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

PETER A. SHELTON, ALAN J. BOYD, AND MICHAEL J. ARMSTRONG
Sea Fisheries Research Institute
Private Bag X2
Rogge Bay 8012
Cape Town, South Africa

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

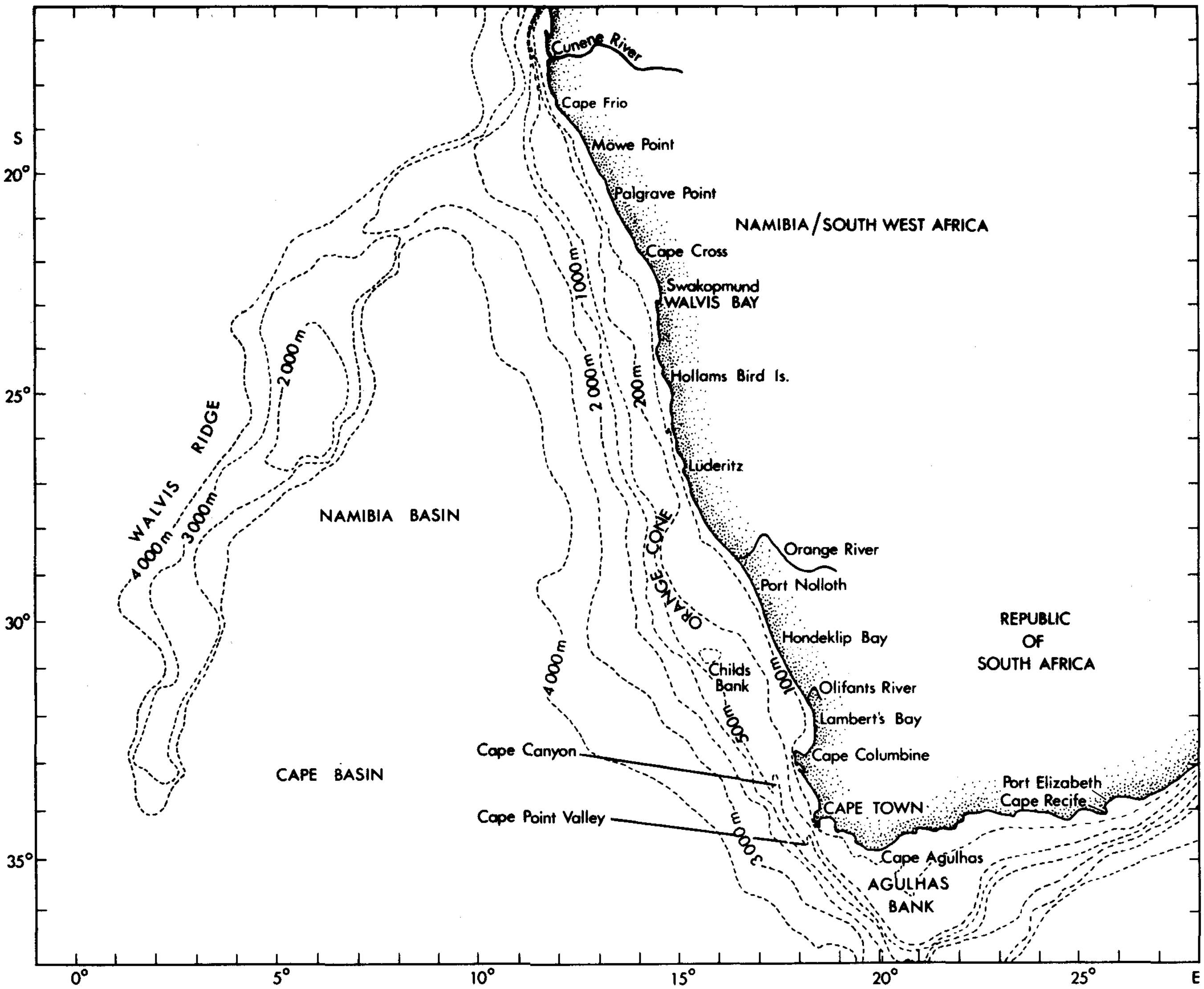


Figure 1. Bathymetry of the Benguela eastern boundary current region.

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.

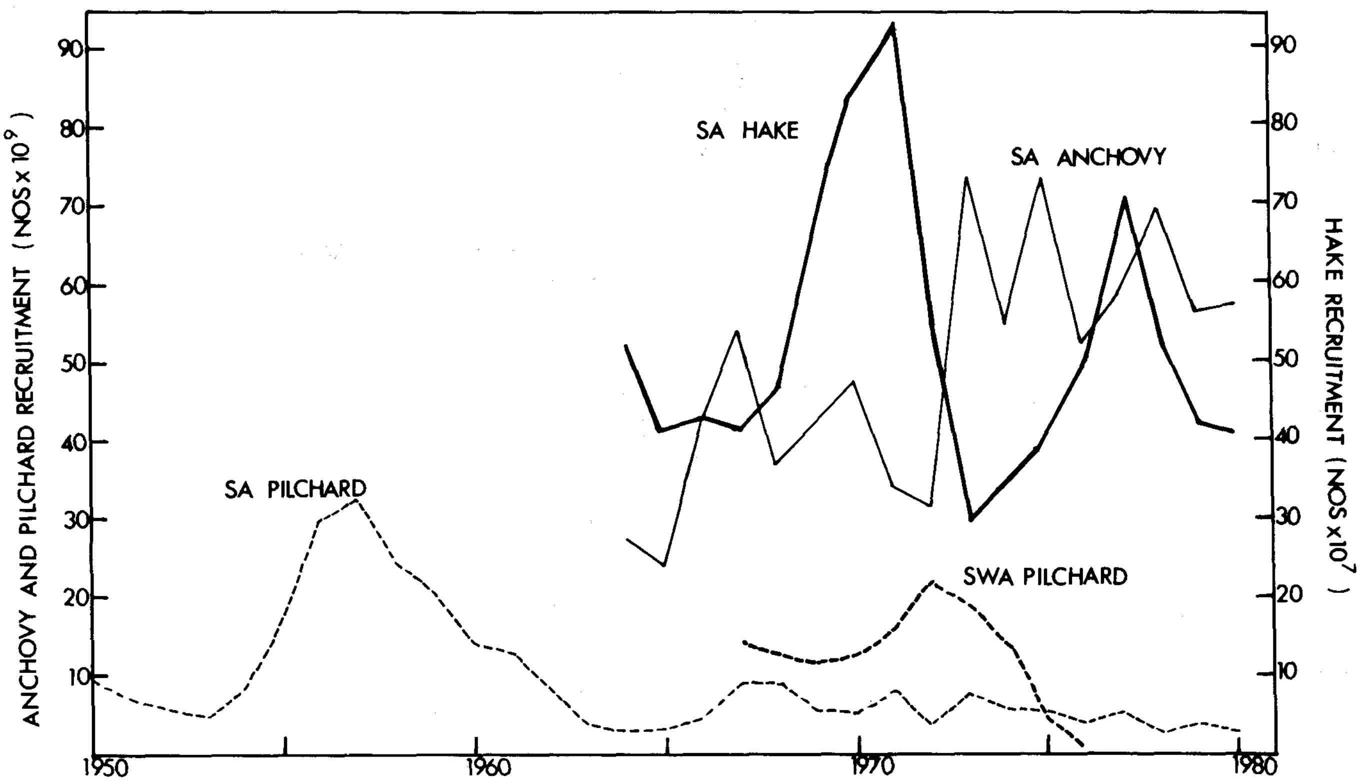


Figure 2. Recruitment calculated by cohort analysis for a number of neritic fish populations inhabiting the Benguela system.

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

[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.

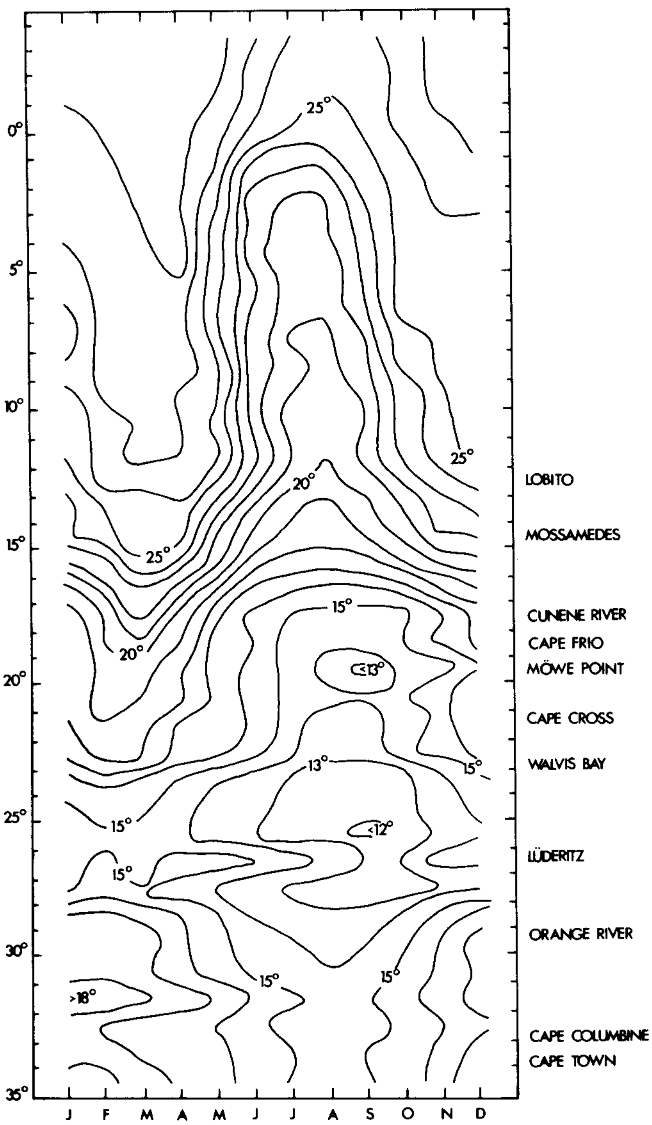


Figure 3. Monthly mean SST measurements for the coastal area of the Benguela system (from Wooster, W.S. 1973. Upwelling in the Eastern Atlantic. Abstracts of the South African National Symposium, Cape Town, 6-10 August 1973).

