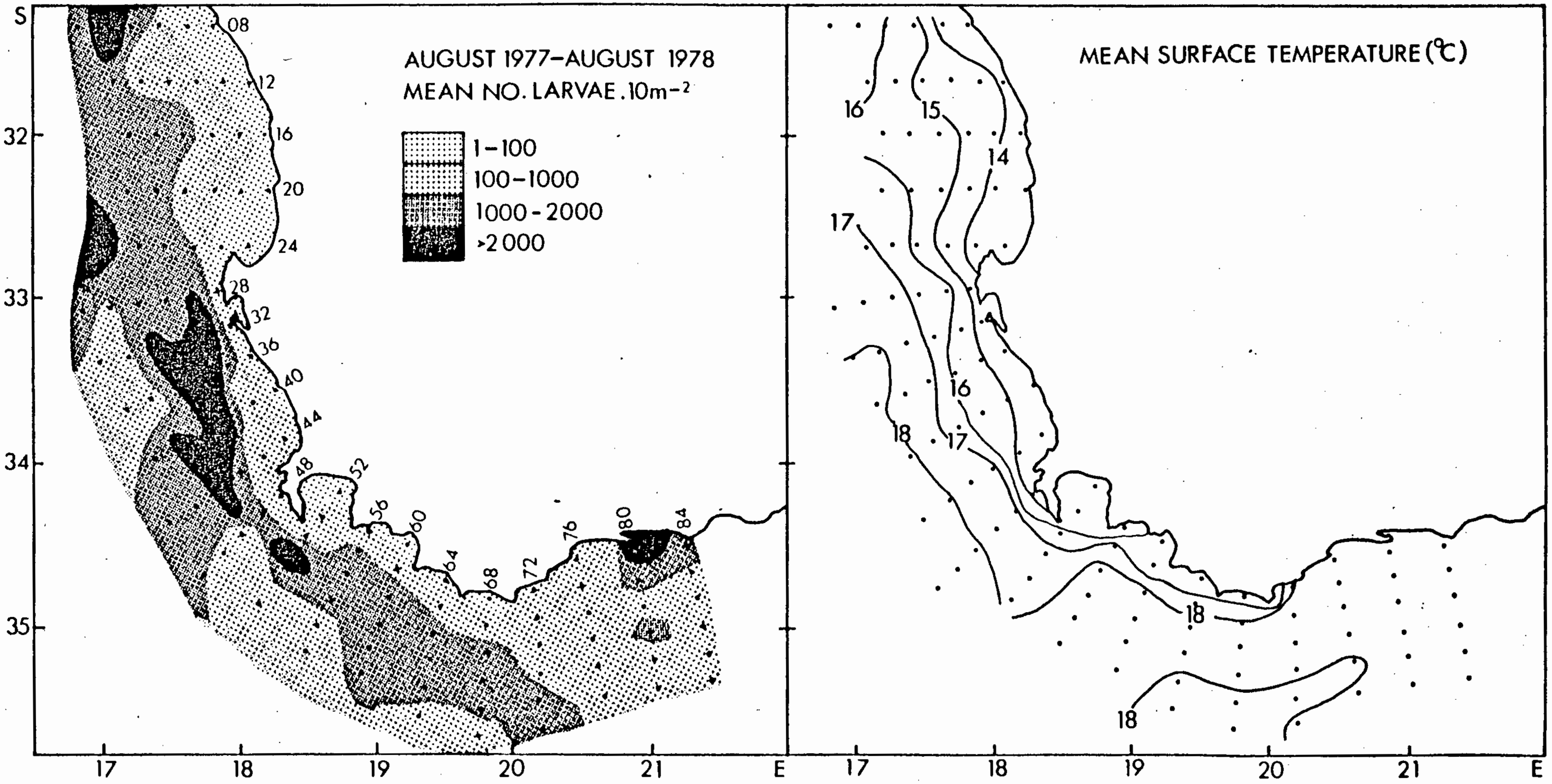


Fig. 5.6 Mean total number of larvae of all species between August 1977 and August 1978 and bottom topography over the CELP grid.

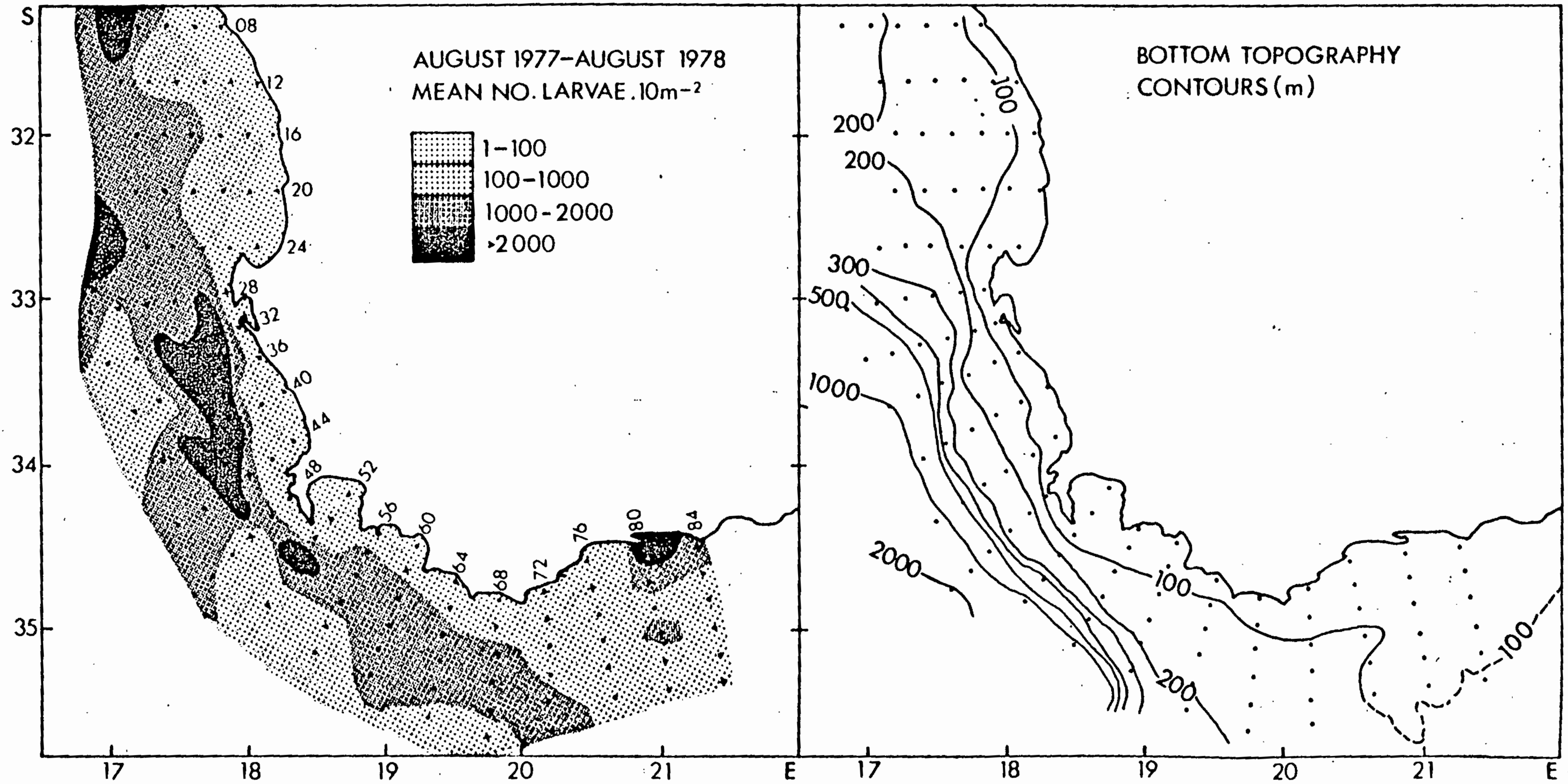


Fig. 5.7 Mean total number of larvae of all species ~~between~~ and mean SST over the CELP grid between August 1977 and August 1978.

The pattern of abundance of the mean total number of larvae of all species in relation to the mean abundance of plankton volume, (Fig. 5.8) shows that larvae were most abundant outside the main area of dense plankton associated with the upwelling centres at Cape Point (lines 36-48) and Cape Columbine (lines 20-32). At these stations the plankton was dominated by small copepods, amphipods and chain forming diatoms, with euphausiids and chaetognaths also present (See Section 3.2). While most of these components of the plankton are a suitable food source for the post-larval stages, several are potential predators of eggs and early stage larvae. East of Cape Point the area of greater plankton volume corresponds roughly with the region of more than 1000 larvae per $10m^2$. The 100mg per m^2 isoline of chlorophyll-a (Fig. 5.9) corresponded very closely with the 17°C isoline, or outer edge of the front, and therefore much of the area of enhanced larval numbers occurred on the edge or just outside the area dense chlorophyll-a concentration. To some extent the pattern of mean microplankton concentration was similar to that of the chlorophyll, but moderate values were more widespread over the Agulhas Bank (Fig. 5.9). The area of mean abundance of larvae greater than 1000 per $10m^2$ overlapped the the area of enhanced microplankton concentration, but areas of dense microplankton concentrations occurred well inshore of the area where larval numbers were greatest (Fig. 5.10).

The spatial mismatch between larval abundance and plankton standing stocks is of considerable interest. Either fish larvae are in general not able to maintain themselves in the inshore areas because of cold temperatures, upwelling and offshore Ekman transport, or their numbers are reduced by predatory zooplankton, which also produce the juvenile stages on which the larvae predominantly feed; or food availability is not the primary factor in determining larval abundance patterns. Although the greatest concentration of plankton in some months occured within the frontal zone, the concentrations sampled with the Bongo nets

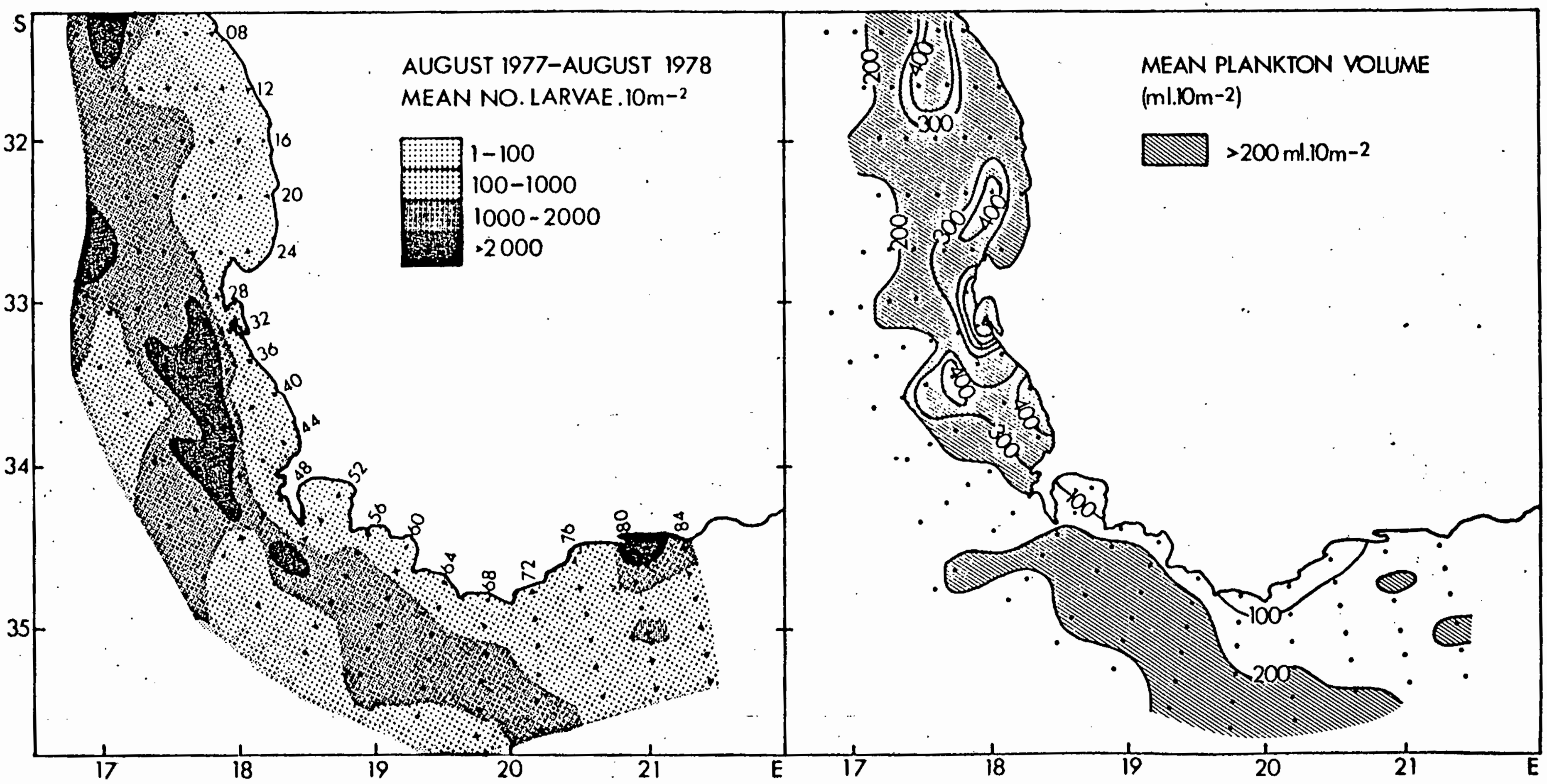


Fig. 5.8 Mean total number of larvae of all species and mean plankton volume over the CELP grid between August 1977 and August 1978.

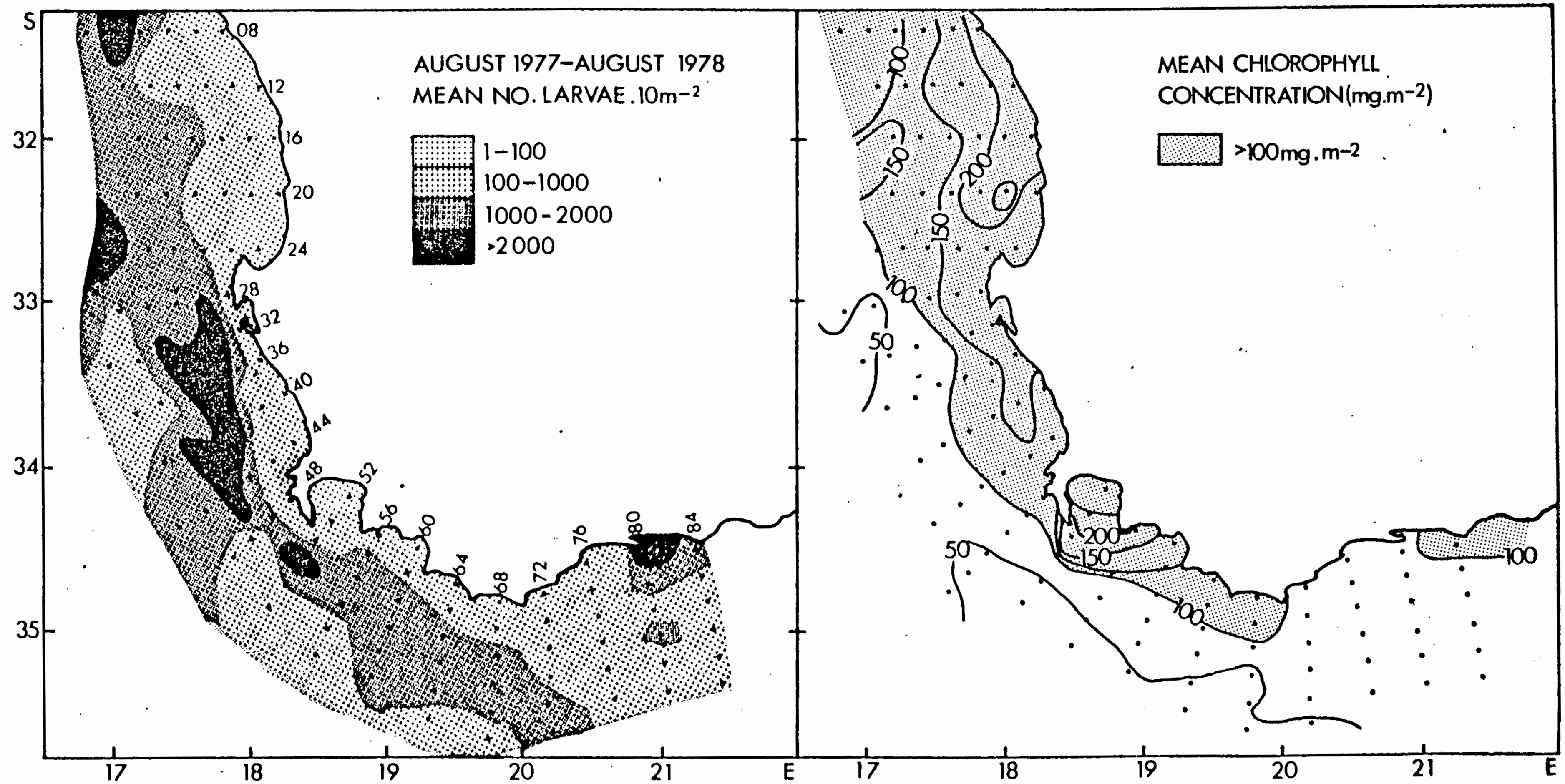


Fig. 5.9 Mean total number of larvae of all species and mean chlorophyll-a concentration over the CELP grid between August 1977 and August 1978.

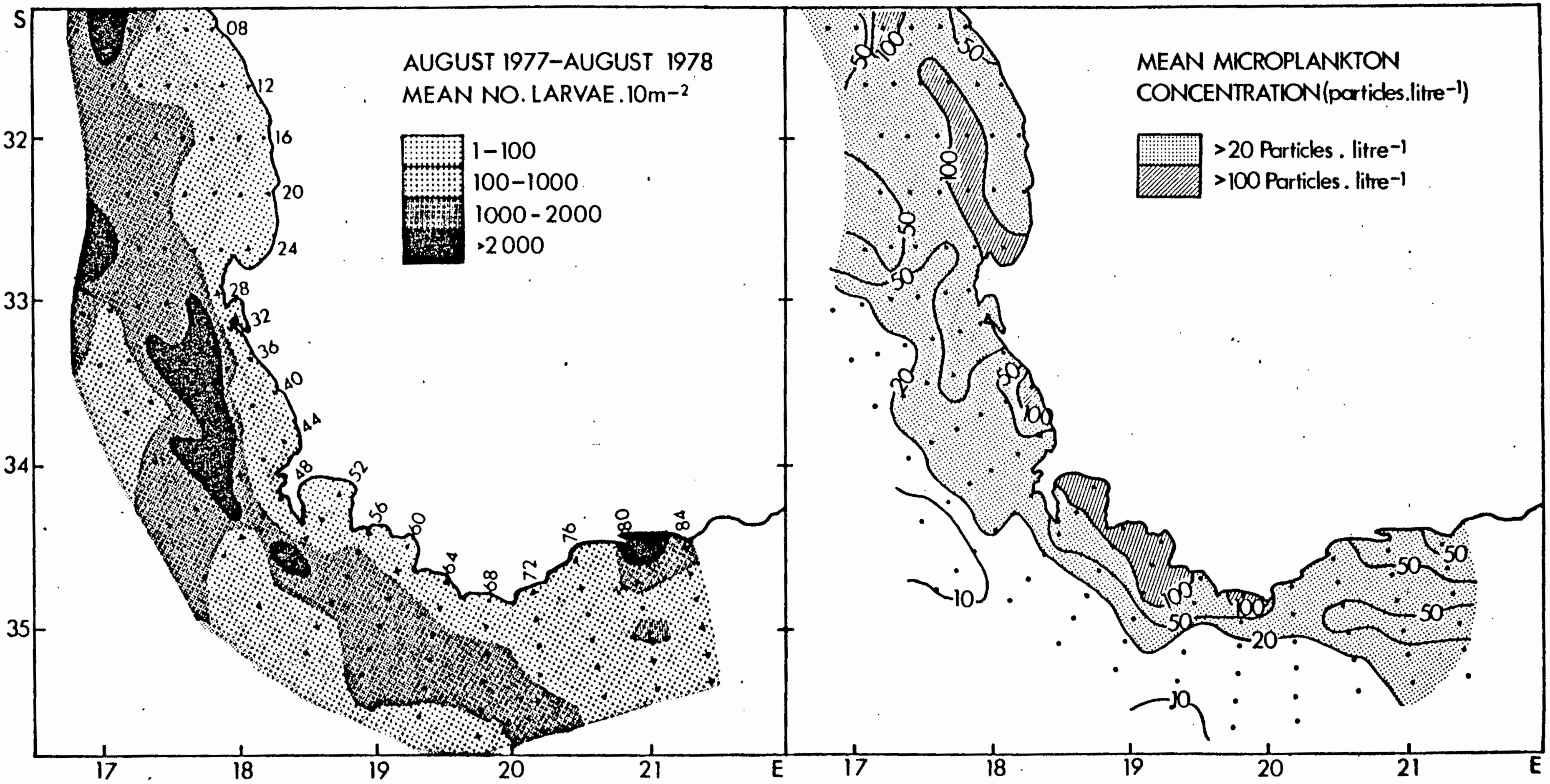


Fig. 5.10 Mean total number of larvae of all species and mean microplankton concentration over the CELP grid between August 1977 and August 1978.

and flights of bottles was often greater inshore of the front. It is possible that sampling of the microscale patchiness of the plankton, using, for example, special bottle arrays such as that designed by Owen (1980), might cast a different light on the abundance patterns of larvae and their food, especially with respect to the front.

The spatial pattern of the mean species diversity of larvae in the samples is compared with various environmental factors in Figs. 5.11-15. The area with a mean species diversity of greater than 10 species per plankton tow corresponded closely with the area in which the water depth exceded 200m (Fig. 5.11). The stations at which a diverse larval assemblage was sampled coincided less closely with the region of elevated SST found offshore of the front (Fig. 5.12), and occurred almost entirely within an area of reduced plankton, chlorophyll-a and microplankton concentrations (Fig, 5.13-15). As indicated in Section 4, the increased diversity of larvae at deep water stations was caused by the increase in the larvae of deep water forms in the samples, although these seldom occurred in large numbers, and is not associated with a higher standing stock of plankton.

Anchovy eggs were most abundant in the plankton in the spring month of October 1977 and the spatial pattern of abundance in this month is compared with environmental factors in Figs. 5.16-20. Since anchovy eggs were most abundant at the inshore stations east of Cape Point, they occurred in the shallow water associated with the Agulhas Bank (Fig. 5.16), and within an SST range of 16°C to 18°C (Fig. 5.17.) In comparison with November 1977 and 1978 and November surveys of the more extensive area in 1983-1985, anchovy eggs were abundant closer inshore in October 1977 than in other months and in other years (see Section 4, Figs. 4.8, 4.9, 4.11 and 4.12). The reason for this is not apparent from an examination of the SST in the various months (see Section 2.1). However, in

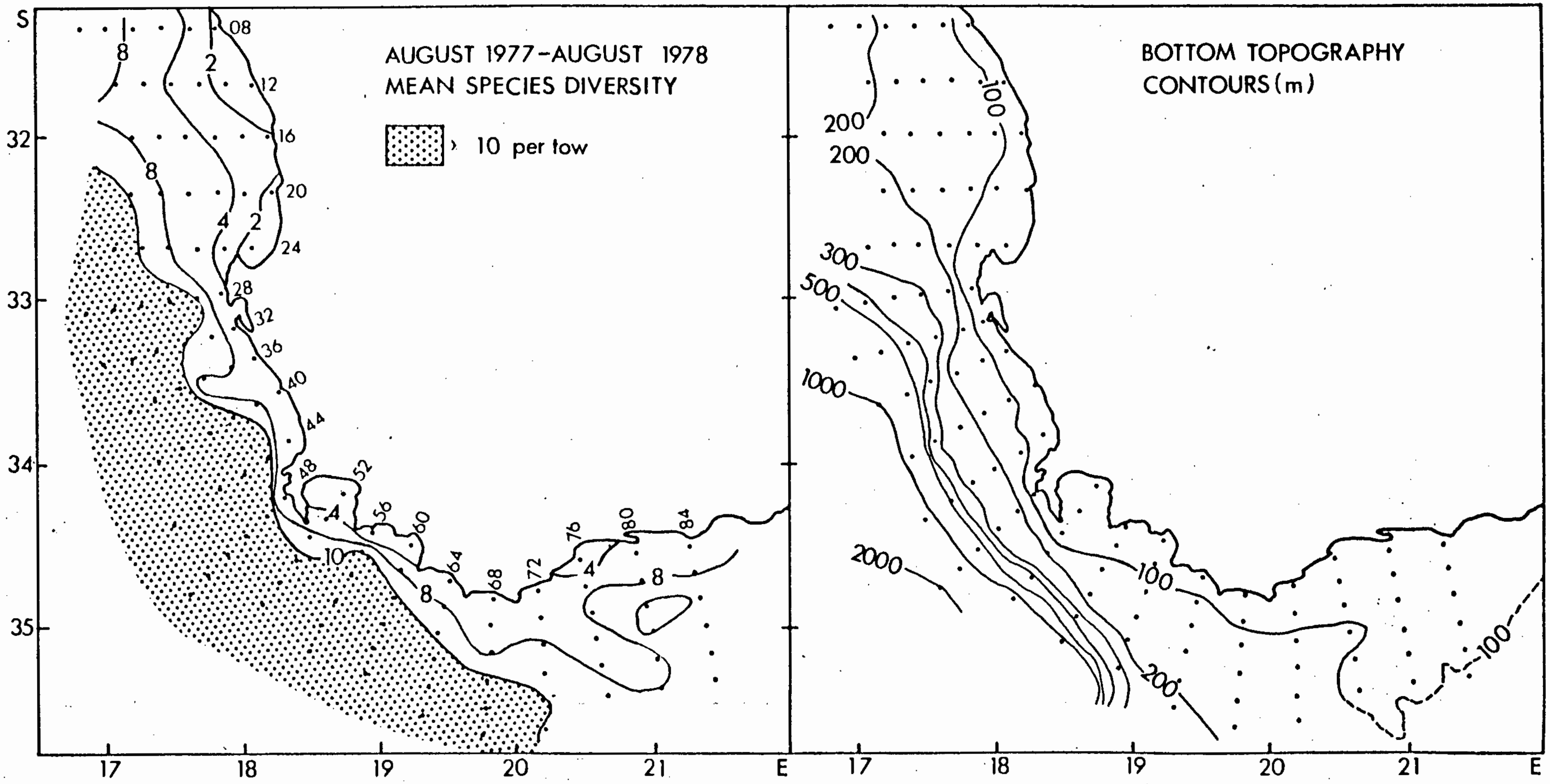


Fig. 5.11 Mean species diversity between August 1977 and August 1978 and bottom topography over the CELP grid.

