**Abstract.**–Seasonal advection of warm western-boundary current water into the southern Benguela eastern-boundary current region from late spring to early autumn coincides with increased coastal upwelling activity. The combined effect of these two processes is to stabilize the system through intensification of temperature fronts and thermoclines, providing conditions favoring anchovy spawning and larval survival. These conditions appear to be robust to short periods of intense storm mixing and downwelling during summer, and weaken and disappear only with the onset of winter when there is diminished influence of the warm western-boundary current water, downwelling conditions, and increased frequency of storms.

Manuscript accepted 24 November 1989.
Fishery Bulletin, U.S. 88:323–338.

# Ocean Stability and Anchovy Spawning in the Southern Benguela Current Region

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The extension of the Hjort (1914) hypothesis by Lasker and his coworkers (Lasker 1975, 1978, 1981a,b) to include the role of a stable ocean in determining fish recruitment has had a profound influence on research into the early life history of marine fish. Lasker's extended hypothesis suggests that ocean stability influences food aggregations for larvae and larval drift and, hence, recruitment strength (Lasker 1981b). In support of Lasker's hypothesis, strong wind events have been found to disrupt anchovy larval food aggregations, and, by inference, to effect larval mortality off California (Lasker 1975) and Peru (Walsh et al. 1980). During such events, larvae can also be entrained within increased offshore Ekman flow and placed outside suitable feeding areas (Walsh et al. 1980, Lasker 1981b). A significant linear relationship between anchovy larval mortality rate and the frequency of calm, low wind-speed periods during the spawning season off California (Peterman and Bradford 1987) provides further evidence of the importance of event-scale disruption of ocean stability.

Parrish et al. (1983) compared the seasonality and geography of sardine and anchovy reproduction in the California, Peru, Canary, and Benguela Current systems with corresponding features of the environment and suggested that patterns of correspondence may indicate the most crucial processes affecting reproductive success. They found that spawning was adapted to avoid times and places characterized by intense turbulent mixing and strong offshore transport.

In this paper we use survey data to provide a finer-scaled description of ocean stability and anchovy spawning than that of Parrish et al. (1983), and suggest that in the southern Benguela Current system anchovy spawning is adapted to seasonal patterns of ocean stability that are resistant to event-scale processes. Local conditions are briefly compared with those in the Southern Californian Bight where Lasker's studies took place, and conclusions are drawn with respect to the influence of ocean stability on survival of the planktonic stages and recruitment in the southern Benguela Current region.

## Methods

During the Cape Egg and Larval Programme (CELP), plankton and the environment were sampled at approximately monthly intervals between August 1977 and August 1978 from a grid of stations in the southern Benguela Current region. The purpose of the program was to determine general spawning habitat and time for the major fish species of commercial importance (Shelton 1986). The grid comprised 120 stations posi-

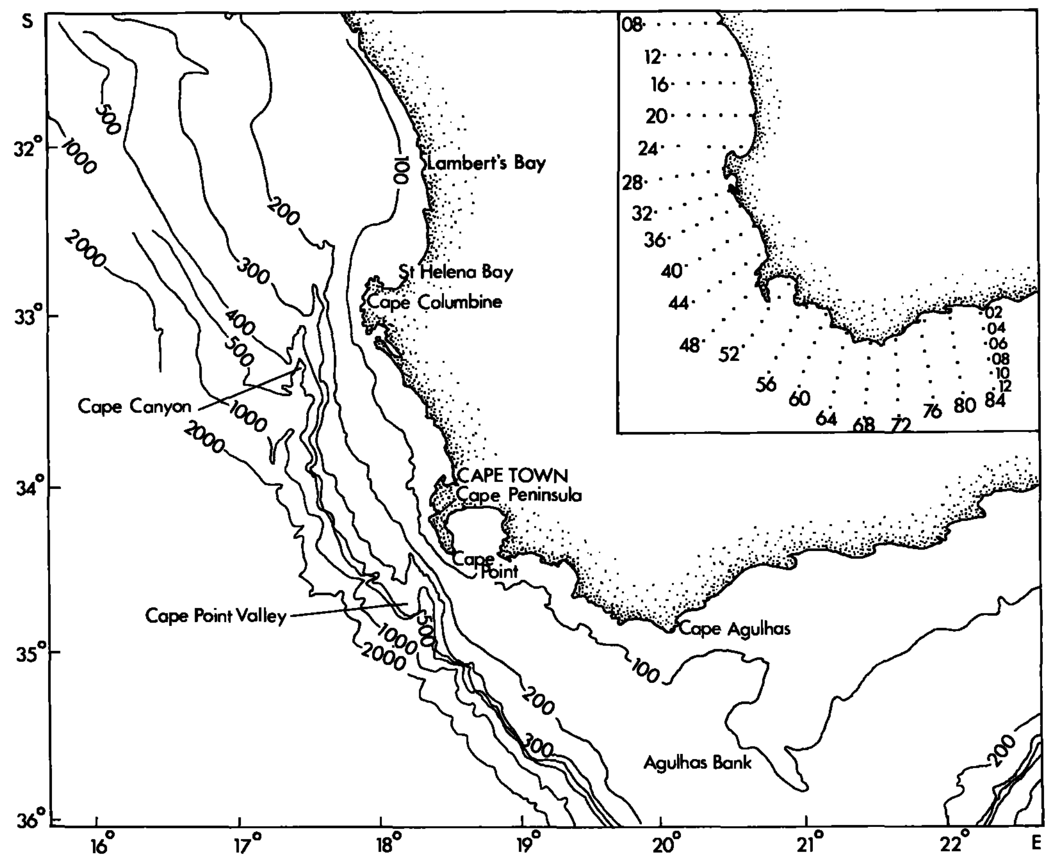



**Figure 1**
Cape Egg and Larval Programme (CELP) survey grid, southern Benguela Current region, sampled monthly August 1977–August 1978, and general topography of the survey area (depth contours in meters).

tioned at 10-nautical-mile intervals (18.5 km) on 20 transects (Fig. 1).

Vertical profiles of temperature and water samples for measurement of salinity, chlorophyll-*a* concentration, and microplankton density were collected from the water column. Chlorophyll analysis, described in Shannon et al. (1984), was by means the standard photometric method of SCOR/UNESCO Working Group 17 (1966). Microplankton particle concentration was determined by prefiltering 2 liters of the water sample through a 100-μm filter and collecting those particles retained by a 37-μm filter. Particles between 37 and 100 μm correspond to the size fraction considered to be important for first-feeding anchovy larvae (Arthur 1976, Hunter 1977). Particles were counted under a light microscope at 20× magnification and expressed as number per liter. Although all particles were enumerated, only the maximum density at each station of total "esculent" (nutritious to fish larvae [Sharp 1980]) particles are presented, such as copepod eggs, nauplii, copepodite stages, and dinoflagellates. Wind strength and direction were estimated by the lighthouse keeper at Cape Point throughout the period. In order to examine surface drift patterns, 20 plastic drift cards (Duncan 1965) were released monthly at each station sampled.

Fish eggs and larvae were sampled by means of a double oblique haul of a Bongo sampler down to a maximum depth of 100 m. The sampler had a mouth opening of 57 cm and was fitted with 300-μm and 500-μm mesh nets. Counts of anchovy eggs and larvae from the 300-μm unit were standardized to volume or numbers under 10 $m^2$ using the formula given in Smith and Richardson (1977). In November 1979 and November 1984 the vertical distribution of anchovy eggs and temperature profiles was measured at two localities. Eggs were sampled with Miller nets (Miller 1961) as described in Shelton and Hutchings (1982). Anchovy egg and early-stage larval abundance data from a more extensive grid of stations sampled in November 1983 using a CalVET net (Smith et al. 1985) are also presented.

## Results and discussion

### Seasonality in temperature and spawning

Both the mean and the coefficient of variation (CV) of sea surface temperature measured over the CELP grid peaked in summer (Fig. 2). This is caused by the seasonal advection of warm water orginating from the western-boundary Agulhas Current into the southern Benguela Current region (Shelton et al. 1985) and the simultaneous increase in coastal upwelling (Andrews and Hutchings 1980). Strong cross-shelf temperature gradients, or fronts, are set up between advected and upwelled water, reflected by the increase in the surface temperature CV. In winter the influence of western-boundary current water is diminished and upwelling is less frequent and less intense (Shelton et al. 1985, Andrews and Hutchings 1980). Consequently, cross-shelf temperature gradients weaken and disappear and mean SST values are lower and have a lower CV, reflecting cool, more isothermal conditions.