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

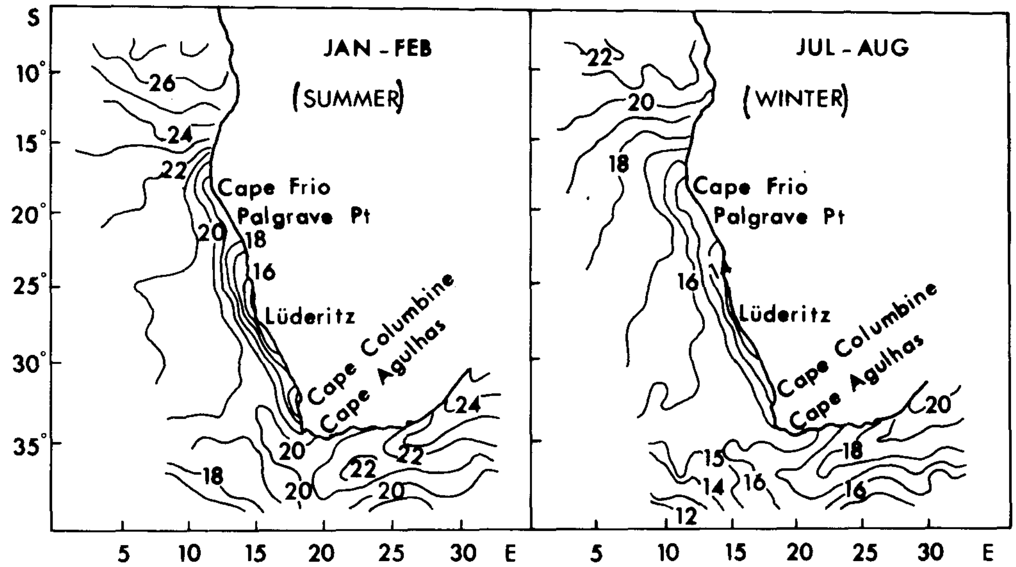


Figure 4. Summer and winter mean SST measurements for one-degree squares in the Benguela system (from Parrish et al. 1983).

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).

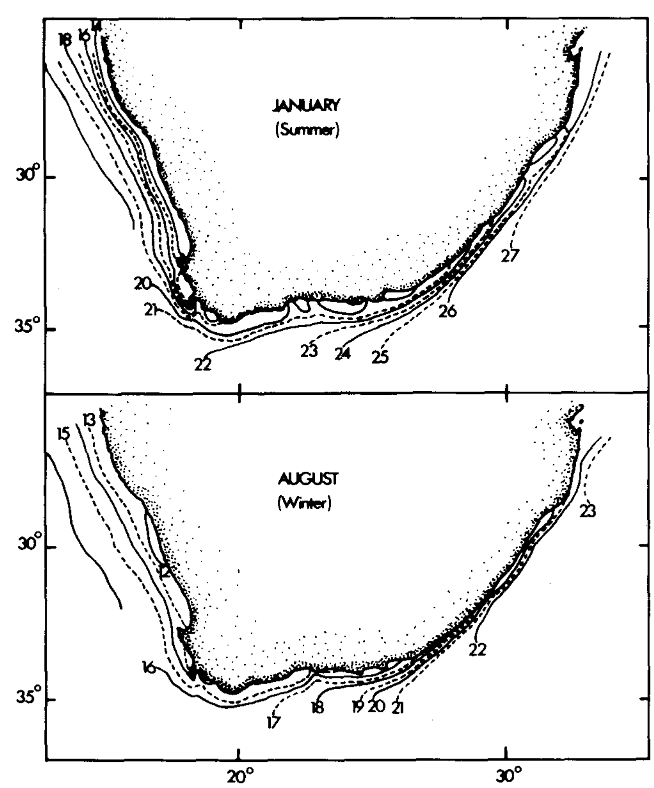


Figure 5. Summer and winter mean SST from an analysis of ten-day mean values from 1968 to 1978 for the coastal area off southern Africa (from Christensen 1980).

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-

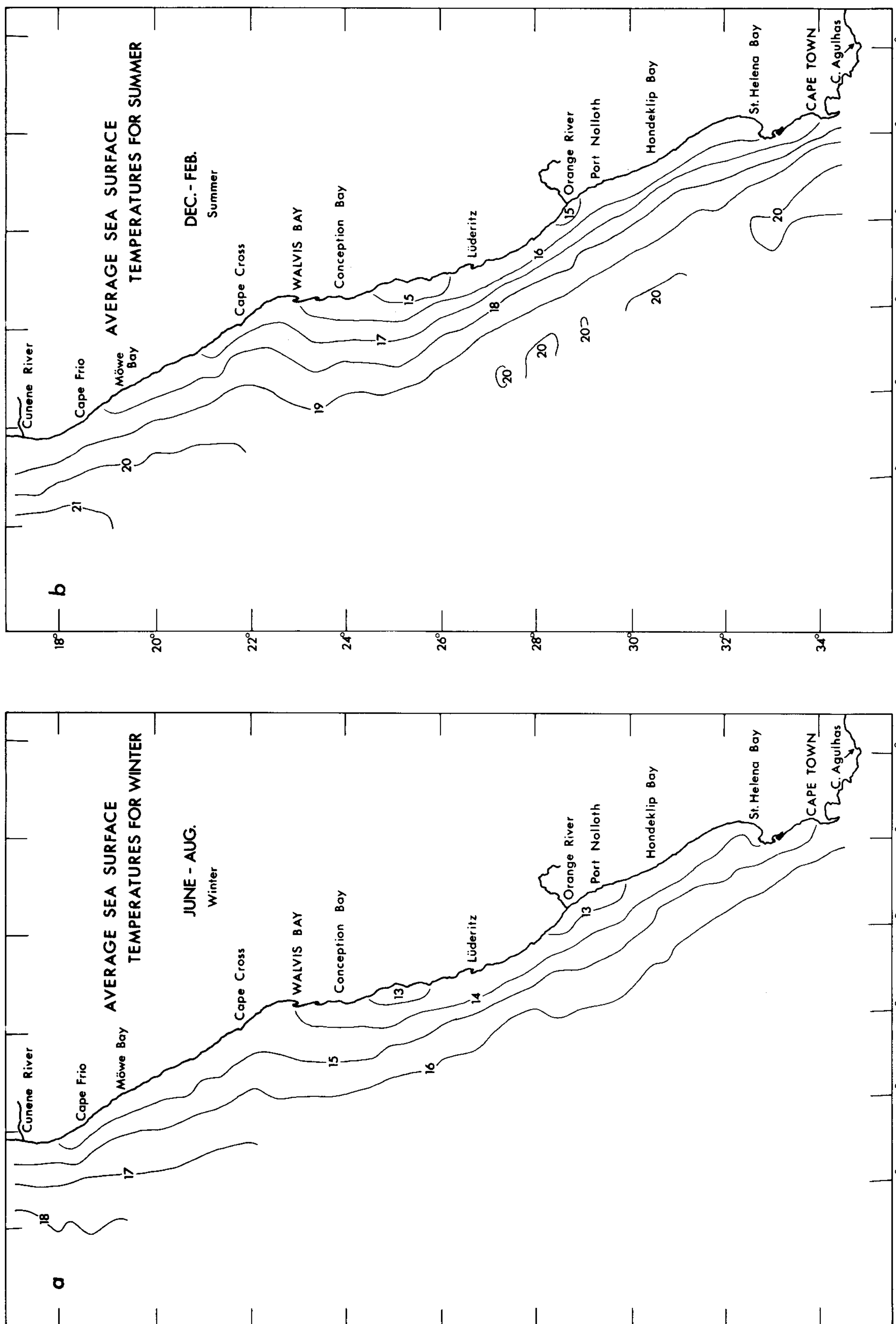


Figure 6. Winter and summer mean SST from an analysis of ten-day mean values for the Benguela system (from Boyd and Agenbag, in press).