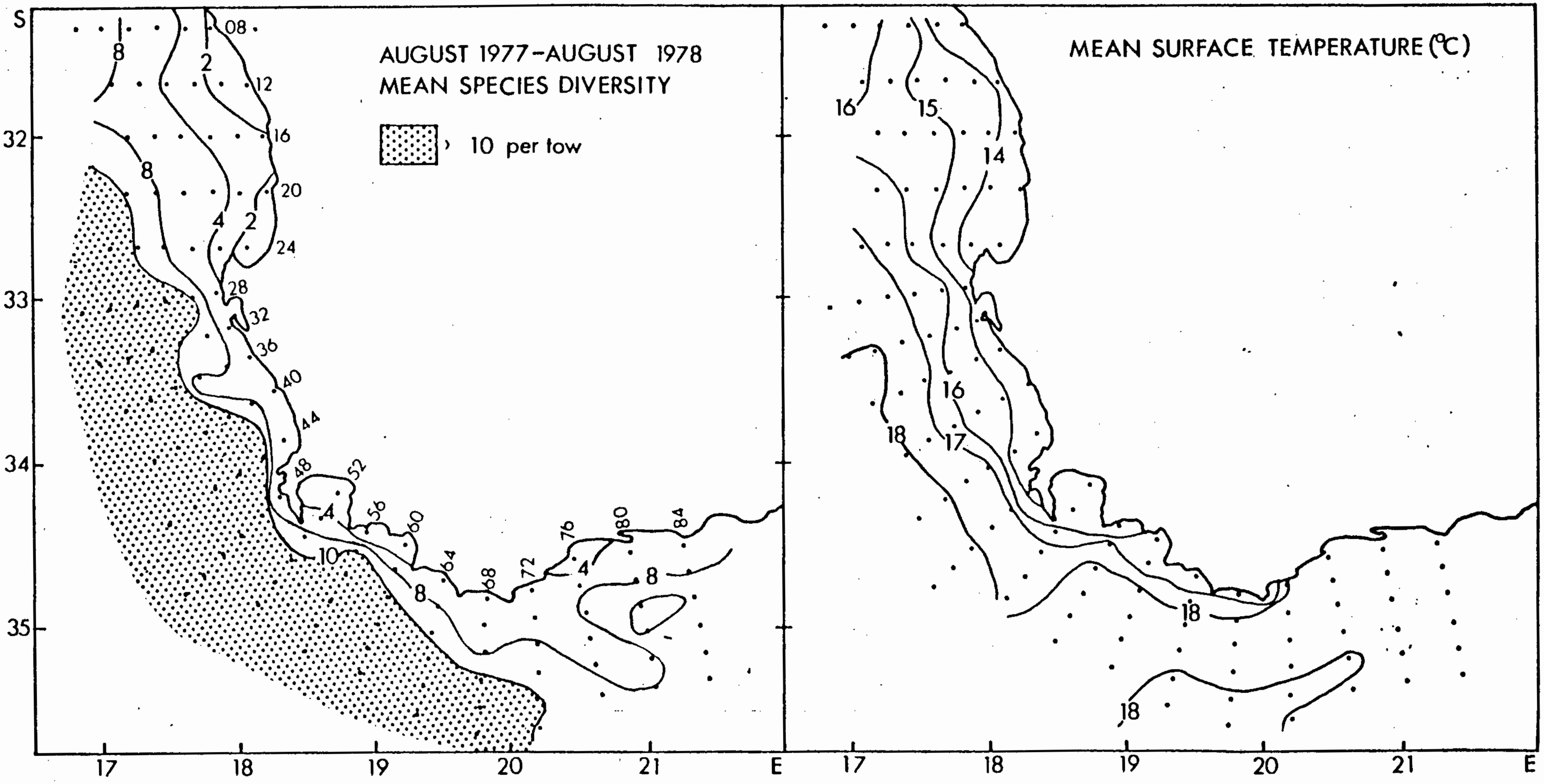


Fig. 5.12 Mean species diversity and mean SST over the CELP grid between August 1977 and August 1978.

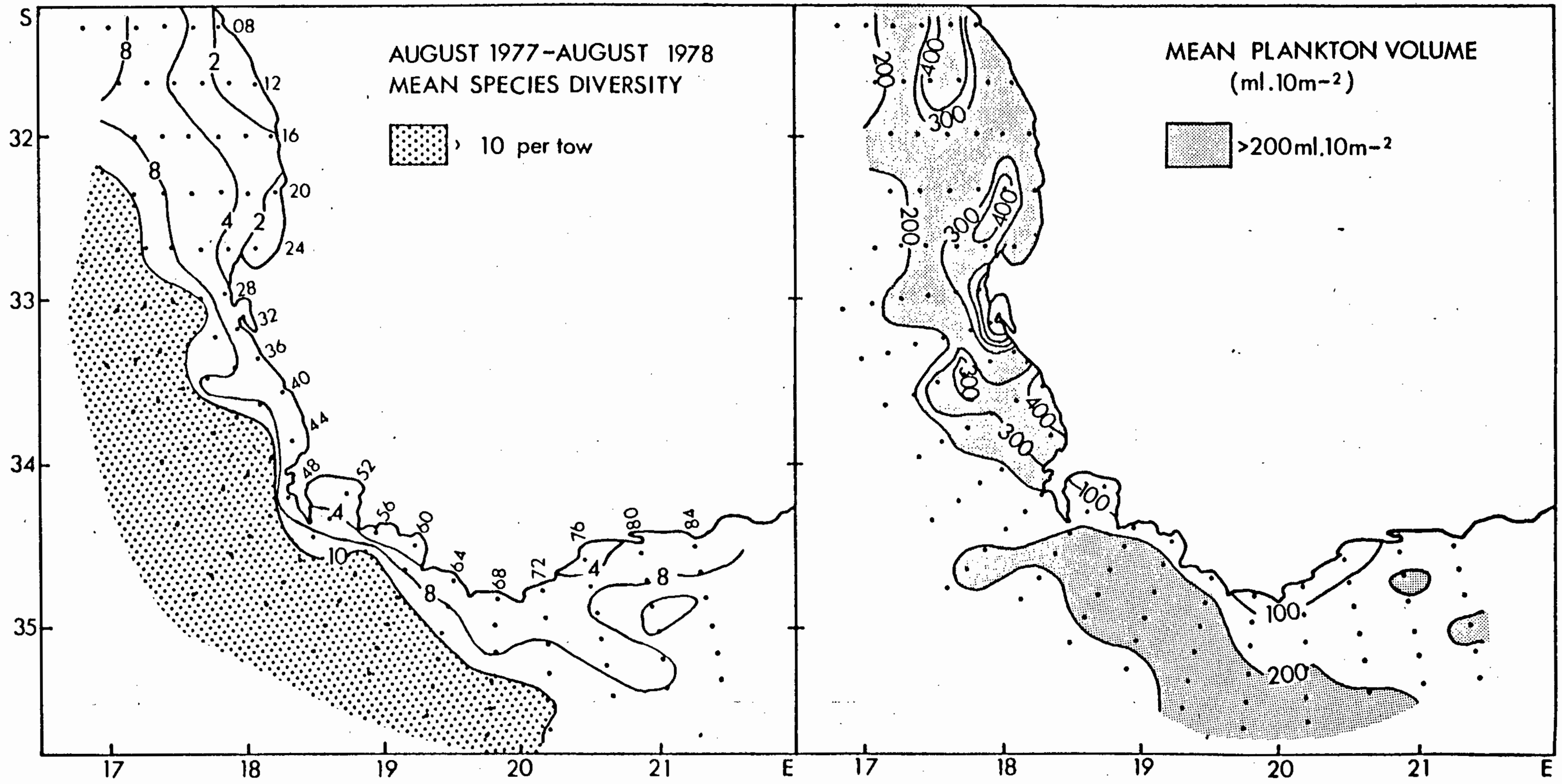


Fig. 5.13 Mean species diversity and mean plankton volume over the CELP grid between August 1977 and August 1978.

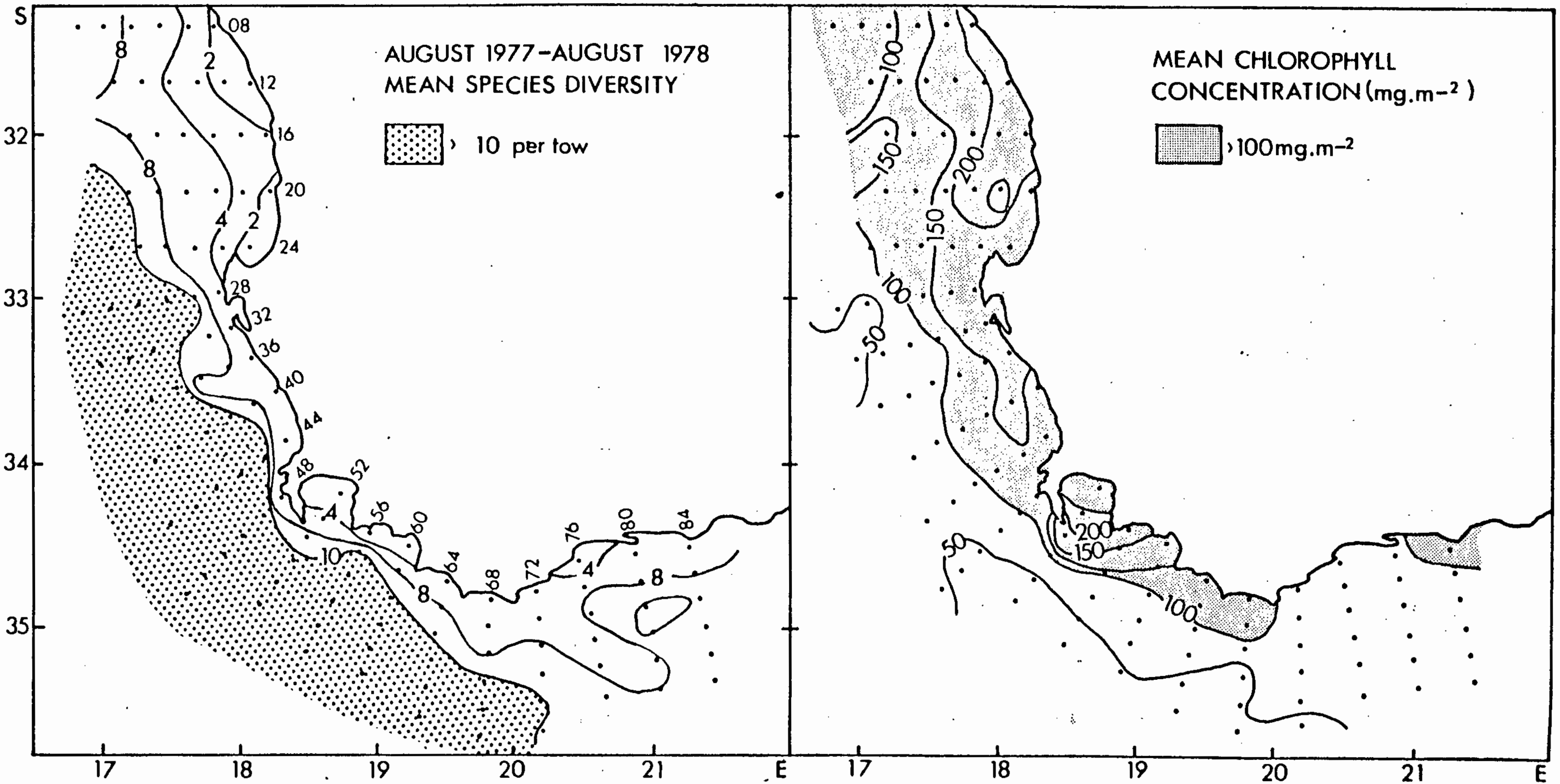


Fig. 5.14 Mean species diversity and mean chlorophyll-a concentration over the CELP grid between August 1977 and August 1978.

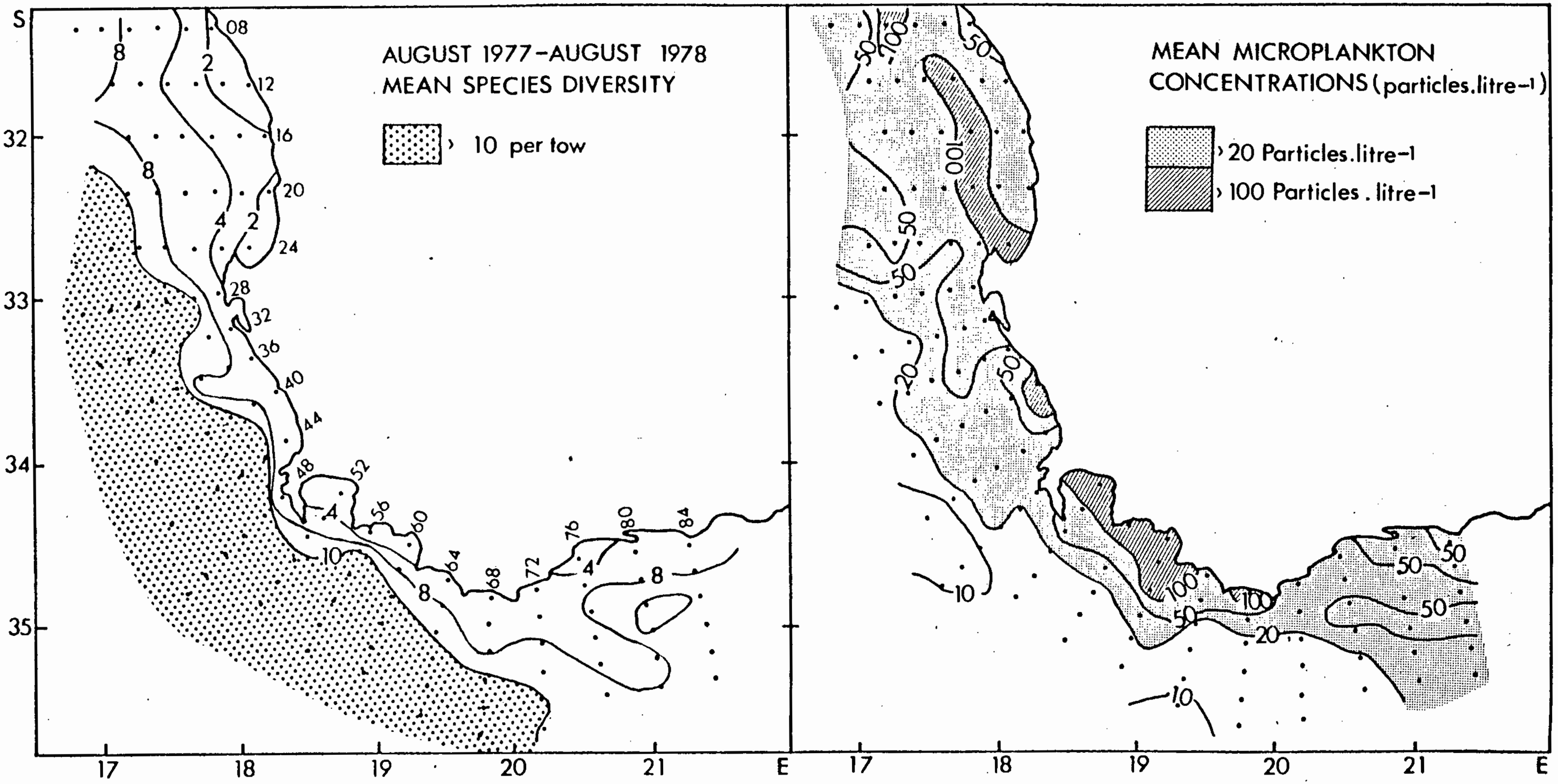


Fig. 5.15 Mean species diversity and mean microplankton concentration over the CELP grid between August 1977 and August 1978.

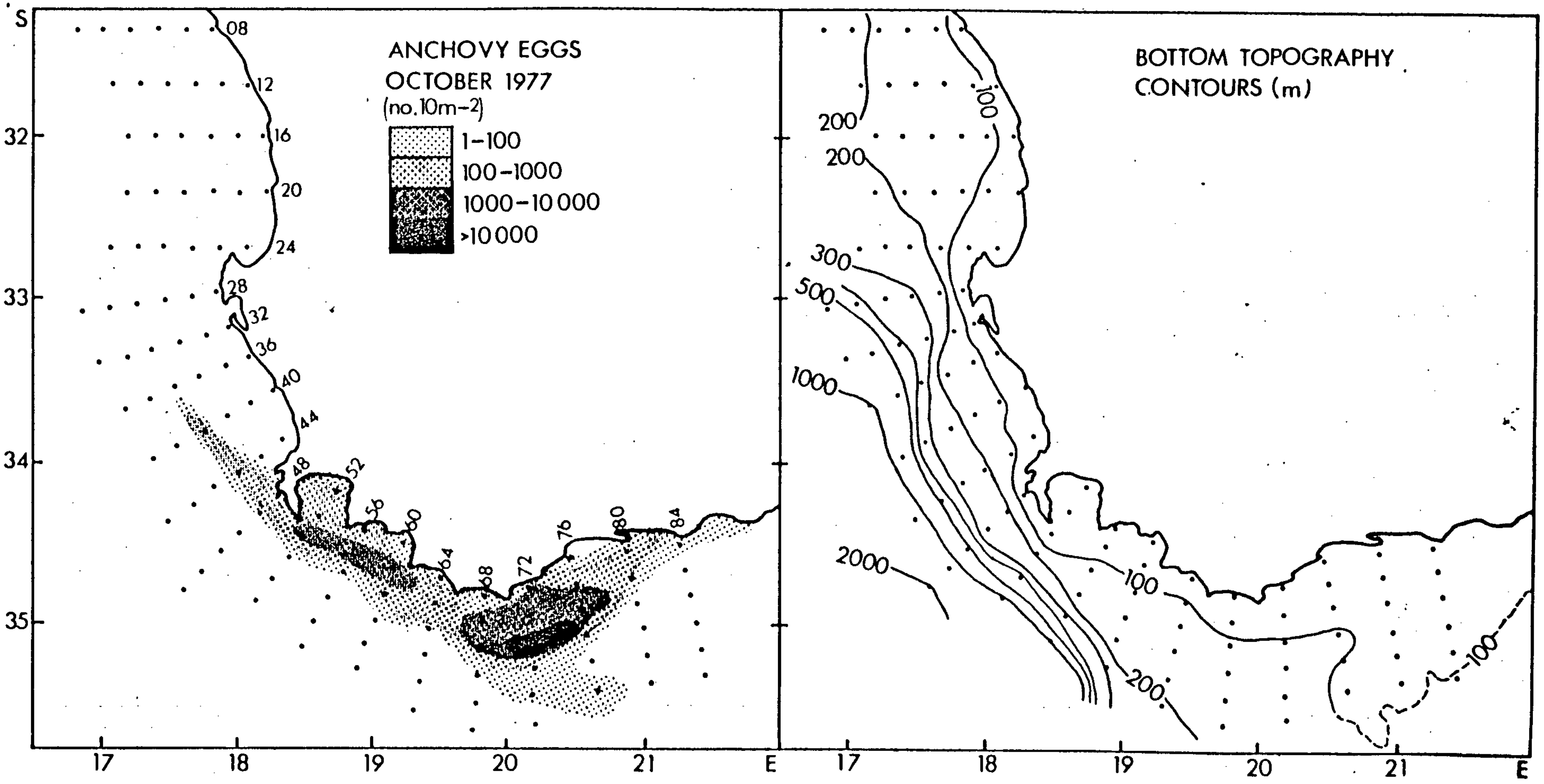


Fig. 5.16 Abundance of anchovy eggs and bottom topography over the the CELP grid in August 1977.

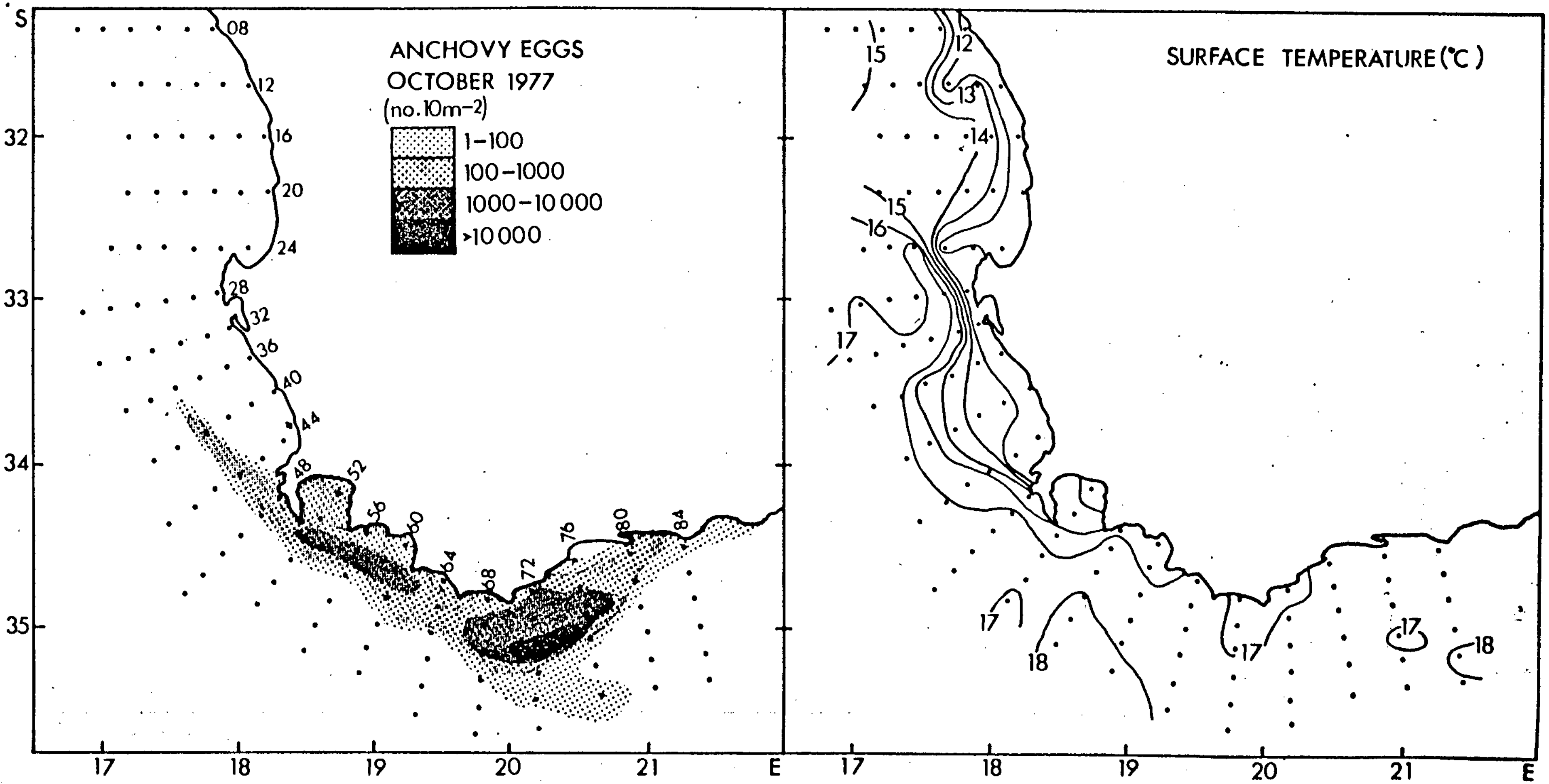


Fig. 5.17 Abundance of anchovy eggs and SST over the CELP grid in August 1977.

October 1977 the water column was well mixed with an almost uniform temperature of 17°C over most of the Agulhas Bank east of Cape Agulhas (Section 2.4, Fig. 2.4.12). By comparison, the characteristic summer vertical temperature structure in this area is an exceptionally strong thermocline at about 50m caused by the simultaneous movement of cold water onto the Bank along the bottom and warm water at the surface (see Section 2.1). The more extensive anchovy surveys carried out in 1983-85 clearly show that anchovy eggs regularly occurred out to the edge of the Agulhas Bank in summer and that abundance is normally greater nearer the edge of the Bank (200m contour) than closer inshore as suggested by the pattern in October 1977. Anchovy eggs were not encountered off the shelf or in areas where undiluted Agulhas Current Water (22°C or warmer) penetrated onto the shelf during the 1983-1985 surveys.

There did not appear to be any relationship between the pattern of abundance of anchovy eggs and plankton volume (Fig. 5.18.), although areas of large plankton volume did overlap areas of large egg abundance. There was some correspondence between the chlorophyl-a 50mg per m^2 isoline and the outer edge of anchovy spawning over the Agulhas Bank (Fig. 5.19). Reduced chlorophyll levels at outer stations of the Agulhas Bank corresponded fairly closely with the area where the upper mixed layer was deeper than 60m (see Section 2.2), suggesting that the reduced plankton concentration may have been a result of nutrient rich water being deeper than the euphotic zone. It is of interest that anchovy did not spawn in the very dense chlorophyll water found in the St Helena Bay area between lines 12 and 24 and inshore on line 36, but rather in water with moderate levels of chlorophyll, normally concentrated into a subsurface layer associated with the thermocline, on the Agulhas Bank. Shelton and Hutchings (1982) have suggested a mechanism whereby anchovy could be transported towards the area of high chlorophyll concentrations in St Helena Bay from the Agulhas Bank spawning area.

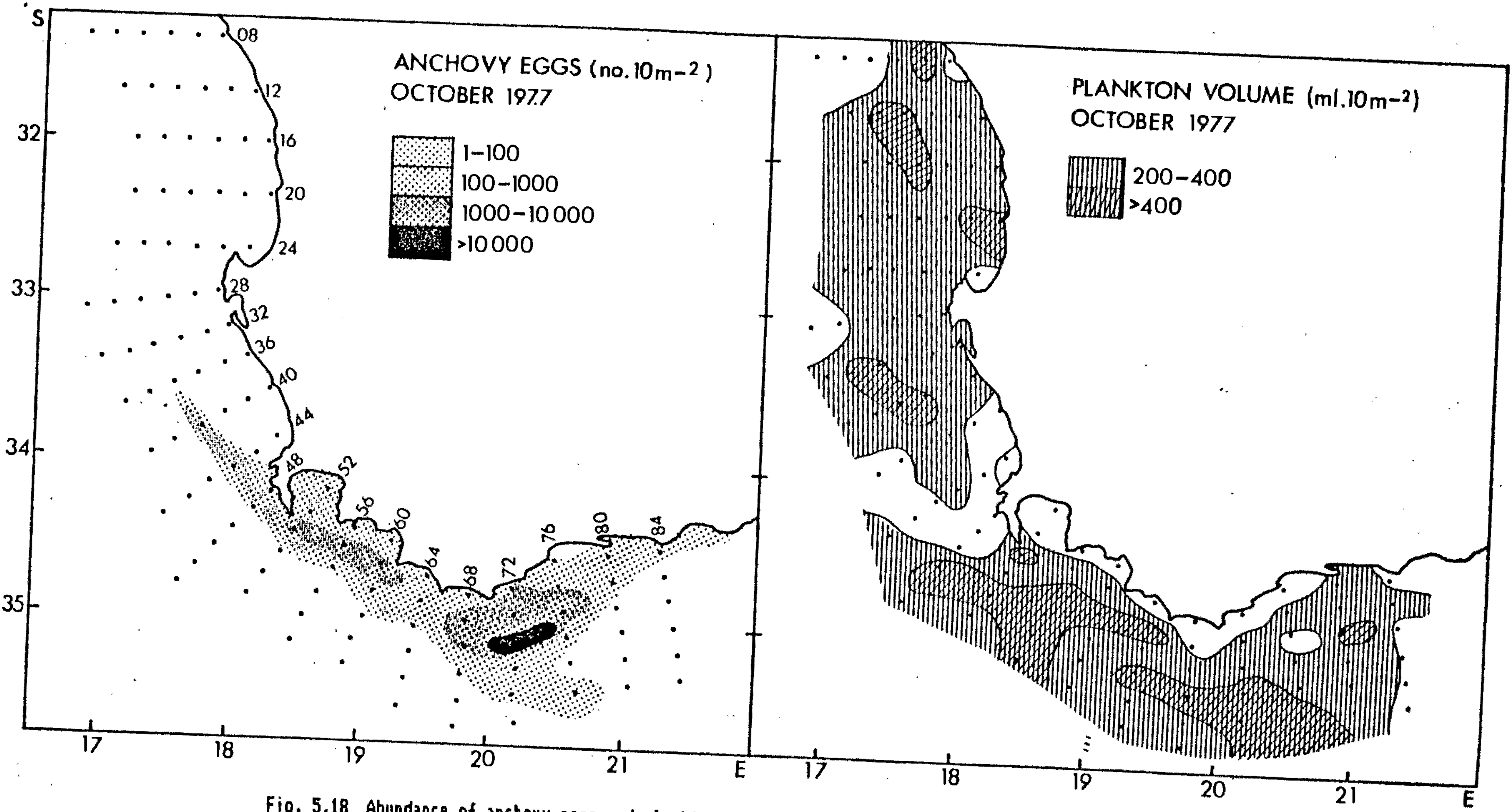


Fig. 5.18 Abundance of anchovy eggs and plankton volume over the CELP grid in August 1977.