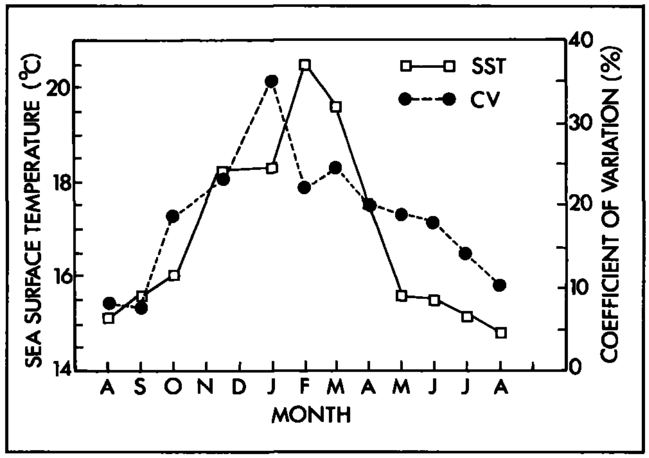



**Figure 2**
Monthly means and coefficents of variation (CV) of sea-surface temperature (SST) values over the CELP survey grid, southern Benguela Current region, for the period August 1977–August 1978.

### Horizontal structure

The changes in temperature structure described above, as well as associated changes in the patterns of abundance of microplankton and chlorophyll-*a*, can be seen in contour diagrams of values for summer and winter (Fig. 3). The strong temperature front that develops along the west coast in summer is clearly visible. Although this front is most persistent between Cape Point and Cape Columbine, and was considered by Bang (1973) to "pivot" at Cape Point, it may extend as far south as Cape Agulhas when upwelling occurs at capes east of Cape Point. At Cape Columbine isotherms tend to diverge offshore, and further north the front is generally weaker and more variable. The density of potential food particles for early-stage larval feeding, as indicated by microplankton and chlorophyll-*a* concentrations, are highest inshore of the temperature front in summer, indicating that the front constrains the offshore Ekman drift of productive upwelled water. In winter when the front disappears, microplankton and chlorophyll-*a* concentrations are generally lower and more dispersed.

Arrows indicating major directions of surface drift over the survey area in summer (January 1978) and winter (August 1977) based on drift-card recoveries are plotted in Figure 4. Of the 24,000 cards released in each month there was a 5% recovery in January 1978 and a 7% recovery in August 1977. There was no clear seasonality in the overall recovery rate. In summer the southern Agulhas Bank area was characterized by onshore surface flow with a westerly component. Some cards released over the western Agulhas Bank moved around Cape Point and up the west coast, and the general pattern of flow inshore of the strong temperature front on the west coast was northwards. North of Cape Columbine there was some evidence of onshore flow. There were very few southern African recoveries offshore of the front, although several cards were recovered along the eastern coast of South America, indicating general offshore flow into the South Atlantic gyre at stations offshore of the front.

In winter, flow in the south was again predominantly onshore, although this time with a marked easterly component east of Cape Agulhas and a westerly component to the west. Several cards released on the western Agulhas Bank were found substantial distances up the west coast, although one card released in the extreme north of the grid travelled against this flow and was recovered on the east coast. Again, few cards were recovered on the coast of southern Africa from releases on the west coast, although there were 10 recoveries from the coast of South America and one recovery from southern California. In comparison with summer, several of these recoveries came from cards released at inshore stations, indicating widespread offshore flow along the west coast in the absence of the front.

### Vertical structure

Summer and winter vertical structure of temperature, microplankton density, and chlorophyll-*a* concentration are shown for three representative sections over the survey area in Figures 5–7. A section over the Agulhas Bank (Fig. 5) shows the existence of a strong thermocline in summer between warm water of Agulhas

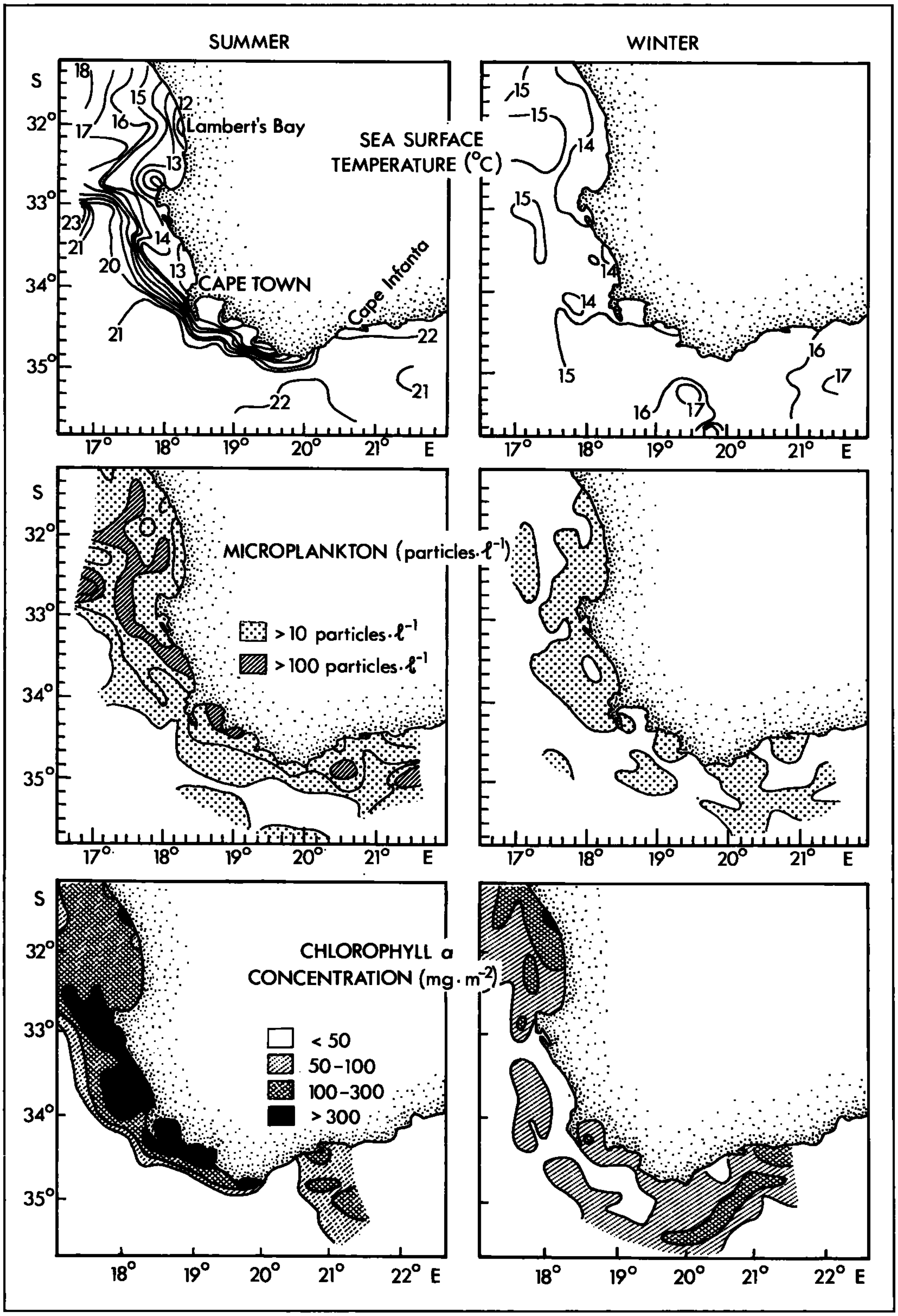



**Figure 3**

Typical summer (January 1978) and winter (August 1977) patterns of sea-surface temperature, microplankton particle concentrations, and chlorophyll-*a* concentrations over the CELP survey grid, southern Benguela Current region.