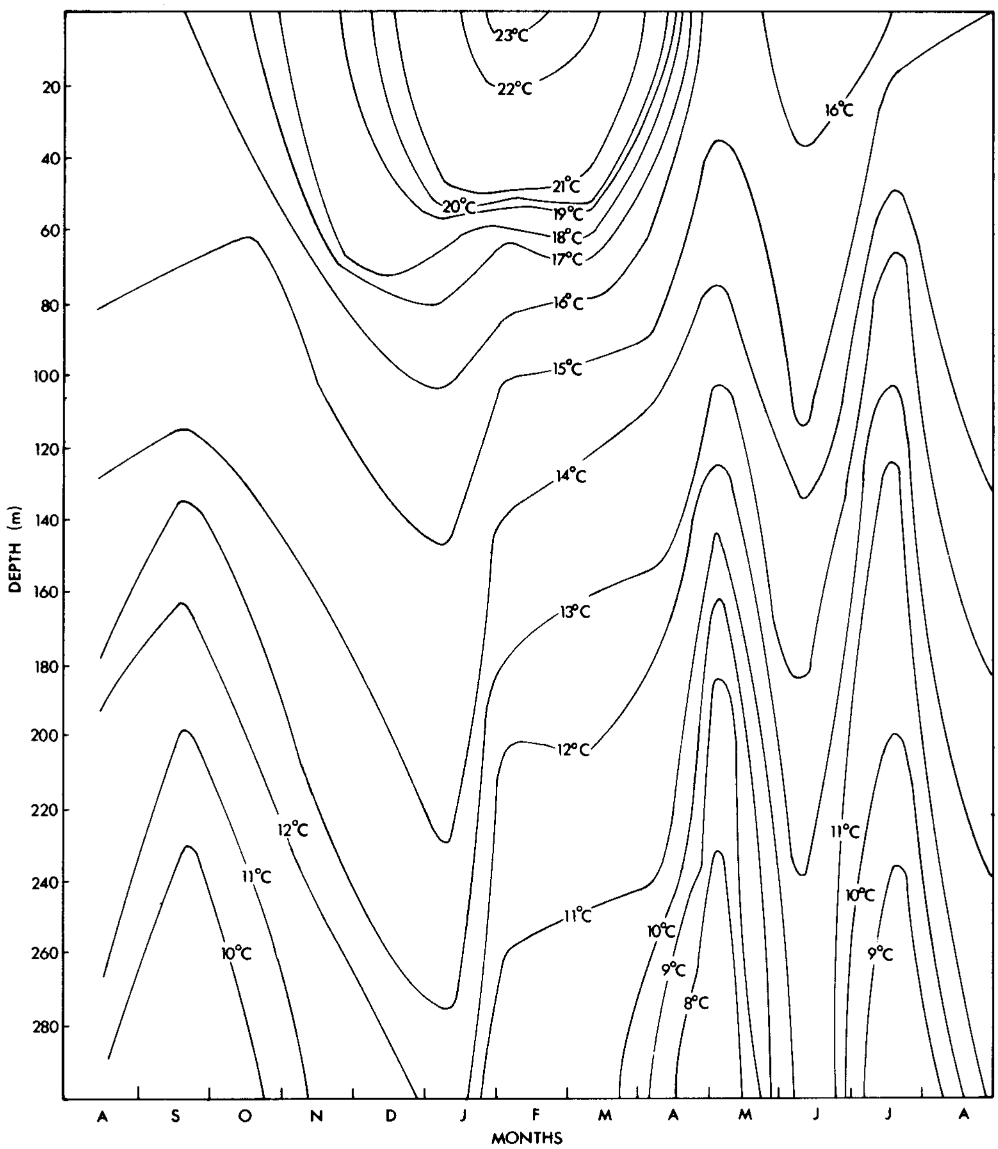


Figure 7. Temperature section from monthly measurements taken about 110 kilometers west of Cape Columbine between August 1977 and August 1978.

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

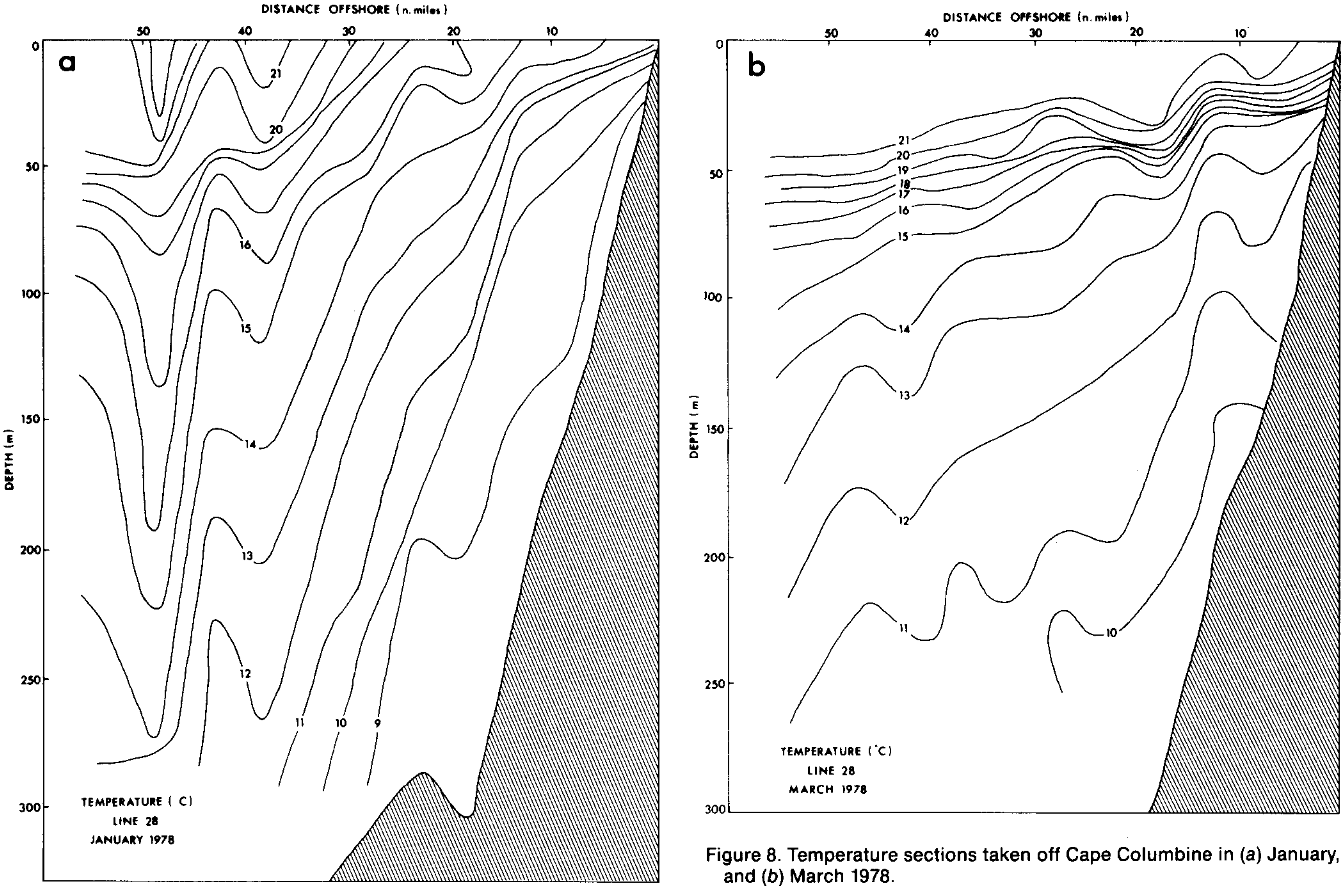


Figure 8. Temperature sections taken off Cape Columbine in (*a*) January, and (*b*) March 1978.

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

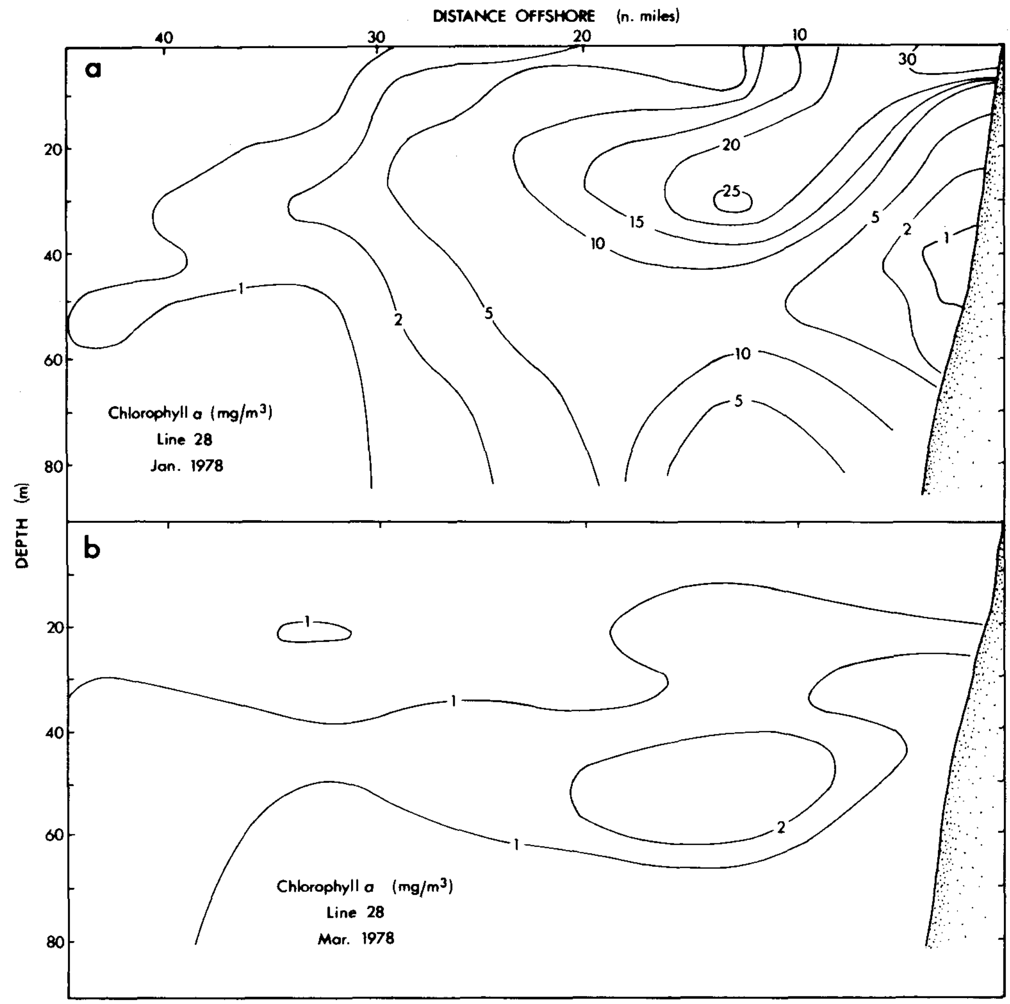


Figure 9. Chlorophyll *a* section off Cape Columbine in (*a*) January, and (*b*) March 1978.