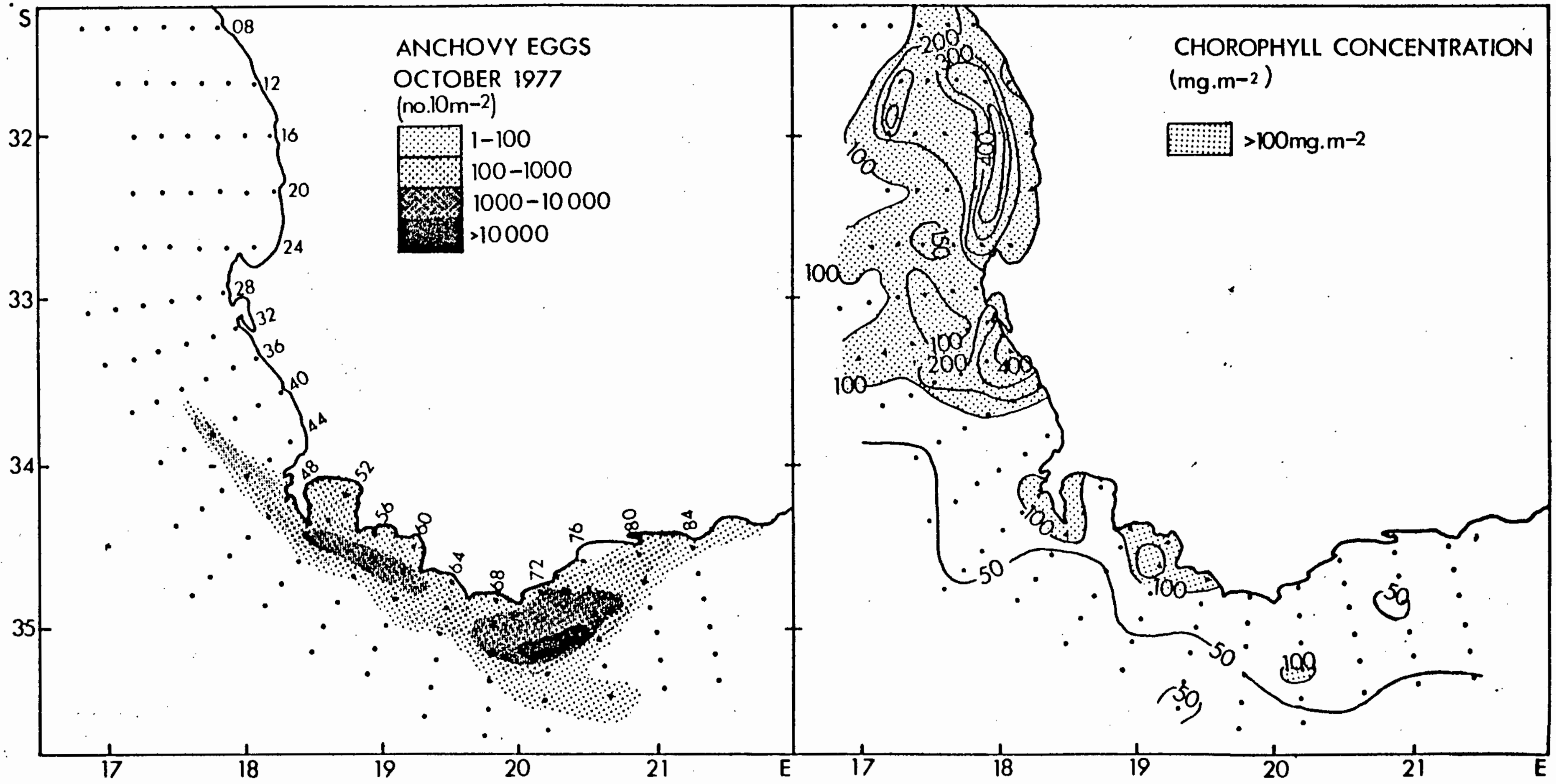


Fig. 5.19 Abundance of anchovy eggs and chlorophyll-a concentration over the CELP grid in August 1977.

The pattern of abundance of microplankton in October 1977 (Fig. 5.20) was very similar to that of chlorophyll with more than 20 particles per litre occurring at inshore stations east of Cape Point in the area where anchovy spawing occurred, and more extensively north of line 36 where anchovy recruiment takes place. The offshore area of the grid over the Agulhas Bank, where the microplankton concentration was less than 10 particles per litre, corresponded reasonably well with the region where the upper mixed layer depth exceeded 60m, as was the case with chlorophyll.

In November 1979 the vertical pattern of abundance of anchovy eggs was examined across the ribbon like area of high abundance, found as a persistent feature on the west coast in the vicinity of the Cape Peninsula during the spawning season, and clearly visible in October 1977. Eggs were concentrated in close proximity to the temperature front (Fig. 5.21). The transect was resampled in November 1980 when the front was less distinct at the surface. The weakening of the front allowed warm water to move onshore, and as a consequence anchovy eggs were found closer to the coast, but still in association with the weak front. Six further stations located in an area of high anchovy egg density on the Agulhas Bank were sampled in November 1984 using an RMT multiple opening and closing net (Fig 5.22). At all stations eggs were abundant in the top 20m of the water colummn. At station A2134 eggs were also abundant at depths of between 50 and 60m, beneath a strong thermocline. In general, eggs were not abundant in water with a temperature of less than 15°C, which corresponded approximately to the bottom of the distinct thermocline which generally extended between a depth of 40 and 50m, but were more abundant within or just above the thermocline.

The reason why anchovy spawn over the shallow Agulhas Bank area, where upwelling is reduced and where dense concentrations of plankton are limited to

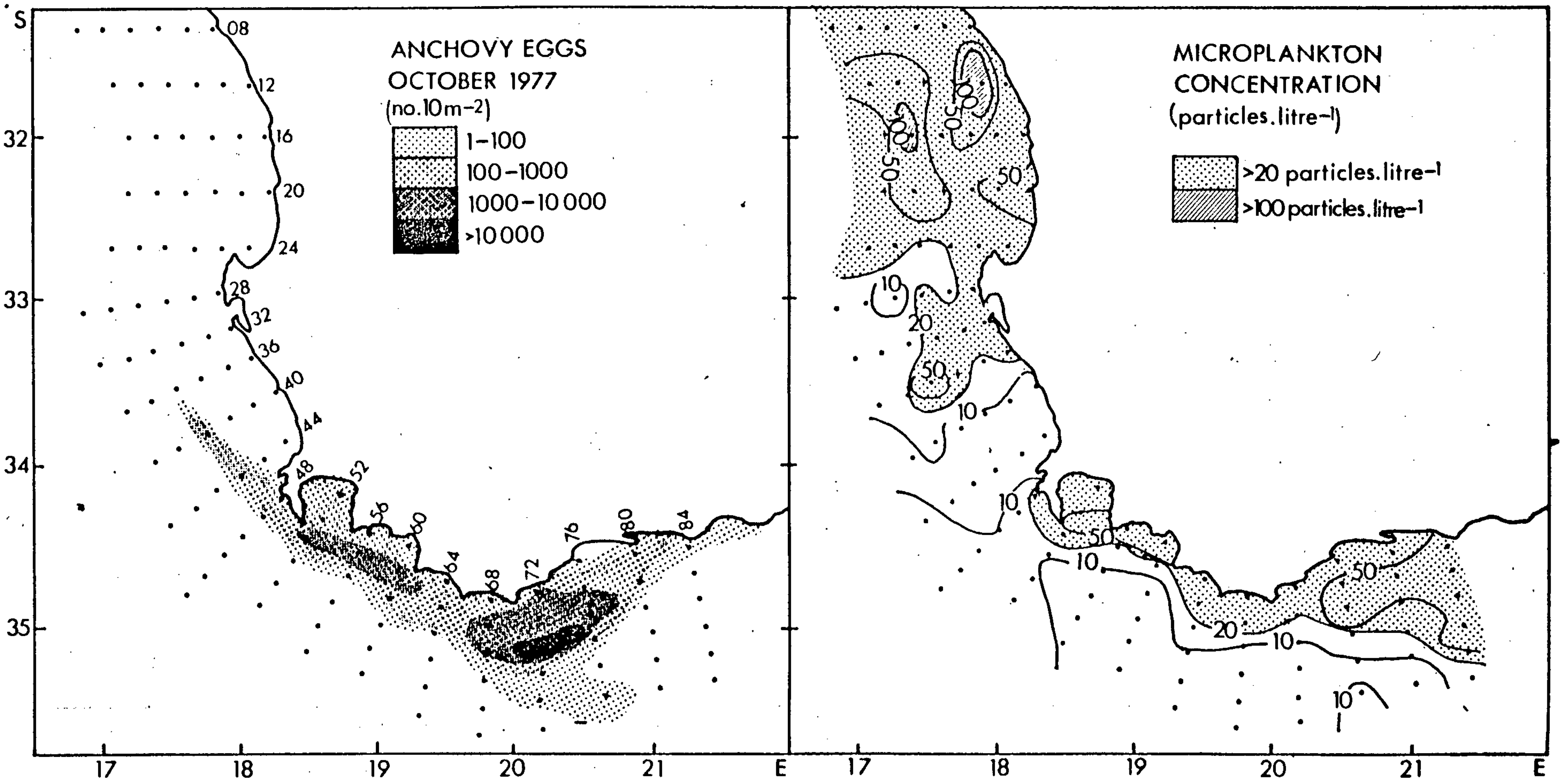


Fig. 5.20 Abundance of anchovy eggs and microplankton concentration over the CELP grid in August 1977.

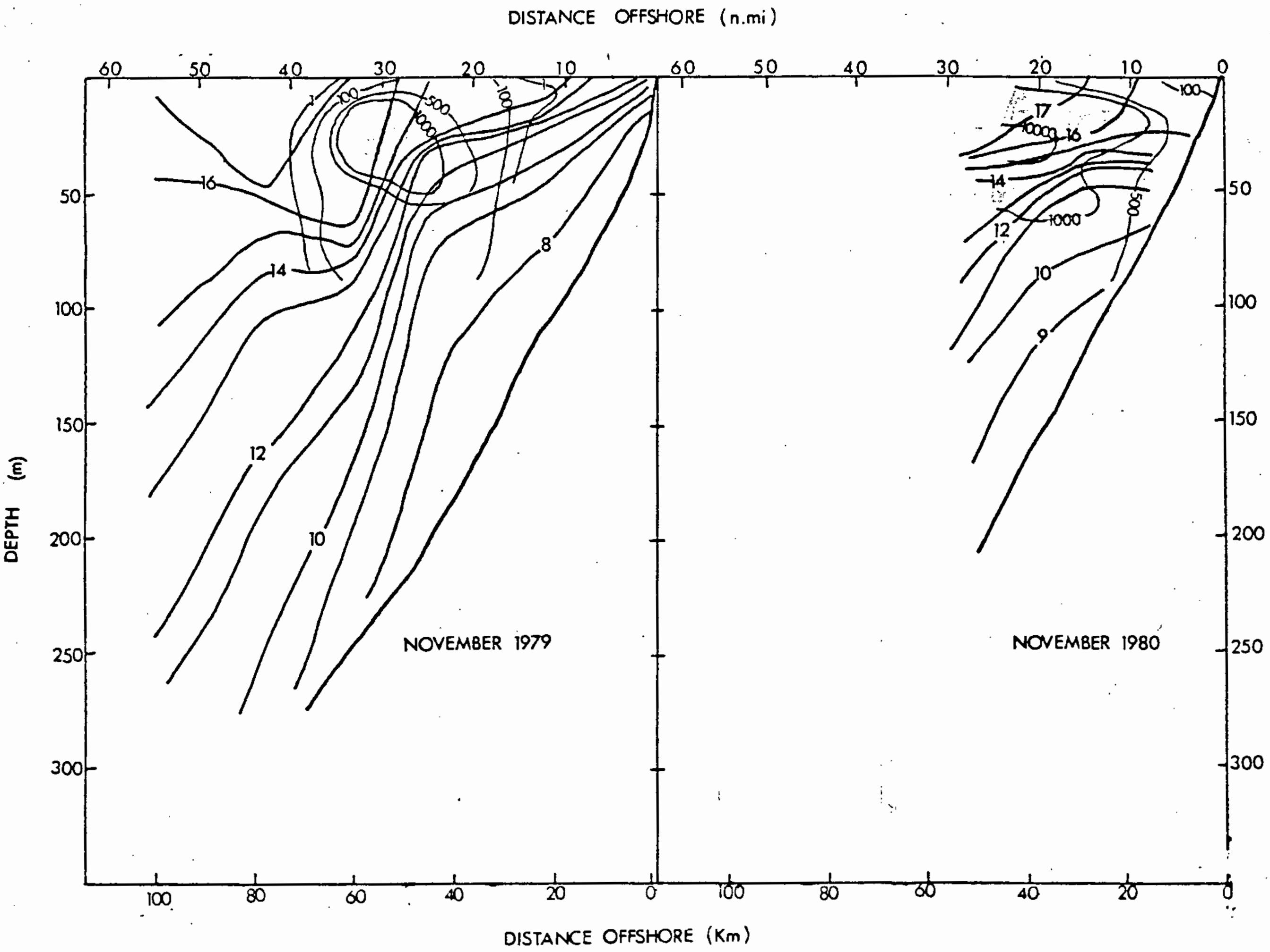


Fig. 5.21 Vertical pattern of abundance of anchovy eggs sampled using Miller nets, and temperature isolines along a line of stations off the Cape Peninsula surveyed in November 1979 and again in November 1980.

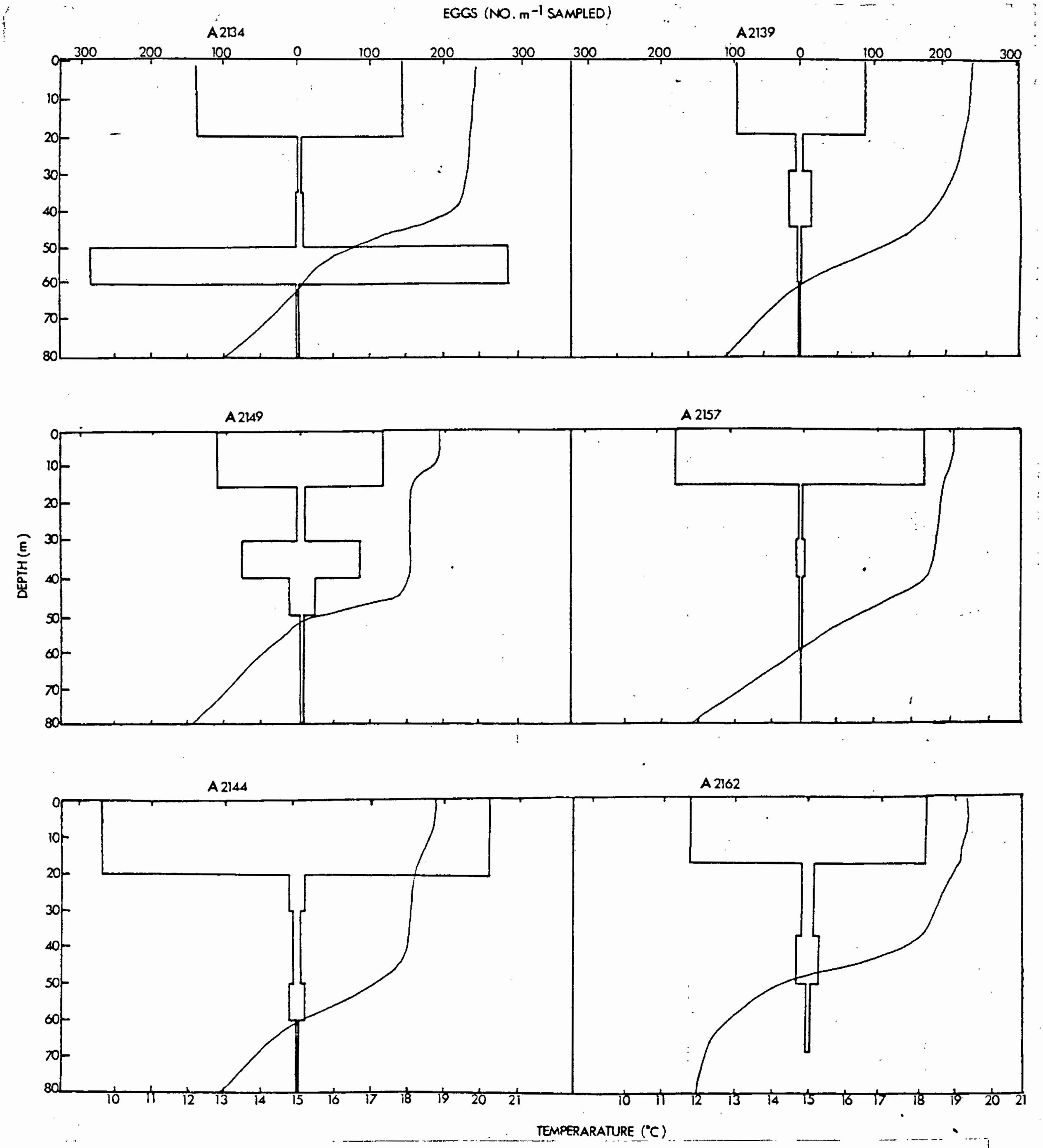


Fig. 5.22 Vertical pattern of abundance of anchovy eggs sampled using an RMT mutltiple opening and closing net, and temperature structre at 6 stations surveyed on the Agulhas Bank in November 1984.

the vicinity of the summer thermocline, may be to avoid the cold temperatures associated with upwelling along the west coast. King et al. 1978 found that normal embryonic development was inhibited at temperatures of 13.6°C and below. In order to make use of the enhanced plankton standing stocks downstream of the southern Benguela region upwelling cèntres off the Cape Peninsula and Cape Columbine, the larvae need to be entrained by the frontal jet current, as demonstrated by Shelton and Hutchings (1982), and transported a considerable distance northwards. An alternative spawning ground would be the broad shelf area north of Cape Columbine, but it is possible that the Agulhas Bank site is favoured because of warmer water associated with the mixing of Agulhas Current Water over the Agulhas Bank, reduced offshore Ekman transport and possibly a greater chance of being entrained into the St Helena Bay eddy after being transported northward in the frontal zone. It is, however, of interest to note that before the precipitous decline of the pilchard in the southern Benguela region, a major spawning ground frequented by the older age classes of pilchard, occurred off Cape Columbine in winter/spring (Anders, SFRI, unpublished charts).

Anchovy larvae were most abundant in the plankton in November/December 1977 and were widespread over the Agulhas Bank and up the west coast, particularly over the shelf break (Fig. 5.23). In relation to SST, anchovy larvae were abundant in the the warm water that covered the Agulhas Bank, particularly in the 22°C water of Agulhas Current origin that penetrated the grid in the south (Fig. 5.24). Along the west coast anchovy larvae were abundant within the frontal zone, which roughly coincided with the position of the shelf break. The significance of the Columbine divergence (see Section 2.5) can be seen from the fact that bottom contours, SST isolines and anchovy larval abunance isolines all diverged offshore in the vicinity of line 24 (Figs. 5.23 and 5.24). As suggested in Section 2.5 and convincingly shown here, the Columbine divergence is an important potential

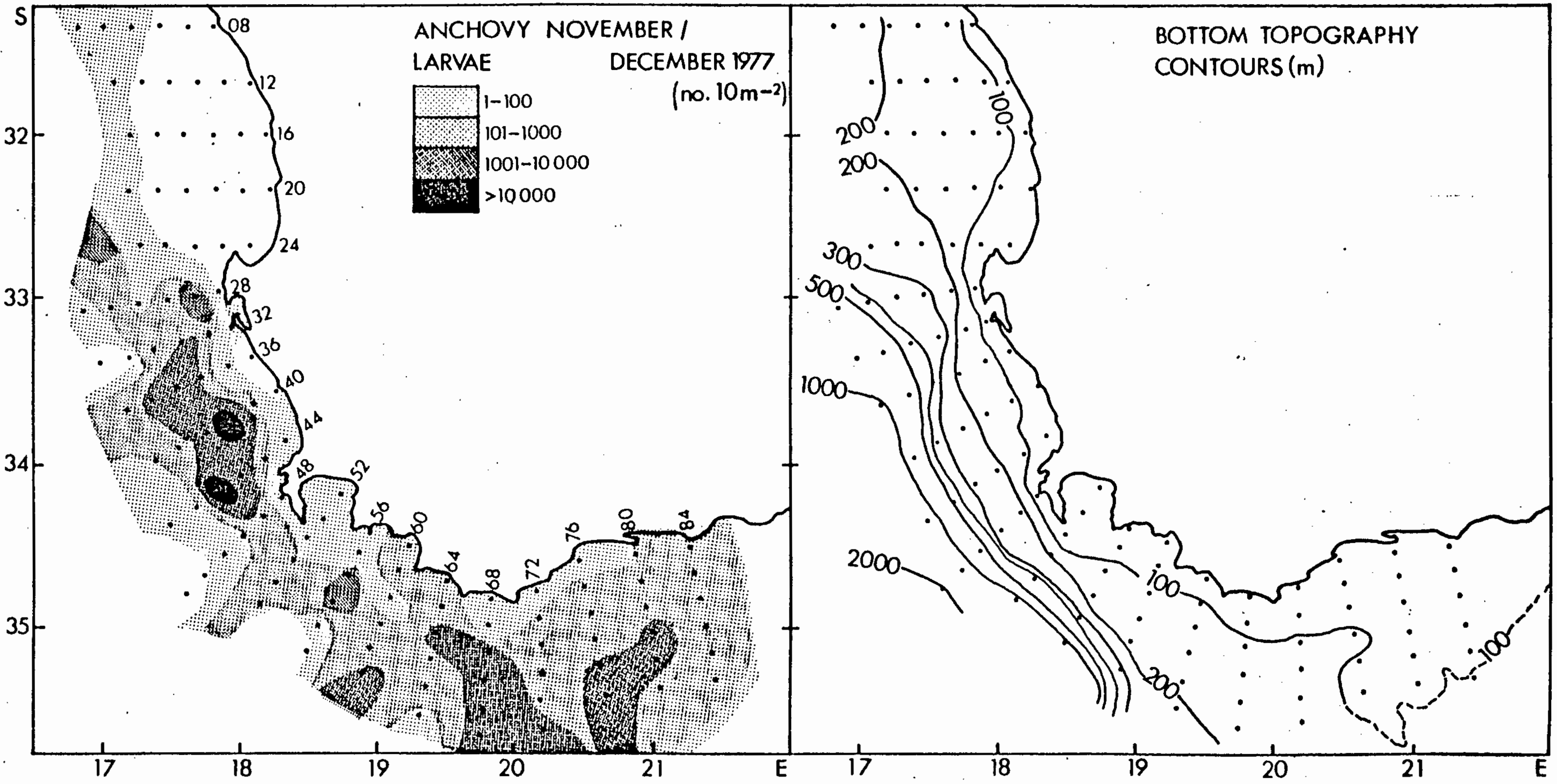


Fig. 5.23 Abundance of anchovy larvae in November/December 1977 and bottom topography over the CELP grid.

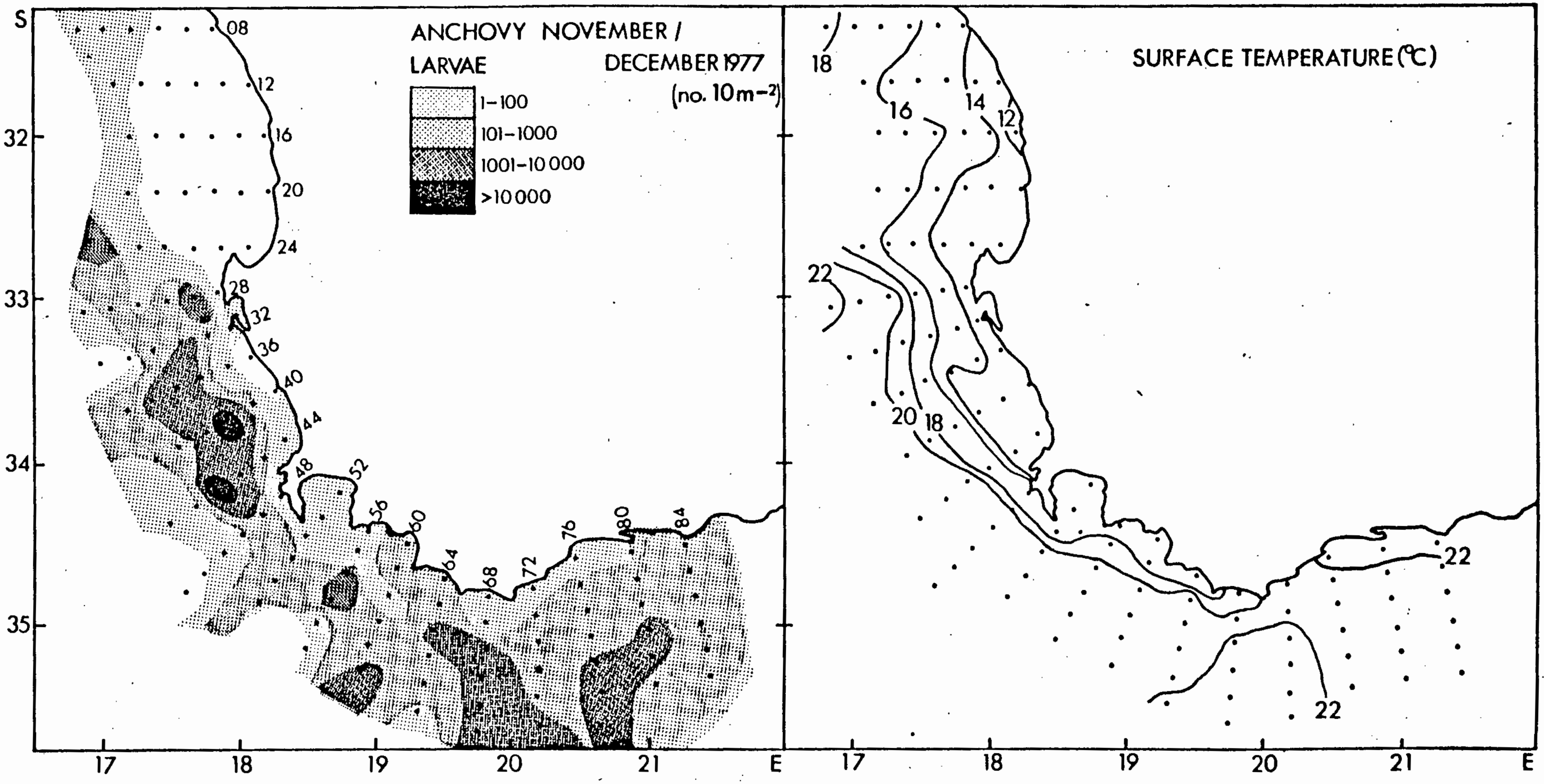


Fig. 5.24 Abundance of anchovy larvae and SST over the CELP grid in November/December 1977.

cause of the loss of larvae from the inshore zone once they have been transported northwards from the Agulhas Bank spawning grounds in the frontal jet. Based on drift card recoveries (see Section 2.2), there is little evidence that these larvae would return to the inshore zone further north. More likely they will be become entrained within the South Atlantic Gyre, as was the fate of a suprisingly high proportion of the drift cards released within the inshore zone, especially in the late winter, spring and summer months. Once in the Gyre their survival rate can be expected to be very poor.