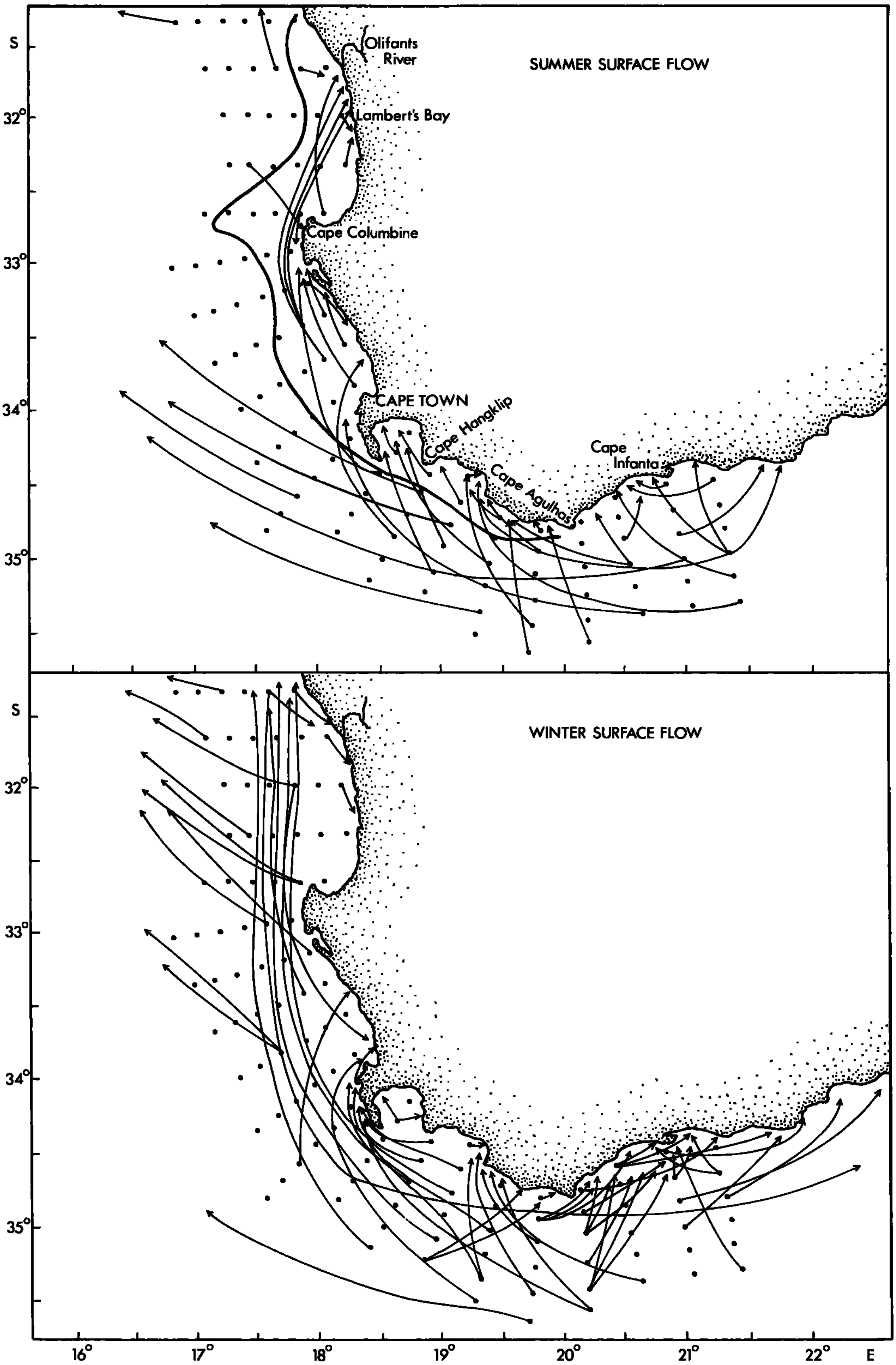



**Figure 4**

Summer and winter patterns of surface flow in the southern Benguela Current region, gauged from drift-card recoveries from releases of 20 cards at each station in January 1978 and August 1977. Arrows may represent more than one recovery and indicate general direction of flow.

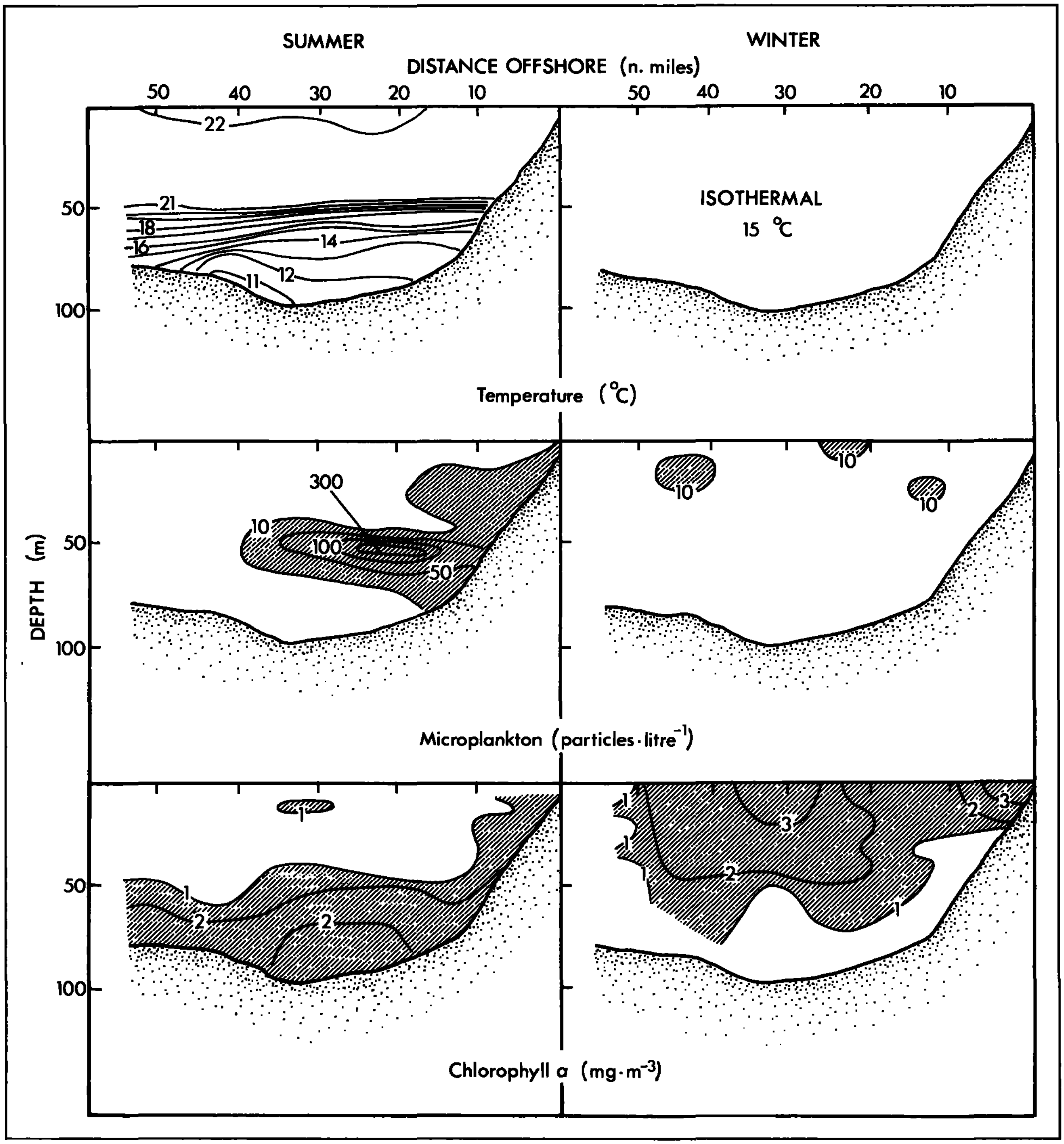



**Figure 5**

Summer (January 1978) and winter (August 1977) sections of temperature, microplankton, and chlorophyll-*a* values along line 76 over the Agulhas Bank, southern Benguela Current region.

Current origin forming an upper mixed layer and cold water that moves onto the Bank along the bottom in summer. The warm layer had very low plankton densities, but enhanced microplankton density and phytoplankton-*a* concentration were associated with the thermocline.

With the onset of winter, the influence of the warm Agulhas Current water over the Agulhas Bank becomes less and heat loss to the atmosphere increases, causing a cooling of the surface layer. Surface cooling combined with the movement off the shelf of the cold bottom layer makes the water column less stable and susceptible to mixing by winter storms (Shannon et al.