(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

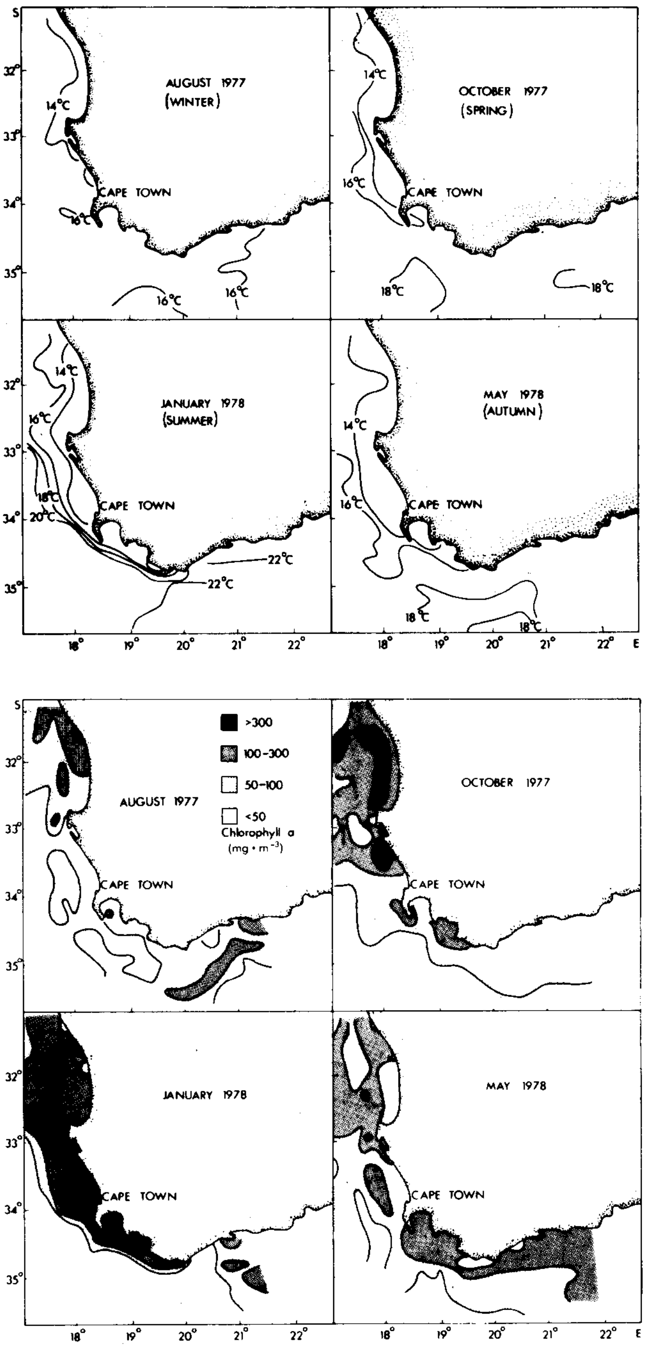


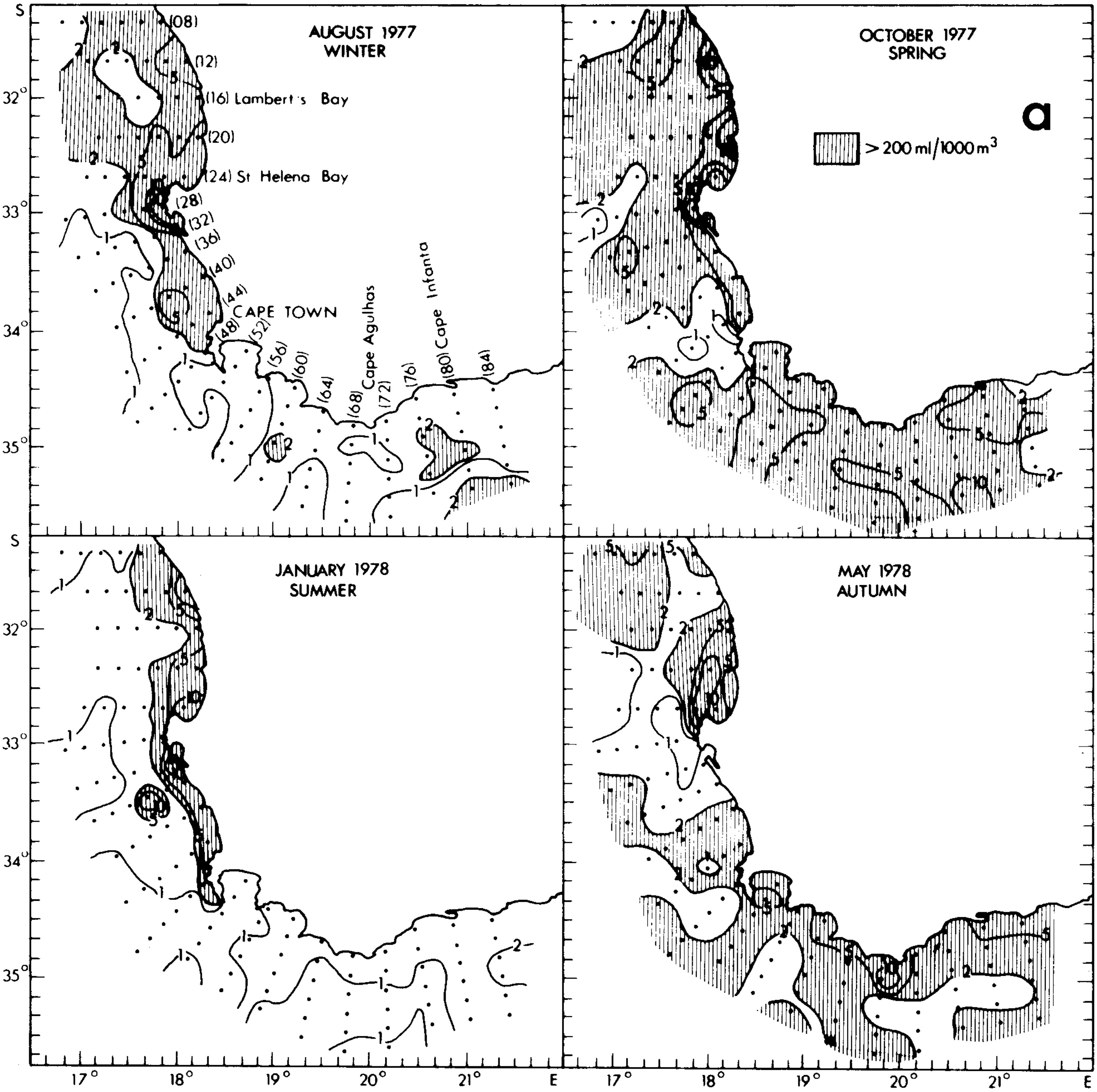
Figure 10. Seasonal pattern of surface temperature and chlorophyll *a* distribution in the southern Benguela region in 1977-78 (from Shannon et al. 1984).

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).



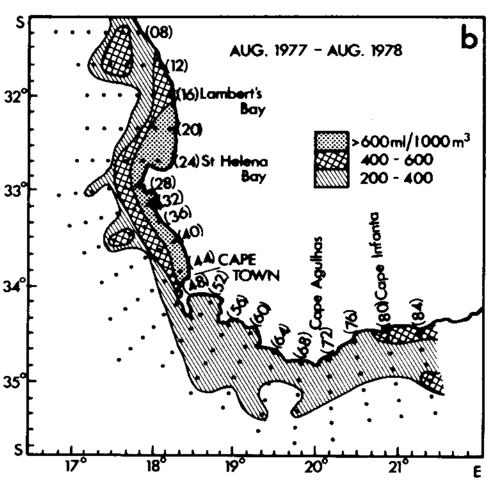


Figure 11. Southern Benguela region: (*a*) seasonal pattern of plankton standing stock from a double oblique tow with a bongo net fitted with 300-micron mesh, taken down to a maximum depth of 100 m; (*b*) mean distribution of plankton retained by the 300-micron mesh net from monthly surveys conducted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