Plankton volume in November/December 1977 was greatest in the vicinity of, and to the north of, Cape Columbine (Fig. 5.25). Larvae up to the size caught by the Bongo sampler were not abundant in this area. Enhanced chlorophyll concentration in November/December 1977 occurred almost entirely within water with a temperature range of less than 20°C, and thus extended west and north of Cape Agulhas (line 72) as an inshore band, broadening offshore in the vicinity of the Columbine divergence and further north (Fig. 5.26). Chlorophyll was particularly abundant in the St Helena Bay region. Anchovy larvae were only abundant along the outer edge of the chlorophyll rich band along the west coast. The pattern of abundance of microplankton in the same month (Fig. 5.27) was similar to that of chlorophyll, with the exception that enhanced levels of miroplankton extended a little further offshore, and therefore overlapped slightly more with the area where anchovy larvae were abundant. The greatest concentrations of microplankton were found in the vicinity of St Helena Bay where early stage anchovy larvae were totally absent.

Since anchovy larvae larger than 10mm were seldom captured by the Bongo sampler, their pattern of abundance was, until recently, unkown until they appear at about 60mm in length in the purse seine fishery, when they are seined

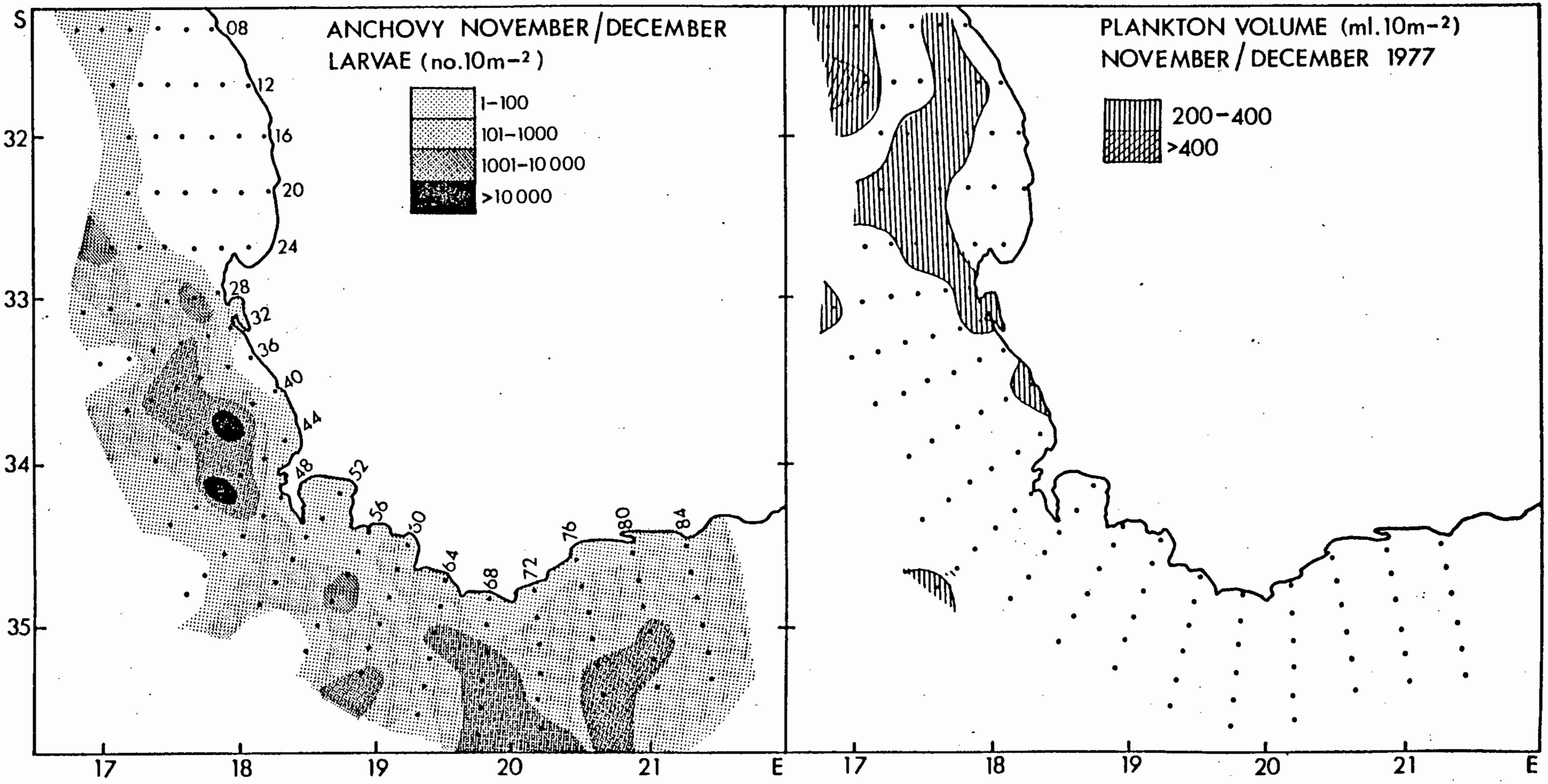


Fig. 5.25 Abundance of anchovy larvae and plankton volume over the CELP grid in November/December 1977.

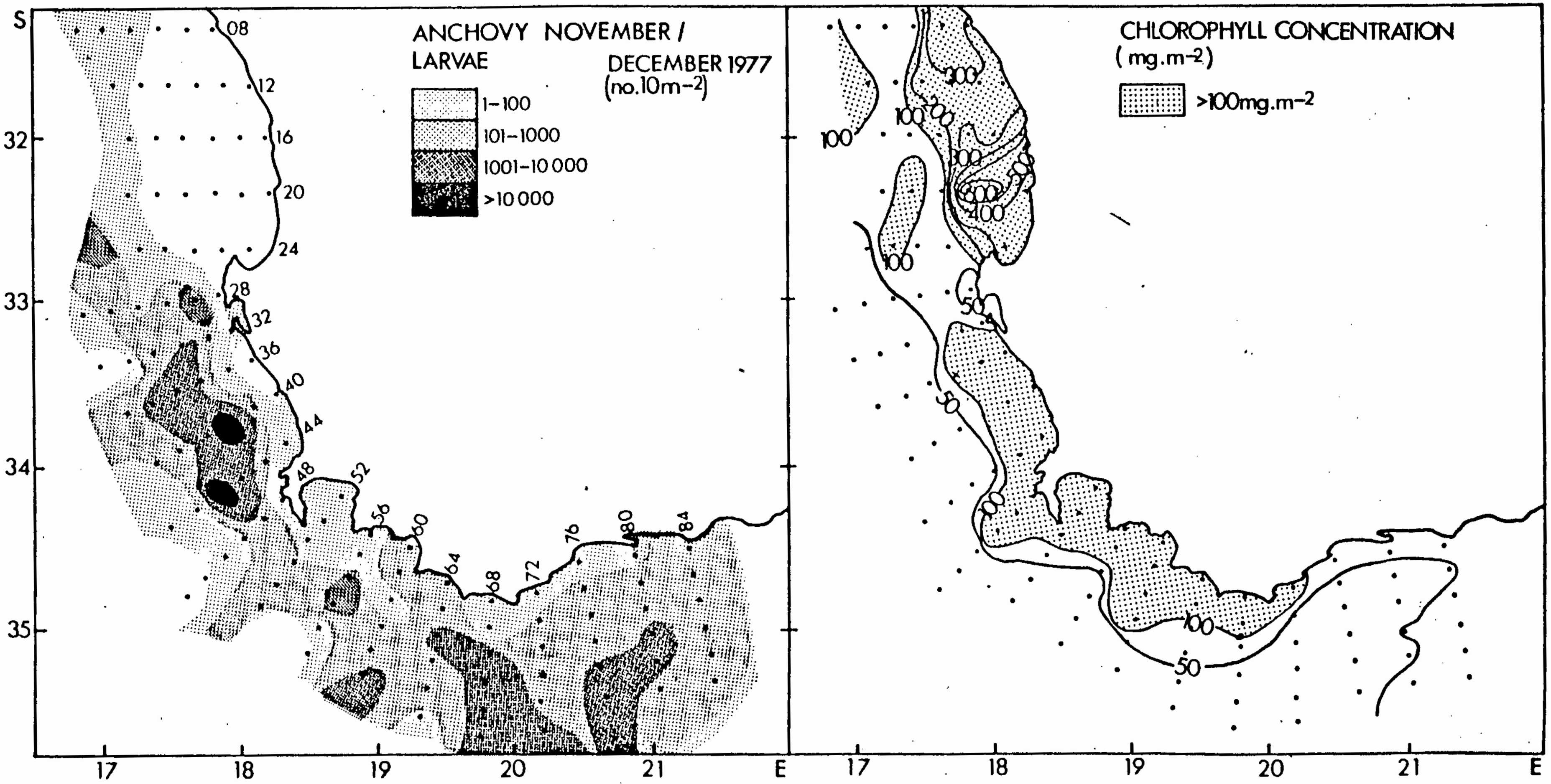


Fig. 5.26 Abundance of anchovy larvae and chlorophyll-a concentration over the CELP grid in November/December 1977.

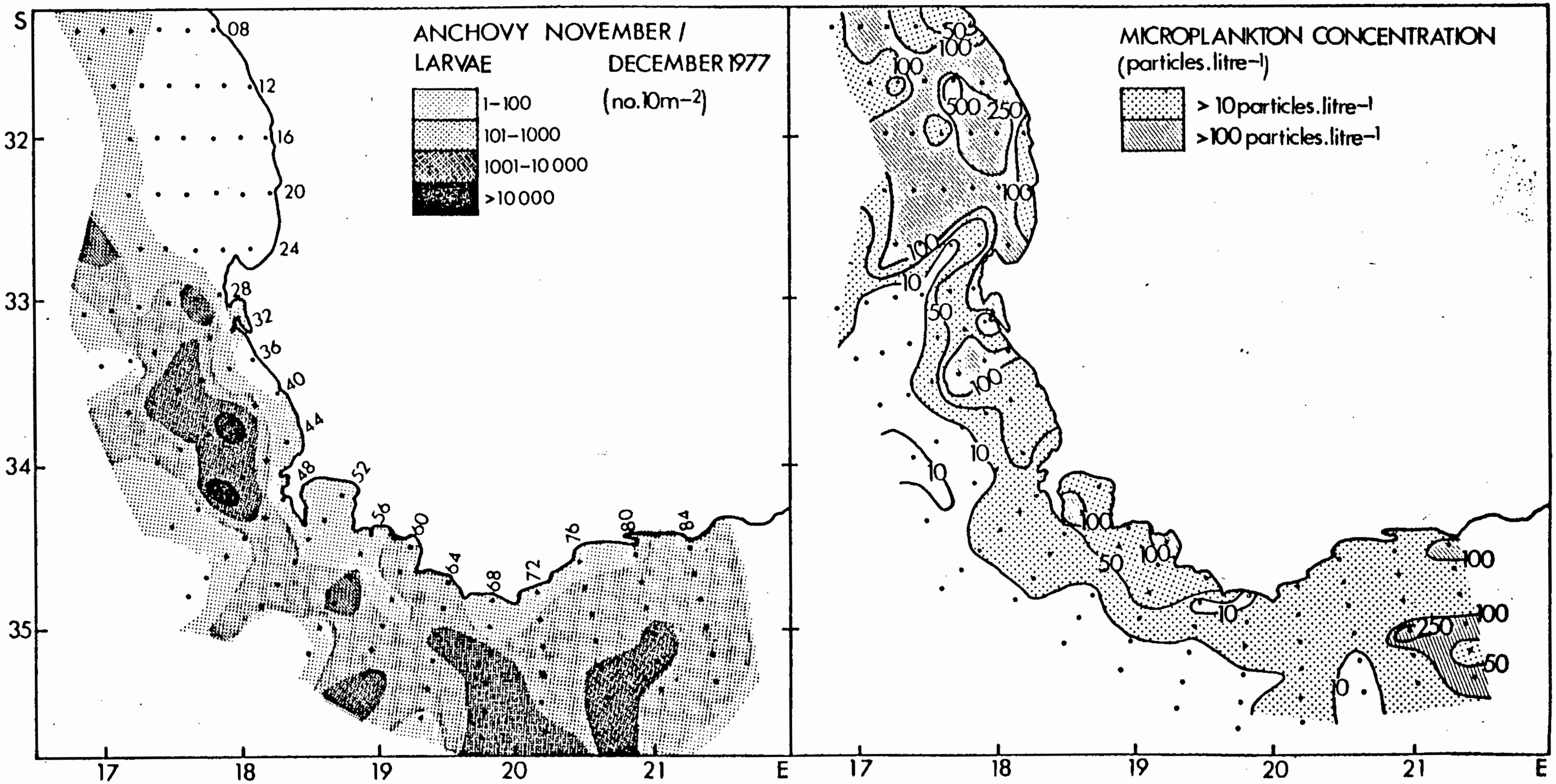


Fig. 5.27 Abundance of anchovy larvae and microplankton concentration over the CELP grid in November/December 1977.

predominantly in inshore waters north of Cape Columbine (Crawford 1980). Recent surveys of anchovy recruits using the RS Africana have confirmed the interpretation of Crawford (1980) and have shown recruits to be abundant at inshore stations from the Cape Peninsula to the Orange River, but particularly in the vicinity of St Helena Bay and the area just north (I. Hampton and M. Armstrong, SFRI, pers. comm.). At some size greater than 10mm anchovy develop the capability to invade and maintain themselves in the coastal zone where plankton standing stocks are consistently well above mean values and where juvenile growth will be rapid.

Lanternfish eggs were most abundant in the plankton in August 1978 and the spatial pattern of abundance shows that spawning was most intense in a band between line 24 and line 56 which roughly followed the shelf break (Fig. 5.28). The area of elevated lanternfish egg abundance broadened and extended further offshore at Cape Columbine (line 28), corresponding to the offshore divergence of the greater than 200m isobaths. The SST structure in August 1978 was typical of winter conditions with cool 15°C water extending out to the edge of the station grid on the west coast and over a large portion of the Agulhas Bank (Fig. 5.29). There was no indication from the SST structure of a divergence off Cape Columbine (line 28). Lanternfish spawning did not occur to any great extent inshore of the of the 14°C isotherm and the southward extent of spawning may have been curtailed by water with an SST range of 16°C-18°C which penetrated the grid between lines 56 and 68. The intrusion of 15°C water on the west coast between lines 28 and 36 coincided quite closely with the greatest concentration of anchovy eggs. Plankton retained by the Bongo sampler was not abundant in the same area as lanternfish eggs, but was instead concentrated closer inshore with plume-like north-westerly extensions off the Cape Peninsula and Cape Columbine, a result of winter upwelling activity (Fig. 5.30). Similarly, chlorophyll-a levels

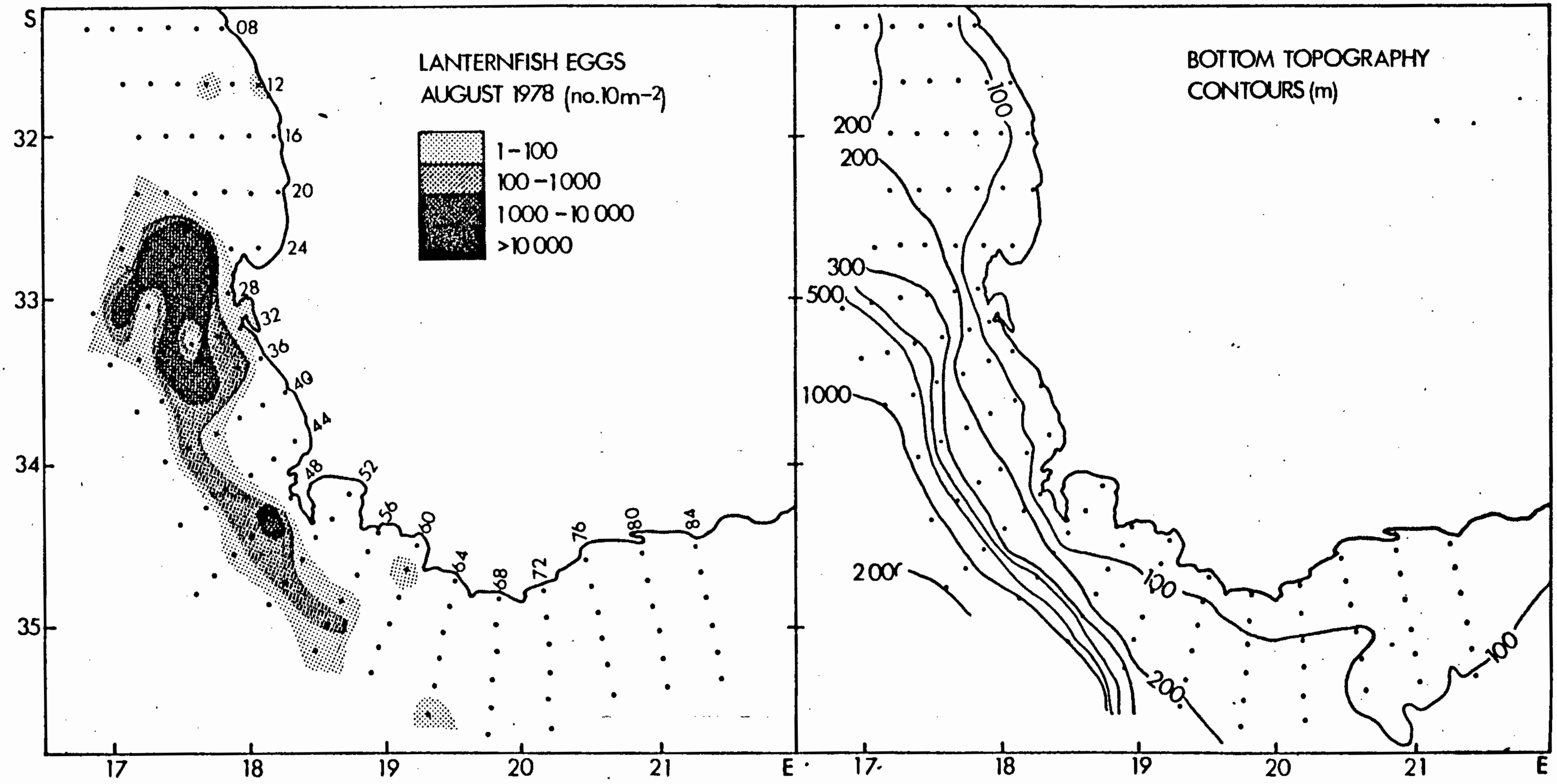


Fig. 5.28 Abundance of lanternfish eggs in August 1978 and bottom topography over the CELP grid.

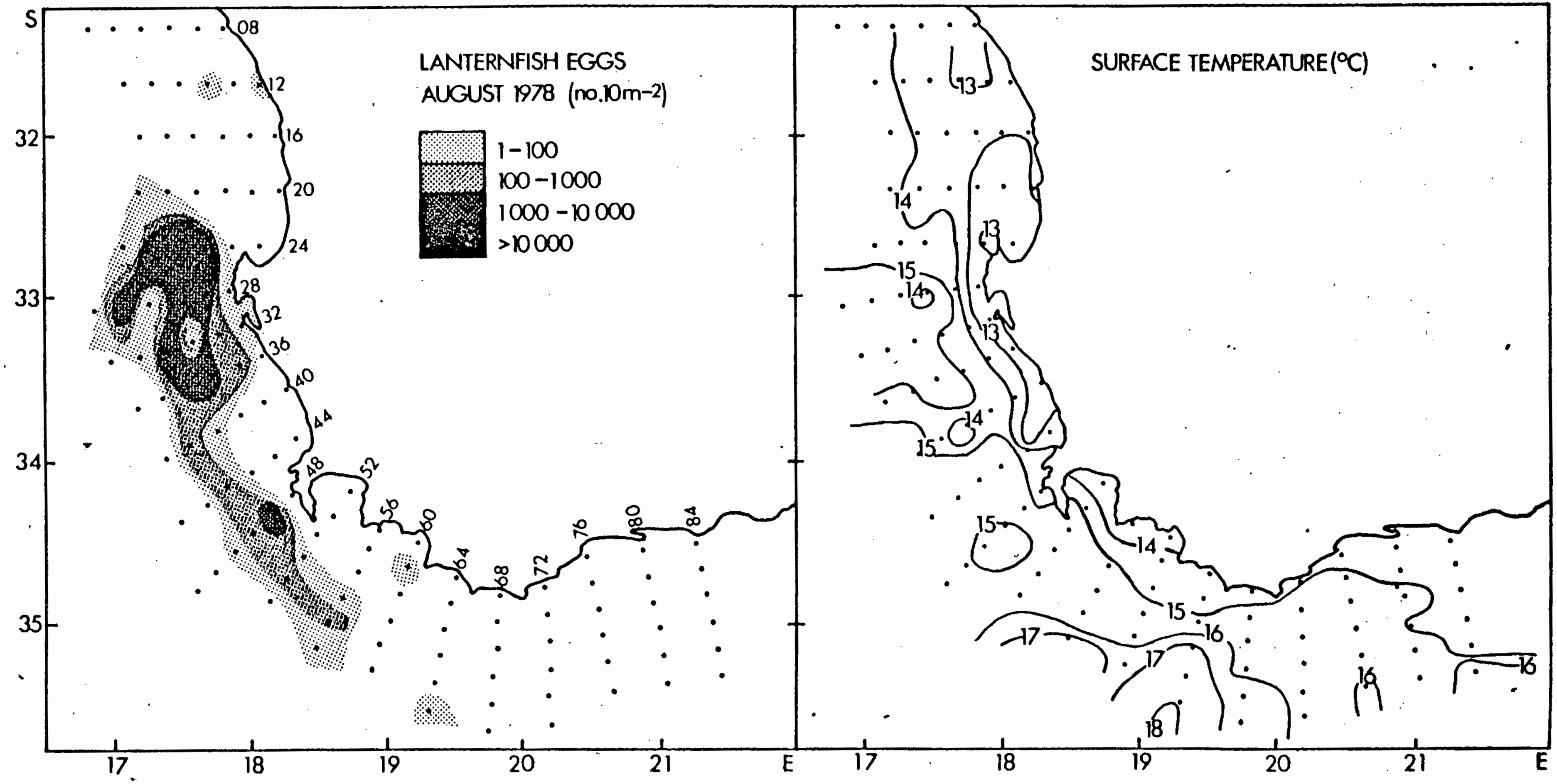


Fig. 5.29 Abundance of lanternfish eggs and SST over the CELP grid in August 1978.

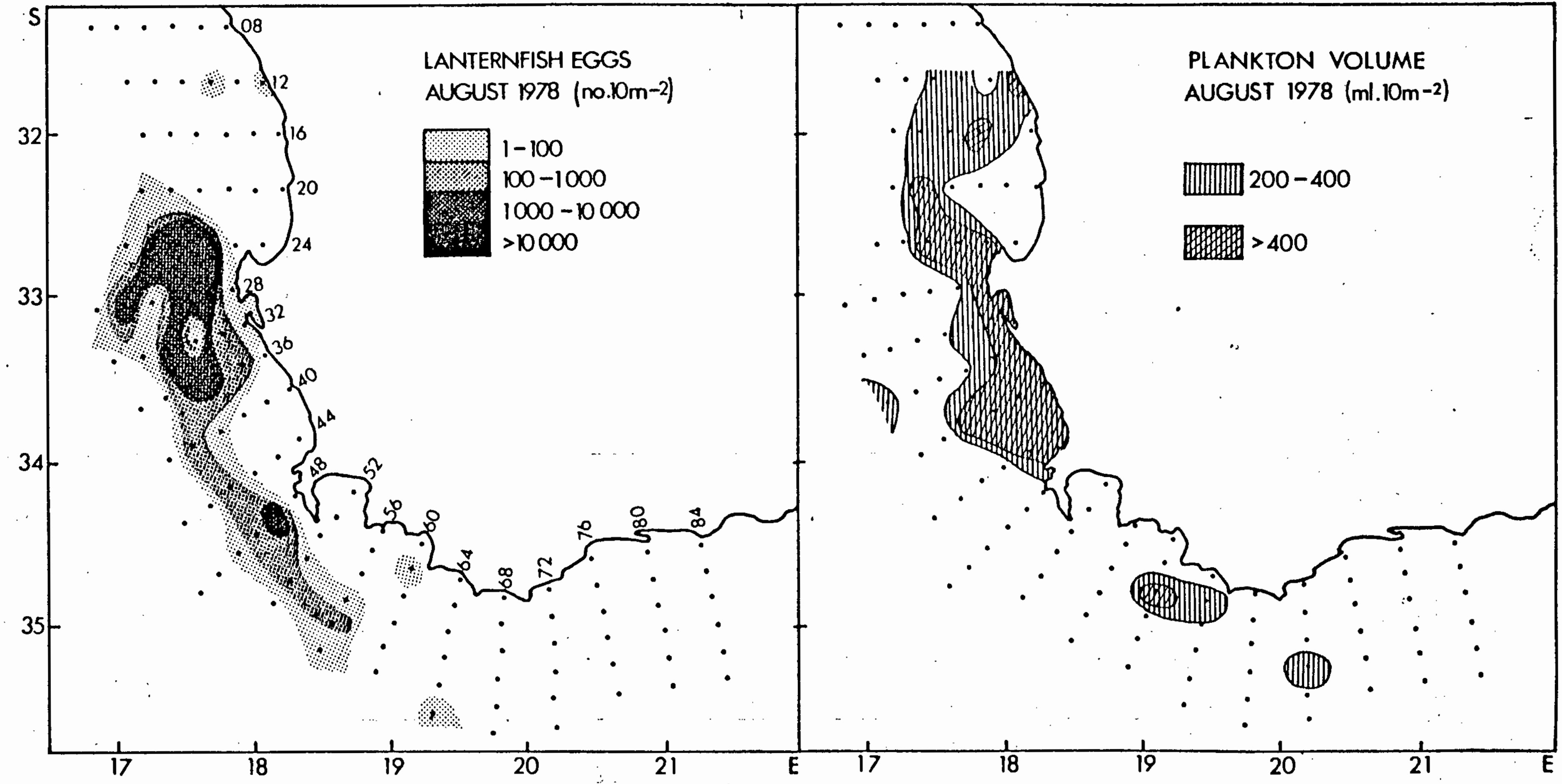


Fig. 5.30 Abundance of lanternfish eggs and plankton volume over the CELP grid in August 1978.

of greater than 100 mg per m^2 only occurred inshore of lanternfish eggs (Fig. 5.31). Chlorophyll-poor water offshore on line 32 overlapped the area where lanternfish eggs were particularly abundant and where an intrusion of slightly warmer water occurred. Chlorophyll levels were greatest in St Helena Bay. Microplankton levels of more than 20 particles per litre was found over a fairly large portion of the survey grid in August 1978 (Fig. 5.32), typical of winter conditions. Concentrations of more than 100 particles per litre were restricted to the inshore area north of the Cape Peninsula, in the vicinity of Cape Columbine and in St Helena Bay. Levels of less than 20 particles per litre coincided with the intrusion of slightly warmer water and minimal chlorophyll concentration off Cape Columbine.