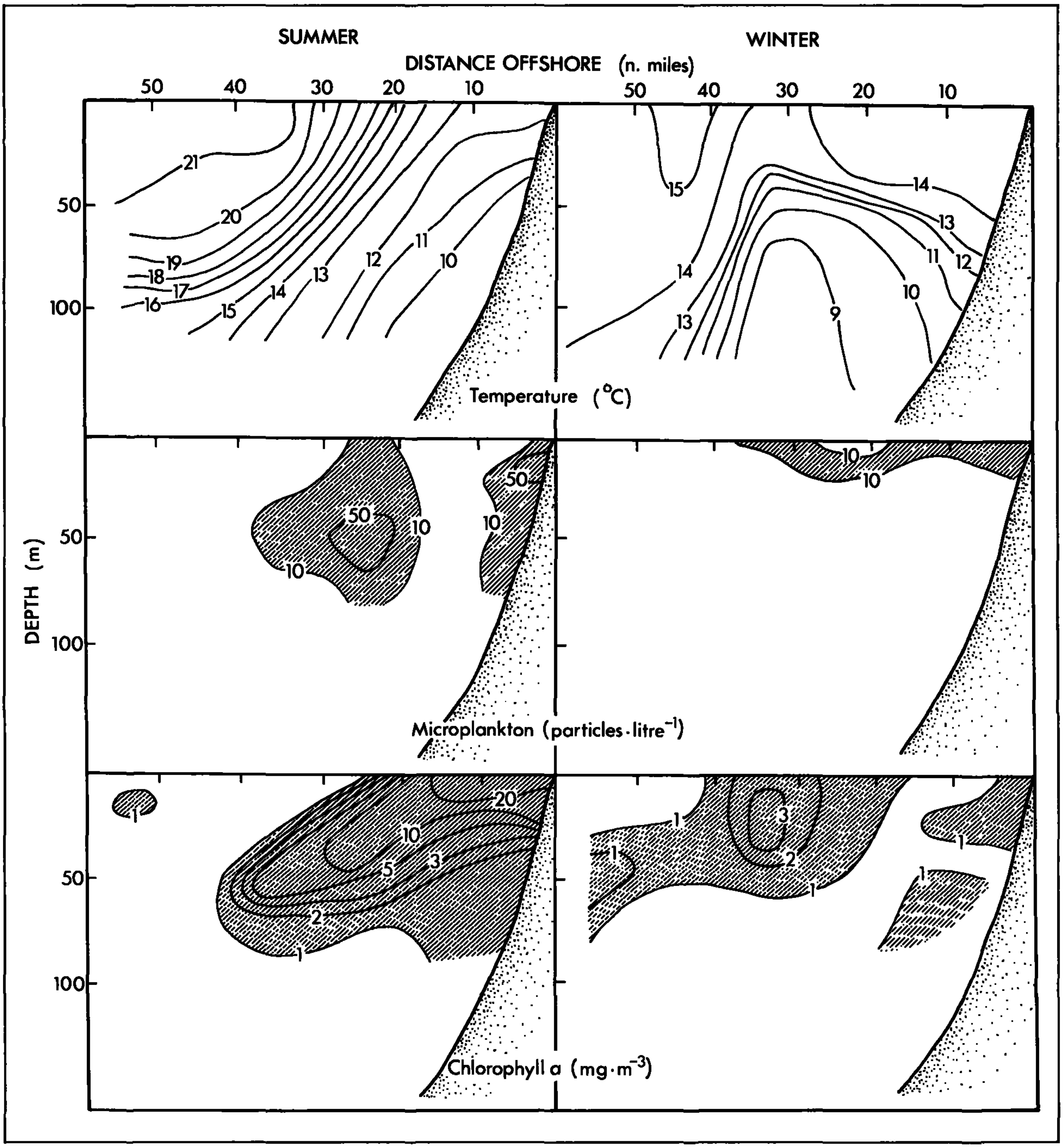



**Figure 6**

Summer (January 1978) and winter (August 1977) sections of temperature, microplankton, and chlorophyll-*a* values along line 44 just north of Cape Town, South Africa.

1984, Largier and Swart 1987). Microplankton particle concentrations tend to be low in the well-mixed water column but chlorophyll-*a* concentrations can be quite high, either if nutrients accumulated in bottom sediments are mixed into the euphotic zone by strong storm action (Shannon et al. 1984), or if periods of calm weather persist long enough for the water column to stabilize, albeit weakly, and phytoplankton is thereby allowed to remain in the euphotic zone long enough to grow.

A section just north of Cape Town (Fig. 6) shows the strong temperature front in summer between cold upwelled water inshore and warm water offshore. Enhanced levels of microplankton occurred in the vicinity

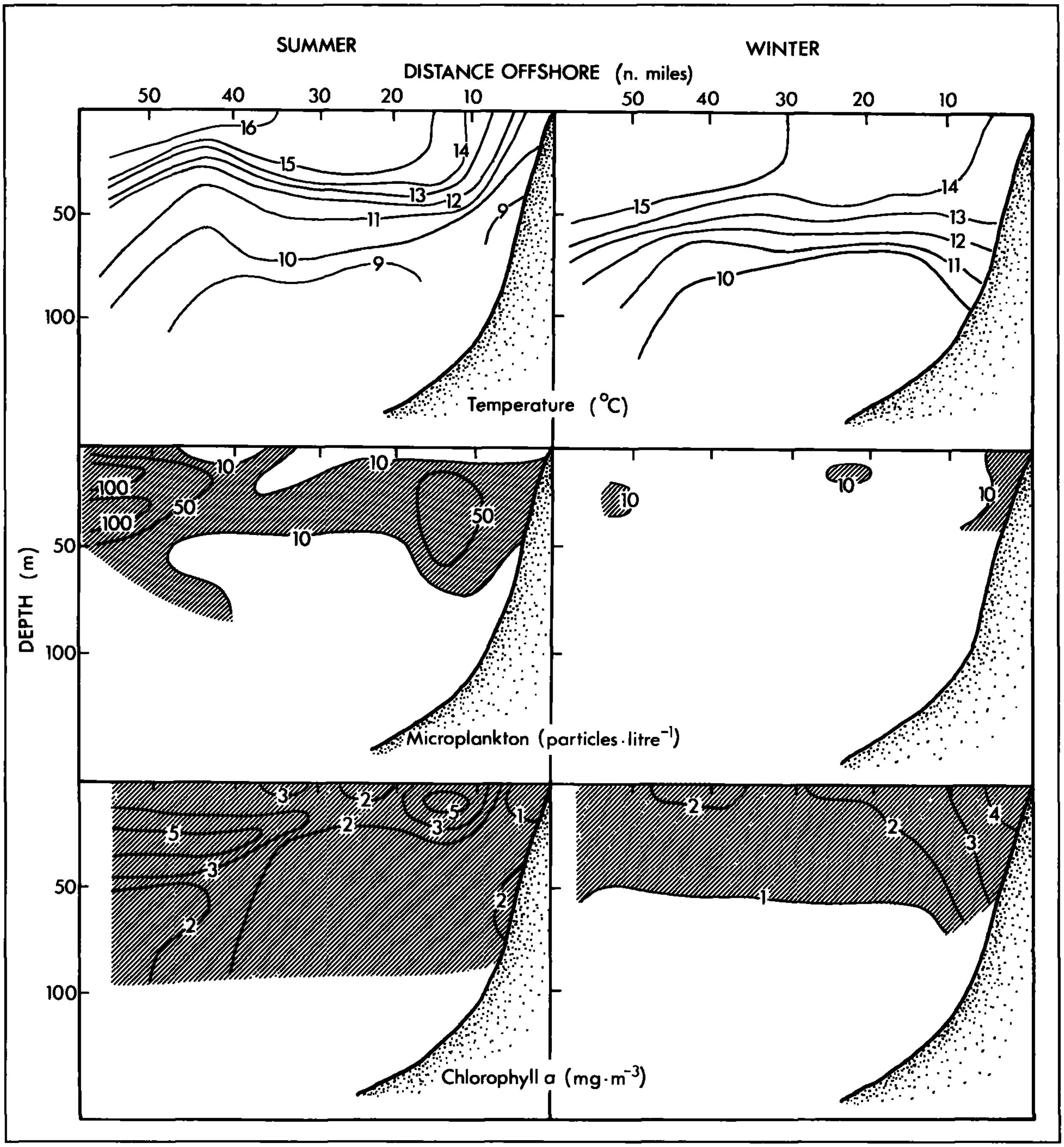



**Figure 7**
Summer (January 1978) and winter (August 1977) sections of temperature, microplankton, and chlorophyll-*a* values along line 16 in the vicinity of Lambert's Bay, South Africa.