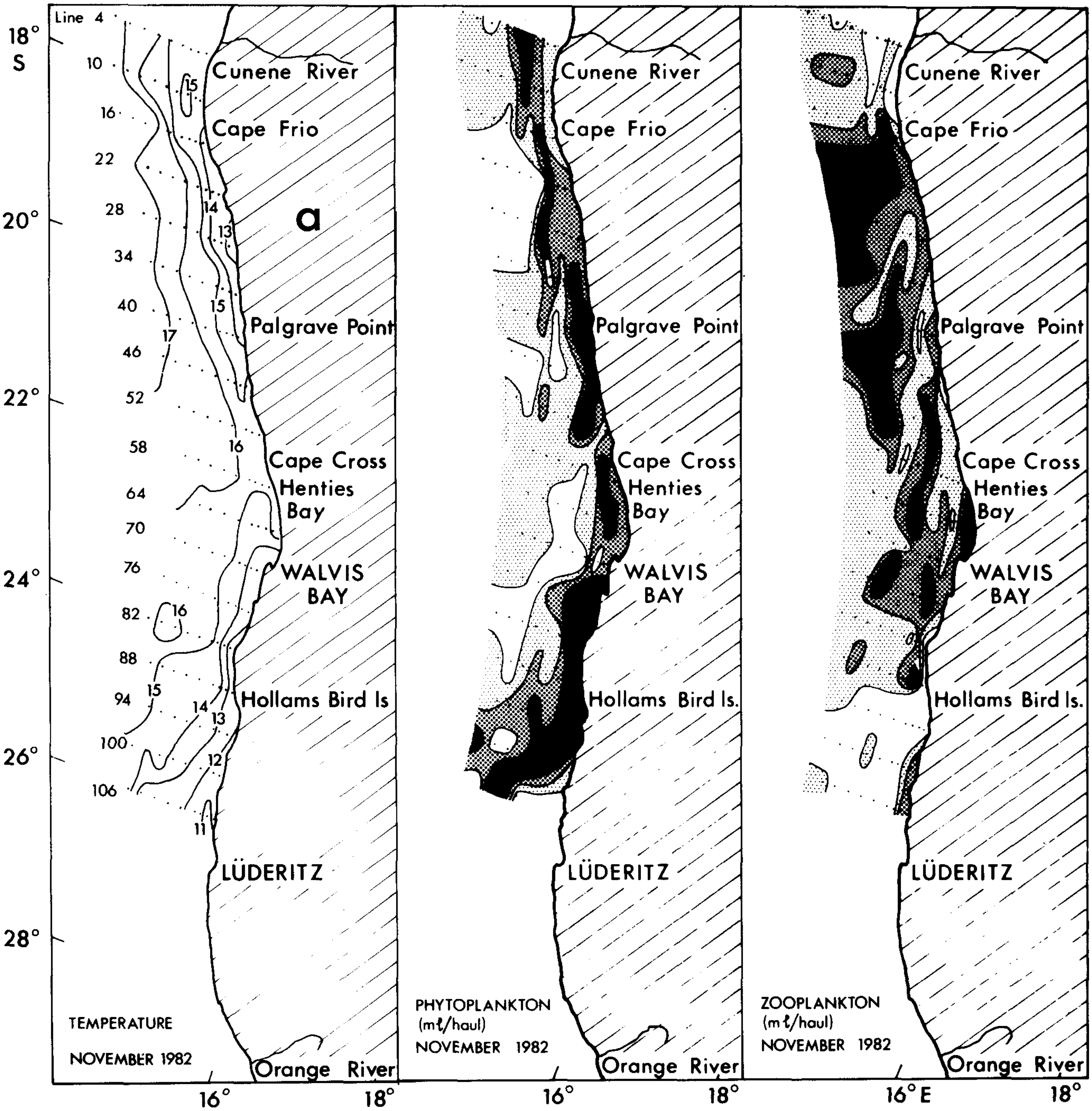


Figure 12a. Northern Benguela region surface temperature and plankton displaced volume from vertical tows from 50 m to the surface with a 50-cm-diameter net fitted with 80-micron mesh for November 1982 (from Kruger and Boyd 1984).

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

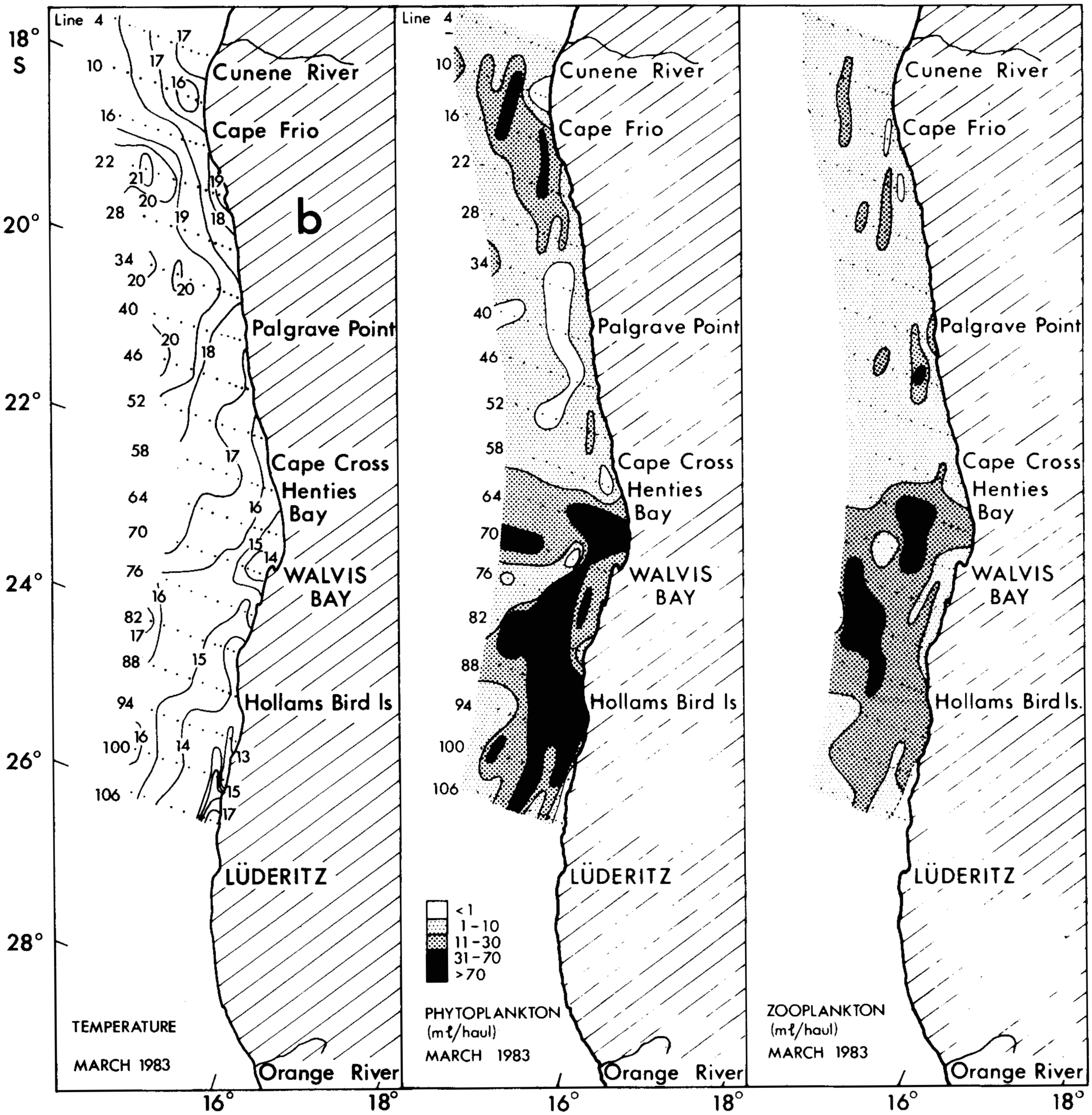


Figure 12b. Northern Benguela region surface temperature and plankton displaced volume from vertical tows from 50 m to the surface with a 50-cm-diameter net fitted with 80-micron mesh for March 1983 (from Kruger and Boyd 1984).

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

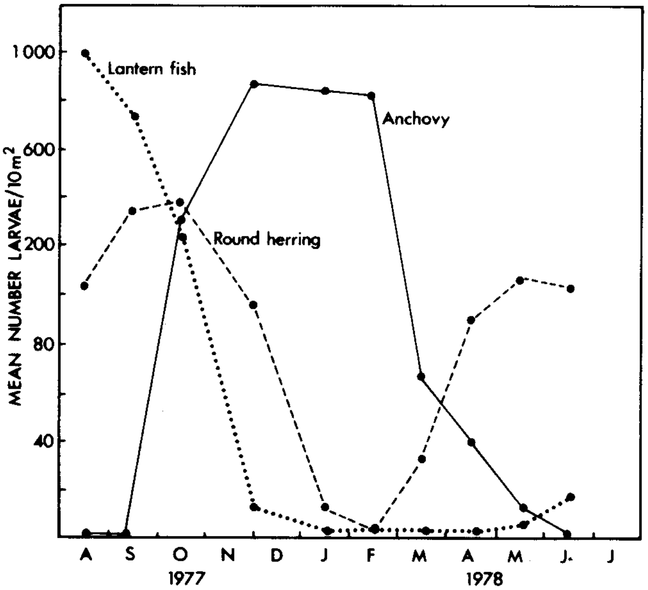


Figure 13. Mean number of anchovy, lantern fish, and round herring larvae from monthly bongo net tows in the southern Benguela region between August 1977 and June 1978.

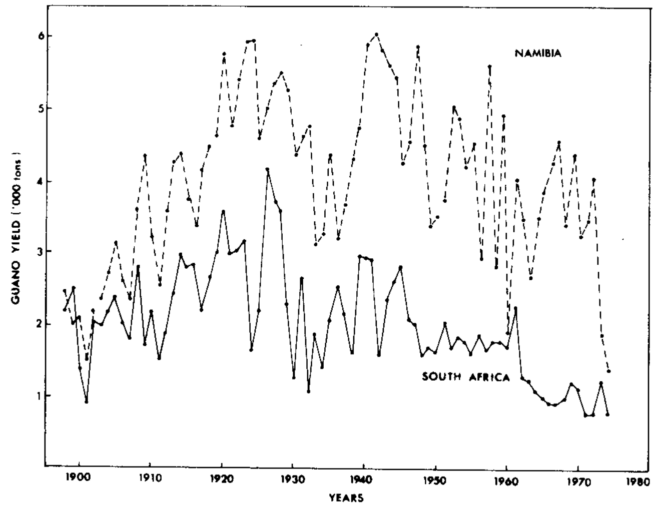


Figure 14. Guano yield from islands off South West Africa/Namibia and South Africa.