In their comparison of eastern boundary current regions, Parrish et al. (1983) found that spawning anchovy and sardine (pilchard) avoid areas of turbulent mixing and offshore transport. Although CELP data on the effect of the wind represent limited samples during the spawning season, rather than means over longer periods, it can be seen from the data for October 1976 that anchovy eggs tended to be most abundant where the Ekman velocity was zero or near zero (Fig. 5.33). By comparison, during August 1978, when lantern fish spawning was at a maximum, there was a considerable amount of onshore transport as well as some offshore transport at stations where lanternfish eggs were most abundant. No meaningful relationships between the amount of turbulence or the depth of the upper mixed layer (partly a function of turbulence) could be detected from the data collected simultaneously with the plankton samples. While the disadvantage of offshore tranport in anchovy is clear, since recruitment takes place in the highly productive inshore waters, in the case of lanternfish, a degree of onshore transport from the spawning ground, which occurs some distance from the coast, may be advantageous in keeping larvae close to the region of enhanced plankton

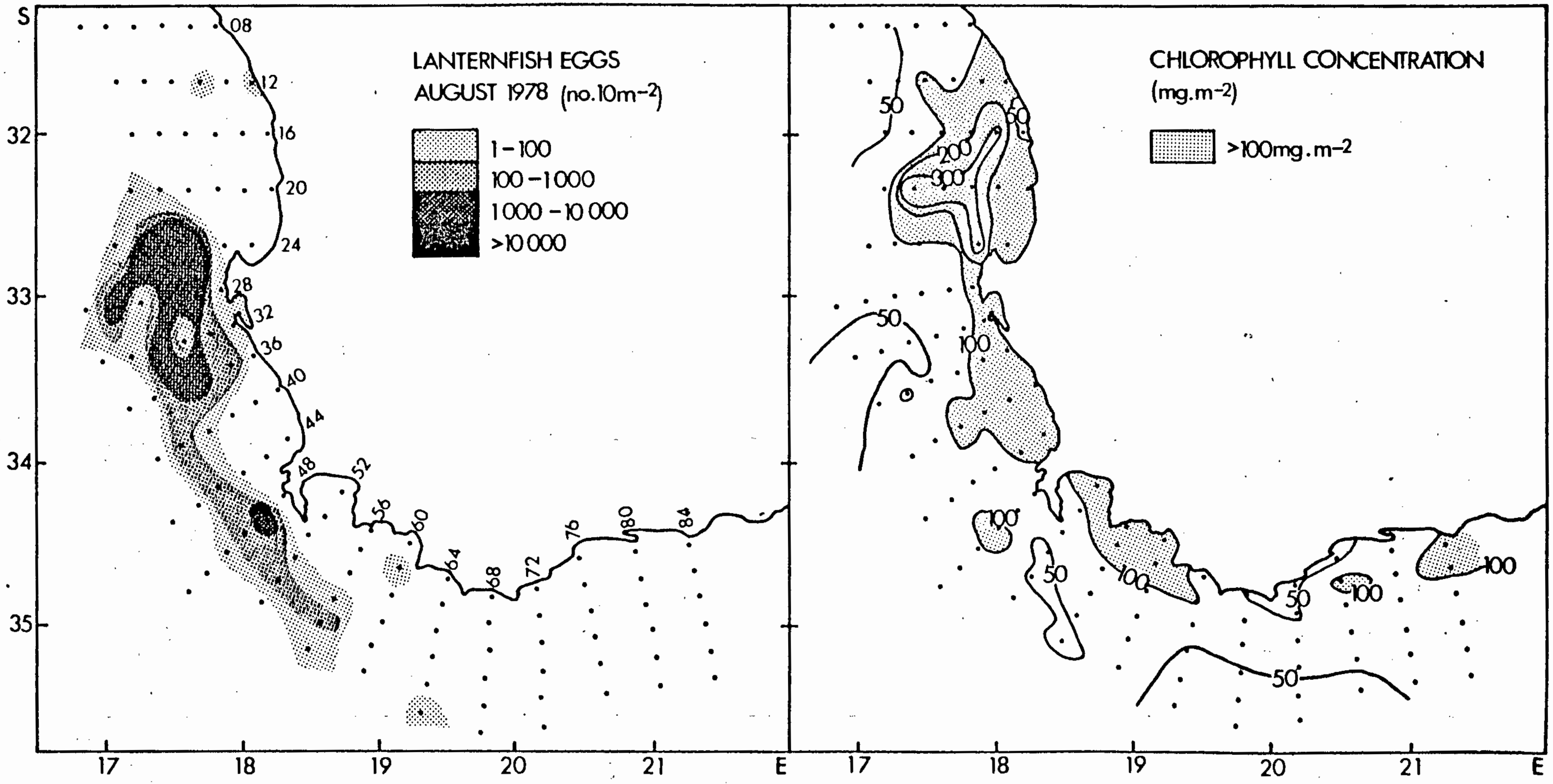


Fig. 5.31 Abundance of lanternfish eggs and chlorophyll-a concentration over the CELP grid in August 1978.

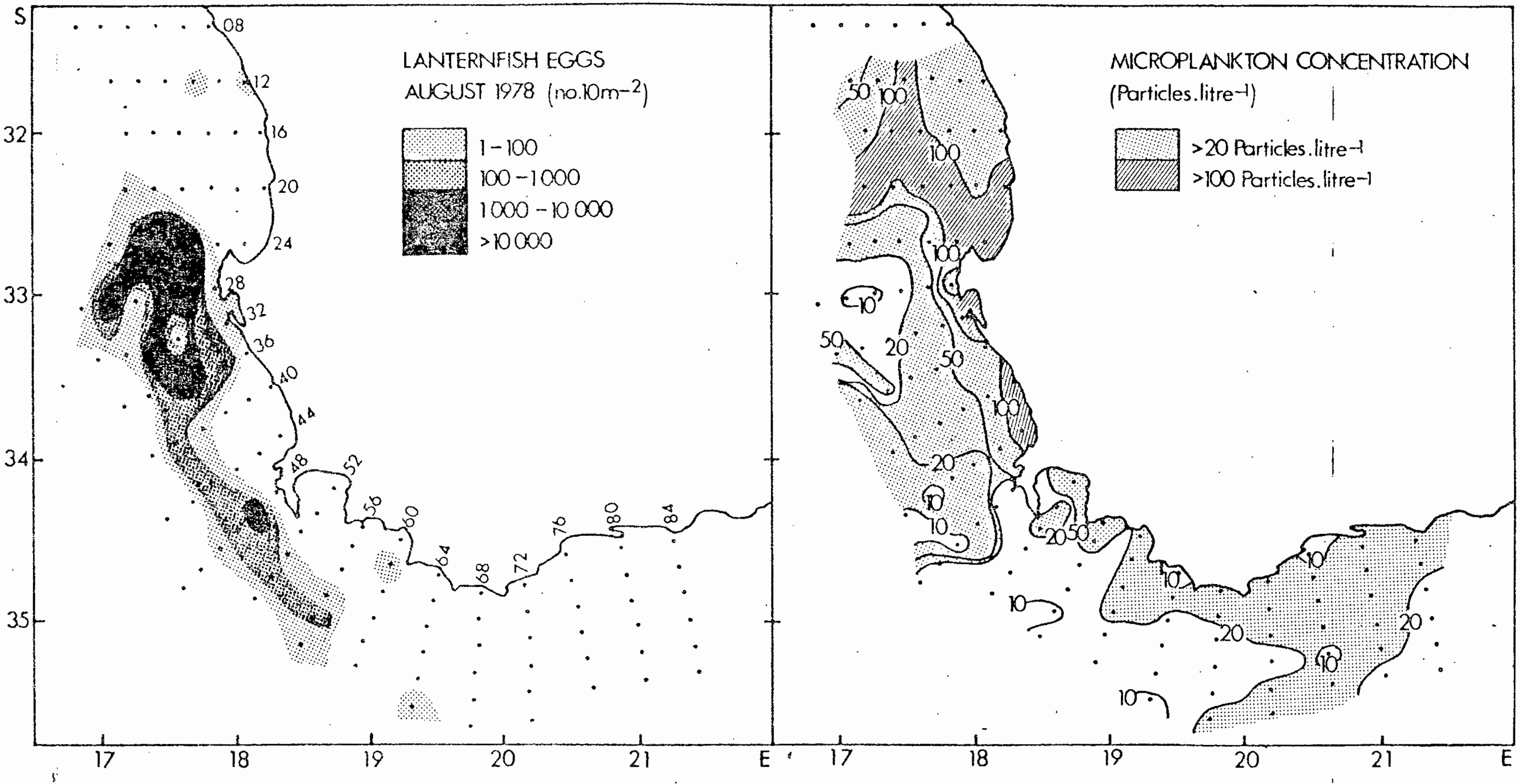
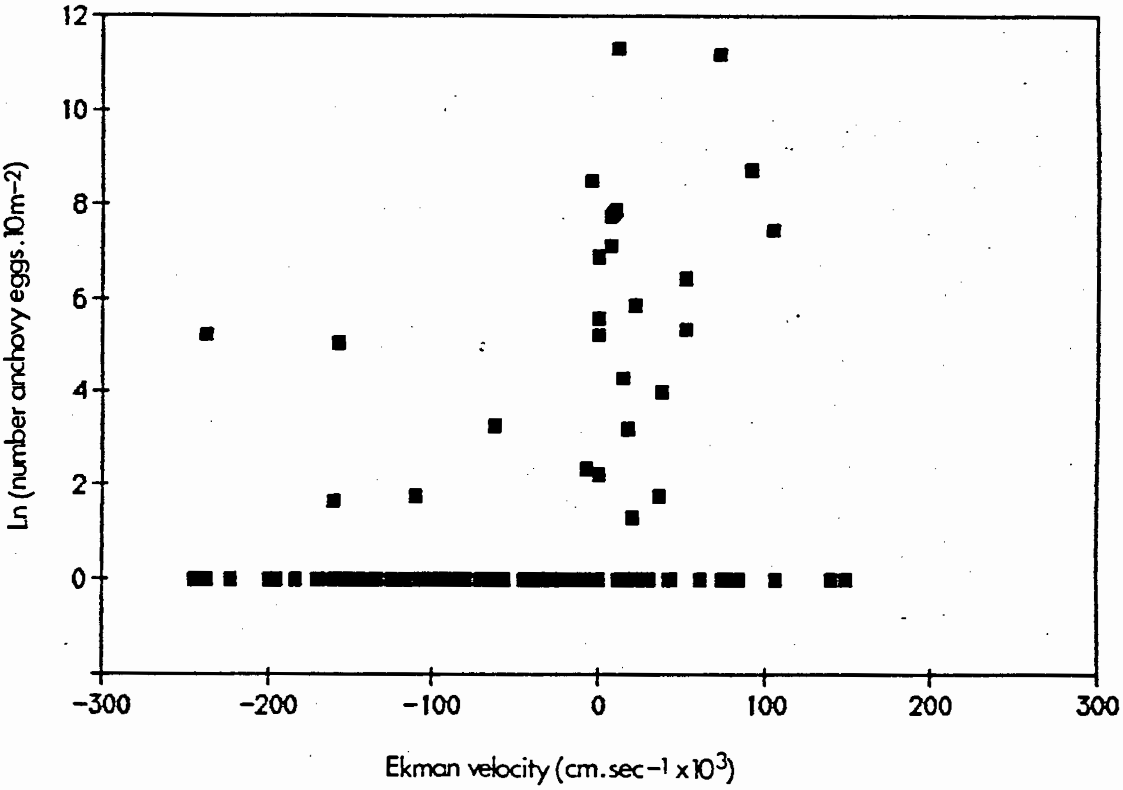


Fig. 5.32 Abundance of lanternfish eggs and microplankton concentration over the CELP grid in August 1978.



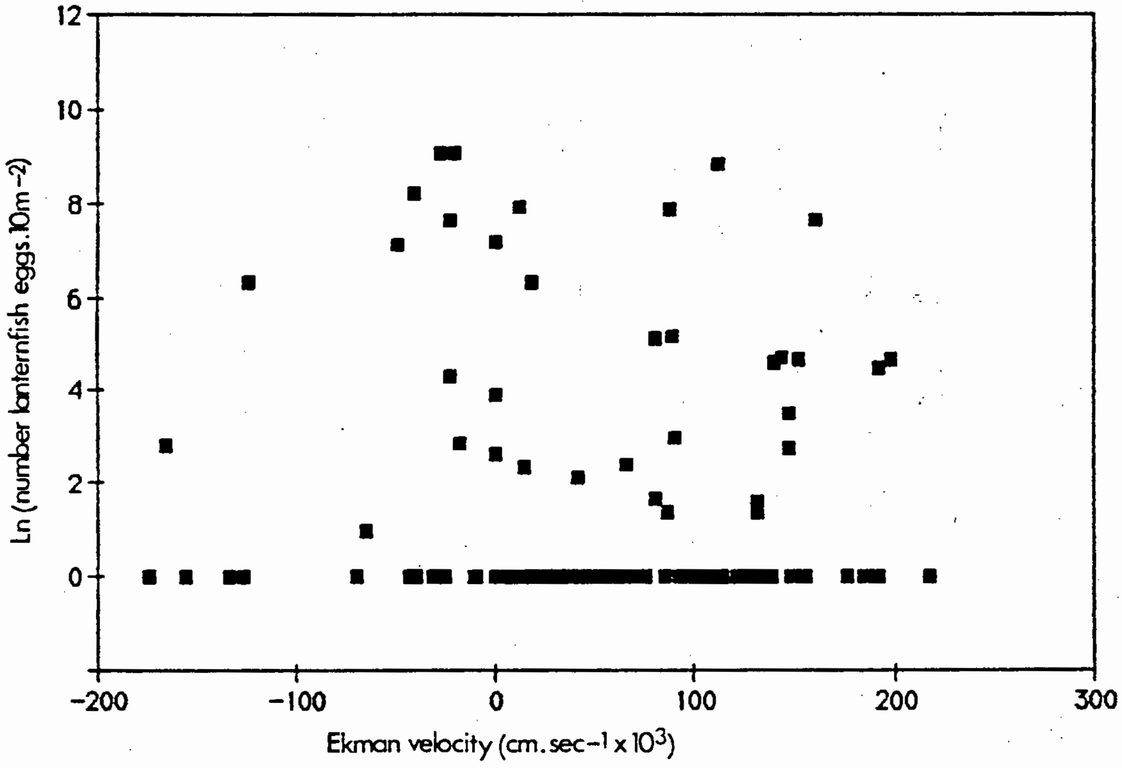


Fig. 5.33 Natural logarithm of the abundance of anchovy eggs in October 1977 and lanternfish eggs in August 1978 plotted against onshore/offshore Ekman velocity over the CELP grid. A negative velocity vector indicates offshore transport.

production near the sites of upwelling. However, since the lanternfish eggs are likely to be abundant some distance below the sea surface, it is possible that the amount of onshore/offshore movement is less at the depth of maximum egg and larval abundance.

Lanternfish larvae were most abundant in the plankton in August 1977 and covered the whole CELP area, but were most numerous offshore of the 100m contour (Fig. 5.34). Larvae were absent east of Cape Agulhas and inshore in the vicinity of the Cape Peninsula (lines 44 and 48), Cape Columbine (line 28) and in St Helena Bay (line 24). The pattern of abundance of lanternfish larvae and SST were not similar except for the general scarcity of larvae within the area of cool water demarcated by the 14°C isotherm running north from line 32 (Fig. 5.35). Plankton displaced volumes in August 1977 were greatest in the inshore area from Cape Columbine north and only partly overlapped with dense concentrations of lanternfish larvae (Fig. 5.36). Chlorophyll-a and microplankton values were uniformly small in August 1977 (Figs. 5.37 and 5.38) and did not match the pattern of abundance of lanternfish larvae.

Hake larvae were also most abundant in the plankton in August 1977 and covered most of the area surveyed without any distinctive pattern, except for an almost complete absence at inshore stations, corresponding to a water depth of less than 100m (Fig. 5.39). There was little correspondence between the pattern of abundance of hake larvae and SST (Fig. 5.40), although larvae were scarce within the body of water with an SST of less than 14°C in the St Helena Bay area, and more than 100 larvae per $10m^2$ occurred where the SST was warmer than 16°C in the extreme south of the grid. Hake larvae were not abundant in areas where net plankton, chlorophyll-a or microplankton were concentrated (Figs. 5.41-43).

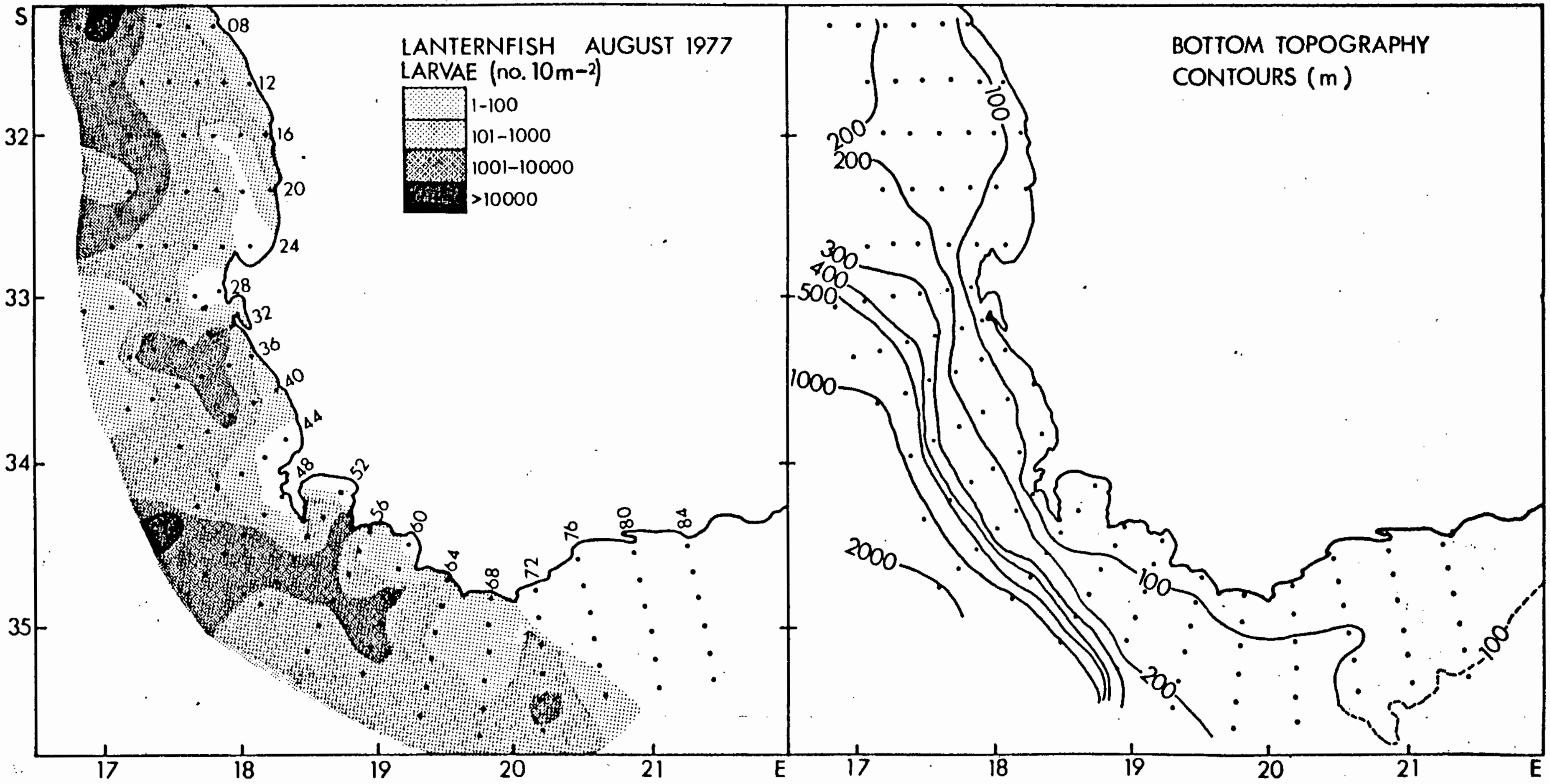


Fig. 5.34 Abundance of lanternfish larvae in August 1977 and bottom topography over the CELP grid.

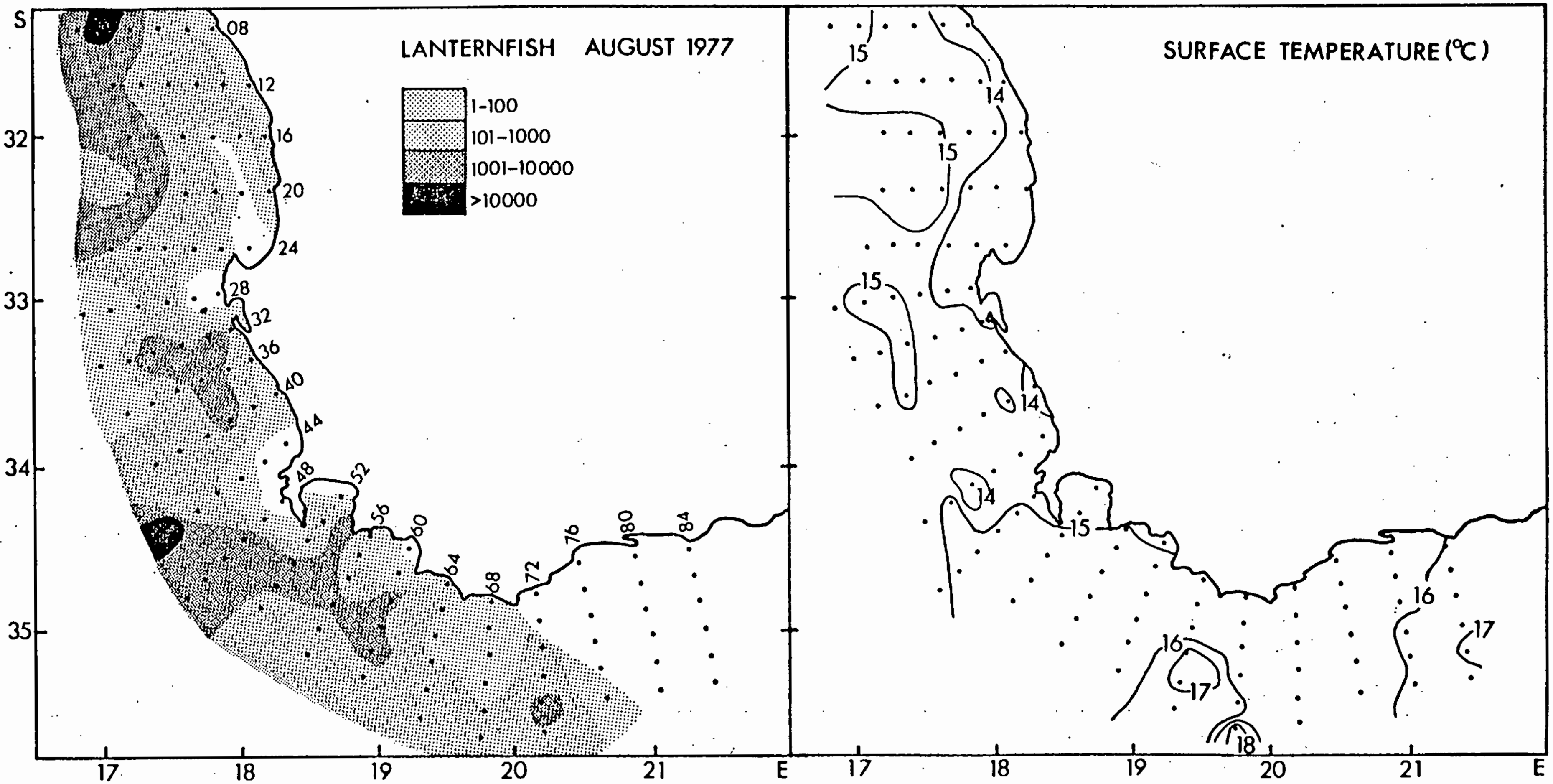


Fig. 5.35 Abundance of lanternfish larvae and SST in August 1977 over the CELP grid.

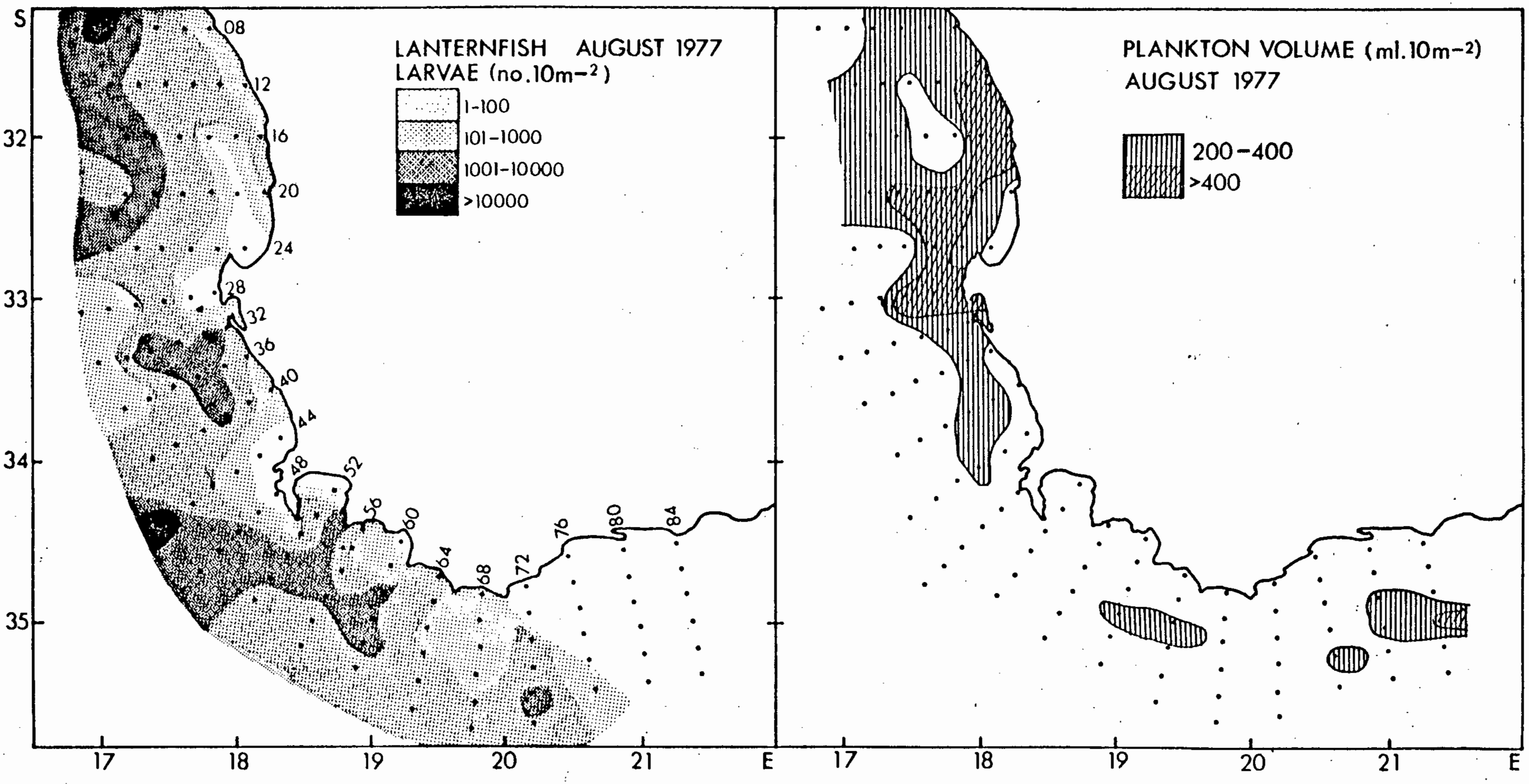


Fig. 5.36 Abundance of lanternfish larvae and plankton volume in August 1977 over the CELP grid.