of the front as well as close inshore, and high levels of chlorophyll-*a* were found inshore near the surface, declining in concentration and following the isotherms into deeper water in the vicinity of the front. Offshore of the front, both chlorophyll-*a* and microplankton levels were negligible. A similar pattern was noted in a transect of the front off Cape Columbine in December 1984, with copepod nauplii and copepodites concentrated in the front and chlorophyll-*a* values increasing towards the coast, inshore of the front (Armstrong et al. 1987). Although the front may persist as a subsurface feature in winter, even during prevalent downwelling conditions, it is much weaker as a consequence of cooler water offshore. Microplankton and chlorophyll-*a*

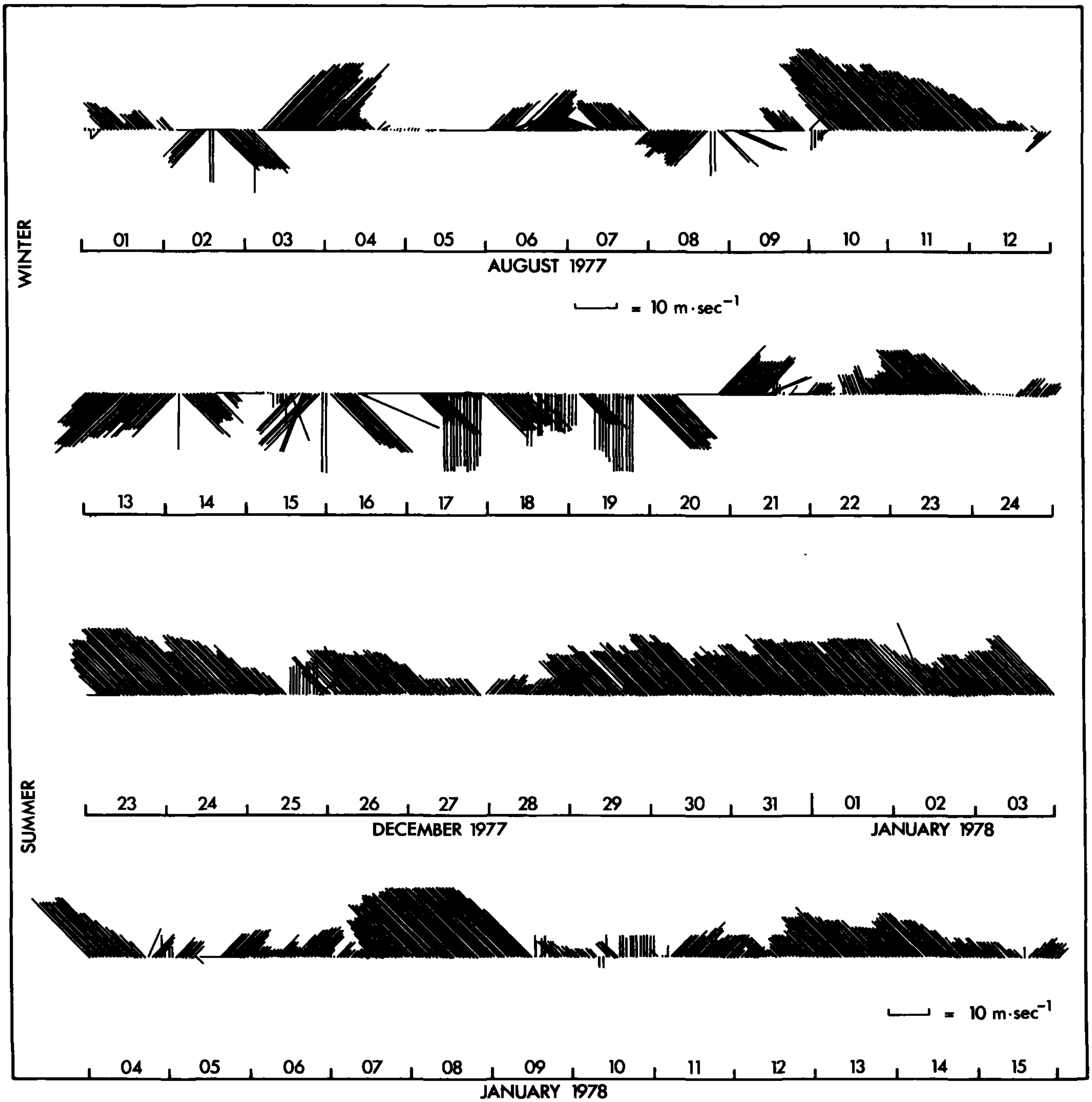



**Figure 8**

Wind stick diagram for the period 23 December 1977–15 January 1978 and 1–24 August 1977, showing tyical summer and winter patterns of wind stress measured at the lighthouse at Cape Point, South Africa.

values are generally much lower and more dispersed over the west coast between Cape Point and Cape Columbine in the absence of the surface front in winter.

A section on the west coast off Lambert's Bay (Fig. 7) shows a moderately strong thermocline with coastal upwelling in summer. Moderate-to-high levels of microplankton and chlorophyll-*a* extending to the limit of the grid in the top 50 m are typical of the area at this time. In winter the thermal structure is similar, but with less upwelling activity and cooler water offshore. Although microplankton levels were low in the section shown, widespread moderate levels of chlorophyll-*a* are quite

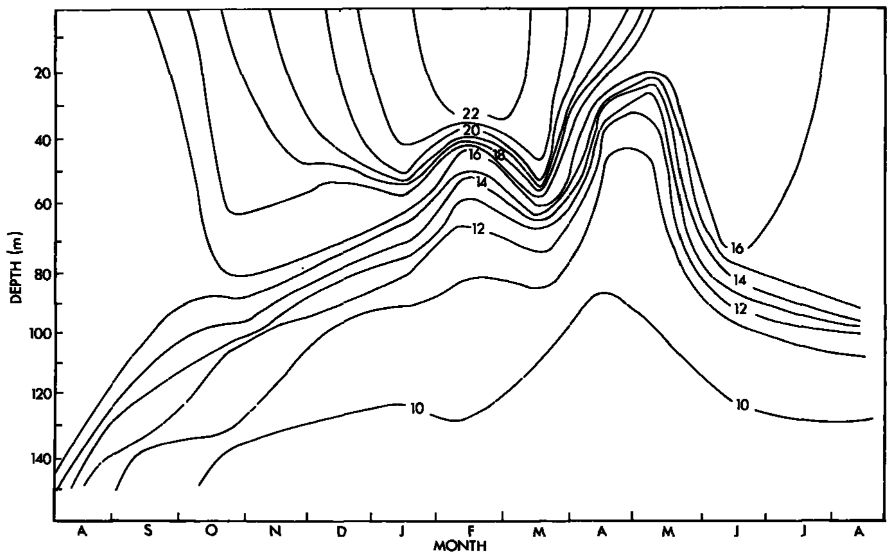



**Figure 9**
Variability in the vertical temperature structure at station 64-06 on the Agulhas Bank, southern Benguela Current region.

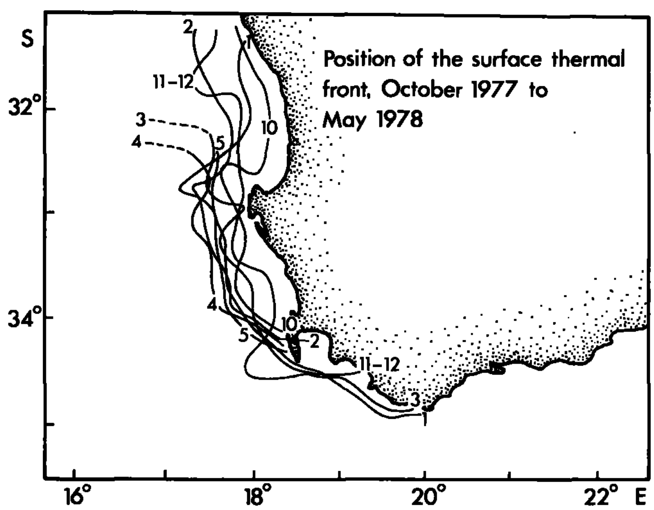



**Figure 10**
Variability in the position of the surface temperature front in the southern Benguela Current region, spring 1977 through autumn 1978. (Numbers refer to months of the year, e.g., 10 = October 1977, 2 = February 1978.)