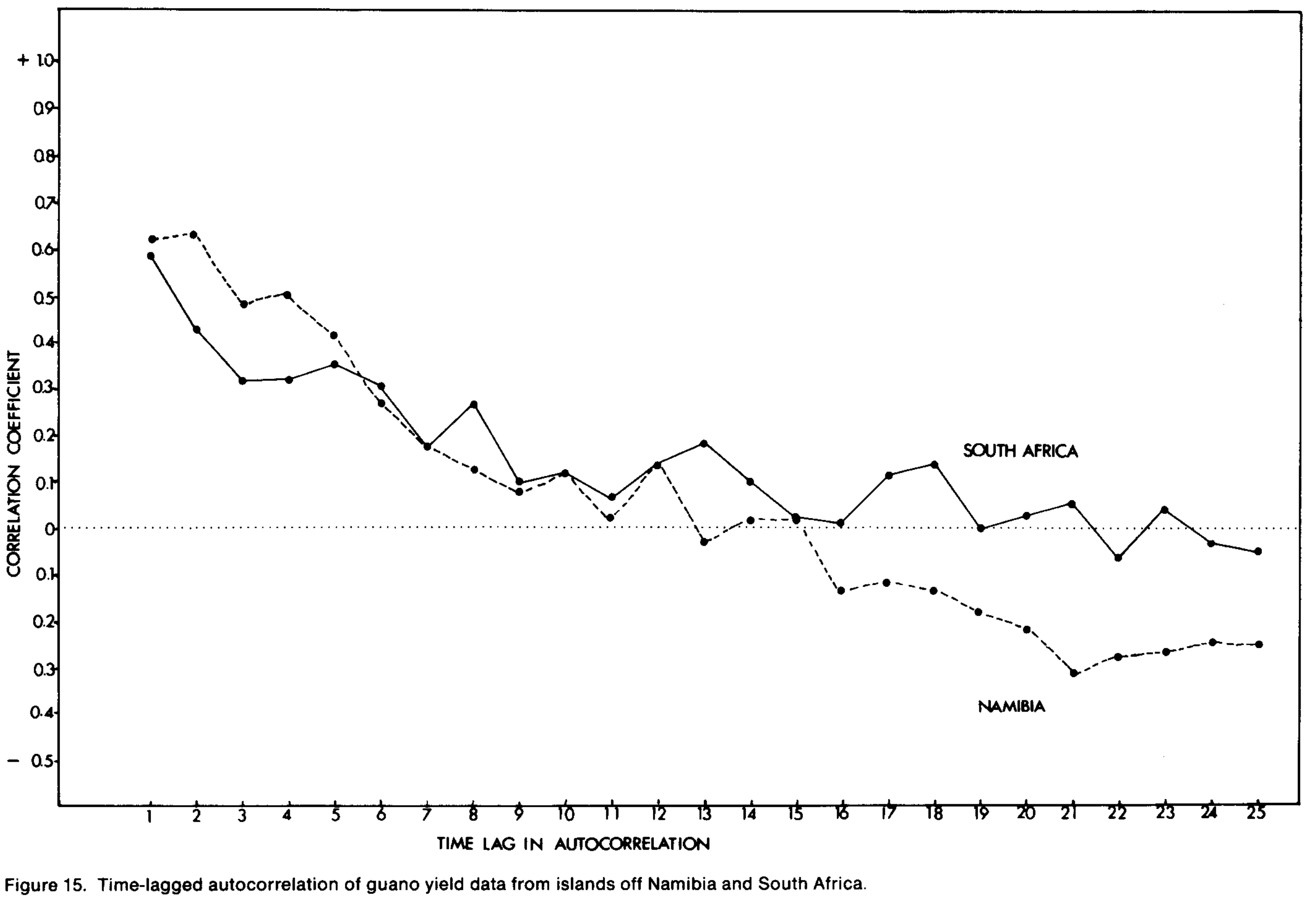


Figure 15. Time-lagged autocorrelation of guano yield data from islands off Namibia and South Africa.

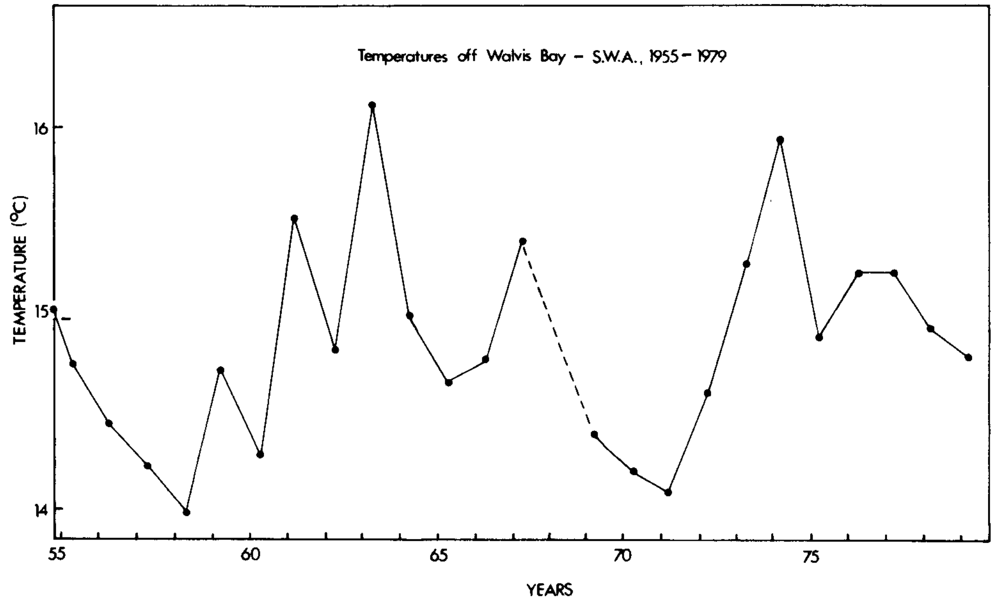


Figure 16. Mean annual SST measurements from a site near Walvis Bay for the period 1955-79. The temperatures for 1955-67 were from hydrological data, those from 1969-79 from general shipping. The latter data were adjusted to have the same mean as the former. Means were computed for each 12-month period 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).

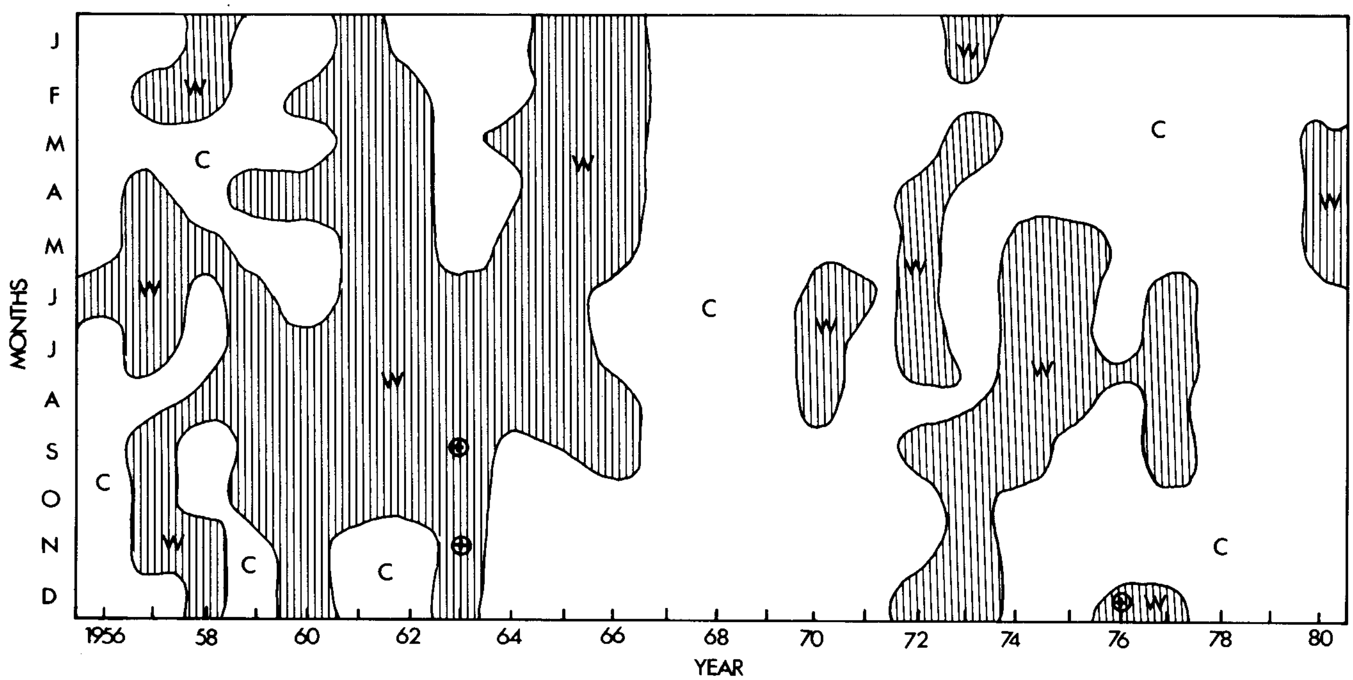


Figure 17. Mean monthly SST measurements from Table Bay near Cape Town for the period 1956-80, showing positive (hatched) and negative temperature anomalies. The (+) indicates a positive anomaly of more than 2°C (from M. Jury, Sea Fisheries Research Institute, Cape Town, unpublished data).