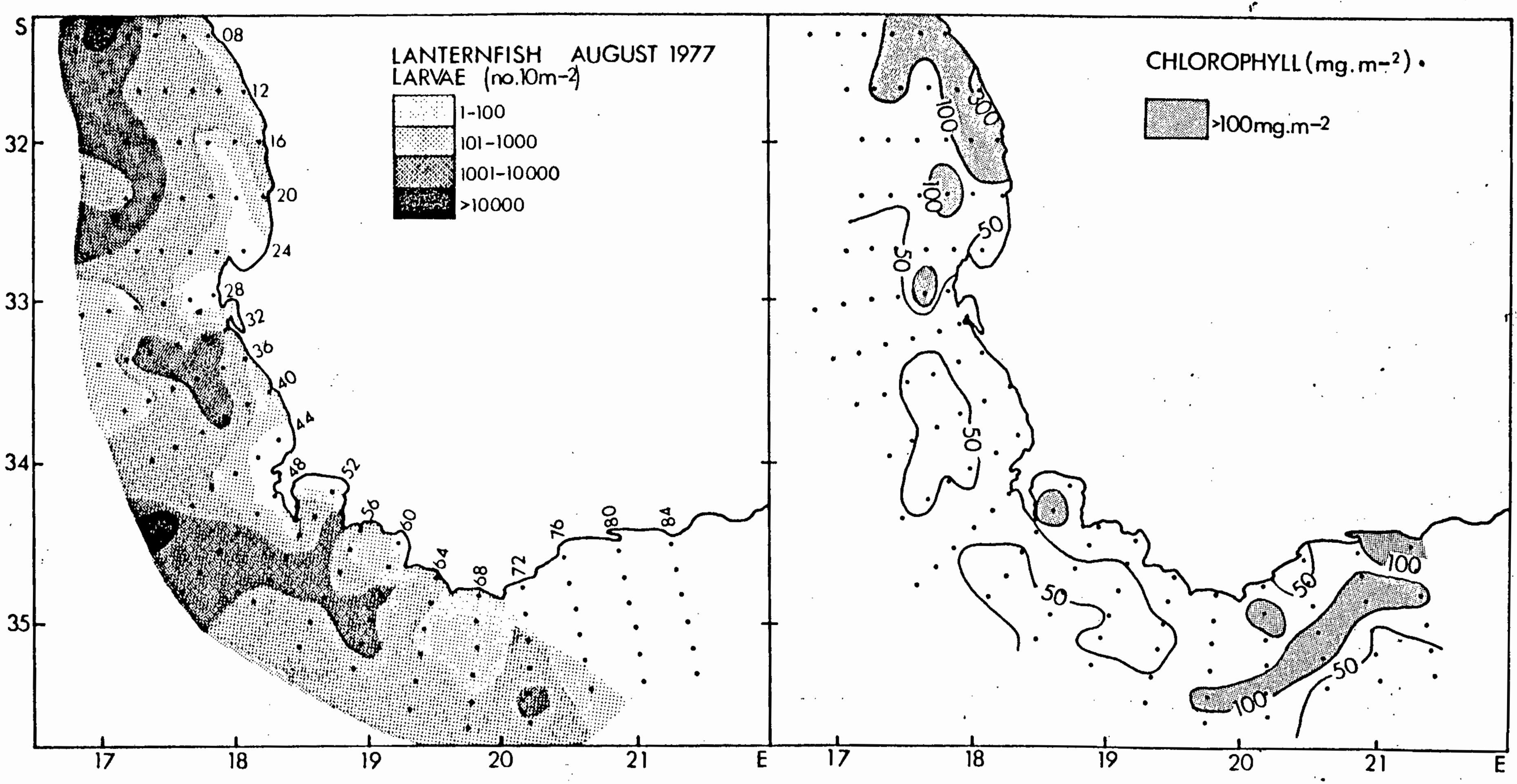


Fig. 5.37 Abundance of lanternfish larvae and chlorophyll-a concentration in August 1977 over the CELP grid.

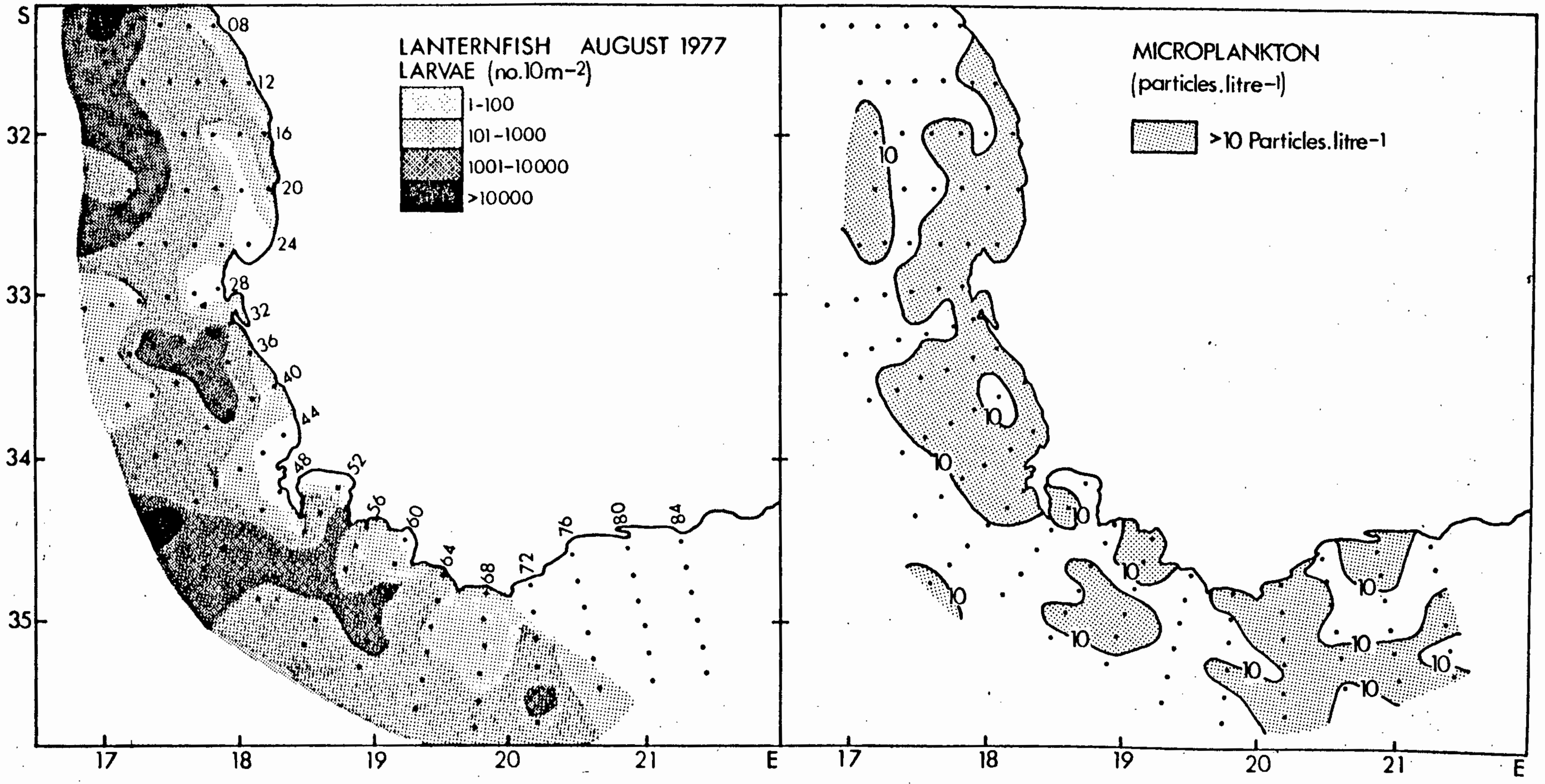


Fig. 5.38 Abundance of lanternfish larvae and microplankton concentration in August 1977 over the CELP grid.

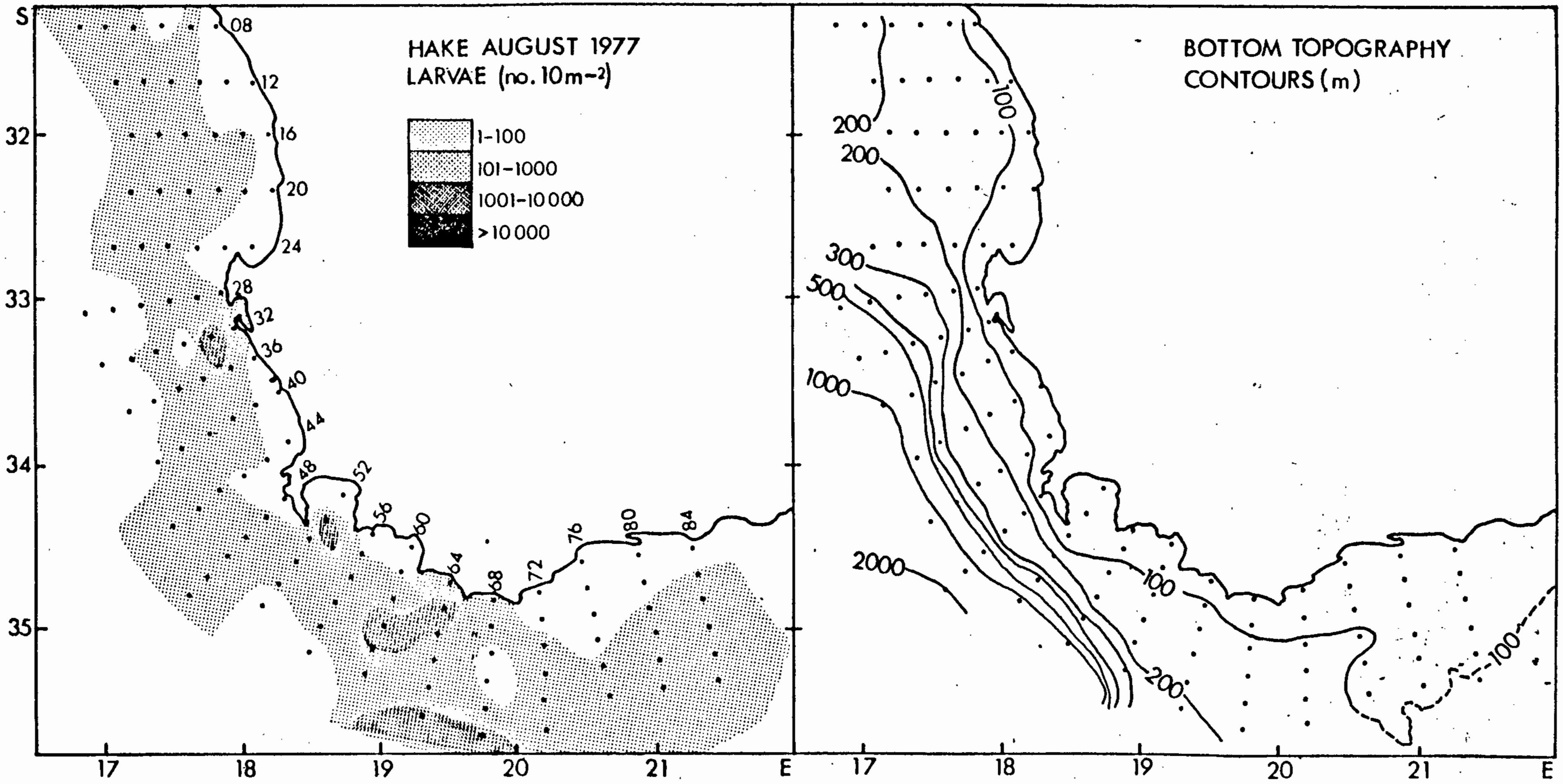


Fig. 5.39 Abundance of hake larvae in August 1977 and bottom topography over the CELP grid.

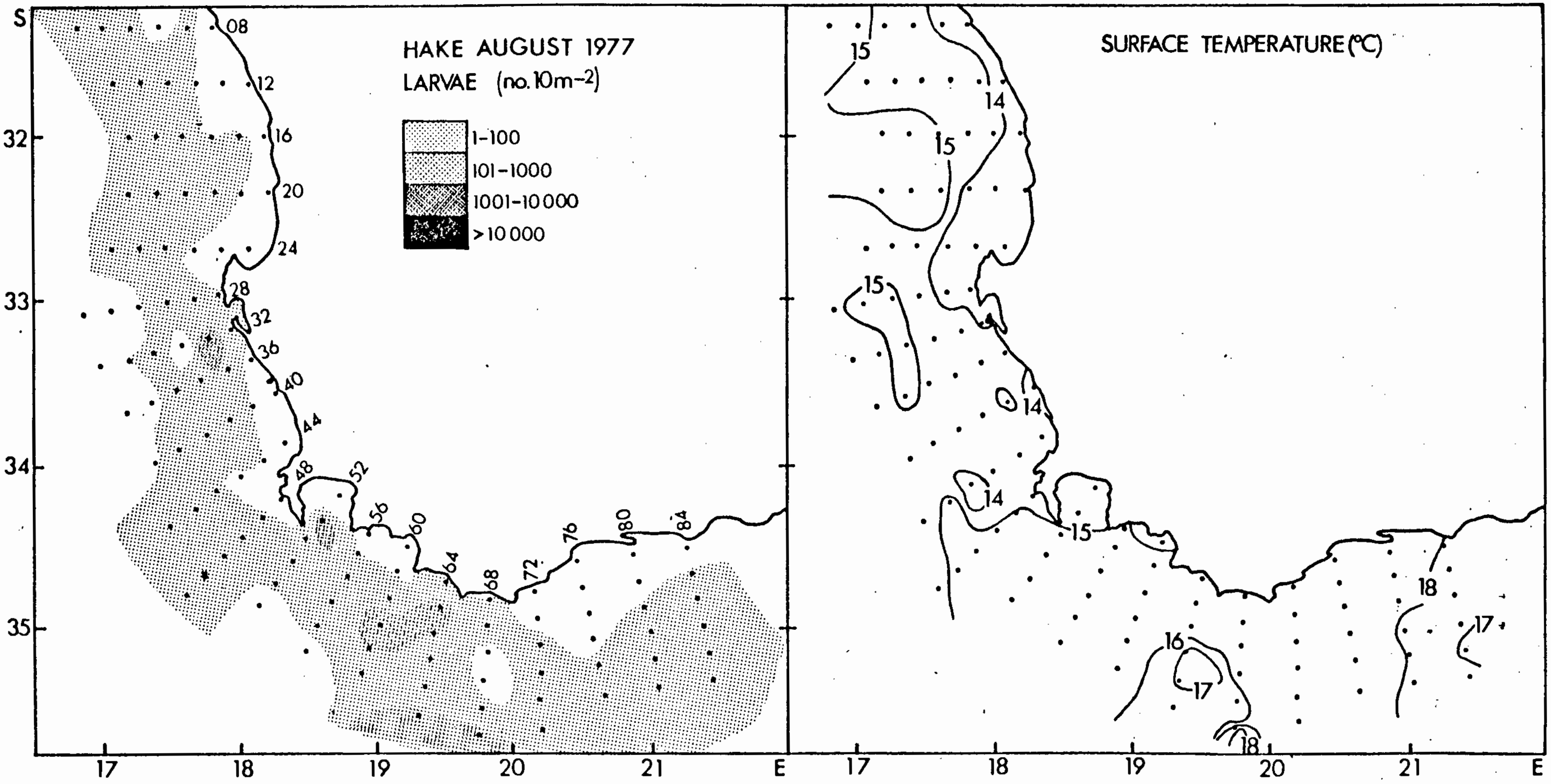


Fig. 5.40 Abundance of hake larve and SST over the CELP grid in August 1977.

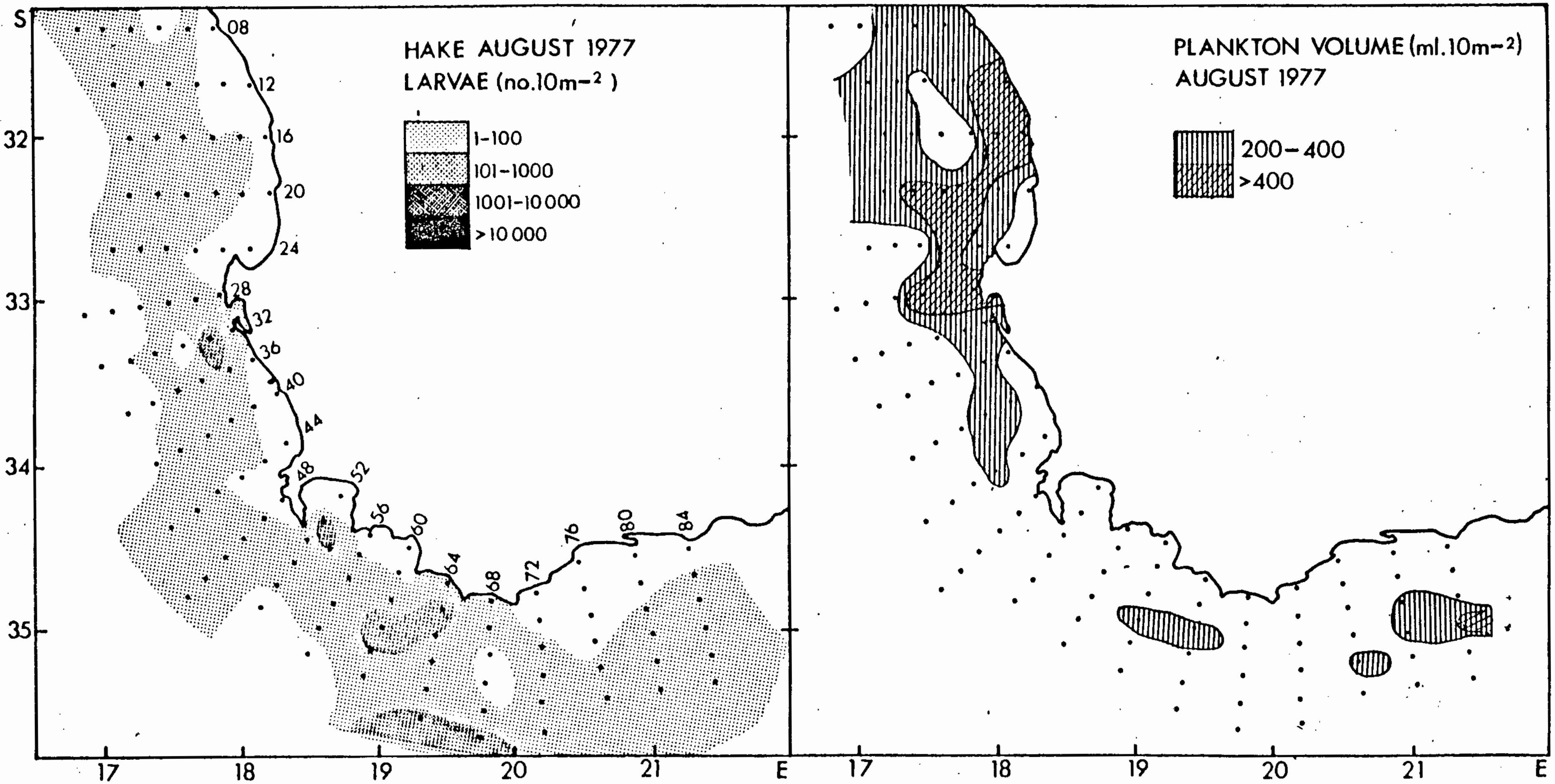


Fig. 5.41 Abundance of hake larve and plankton volume over the CELP grid in August 1977.

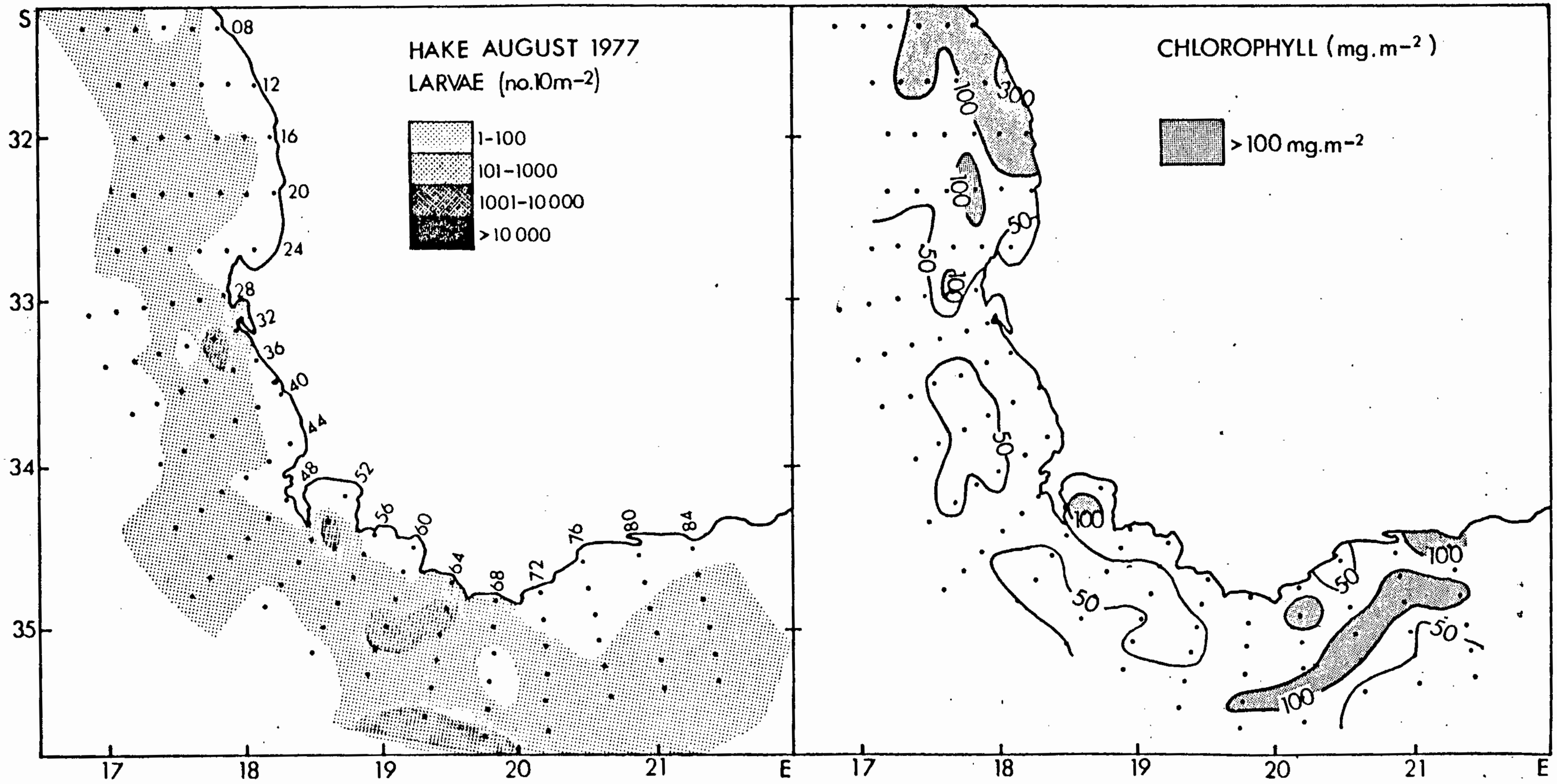


Fig. 5.42 Abundance of hake larve and chlorophyll-a concentration over the CELP grid in August 1977.

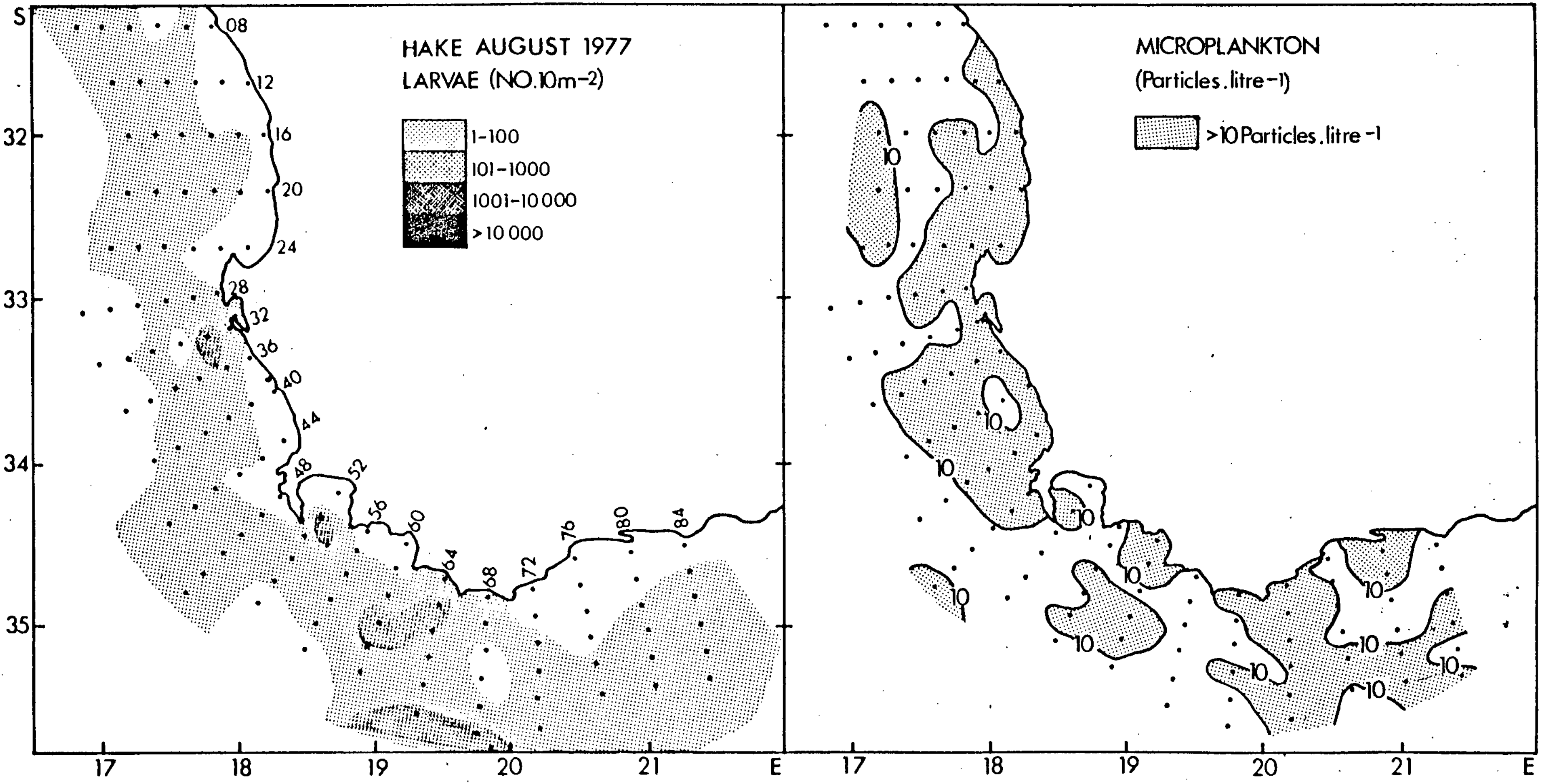


Fig. 5.43 Abundance of hake larve and microplankton concentration over the CELP grid in August 1977.

The 5 sample groups that were fairly persistent throughout the survey (see Section 4), labelled A-E, are plotted together with the bottom topography (Fig. 5.44) and SST (Fig. 5.45). Lanternfish eggs and larvae were commonly found in Groups A and E, hake larvae were commonly found in Group A and anchovy eggs and larvae were found almost exclusively in Group B In Fig. 5.44 it is evident that stations in Group A were associated with the shelf break along the west coast, but were more widespread north of Cape Columbine (line 28) where the shelf widens and the shelf slope is less steep and further offshore. Stations in Group B were most frequently found between the 100m and 200m contours over the western portion of the Agulhas Bank, extending northwards just inside of the shelf edge in some months. Stations in Group C were located over the eastern portion of the survey grid in that part of the Agulhas Bank where the water was shallower than 100m. Stations in Group D generally occurred inshore of the 200m bottom contour on the west coast whereas stations in Group E were over the shelf slope on the west coast.