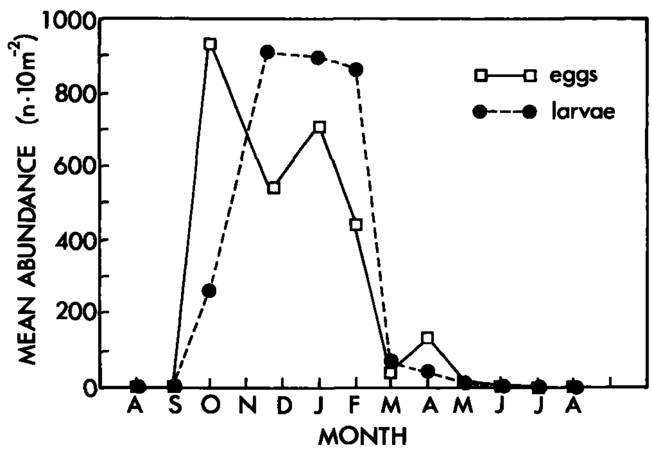



**Figure 11**
Monthly mean abundance of anchovy eggs and larvae over the CELP survey grid, southern Benguela region, for the period August 1977–August 1978.

typical for the recruitment area in winter, as shown in Figure 3.

## Robustness to event-scale processes

Wind stick diagrams of wind strength and direction estimated by the lighthouse keeper at Cape Point (Fig. 8) show that winter is characterized by frequent periods of strong northerly wind interspersed with southerly winds and calm, whereas in summer strong upwelling-favorable southeasterlies dominate, alternating with brief periods of calm and occasional wind reversals. Despite event-scale forcing of this nature, contoured monthly temperature profiles through the water column over the Agulhas Bank show strong stratification persisting over several months of the spring-to-autumn period, weakening and disappearing with the onset of winter (Fig. 9). Similarly, although erratic in appearance and position to the north and south, the temperature front in the transport area between Cape Point and Cape Columbine persists as a stable feature for up to 8 months of the year (Fig. 10), despite event-scale variability in the wind field. During lulls in upwelling the front may weaken at the surface and move inshore, at which time the temperature discontinuity may be most apparent in the form of a thermocline, but it persists as a subsurface feature further offshore (Shelton

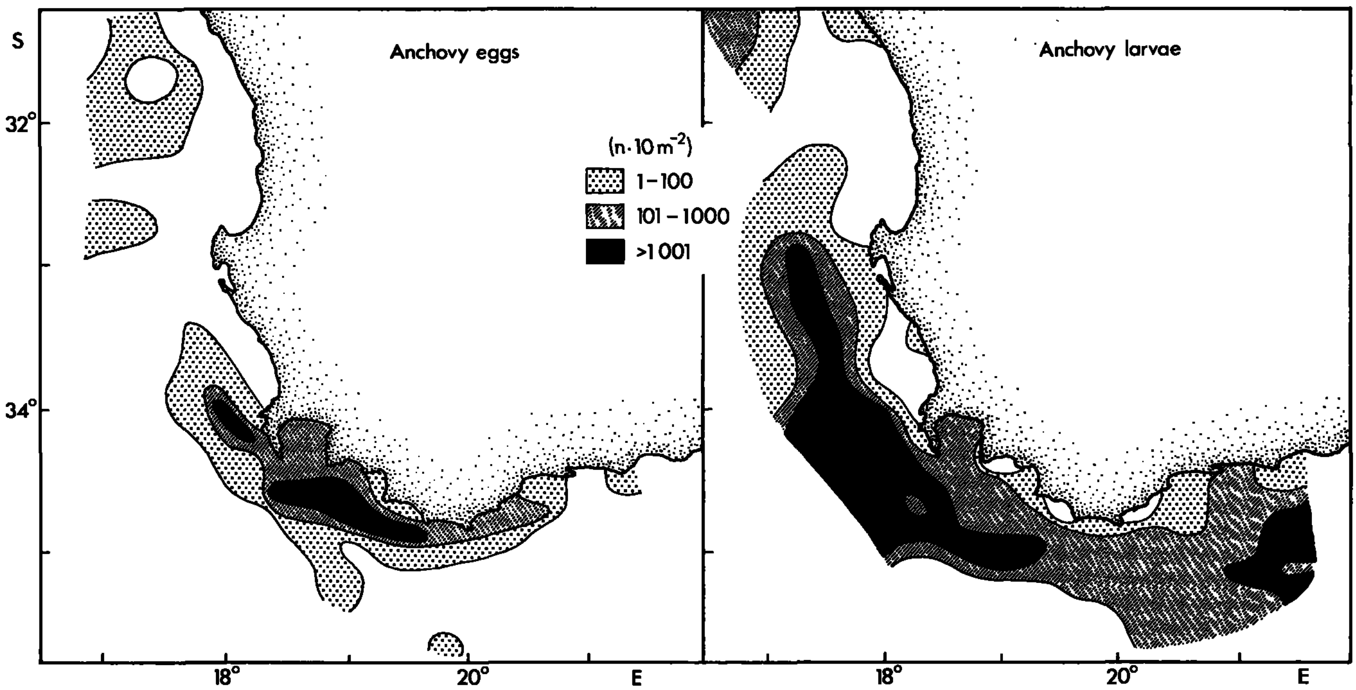



**Figure 12**
Anchovy egg and larval abundance patterns over the CELP survey grid, southern Benguela Current region, in January 1978, a month of peak spawning.

1986). With the next pulse of upwelling, the isotherms flip to a more vertical orientation and the front moves offshore again, to an average position over the inner shelf break (200-m contour).

## Anchovy spawning, transport, and recruitment in relation to ocean stability

Anchovy eggs are generally absent or in very low abundance in the plankton in autumn and winter when the region is cool and isothermal (March–August, Fig. 11). With the onset of spring (September–November) both egg and larval abundance increases rapidly, reaching a peak in late spring or early summer when both the mean temperature and the CV are high, and then decreasing to low numbers over the autumn.

Anchovy spawning is typically most intense south and east of Cape Point over the broad Agulhas Bank (Fig. 12). The vertical distribution of anchovy eggs in the spawning area on the Agulhas Bank (Fig. 13a) is restricted almost entirely to the warm upper mixed layer, above the strong thermocline that forms in summer at about 50 m. On the west coast a transect bisecting the front in the vicinity of the Cape Peninsula shows that anchovy eggs extending up the west coast are concentrated within the frontal zone (Fig. 13b). Anchovy larvae (Fig. 12) are generally more widespread over the Agulhas Bank than the eggs as a result of dispersal, and in particular extend further up the west coast, often as far as Cape Columbine, in the vicinity of the front. Recent samples from a more extensive grid of stations confirm these patterns (Fig. 14).

Based on these patterns of anchovy eggs and larval abundance and the catch pattern of recruits in the commercial fishery (Crawford et al. 1980 and Crawford 1980), the habitat of the anchovy in the southern Benguela region can be divided into spawning, transport, and recruitment areas (Fig. 15). The role of ocean stability in each of these three areas can be evaluated.