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-

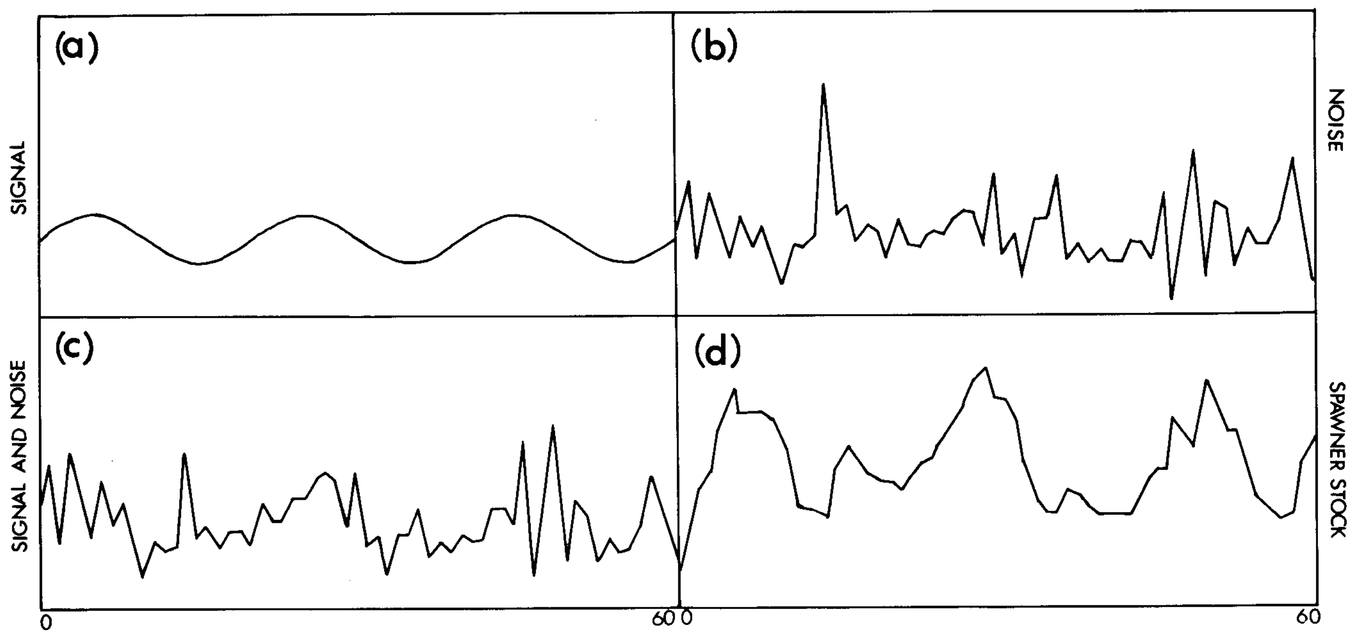


Figure 18. A sine wave with a wavelength of 20 years and an amplitude of 0.67 to 1.33 of the mean value (*a*), used multiplicatively to vary the central tendency of a log-normally distributed random number sequence with a range of 0.5 to 2.0 times the mean value (*b*). This resulted in the signal (*c*),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

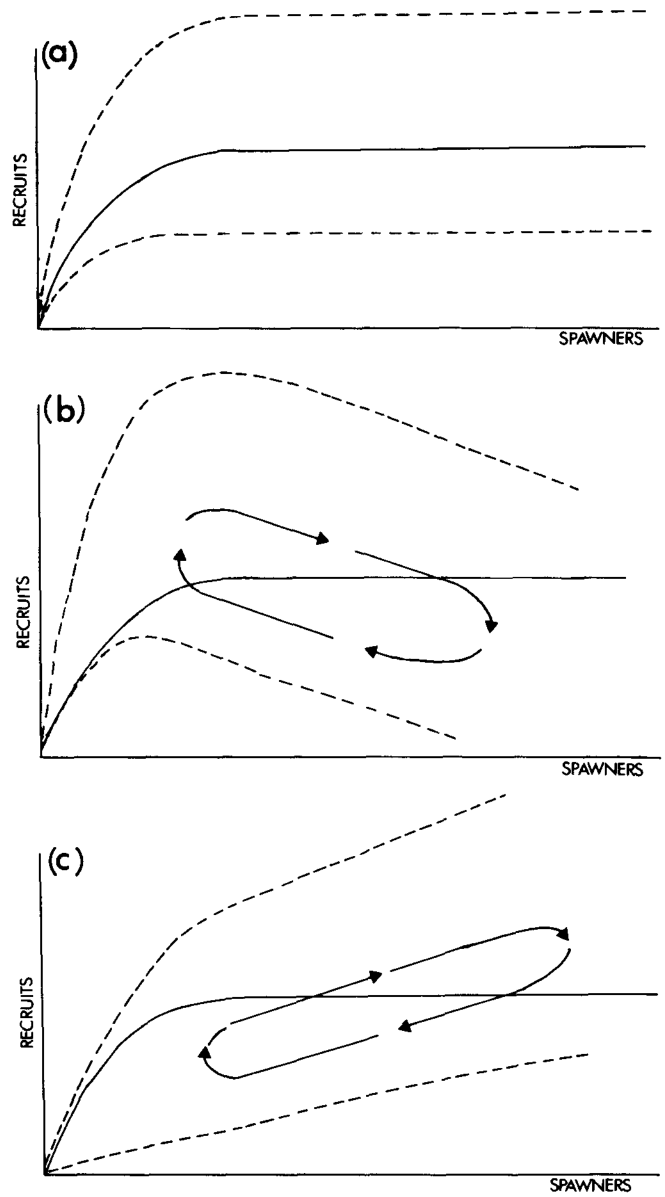


Figure 19. Theoretical stock-recruit functions for fish species, showing possible ranges of recruitment variability (broken lines): (*a*) with no autocorrelation in the environmental variable affecting recruitment, (*b*) with autocorrelation in environment exhibiting a periodicity of approximately double 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.

LITERATURE CITED

Armstrong, M.J. 1984. An analysis of yield variability from three harvesting strategies in the South African anchovy fishery, under conditions of randomly fluctuating recruitment success. S. Afr. J. Mar. Sci. 2:131-144.

Badenhorst, A., and A.J. Boyd. 1980. Distributional ecology of the larvae and juveniles of the anchovy *Engraulis capensis* Gilchrist in relation to the hydrological environment off South West Africa, 1978/79. Fish. Bull. S. Afr. 13:83-106.

Bailey, G. 1979. Physical and chemical aspects of the Benguela Current in the Lüderitz region. M.S. thesis, Univ. Cape Town, S. Africa, 225 p.

Bang, N.D. 1971. The southern Benguela Current region in February 1966: Part II. Bathythermography and air-sea interactions. Deep-Sea Res. 18:209-224.

———. 1973. Characteristics of an intense ocean frontal system in the upwell regime west of Cape Town. Tellus 25:256-265.

Bang, N.D., and W.R.H. Andrews. 1974. Direct current measurements of a shelf-edge frontal jet in the southern Benguela system. J. Mar. Res. 32(3):405-417.

Batchelor, A.L., and G.J.B. Ross. 1984. The diet and implications of dietary change of Cape gannets on Bird Island, Algoa Bay. Ostrich 55(2):45-63.

Beddington, J.R., and R.M. May. 1977. Harvesting natural populations in a randomly fluctuating environment. Science 197:463-465.

Bernal, P.A. 1981. A review of the low-frequency response of the pelagic system in the California Current. CalCOFI Rep. 12:49-62.

Boyd, A.J. 1979. A relationship between sea-surface temperature variability and anchovy *Engraulis capensis* recruitment off South West Africa, 1970-1978. Fish. Bull. S. Afr. 12:80-84.

Boyd, A.J., and J.J. Agenbag. In press. Seasonal trends in the longshore distribution of surface temperatures off southwestern Africa 18-34°S, and their relation to subsurface conditions and currents in the area 21-24°S. Investigación Pesquera.

Boyd, A.J., and J.D. Hewitson. 1983. Distribution of anchovy larvae off the west coast of southern Africa between 32° 30′ and 26° 30′, 1979-1982. S. Afr. J. Mar. Sci. 1:71-75.

Boyd, A.J., and R.M. Thomas. 1984. A southward intrusion of equatorial water off northern and central Namibia in March 1984. Tropical Ocean-Atmosphere Newsletter 27:16-17.

Boyd A.J., J.D. Hewitson, I. Kruger, and F. Le Clus. In press. Temperature and salinity trends off Namibia from August 1982 to August 1984 and their relation to plankton abundance and the reproductive success of pelagic fish. Colln. Scient. Pap. Int. Commn. SE. Atl. Fish. 12.

Brown, P.C., and L. Hutchings. In press. Phytoplankton distribution and dynamics in the southern Benguela Current. Investigación Pesquera.

Brundrit, G.B. 1981. Upwelling fronts in the southern Benguela region. Trans. Roy. Soc. S. Afr. 44(3):309-313.

———. 1984. Monthly mean sea level variability along the west coast of southern Africa. S. Afr. J. Mar. Sci. 2:195-203.

Brundrit, G.B., B. de Cuevas, and A.M. Shipley. 1984. Significant sea-level variations along the west coast of southern Africa 1979-83. S. Afr. J. Sci. 80:(2)80-82.

Butterworth. 1983. Assessment and management of pelagic stocks in the southern Benguela region. *In* G.D. Sharp and J. Csirke (eds.), Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. 291(2):329-405.

Caddy, J.F. 1979. Long-term trends and evidence for production cycles in the Bay of Fundy scallop fishery. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 175:97-108.

Chelton, D.B., P.A. Bernal, and J.A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40(4):1095-1195.

Christensen, M.S. 1980. Sea-surface temperature charts for southern Africa south of 26°S. S. Afr. J. Sci. 76:541-546.