The correspondence between the station groups and SST was less clear than with bottom topography (Fig. 5.45) and varied seasonally. In August 1977 stations in Group B were found in water with an SST of greater than 15°C over the western portion of the Agulhas Bank, whereas in the same month stations in Group C were associated with the warmer water which covered the eastern part of the grid at lines 80 and 84. In October 1977 stations in Group A were found mostly in water with an SST of between 14°C and 16°C along the west coast, whereas stations in Group D were largely restricted to the cooler water inshore. In January 1978 stations in Group A were associated with the well developed temperature front. In May 1978 only stations from Group D were found in the cool less than 14°C water along the west coast.

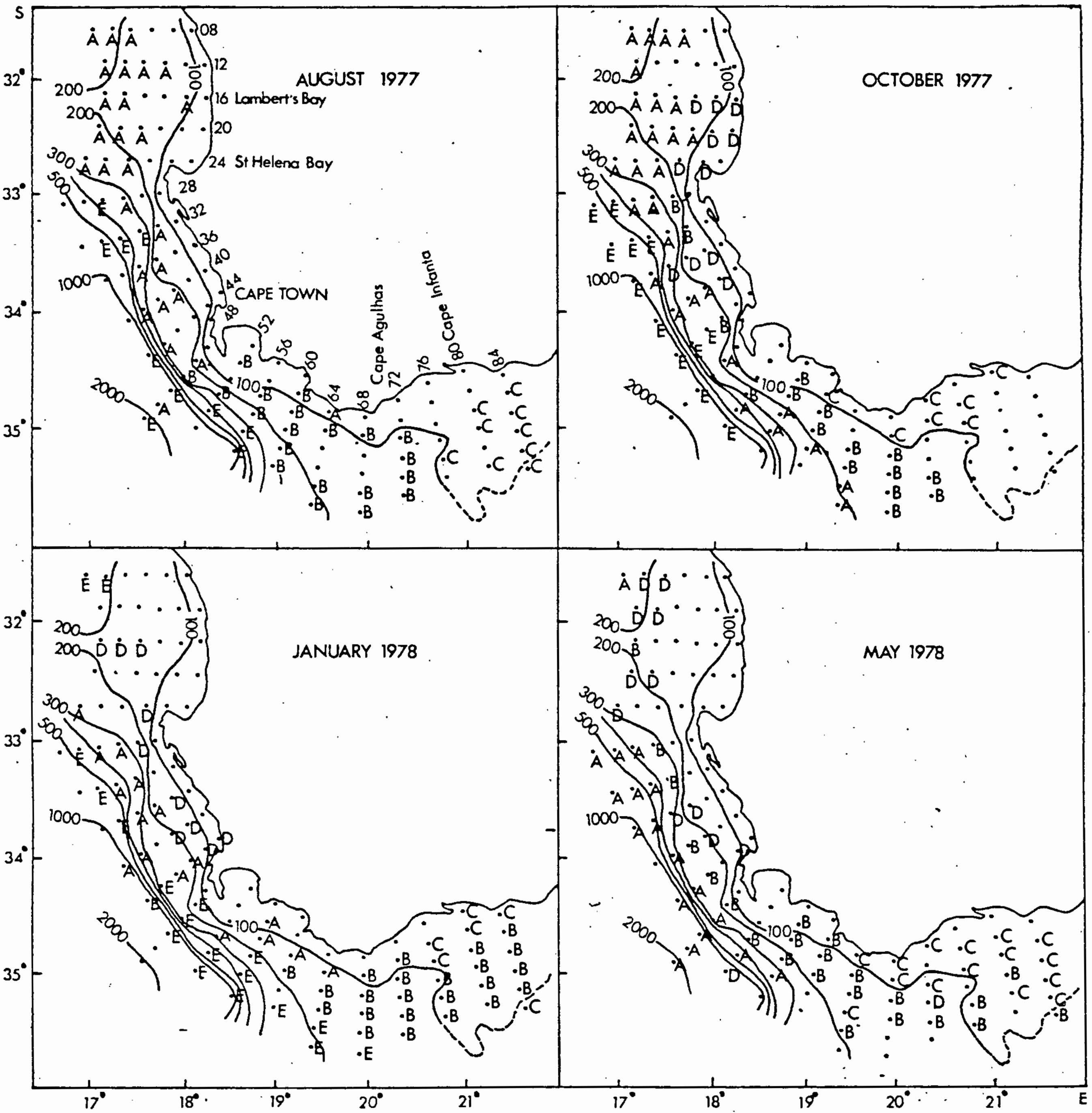


Fig. 5.44 Postion of stations belonging to Groups A-E defined by cluster analysis in relation to bottom topography in August 1977, October 1977, January 1978 and May 1978.

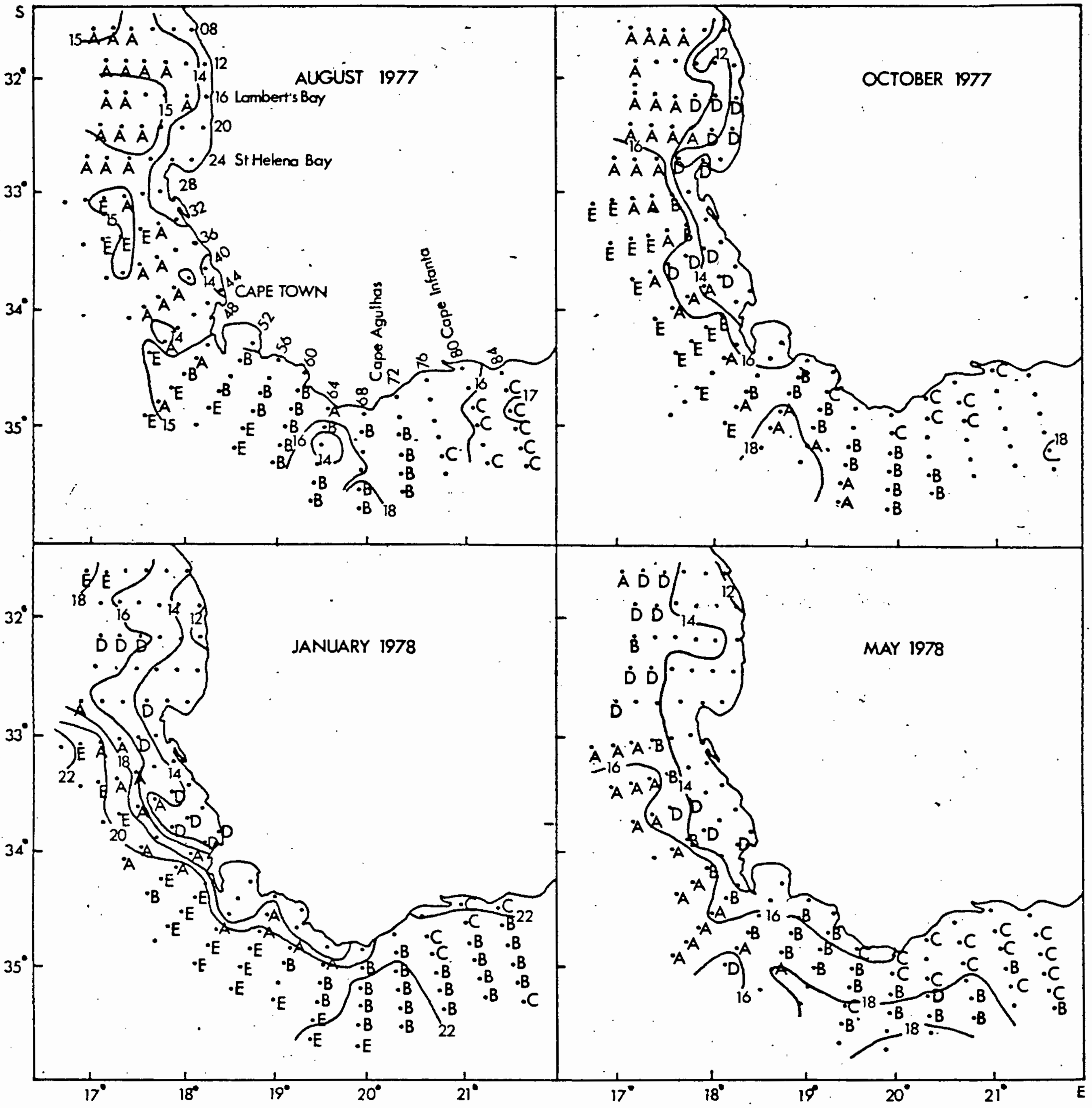


Fig. 5.45 Postion of stations belonging to Groups A-E defined by cluster analysis in relation to SST in August 1977, October 1977, January 1978 and May 1978.

Comparison of spawning strategies

The very different spawning strategies of anchovy, lanternfish and hake suggests that the kind of anomalies in the environment that are likely to significantly influence recruitment will vary between species. Since the spawning season in anchovy is timed so that larvae are most abundant during the period of maximum upwelling, when the seasonal increase in plankton standing stocks occurs, and when the environment is most structured in terms of fronts and thermoclines, it seems likely that the survival of early stage larvae may be influenced by the disruption of the thermocline on the Agulhas Bank, and by the dynamics of the front on the west coast. In particular eddies, such as the one found in the vicinity of St Helena Bay, and other cross-frontal mixing process, which may facilitate the invasion by larvae of the productive inshore areas downstream of the main west coast upwelling sites, may be important in determining survival. Subtle changes in the dynamics of the front or in the position of larvae within the frontal gradient may mean the difference between being swept offshore at the divergence off Cape Columbine or in the general offshore surface Ekman transport, or being carried inshore.

The seasonality in lanternfish spawning is largely out of phase with the annual plankton production cycle and occurs when the environment is least structured in terms of fronts and thermoclines. Spawning is largely offshore of the shelf break, but since the shelf is particularly narrow off Cape Columbine and the Cape Peninsula, eggs are found close to the coast in these areas and there is an extensive invasion of the neritic habitat by larvae. Although plankton standing stocks are reduced in winter, the pattern of abundance of plankton is more uniform at this time and moderate levels of plankton extend offshore. It would seem likely that the survival of lanternfish larvae would be reduced by anomalous warm water advection, or persistent downwelling in winter/spring which would limit the offshore abundance of plankton and reduce the amount of overlap between larvae and potential food particles.

The ubiquitous spawning strategy adopted by hake gives few clues to the kind of environmental conditions which are likely to cause poor recruitment, except that the anomaly would have to be prolonged and cover a wide area. Since larvae were generally scarce in the cold inshore area, it is possible that an extended cool period with concomitant decrease in stratification and increase in offshore transport of a deep layer of water would be unfavourable to hake larval survival.

The spawning strategies adopted by anchovy, lanternfish and hake reveal very different adaptations to the highly variable neritic and shelf slope environments of the southern Benguela upwelling region. The clearly defined temporal and spatial pattern of spawning in anchovy points to a strategy that is adapted to predictable intra-annual environmental processes. While adult lanternfish are largely associated with the shelf slope rather than the shelf, the spawning strategy appears to be adapted to utilize the enhanced levels of plankton production associated with the southern Benguela Current region, since the larvae cover a large portion of the shelf where plankton concentrations are greater than further offshore. Spawning time and area differ from the anchovy but also appear to be adapted to predictable intra-annual environmental processes. Hake have a relatively ubiquitous temporal and spatial pattern of spawning, suggesting either that predictable intra-annual processes are not a feature of their environment, or that other influences, such as intraspecific competition, have had greater effect in determining spawning strategy.

5.4 Conclusion

SST and the abundance of various components of the plankton show considerable variability at the seasonal time scale. As a result, the overall diversity and abundance of fish larvae in the plankton also vary seasonally. However, individual species show significant differences related to habitat, suggesting that dominant environmental processes differ between habitats. Anchovy spawning appears to be related to the increase in SST and plankton concentration during spring, and survival of larvae is likely to benefit from the physical patterning of food particles by fronts and thermoclines over the summer period. In comparison, lanternfish spawning is completely out of phase with anchovy spawing and occurs further offshore, over the shelf slope. The survival of lanternfish larvae in winter may benefit from the more homogeneous nature of the neritic environment and the increased offshore influence of productive coastal water at this time, which results from decreased onshore advection of warm water and the consequent weakening of the temperature front. The relatively ubiquitous spawning behaviour of hake suggests that their habitat is not predictably influenced by seasonal processes, or that the influence of other effects, such as intraspecific competition, is greater. The present study points to processes which are potentially important in determining survival in anchovy, hake and lanternfish. As a second step it is necessary to determine the nature of the variability in these processes that are likely to influence the populations, given the life history adaptations that have taken place to cope with the expected degree of variability in each habitat.

6. LIFE HISTORY STRATEGIES IN A VARIABLE ENVIRONMENT

6.1 Introduction

Variability in the physical environment may have a number of components which have different periods and account for different proportions of the total variance. Fish populations in the Benguela Current system are affected by the environment continuously and can adapt their life history strategies according to the dominant components of variability in their particular habitats. Thus anchovy and lanternfish have adapted time of spawning to seasonal events, suggesting that the seasonal component accounts for a significant proportion of the variability in their habitats, whereas hake spawning is more uniformly distributed with respect to time (see Section 5). Life history strategies can also be adapted to spatial predictability, with the result that anchovy and lanternfish select specific areas for spawning in response to a non-uniform environment, whereas hake are relatively ubiquitous spawners. In habitats where a number of different components contribute roughly equal proportions of the total variance of key environmental variables influencing survival, species will have to develop "risk-spreading" or "bet-hedging" (Stearns 1976) strategies.

I use the terms "strategy" and "bet-hedging" with reservation because their cognitive connotation is not compatible with natural selection theory.

6.2 Bet-hedging

The importance of bet-hedging in animal populations in general and in marine fish populations in particular has come to be widely recognised (e.g. Den Boer 1968, Murphy 1968, Stearns 1976, Leggett and Carscadden 1978, Hewitt 1982, Lambert and Ware 1984, Longhurst 1984). The high fecundity associated with most marine fish species is evidence of a bet-hedging strategy to cope with uncertain progeny survival, since approximately only two progeny need to reach maturity over the entire lifespan of each female to ensure replacement of the breeding population. Essentially bet-hedging involves the spreading of risk over both time and space in order to maximize survival in a patchy or variable environment. It is the opposite of a "big bang" strategy which may be adopted in a predictable environment, uncomplicated by the presence of several different components contributing roughly equal amounts of variability. In the big bang strategy an individual's entire reproductive output is released at the same time and in the same place, probably together with the reproductive products of the rest of the population, in response to a predictable environmental signal.

Den Boer (1968) considered the spreading of risk in space to be a widespread phenomenon contributing significantly to population stability. Although the egg and larval stages of most species sampled during CELP were found over a farily large portion of the survey grid, the pattern was, in all instances, significantly different from random (see Section 4). The eggs and larvae of anchovy were most patchy, lanternfish less patchy and hake least patchy, suggesting a greater degree of spatial risk-spreading in the latter species in response to a spatially less predictable environment.

The significance of density-dependent as opposed to risk-spreading influences in the pattern of abundance of all three species needs to be considered. Two potential density-dependent mechanisms are intraspecific competition between larvae and cannibalism by larvae. Lambert (1984) and Lambert and Ware (1984) suggest that the time and space separation between larval cohorts of a number of demersal and pelagic spawning fish species is related to their capacity for competition, with greater spacing associated with a greater capacity for competition. Brownell (1985) has found that large anchovy larvae are able to cannibalise larvae of a size approaching half their own body length in the laboratory, and this may be and important interaction influencing pattern in the field, not only in anchovy. Thus the capacity for intraspecific interaction by anchovy, hake and laternfish may influence the pattern imparted by the adults on their reproductive stages at spawning.

The most obvious strategy for spreading risk over time is longevity and repeated spawning over several spawning seasons, or iteroparity as noted by Longhurst (1984). The significance of this strategy in animals was first shown with respect to clupeoid fish. Using a simple simulation model of competition between anchovy and sardine (pilchard), Murphy (1968) demonstrated that, when the interspecific interaction coefficients were equal and population growth was not affected by environmental variablity, anchovy, which was shorter lived, had a faster population growth rate and a smaller carrying capacity in Murphy's model, increased more rapidly and then collapsed, while the sardine population continued to grow to carrying capacity. By adjusting, the interaction coefficients he brought both populations into equilibrium in the model and then introduced uniform random variability. In all instances, even when the equilibrium population size of sardine was set below that of anchovy, the sardine population always won as a result of the greater degree of iteroparity. Schaffer (1974) extended Murphy's conclusions, and life history strategies in stochastic environments are discussed in Stearns (1976, 1977). When the survival of premature stages is highly variable, reduced reproductive effort, smaller numbers of young produced at a time, and longevity, and therefore iteroparity, will be favoured. In contrast, when adult survival is variable, increased reproductive effort, greater number of young produced at a time, and short life span, leading to semelparity will be favoured.

The fact that a number of different life history tactics can be identified within the species assemblage in the southern Benguela region points to differences in the environmental variability characteristic of different habitats in the neritic and shelf slope zones sampled during CELP. This is explored further by considering the habitats of anchovy, hake and lanternfish.

6.3 Habitat characteristics

The habitats occupied by adult anchovy, hake and lanternfish can be classified, respectively, as the upper mixed layer (UML) and bottom mixed layer (BML) habitats over the shelf and the midwater (MW) habitat over the shelf slope. The relative positions of these three habitats are shown in Fig. 6.1. The UML and the BML are often separated by a thermocline which may vary in depth (see Section 2.4). During upwelling the thermocline may outcrop at the surface and form a surface temperature front, and when this occurs the distinction between the UML and the BML largely disappears. In addition, reduced stratification during winter, as result of reduced warm water advection, less upwelling activity and less solar heating allows strong winds associated with winter storms to increase the depth of the upper mixed layer, and over shallower areas such as the Agulhas Bank, the entire water column may become mixed. The MW habitat occurs over the shelf slope and is associated with oceanic water of intermediate depth. This water mass migrates closer to the shelf during summer, especially in the vicinity of the undersea canyons off Cape Columbine and Cape Point.

Ideally power spectra for key variables thought to influence fish larval survival should be available for the three different habitats described above to allow a quantitative comparison. Brundrit (1984) has examined the variation in sea level measured at various sites along the coastline of the Benguela Current system

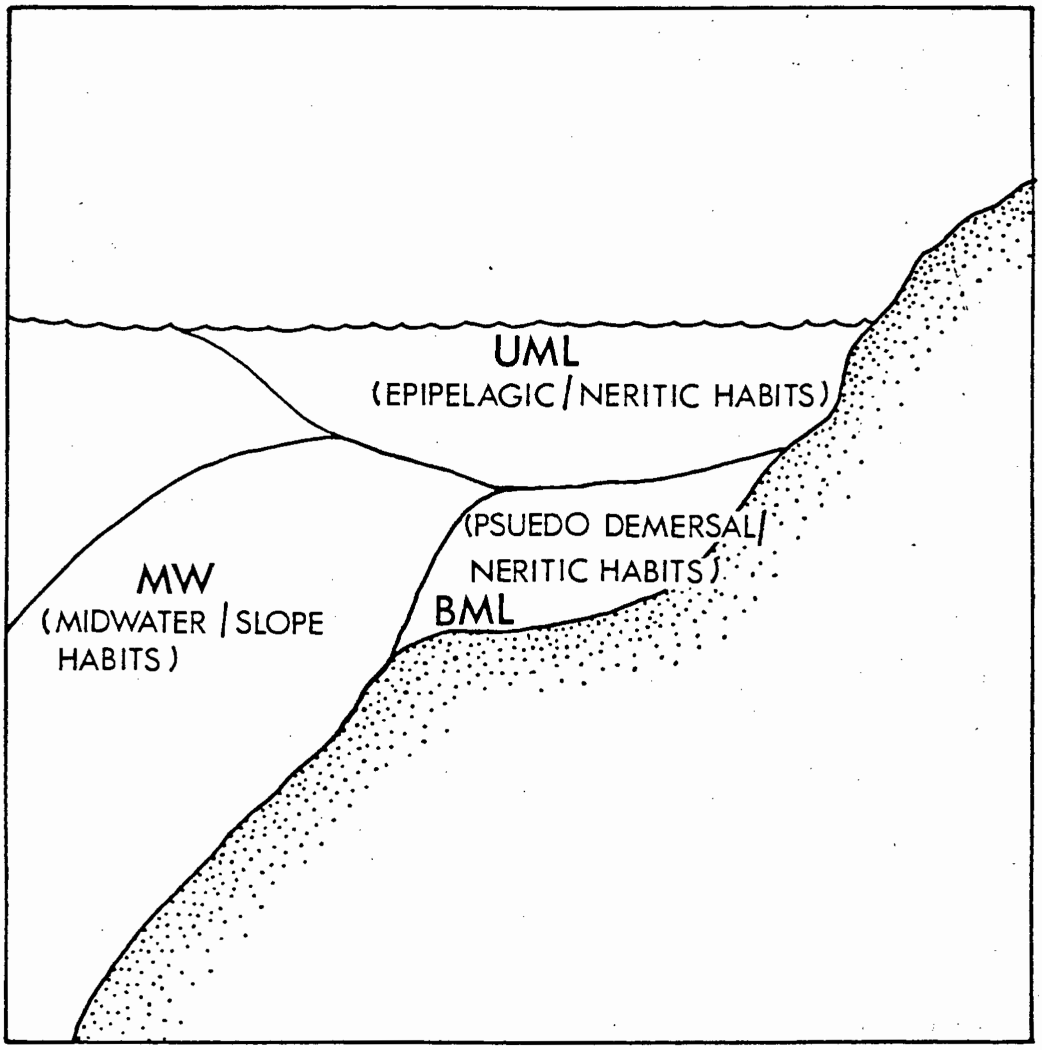


Fig. 6.1 Schematic cross section of the shelf and slope showing the upper mixed layer (UML) inhabited by epipelagic/neritic species such as the anchovy, the bottom mixed layer (BML) inhabited by psuedo-demersal/neritic species such as the hake, and the mid water (MW) midwater zone inhabited by midwater/slope species such as lanternfish.

after removing the tidal and local atmospheric components. This gives an indication of variability in the neritic habitat in general. The first component accounted for over 55% of the variability and this was attributed to the 3 to 7 day frequency of coastal lows which interact with the South Atlantic High and reduce offshore Ekman transport (Andrews and Hutchings 1980, Nelson and Hutchings 1983). The seasonal component accounted for about 25% of the variability and was attributed to the seasonal north-south shift in the upwelling-favourable winds. The final component was associated with interannual variability and was found to be well correlated with the occurrence of the El Nino phenomenon in the eastern equatorial Pacific Ocean, and there was also good agreement with long term trends in SST. The significance of the seasonal and longer term components of variability in sea surface temperature (SST) in the Benguela Current system are considered in McLain et al. (1985) and Shelton et al. (1985). The description of variablity by Brundrit (1984) is in marked contrast with that of Steele and Henderson (1984) who considered the variance per unit frequency interval of variability in the sea to increase as the period increases from days to decades. They termed this "red" noise in comparison with "white" noise in which the variance is constant with respect to frequency. In contrast, the variability described by Brundrit (1984) is "bluish" if not "violet" in nature because the variance decreases with increasing period. In the absence of statistical descriptions of the variability in the UML, BML and MW habitats, it is suggested that shorter period variability is progressively filtered out down the water column and away from the coast, with the open ocean approximating to the model of Steele and Henderson (1984). If this is roughly correct, corresponding adaptations in the life history strategies of the component species may be expected.

6.4 Life history traits

Important life history traits of anchovy, lanternfish and hake and the references from which the information was obtained are listed in Table 6.1. Anchovy, which inhabit the UML, are obligatory schoolers which partake in extensive seasonal, longshore migrations. The eggs are patchy in time and space as a result of a distinct spring/summer spawning season, coinciding with the seasonal increase in plankton production, and the selection of a specific spawning area within the southern Benguela region. Maturity can be reached within one year of age but fish ~~older~~ more than 3 years ~~of age~~ old are rare. Fecundity is high and repeated spawning can occur with a frequency of up to seven days.

Lanternfish, which occur predominantly in the MW habitat, form dispersed layers and partake in a diel vertical migration but do not perform extensive longshore movements. Spawning occurs over a restricted period of the year, but is out of phase with the seasonal increase in plankton in general. There is a specific spawning area as reflected by the CELP survey grid, but spawning probably occurs further offshore as well. As a result of the distinct spawning area and season the occurrence of eggs in the plankton was patchy, but less so than anchovy eggs. Most lanternfish reach maturity at one year of age and few survive to spawn the following year. Only one batch is produced per individual per season and fecundity per gram is smaller than anchovy.

Hake, which are commonly found in the BML over the shelf have a relatively uniform pattern of abundance, carry out a diel vertical migration and appear to migrate offshore as they become older. There is no significant longshore migration. Spawning is widespread in the southern Benguela region and occurs throughout the year, although the months of November/December and February/March appear to be favoured (Botha 1986). As a result the pattern of abundance of eggs over the CELP survey area was comparitively uniform. Maturity is delayed, fecundity per gram is comparitively small but multiple year classes carry out spawning as a result of their longevity. Botha (1980) found little evidence for serial spawning in hake but Botha (1986) deduced from the long spawning season that either serial spawning occurs or only a small proportion of the mature population spawns each day. The later explanation is simpler and is assumed to be the correct one in the absence of more detailed information.

6.5 Sensitivity of life history strategies to different kinds of environmental variability

In order to examine the sensitivity of anchovy, lanternfish and hake life history strategies to the environment, and thereby obtain an idea of what kinds of variability will be worth monitoring in order to build predictive models of recruitment strength, or to understand the mechanisms determining year class strength, the performance of each strategy was examined using simulation under a variety of environmental forcing functions. A strategy that is adapted to a particular kind of variability can be expected to be able to filter out much of the variance and return a relatively stable population, whereas a strategy that is poorly adapted will result in a large variance in population size, frequent low population levels and even collapse. Alternatively, some species may be adapted to track some components of variability. These opportunistic species will display large changes in population size. Assuming that the model is realistic, variability that does not elicit a response in the model population is unlikely to be worth monitoring in nature.

Similar simulation models were built for anchovy, hake and lanternfish using the parameters in Table 6.1. Since the progeny of each night's spawning may

Table 6.1

Important life history traits displayed by anchovy, lanternfish and hake in the southern Benguela region.

Trait	Anchovy	Lanternfish	Hake
Degree of schooling	obligatory[1]	dispersed layers[1]	uniform pattern[1]
Migration behaviour	extensive seasonal longshore[2]	diel vertical[3]	diel vertical + lifetime inshore to offshore[4]
Time of spawning	spring/summer[5]	winter/spring[5]	throughout year[5]
Spawning season month start-end	10-2[5]	8-10[5]	1-12[5]
Frequency of batches	1 per 7 days[6]	1 per season[7]	1 per season[8]
Eggs=a+b*female wt *number of batches	a=-5102[6] b=922	a=493[7] b=375	a=11886[9] b=252
Egg size (mm)	1.4 ~~*~~ by 0.66	0.70 ~~*~~ by 0.65	1.33
Patchiness of eggs	highly patchy[5]	moderately patchy[5]	probably uniform[5]
Length (cm) at 50% maturity	9 caudal length[10]	4.5 caudal length[7]	43 total length[11]
Length (cm) at 100% maturity	12 Lc[10]	6 Lc[7]	60 Lt[11]
Prop. matt= a+b*length	a=-1 b=0.17	a=-1 b=0.33	a=-0.76 b=0.03
Instantaneous rate of natural mortality	1[12]	2.37[7]	0.3[13]
Annual mortality	0.63	0.93	0.26
Monthly survival	0.920485	0.801232	0.975220
Growth parameters			
L_∞	14[14]	7[7]	125.4[13]
K	1.586	1.66	0.113
t_0	-0.0012	0.06	-0.0396
Length to weight conversion	$(0.0034 * Lt^{3.25})$[15]	$(0.0242 * Lc^{2.6838})$[16]	$(0.0095 * Lt^{2.8852})$[17]
B_{max} (tons*10^6)	2.0[1]	10.0[18]	0.5[13]

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[1] SFRI, unpublished data; [2] Crawford (1980a); [3] Gjosaeter and Kawaguchi (1980); [4] Botha (1973); [5] Section 4 of this thesis; [6] M.J. Armstrong, SFRI, pers. comm.; [7] Prosch (1986), [8] Botha (1980); [9] Calculated using fecundity data for the Pacific hake ***Merluccius productus*** from Nelson and Larkins (1970) and length-weight relationships for the Cape hake stock from Draganik (1976); [10] Shelton and Armstrong (1983); [11] Botha 1986; [12] Armstrong (1984); [13] Leslie (1985), [14] Prosch (in prep); [15] Robinson (1966); [16] Crawford (1980b); [17] Draganik (1976); [18] Educated guess.

encounter a different set of environmental conditions, a one day time step was used for egg production and subsequent survival, while other parameters such as length, weight, fecundity and maturity were updated in monthly increments. The time horizon for each simulation was 140 years and the same series of random numbers was used in each run. Ideally Monte Carlo simulations should be carried out to determine the population variance, however the single "sample simulation" over a long time horizon provides an adequate approximation of the variance, and since the same sequence of random numbers was used throughout, comparisons of the variance between species are valid. During the first 20 years of each simulation the survival of eggs was determined by a density dependent survival function in the absence of any environmental variability. After 20 years a subroutine to include environmental variability into post-spawning survival was activated in the simulation and after 40 years a total of 100 annual values of total population size by number were generated and analysed.