Anchovy spawning is highly seasonal, peaking in summer when the southern Benguela region is most structured by temperature fronts and thermoclines under the simultaneous influence of advected warm western-boundary current water and coastal upwelling. The spawning area is characterized by a strongly stratified, stable water column throughout summer. Stratification is resistant to event-scale mixing processes and only weakens with the reduced influence of eastern-boundary current water on the Bank and the retraction of the cold bottom layer with the onset of winter. Winter storms are then able to mix the entire water column creating isothermal conditions which persist until the onset of summer. The warm, uniform surface layer over the Agulhas Bank in summer provides conditions conducive to rapid anchovy egg development; below 14°C anchovy egg development in the

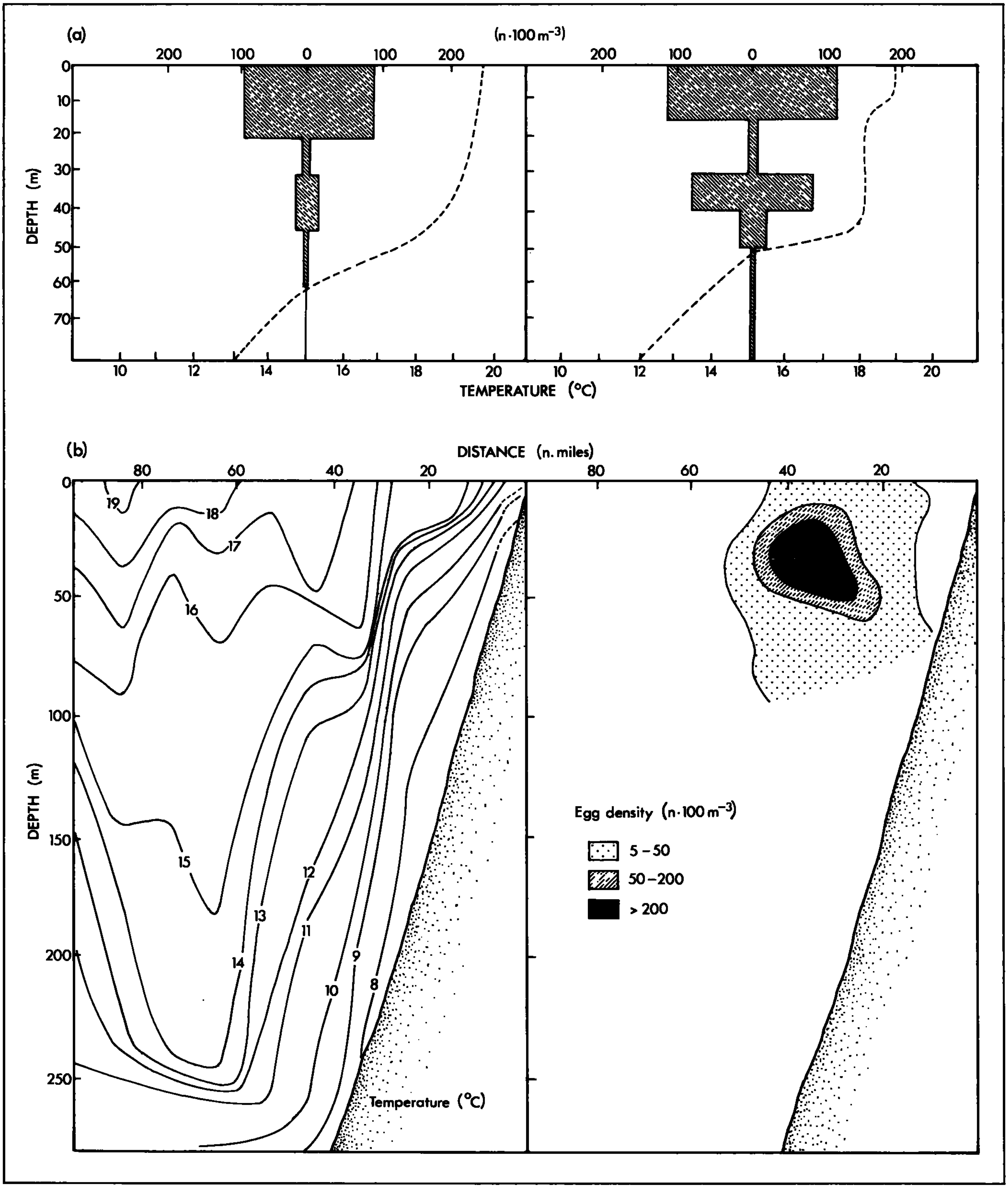
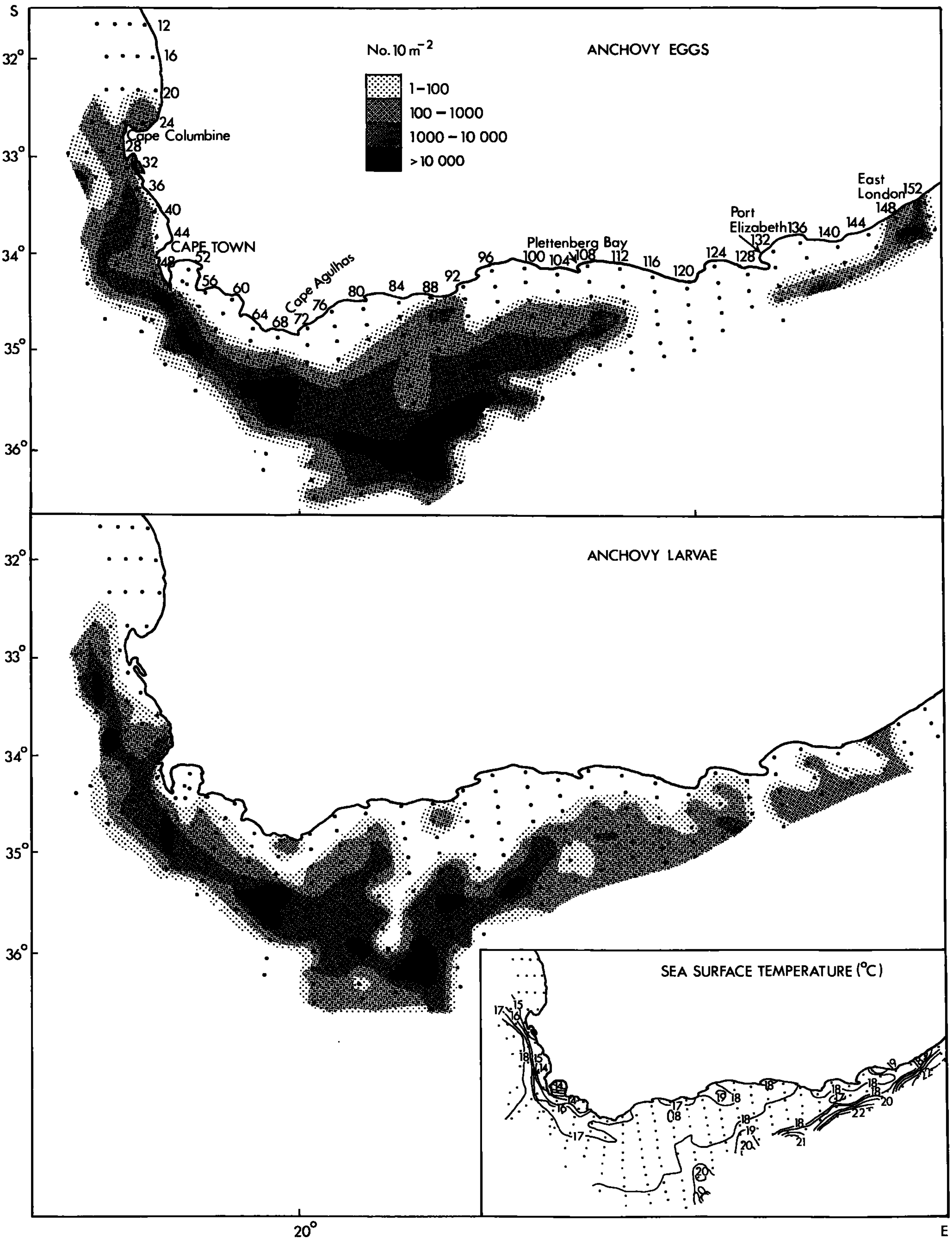



**Figure 13**
(a) Vertical distribution of eggs and temperature at depth for two stations in the anchovy spawning area, southern Benguela Current region, November 1984. (b) Vertical sections of temperature and anchovy egg abundance measured along a transect bisecting the temperature front off the Cape Peninsula, South Africa, November 1979.

**Figure 14**
Pattern of abundance of anchovy eggs and larvae in November 1983 from an extensive survey grid covering nearly the entire anchovy spawning area in the southern Benguela Current region.