Crawford, R.J.M. 1980. Seasonal patterns in South Africa's Western Cape purse seine fishery. J. Fish. Biol. 16(6):649-664.

———. 1981a. Distribution, availability and movements of anchovy *Engraulis capensis* off South Africa, 1964-1976. Fish. Bull. S. Afr. 14:51-94.

———. 1981b. Distribution, availability and movements of pilchard *Sardinops ocellata* off South Africa, 1964-1976. Fish. Bull. S. Afr. 14:1-46.

Crawford, R.J.M., and P.A. Shelton. 1978. Pelagic fish and seabird interrelationships off the coasts of South West and South Africa. Biol. Conserv. 14:85-109.

Crawford, R.J.M., P.A. Shelton, and L. Hutchings. 1983. Aspects of variability of some neritic stocks in the southern Benguela system. *In* G.D. Sharp and J. Csirke (eds.), Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. 291(2):407-448.

Cushing, D.H. 1978. Biological effects of climatic change. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 173:107-116.

Cushing, D.H., and R.R. Dickson. 1976. The biological response in the sea to climatic changes. Adv. in Mar. Biol. 14:1-122.

De Decker, A. 1970. Notes on an oxygen-depleted sub-surface current off the west coast of South Africa. Investl. Rep. Div. Sea Fish. S. Afr. 84:1-24.

———. 1984. Near surface copepod distribution in the southwestern Indian and southeastern Atlantic Ocean. Ann. S. Afr. Mus. 93(5):303-370.

Duncan, C.P., and J.H. Nell. 1969. Surface currents off the Cape coast. Investl. Rep. Div. Sea Fish. S. Afr. 76:1-19.

Gilooly, J.F., and N.D. Walker. 1984. Spatial and temporal behavior of sea-surface temperatures in the south Atlantic. S. Afr. J. Sci. 80(2):97-100.

Harris, T.F.W., and L.V. Shannon. 1979. Satellite-tracked drifter in the Benguela Current system. S. Afr. J. Sci. 75(7):316-317.

Hart, T.J., and R.I. Currie. 1960. The Benguela Current. Discovery Rep. 31:123-297.

Hutchings, L., and G. Nelson. In press. The influence of environmental factors on the Cape pelagic fishery. Investigación Pesquera.

Iles, T.D. 1973. Interaction of environment and parent stock size in determining recruitment in the Pacific sardine as revealed by analysis of density-dependent 0-group growth. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 164:228-240.

Iles, T.D., and M. Sinclair. 1982. Atlantic herring: stock discreteness and abundance. Science 215:627-633.

Kawasaki, T. 1983. Why do some pelagic fishes have wide fluctuations in their numbers?—Biological basis of fluctuations from the viewpoint of evolutionary ecology. *In* G.D. Sharp and J. Csirke (eds.), Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. San José, Costa Rica, 19-29 April 1983. FAO Fish. Rep. 291(3):1065-1080.

Kruger, I. 1983. Distribution and abundance of plankton off South West Africa during 1981-82 compared with 1980-81. Colln. Scient. Pap. Int. Commn SE. Atl. Fish. 10(2):121-138.

Kruger, I., and A.J. Boyd. 1984. Investigation into the hydrology and plankton of the surface waters off southwestern Africa in ICSEAF Divisions 1.3, 1.4 and 1.5 in 1982-83. Part 1. The hydrology of the surface waters of southwestern Africa in 1982-83. Colln. Scient. Pap. Int. Commn. SE. Atl. Fish. 11(1):149-158.

Lasker, R. 1978. Ocean variability and its biological effects—Regional review—Northeast Pacific. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 173:168-181.

MacCall, A.D. 1980. The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis*. *In* G.D. Sharp (ed.), Workshop on the effects of environmental variation on the survival of larval pelagic fishes, Lima, Peru, April-May, 1980. IOC Workshop Rep. 28, UNESCO, Paris, p. 201-220.

McLain, D.R., J. Norton, R. Brainard, and D. Husby. 1985. Anomalous warm events in eastern boundary current systems. CalCOFI Rep. 26:(this volume).

Moroshkin, K.V., Bubnov, V.A., and R.P. Bulatov. 1970. Water circulation in the eastern South Atlantic Ocean. Oceanology 10(1):27-34.

Nelson, G., and L. Hutchings. 1983. The Benguela upwelling area. Prog. Oceanog. 12:333-356.

Nelson, W.R., M.C. Ingham, and W.E. Schaaf. 1977. Larval transport and year class strength of Atlantic menhaden, *Brevoortia tyrannus*. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 75:23-41.

O'Toole, M.J. 1976. Distribution and abundance of larvae of hake *Merluccius* spp. off South West Africa 1972-1974. Colln. Scient. Pap. Int. Commn. SE. Atl. Fish. 3:151-158.

———. 1977. Investigations into some important fish larvae in the South East Atlantic in relation to the hydrological environment. Ph.D. thesis, University of Cape Town, S. Africa.

———. 1980. Seasonal distribution of temperature and salinity in the surface waters off South West Africa, 1972-1974. Investl. Rep. Sea Fish. Inst. S. Afr. 121:1-25.

Parrish, R.H., and A.D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. U.S. Fish and Wildl. Ser., Fish. Bull. 167:1-110.

Parrish, R.H., A. Bakun, D.M. Husby, and C.S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *In* G.D. Sharp and J. Csirke (eds.), Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. 291(3):731-777.

Philander, S. 1983. El Niño—Southern Oscillation phenomena. Nature 302:295-301.

Schaaf, W.E. 1979. An analysis of the dynamic population response of Atlantic menhaden, *Brevoortia tyrannus*, to an intensive fishery. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 177:243-251.

Schumann, E.H., L.A. Perrins, and I.T. Hunter. 1982. Upwelling along the south coast of the Cape Province, South Africa. S. Afr. J. Sci. 78:238-242.

Shannon, L.V. 1966. Hydrology of the south west coasts of South Africa. Investl. Rep. Div. Sea Fish. S. Afr. 58:1-62.

———. 1984. The NIMBUS 7 CZCS experiment in the Benguela Current region off southern Africa, February 1980. 2. Interpretation of imagery and oceanographic implications. J. Geophys. Res. 89:4968-4976.

———. In press. The Benguela ecosystem: Part I, evolution of the Benguela, physical features and processes. *In* M. Barnes (ed.), Oceanography and marine science: an annual review. Allen & Unwin, London.

Shannon, L.V., G. Nelson, and M.R. Jury. 1981. Hydrological and meteorological aspects of upwelling in the southern Benguela Current. *In* F.A. Richards (ed.), Coastal upwelling. Coast. and Est. Sci. 1:146-159.

Shannon, L.V., S.A. Mostert, N.M. Walters, and F.P. Anderson. 1983. Chlorophyll concentrations in the southern Benguela Current region as determined by satellite (Nimbus-7 coastal zone colour scanner). J. Plankton Res. 5(4):565-583.

Shannon, L.V., L. Hutchings, G.W. Bailey, and P.A. Shelton. 1984. Spatial and temporal distribution of chlorophyll in southern African waters as deduced from ship and satellite measurements and their implications for pelagic fisheries. S. Afr. J. Mar. Sci. 2:109-130.

Shelton, P.A. 1984. Notes on the spawning of anchovy during the summer of 1982-3. S. Afr. J. Sci. 80(2):69-71.

Shelton, P.A., and L. Hutchings. 1982. Transport of anchovy *Engraulis capensis* Gilchrist eggs and early larvae by a frontal jet current. J. Cons. Int. Explor. Mer 40:185-198.

Shelton, P.A., and F. Kriel. 1980. Surface drift and the distribution of pelagic-fish eggs and larvae off the south-east coast of South Africa, November and December 1976. Fish. Bull. S. Afr. 13:107-109.

Smith, P.E. 1978. Biological effects of ocean variability: time and space scales of biological response. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 173:117-127.

Soutar, A., and J.D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fish. Bull., U.S. 72:257-273.

Stander, G.H. 1963. The pilchard of South West Africa (*Sardinops ocellata*). Temperature: its annual cycles and relation to wind and spawning. Investl. Rep. Mar. Res. Lab. S.W. Afr. 9:1-57.

———. 1964. The pilchard of South West Africa. The Benguela Current off South West Africa. Investl. Rep. Mar. Res. Lab. S.W. Afr. 12:1-43.

Stander, G.H., and A.H.B. De Decker. 1969. Some physical and biological aspects of an oceanographic anomaly off South West Africa in 1963. Invest. Rep. Div. Sea Fish. S. Afr. 81:1-46.

Swartzman, G.L., W.M. Getz, R.C. Francis, R.T. Haar, and K. Rose. 1983. A management analysis of the Pacific whiting (*Merluccius products*) fishery using an age-structured stochastic recruitment model. Can. J. Fish. Aquat. Sci. 40:524-539.

Tyson, T.D. 1981. Atmospheric circulation variations and the occurrence of extended wet and dry spells over southern Africa. J. Climatol. 1:115-130.

Van Foreest, D., F.A. Shillington, and R. Legekis. 1984. Large scale, stationary, frontal features in the Benguela Current system. Cont. Shelf Res. 3:465-474.

Van Loon, H., and R.A. Madden. 1981. The Southern Oscillation. part 1, global associations with pressure and temperature in northern winter. Mon. Weather Rev. 109:1150-1162.

Vines, R.G. 1980. Analysis of South African rainfall. S. Afr. J. Sci. 76:404-409.

Walker, N., J. Taunton-Clark, and J. Pugh. 1984. Sea temperatures off the South African west coast as indicators of Benguela warm events. S. Afr. J. Sci. 80(2):72-76.