Only survival over the first month was subject to environmental variability and density dependence. In subsequent months survival was held constant at the monthly rate shown in Table 6.1. The density dependent survival rate in month i, s_i, was made a function of total population biomass in month i, B_i, so that

$$s_i = e^{-b*B_i^c} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

This is the same form of the density dependence assumed in the Ricker model as modified by MacCall (1980) and tended to reduce oscillation around the equilibrium at high survival rates. A value of c=0.5 was arbitrarily chosen. Values of c of less than one reduce the severity of density dependence, comparable to the situation where the range increases with increasing population size so that density increases more slowly than abundance.

Density independent survival was introduced into the simulation by perturbing the density dependent survival rate, first by using a multiplicative log-normally distributed random number sequence according to the expression

$$S_i = s_i * e^{E_i * \sigma} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2)$$

Where S_i = total survival rate on day i resulting from both density independent and density dependent sources. E_i is a random number, representing environmental effects, with a normal distribution, a mean of zero and a standard deviation, σ. The standard deviation was varied from 0.2 to 0.8 in order to examine the population response to increasing levels of variability. A standard deviation of 0.35 corresponds roughly to 95% confidence limits of half to double in the variability of the environment. Population size values accumulated from the last 100 years of the simulation were log-transformed to normalize the distribution imparted by the log-normal environmental forcing function. The geometric mean, and the coefficient of variation of the log-transformed values was calculated. The 95% confidence limits were expressed as a proportion of the geometric mean. In a second set of simulations density dependent survival was perturbed by a sine wave with an amplitude of 0.67 to 1.33 and periods of 700 and 1500 days. Population size was normally distributed so that log transformation was unnecessary.

The CV of the logarithm of the population size by number increased nearly linearly with increasing SD of the environment in the simulations of all three species (Table 6.2 and Fig. 6.2). The slope for lanternfish was the steepest and the slope for anchovy the least steep with the slope for hake only slightly steeper. At a SD of E_i equal to 0.4, giving a 95% confidence range of slightly more than half to double in the amount of environmental variability, the 95% range in lanternfish population size was 0.27 to 2.62 times the mean number, in hake 0.88 to 1.17, and in anchovy 0.83 to 1.20. This result suggests that the life history strategies of anchovy and hake are able to filter out much of the random variability in the environment whereas random variability in the environment is amplified in the lanternfish population.

Table 6.2

Results of the simulation to examine the sensitivity of anchovy lanternfish and hake populations to increasing variability in the environment.

Species	SD of E	Geometric mean population size (numbers$*10^{-6}$)	CV (%)	95% confidence limits as a proportion of the mean
Anchovy	0.2	17 570.910	0.384	0.93-1.45
	0.4	17 747.501	0.756	0.83-1.20
	0.8	18 379.662	1.491	0.75-1.34
Hake	0.2	731.429	0.458	0.94-1.06
	0.4	735.831	1.015	0.88-1.17
	0.8	746.951	2.829	0.69-1.45
Lanternfish	0.2	37 949.060	4.102	0.42-2.37
	0.4	24 270.090	7.427	0.27-2.62
	0.8	13 670.560	13.101	0.75-12.13

The response in the three populations to cycles in the environment were different (Table 6.3). At periods of 700 and 1500 days the anchovy population displayed roughly the same amount of variability as the cycle, the hake population filtered out part of the variability, while the lanternfish population amplified the cycle, increasingly rapidly and then collapsing.

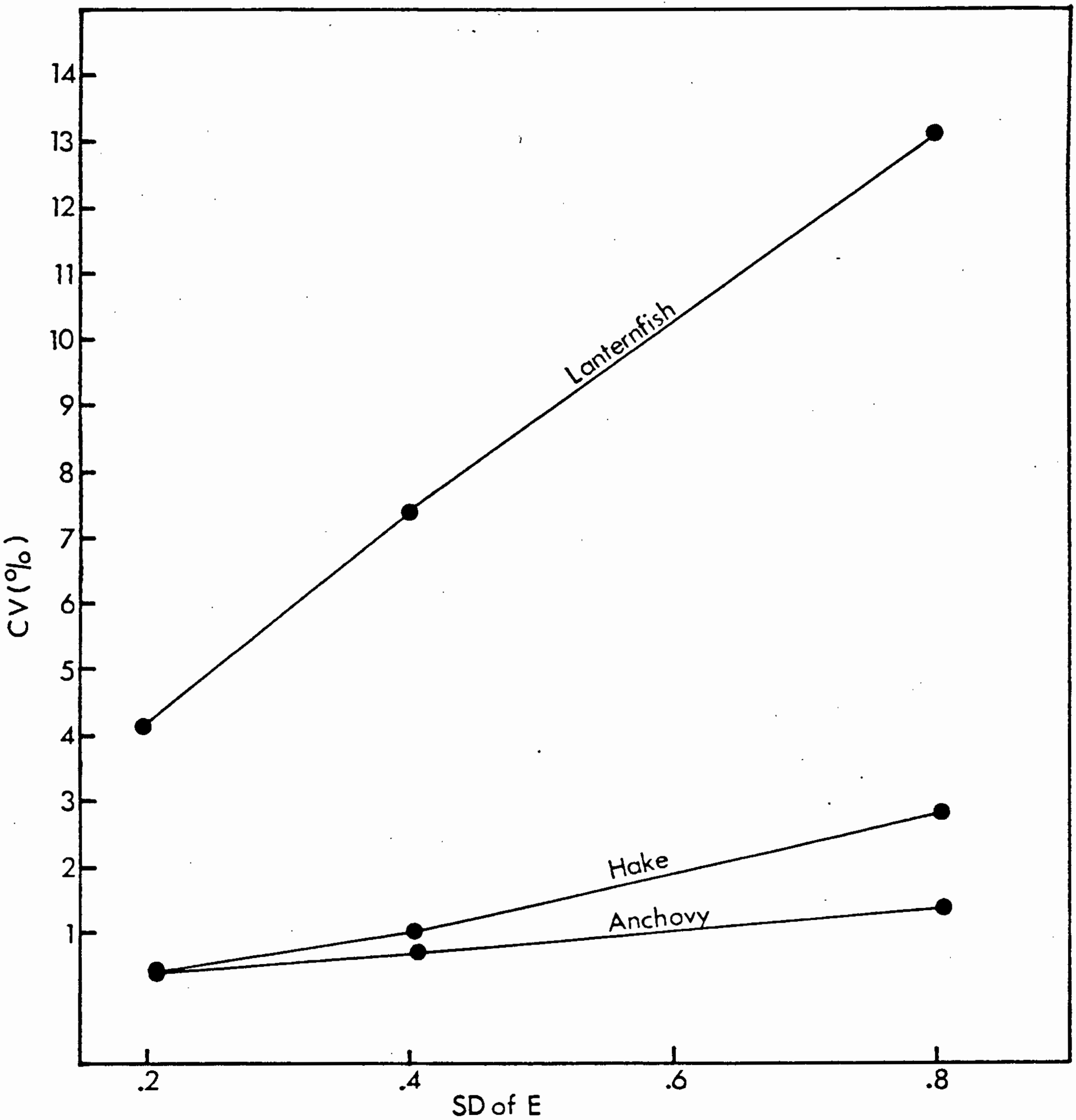

Fig. 6.2 Plots of the coefficient of variation (CV) of the logarithm of population size (number.10^{-6}) versus the standard deviation (SD) of the variable E representing environmental variability, for lanternfish, hake and anchovy.

Table 6.3

Results of the simulation to examine the sensitivity of anchovy, lanternfish and hake populations to environmental variability with periods of 700 and 1500 days.

Species	Period (days)	Mean Pop. size (number*10-6)	CV (%)	95% confidence limits as a proportion of the mean
Anchovy	700	17 609.300	17.280	0.65-1.35
Hake		722.490	3.479	0.93-1.07
Lanternfish		14 102.232	109.133	0.01-3.18
Anchovy	1500	17 051.612	15.375	0.69-1.31
Hake		697.847	8.876	0.82-1.18
Lanternfish		12 171.023	114.214	0.01-3.28

6.6 Discussion

The results of the simulation suggest that anchovy and hake have developed bet-hedging strategies that are efficient at filtering out variability with a large variance. Hake appear to be more effecient than anchovy at filtering cycles. By comparison, the life history strategy adopted by lanternfish is not efficient at filtering out variability or cycles. These dynamics suggest that lanternfish would be unfit to inhabit the neritic environment, but while the adults tend to remain in the vicinity of the shelf slope where spawning takes place, the larvae are widespread over the shelf. If larval survival is influenced by neritic environmental conditions, then large fluctuations in population size would probably occur, as suggested by the model. However, large changes in the catches of this species are traditionally considered to be the result of changes in availability rather than in abundance.

If the long period component of variability only contributes a small proportion of the total variability in the epipelagic environment, then anchovy population size would be expected to remain relatively constant, even after large intra-annual variabilty in processes such as upwelling. It has previously been suggested by Shannon et al. (1984a) that an anomaly that would be likely to influence the dynamics of the anchovy would have to prevail for several months, and Hutchings and Nelson (1985) have concluded that a 3 to 4 month wind anomaly would be needed to "upset" anchovy spawning. The simulation results presented here suggest that the anchovy population is even more robust to short term variability than was previously thought, and that small scale environmental measurements will not contribute substantially towards predicting clupeiod year class strength or to understanding the mechanisms determining year class strength. Essentially these exercises are merely documenting the "mistakes" which the anchovy is adapted to make as part of its life history strategy. Sampling effort could be more usefully directed at measuring large scale, longer period variability, which the simulation study suggests will affect the anchovy population.

In contrast to anchovy, a time series of hake recruitment calculated by cohort analysis is available for the west coast of South Africa, as far east as Cape Agulhas (ICSEAF Area 1.6, Leslie 1985). These data span the years 1964 to 1983 and give a 95% confidence range for recruitment of 0.52-1.91 times the mean. This covered a period over which the estimated spawner biomass decreased by more than a factor of four (Leslie 1985) as a result of heavy fishing pressure, suggesting that the population may now be in that part of the stock-recruit relationship where recruitment declines as a function of decreasing spawner stock. Therefore it is not possible to say whether estimated recruitment variability is compatible with the simulation model predictions.

Spatial risk-spreading is not considered in the simulations, but would, especially in the case of hake which spawns over a wide area, contribute to the population's ability to dampen out variability. The time series of SST measurements analysed in McLain et al. (1985) are very interesting in that they show that in the Canary and Benguela Current systems anomalies are temporally persistent but tend to cover a limited area in the longshore direction, whereas in the California and Peru Current systems, anomalies do not persist but when they do occur they cover extensive longshore areas. Thus temporal risk spreading may be more important in the Benguela and Canary Current systems and spatial risk spreading more important in the California and Peru Current systems.

6.7 Conclusions

The bet-hedging life history strategies adopted by anchovy and hake result in the populations being able to filter out much of the variability that may be expected to be encountered over the shelf in an eastern boundary current upwelling area. These populations will, however, be affected by variability with a period of longer than a year. The measurement and monitoring of the intra-annual components of variability in the environment is therefore unlikely to be of much use in understanding the determinants of, or predicting, year class strength in anchovy and hake. Lanternfish do not appear to be well adapted to the neritic environment, but the larvae do invade the shelf area. This may lead to large fluctuations in population size.

7. GENERAL DISCUSSION

The temporal and spatial patterns of abundance observed in fish eggs and larvae in the plankton is primarily the result of adult spawning behaviour, which may be adapted to ensure optimum survival with respect to larval competition, predation on larvae, and the influence of the environment. Secondarily, it is the result of these processes, i.e mortality due to competition, predation and the environment, and ocean mixing processes which can cause both dispersion and aggregation. A highly predictable environment in which a particular area at a particular time results in substantially better survival than any other area/time combination would provide selection pressure for releasing all the reproductive products in the same place at the same time. This may have the added advantage of predator swamping (Lambert and Ware 1984). However, intraspecific competition may cause the optimum strategy to be a more widespread release of reproductive products over a longer period. For example Lambert (1984) has suggested that cohorts of herring larvae are spaced more widely apart than those of capelin because herring larvae have a greater capability for intraspecific competition.

A highly variable and unpredictable environment causing varying survival of the early stages may also favour the spreading of the reproductive stages widely in time and space to maximise the probability of survival. Bet-hedging strategies such as iteroparity in shad have been suggested by Leggett and Carscadden (1978) to be a response to variable early stage survival, and Sherman et al. (1984) found that whereas peak spawning in some fish species such as anchovy off the north-eastern United States was in synchrony with increasing abundance levels of zooplankton, other species such as hake have adopted an ubiquitous, extended spawning strategy to ensure that at least some of the larvae will encounter sufficient food for growth and survival. However, an ubiquitous spawning strategy could also be an adaptation to a homogeneous environment in which no particular time or place results in greater survival.

The degree of aggregation of the non-planktonic phase also influences the spatial pattern of abundance. For example Hewitt (1981) found that anchovy larvae off California are initially patchy as a result of schooling behaviour in the adults. Subsequently the larvae disperse or become less patchy until they are about 20 days old when patchiness again increases facilitating school formation. Hewitt (1981) suggested that if complete dispersal occurred, schooling behaviour would be adversely affected. As an example of physical processes influencing pattern, Shelton and Hutchings (1982) found that anchovy eggs and early stage larvae spawned over the Agulhas Bank were entrained in a jet current associated with the temperature front off the west coast of South Africa and transported northwards to productive areas downstream of the upwelling centres where recruitment occurs.

The interpretation of pattern in fish eggs and larvae is therefore a complex problem, but broadly consistent temporal and spatial matching between the environment and the abundance of ichthyoplankton may be viewed as adaptive, whereas smaller scale and infrequent associations may be "mistakes", a natural consequence of what in most species are essentially bet-hedging strategies, as implied by large fecundities, repeat spawning and other risk-spreading traits. To determine parameters and processes as well as temporal and spatial scales for measurement, in order to predict year class strength, or to understand the mechanisms determining recruitment, it is important not to be misled into focussing attention on the "mistakes", however dramatic these may appear at the time. As an example of progress in determining general adaptive patterns in eastern boundary current regions, Parrish et al. (1983) found that anchovy and sardine (=pilchard) spawning habits simultaneously minimise both wind-induced turbulent mixing, which disrupts ocean stratification, and offshore-directed transport, which may carry the reproductive stages out of the neritic environment. This is achieved in the southern Benguela Current region by spawning east of Cape Point (see Section 4, Fig. 4.7) where offshore Ekman drift is generally less than on the west coast (see Section 2.2, Fig. 2.2.6 and Section 5, Fig. 5.33), and in summer when turbulence is reduced and the water column strongly stratified east of Cape Point (see Section 2.2, Fig. 2.2.4 and Section 2.1, Figs.2.1.12 to 2.1.14). Prolonged and widespread disruption of these patterns during the spawning season, or over more than one spawning season, will almost certainly elicit a measurable decline in anchovy and pilchard recruitment in the Benguela Current system. This thesis has attempted to extend the description of consistent pattern matching between the environment and the abundance of fish eggs and larvae in the southern Benguela Current region using the data collected during CELP.

It is the conclusion of this thesis that the dominant physical process in the southern Benguela Current region is the interaction between western boundary current and upwelled South Atlantic Central waters, resulting in vertical and horizontal temperature (or density) gradients which intensify in summer and weaken in winter. It is suggested that fish spawning strategies have been adapted with respect to this process and that major perturbations leading to prolonged and widespread disruption of the front or thermocline in summer, or alternatively the development and maintenance of strong temperature gradients in winter, will effect year class strength in different species. However, short term and small scale variability will be compensated by bet-hedging.

The influence of the seasonal advection of warm water into the system is shown in Fig. 7.1 to increase the coefficient of variation of sea surface temperature, plankton displaced volume and chlorophyll-a concentration over the CELP grid. As examples of three very different spawning strategies, anchovy larvae were present in the plankton over the period when the system was most heterogeneous, lanternfish larvae were present during months when the system was more homogeneous and hake larvae were present throughout the year.

The strong temperature gradients over the period when anchovy larvae were present caused chlorophyll and microplankton to be concentrated in the thermocline over the Agulhas Bank and inshore of the temperature front on the west coast (see Section 3.2, Figs. 3.2.6 and 3.2.7 and Section 1.3, Figs. 8 and 9), downstream of the major upwelling centres, particularly in St Helena Bay (see Section 3.2, Figs. 3.2.4 and 3.2.8). Early stage larvae probably benefit from the subsurface food layer on the Agulhas Bank but later stage larvae on the west coast are concentrated in the front and only partly overlap the elevated plankton concentrations inshore. To enter the west coast nursery grounds which occur predominantly in St Helena Bay and further north, late stage larvae must be carried into the inshore zone. This may be facilitated by eddies associated with the front, such as the St Helena Bay eddy (see Section 2.2, Fig. 2.2.10), and other mixing processes, which may vary on short time scales, possibly associated with the passage of atmospheric coastal low pressure systems. For example, during periodic lulls in upwelling, the front will move onshore and weaken (see Section 5, Fig. 5.21), bringing larvae into greater contact with elevated plankton standing stocks inshore. Alternatively, processes that cause the front to shed offshore eddies (Van Foreest et al. 1984), in particular the offshore divergence off Cape Columbine, may result in the loss of larvae from the system. To counteract the short-term variability in circulation, anchovy have developed a suite of

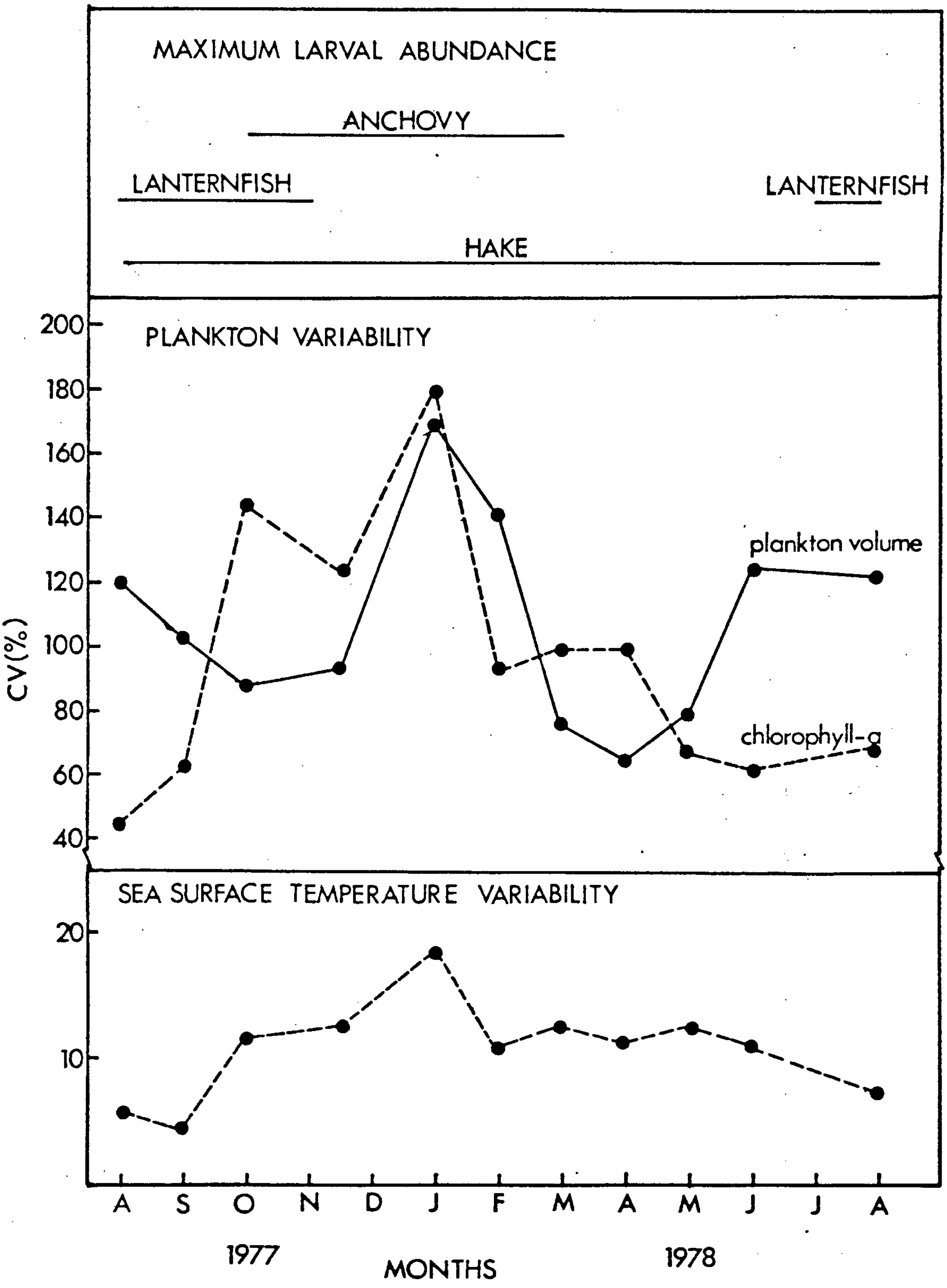

Fig. 7.1 Sea surface temperature, plankton displaced volume and chlorophyll-a concentration variability expressed as monthly percentage coefficients of variation (CV), with the months of maximum anchovy, lantenfish and hake larval abundance superimposed.

bet-hedging traits, including a high fecundity, batch spawning, a fairly long (but distinct), spawning season and more than one reproductively active age class. Simulation modelling showed that as a result of bet-hedging traits, an anchovy population should be able to filter out a large amount of the random variability in the system and filter out part of the autocorrelated variability occurring with a period of less than one year.

Anchovy eggs were significantly more patchy than the eggs and larvae of all other species ($p<0.05$, see Section 4, Table 4.5), reflecting the schooling behaviour of the adults, but although anchovy larvae (all ages combined) were more patchy and more crowded than either hake or lanternfish larvae, the difference was not statistically significant. The patchy distribution of anchovy eggs and larvae suggests that intraspecific competition is limited, so that the advantage of patchiness with respect to subsequent school formation outweighs the negative effects of crowding.

Perturbations which negatively influence year class strength in anchovy are likely to be processes which reduce the intensity of temperature gradients for prolonged periods during the spawning season, disrupting plankton concentrations within the thermocline and between the front and the coast, processes causing an increase in the number of larvae transported offshore, and processes causing an over-dispersed distribution of larvae, inhibiting school formation. Future monitoring should therefore give attention to such processes. There is no evidence from the recent direct surveys of anchovy biomass that large fluctuations in year class strength have occurred since 1983, and more than 200 000 tons have been harvested annually since 1972 without catch rates falling (SFRI unpublished data). Year-class failures may, therefore, be infrequent events. Increased harvesting leading to a reduced age structure may increase their frequency.

Lanternfish spawning is adapted to winter conditions when the system is most uniform (Fig. 7.1). At this time chlorophyll and microplankton standing stocks are small but widespread (see Section 3.1, Fig. 3 and Section 3.2, Fig. 3.2.5). The frequency of winds from the north increases in winter (see Section 2.2, Fig 2.2.2), leading to more frequent onshore transport as indicated by wind measurements at a number of stations where large densities of lanternfish eggs were sampled (see Section 5, Fig. 5.33), and by the increased percentage of drift card recoveries between Cape Point and Cape Columbine in winter (see Section 2.2, Table 2.2.2). Conversely, cool water with moderate to small plankton concentrations was shown to extend further offshore in winter. Lanternfish larvae were found to be much more widespread and closer inshore than the eggs, which are in greatest concentrations over the shelf slope, particularly in the vicinity of the canyons off Cape Columbine and Cape Point (see Section 4, Fig. 4.14). Although lanternfish eggs were significantly more patchy than a number of other components of the ichthyoplankton ($p<0.05$, see Section 4, Table 4.5), including their own larval stages, this may reflect miss-match of the survey grid with the spawning area rather than adaptive pattern, as eggs were most frequently sampled at offshore stations. Lanternfish larvae were less patchy than anchovy larvae, but the difference was not significant. The life history strategy of lanternfish was shown to be relatively ineffecient at filtering out random environmental variability or cycles with various periods. Thus lanternfish appear to be adapted to a uniform environment. Even small perturbations of short duration are likely to lead to large changes in population size.

Of particular importance for monitoring may be processes related to the degree of overlap between lanternfish larvae resulting from offshore spawning and winter standing stocks of plankton produced inshore. The overlap will be reduced either by reduced onshore transport of larvae (less wind stress from the north) or a restriction in the offshore movement of plankton brought about by unseasonal intensification of the front. Although no annual estimates of lanternfish biomass have been made, the catch has fluctuated widely since this species first appeared in the fishery in 1968. This variability has traditionally been attributed to changes in availability (SFRI, unpublished data), but might just as easily be caused by large fluctuations in biomass.

Hake eggs were not routinely identified in the plankton but published accounts of the reproductive biology (Botha 1980, 1986), and the abundance of larvae in the plankton points to a ubiquitious spawning strategy similar to that found by Sherman et al. (1984) for hakes off the north-eastern United States. Simulation modelling suggested that the combination of bet-hedging traits in hake allows the population to filter out random variability almost as efficiently as anchovy, but to be better adapted to filtering out longer period cycles. Hake larvae were the least crowded of all components of the ichthyoplankton, a result of the dispersed pattern of abundance of the psuedo-demersal adults - an advantage with respect to reducing intraspecific competition. The widespread distribution of hake larvae will provide a greater degree of spatial risk spreading than in anchovy or lanternfish, a factor not taken into account in the simulation model. Catches of hake in the southern Benguela region as far east as Cape Agulhas have generally exceeded 100 000 tons since 1955, although, the spawner biomass has apparently decreased considerably over this period and recruitment can be estimated to have varied within a range of half to double (calculated from cohort analysis data presented in Leslie 1985). It is not clear to what extent this reflects the true population variability and what proportion can be attributed to recruitment over-fishing, rather than the environment. Anomalies producing large changes in year class strength will likely have to persist for a number of years before the hake population size will be adversely affected. Perturbations such as extensive and prolonged warm events concentrating larvae in a narrow belt close to the coast may increase mortality from intraspecific competition.

In conclusion, the observed pattern of egg and larval abundance in anchovy, lanternfish and hake from the CELP samples point to very different spawning strategies. Life history strategies also differ greatly between the species, therefore the kinds of anomalies influencing year class strength will be very different. General and consistent temporal and spatial matching observed between the environment and egg and larval abundance patterns suggests adaptation, and points to parameters or processes for monitoring, but miss-matches of short duration may not necessarily cause large perturbations in population size because of bet-hedging.

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