ANCHOVY EGGS
No. 10 m⁻²
1–100
100 – 1000
1000 – 10 000
>10 000
Cape Columbine
CAPE TOWN
Cape Agulhas
Plettenberg Bay
Port Elizabeth
East London
ANCHOVY LARVAE
SEA SURFACE TEMPERATURE (°C)
S
32°
33°
34°
35°
36°
20°
E

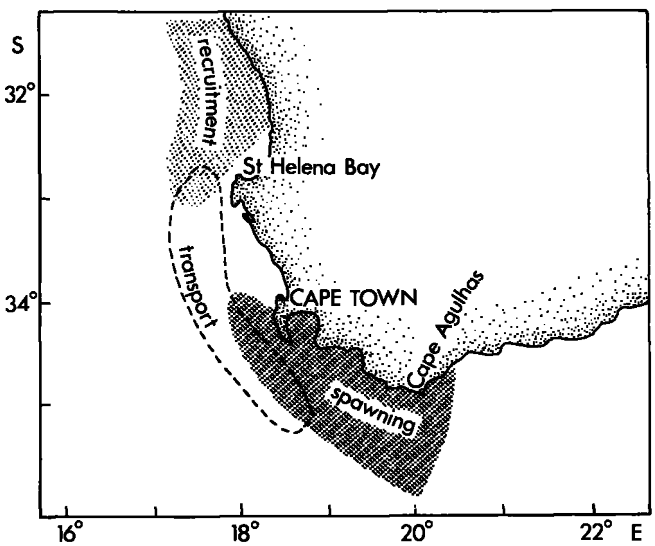



**Figure 15**
A generalized representation of anchovy spawning, transport, and recruitment areas in the southern Benguela Current region.

laboratory is very slow and hatching larvae are deformed (King et al. 1978). Below the warm surface layer a strong thermocline at about 50 m is associated with subsurface maxima of microplankton and chlorophyll-*a*, facilitating the survival of early-stage larvae that require high concentrations of food particles within a suitable size range (Lasker et. al. 1970).

Spawning conditions in the southern Benguela appear to be in marked contrast with conditions in the spawning ground of the Northern anchovy *Engraulis mordax* in the Southern California Bight where Lasker's studies were carried out. Surface temperatures in the Southern California Bight given in Lasker (1981b) are some 3–5°C lower than over the Agulhas Bank during the respective spawning seasons. Vertical temperature structure during the spawning season off southern California, as shown in Lasker (1978), is quite variable, with generally weak stratification susceptible to mixing. The chlorophyll-*a* layer disrupted by storm mixing in April 1984 was at about 15 m (Lasker 1975), in contrast to the deeper maxima on the Agulhas Bank. Although maximum chlorophyll-*a* values before storm mixing in the layer off California in April 1974 are similar to those recorded in the Agulhas Bank layer, microplankton particle concentrations over the Agulhas Bank do not reach the high values recorded by Lasker (1981b) because dinoflagellates are not as common as in the Southern California Bight, possibly due to persistent strong winds (Parrish et al. 1983), which thoroughly mix the relatively deep, upper mixed layer.

From the the spawning area in the south, the drift of eggs and early-stage larvae is primarily northwestwards, into the west coast transport area. Bang (1973) and Bang and Andrews (1974) have documented the presence of a strong northward-flowing jet current associated with the front which is a prominent feature of this area in summer. The role of this jet in transporting anchovy eggs and early-stage larvae from the Agulhas Bank spawning ground to the west coast nursery area has been examined and described in Shelton and Hutchings (1982). Drift-card recoveries for summer support their interpretation. In the transport area, enhanced levels of chlorophyll-*a* and microplankton associated with the inshore and frontal zone may be important in early-larval survival. Despite predominantly southeast winds in summer, facilitating offshore Ekman flow and upwelling at the coast, the offshore loss of eggs and larvae along the west coast may be small because of the constraining influence of the front. However, there is frequently an offshore divergence of the front off Cape Columbine, following the orientation of bottom contours, and this may be associated with the "leaking" of water containing larvae from the productive coastal region (Shelton et al. 1985, Shelton 1986).

Onshore flow north of Cape Columbine facilitates penetration of the productive recruitment area by larvae. Positioned downstream of the major sites of upwelling at Cape Columbine and Cape Point, the frontal structure dominating the transport area in summer gives way to more gently sloping isotherms north of Cape Columbine where the shelf widens. Because of lower average wind speeds (Hutchings et al. 1988), upwelling is milder than in the transport area and a vertically stable water column is a persistent feature. Enhanced levels of microplankton and chlorophyll-*a* characterize the inner shelf in this area throughout the year (Hutchings 1981), providing suitable conditions for the survival and growth of anchovy recruits.

The patterns of ocean stability described above, based largely on survey data, appear to have played a major role in shaping the spawning behavior observed by anchovy in the southern Benguela region. Upwelling generates the high levels of plankton production that support the spawning biomass of up to 2 million tons of anchovy estimated for the area (Armstrong et al. 1988), but the associated processes of turbulence and offshore Ekman flow present special problems to the plankton stages that have to be solved through evolutionary adaptation. In the southern Benguela region this appears to have been brought about by the selection of times and areas of spawning which make best use of seasonal and spatial patterns of ocean stability to provide suitable food concentrations and favorable transport.

Survey data for the southern Benguela therefore tends to confirm the conclusions from the larger-scale comparative study of eastern-boundary currents by Parrish et al. (1983) that the spawning habits of anchovy (and sardine) attempt to minimize both wind-induced turbulent mixing and offshore-directed transport. Bakun (1985) argues that the results of Parrish et al. (1983) strengthen the relevance of Lasker's hypothesis to modeling recruitment and exploratory data analysis. However, if anchovy populations in the different eastern-boundary current regions have essentially "solved" the problems of disruptive turbulence and unfavorable transport, "mistakes" should be rare and difficult to find in the field. The fact that event-scale disruptive turbulence has been observed in the spawning area off southern California and that the incidence of calm periods can be statistically related to daily larval mortality rate (Lasker 1975, 1981b; Peterman and Bradford 1987) suggests that such "mistakes" do occur despite adaptations. Even so, they may be undetectable in recruitment measurements, either because of large and often unquantified measurement error, or because the "mistakes" are masked by a well-developed suite of "bet-hedging" traits (Shelton 1987). Estimates of anchovy recruitment (with error bars) for the southern Benguela population based on direct surveys (Butterworth 1989, Fig. 16) show less variability than anticipated in the literature (e.g., Beddington and Cooke 1983), although the time series is still too short to be conclusive.

If the southern Benguela anchovy population is adapted to local persistent patterns of ocean stability and is well-buffered against event-scale variations through bet-hedging, a prerequisite for detectably poor recruitment at moderate spawning stock sizes may be season-long weakening or disruption of the stability patterns in either the spawning, transport, or recruitment areas. Such conditions would probably arise if the influence of Agulhas Current water over the Agulhas Bank and on the west coast were reduced, particularly over the summer period.

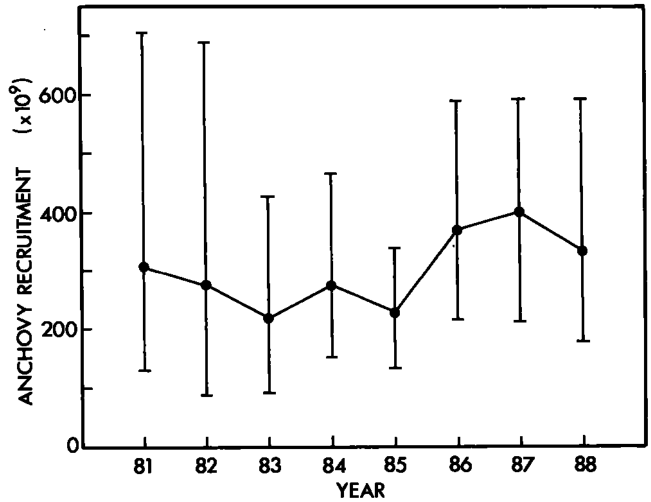



**Figure 16**

Estimates (median and 95% confidence interval) of annual anchovy recruitment for the southern Benguela population, deduced from direct survey results to July 1988 (Butterworth 1989).

## Acknowledgments

We acknowledge the input of several of our colleagues at the Sea Fisheries Research Institute, Cape Town, to the Cape Egg and Larval Programme. In particular, Garth Newman and Vere Shannon provided much of the impetus for the initiation of CELP, and Alan Robertson, Hennie Crous, Frans Kriel, Deon Horstman, Donald Alexander, Robert Cooper, Gustav Wehmeyer, Jan Van der Westhuizen, Chris Jeenes, John Giddey, and Christine Illert gave excellent technical support during its execution. Colleagues at the NMFS Southwest Fisheries Center, La Jolla, particularly the group formally headed by Reuben Lasker, are thanked for their advice and encouragement with respect to the studies of anchovy early-life history in the Benguela Current system. We dedicate this paper to the memory of Reuben.

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