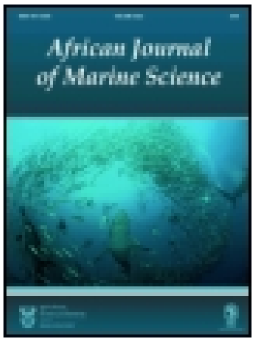

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THE 1980s — A DECADE OF CHANGE IN THE BENGUELA ECOSYSTEM

L. V. SHANNON, R. J. M. CRAWFORD*, D. E. POLLOCK*, L. HUTCHINGS*, A. J. BOYD*, J. TAUNTON-CLARK*, A. BADENHORST*, R. MELVILLE-SMITH*, C. J. AUGUSTYN*, K. L. COCHRANE*, I. HAMPTON*, G. NELSON*, D. W. JAPP* and R. J. Q. TARR**

Changes that occurred in sea surface and some deeper temperatures, surface winds, currents, plankton and some dominant crustacean (rock lobster *Jasus lalandii*), molluscan (squid *Loligo vulgaris reynaudii* and abalone *Haliotis midae*), fish (anchovy *Engraulis capensis*, pilchard *Sardinops ocellatus*, Cape hakes *Merluccius* spp., sole *Austroglossus pectoralis*, kingklip *Genypterus capensis* and various species of linefish) and seabird (Cape gannet *Morus capensis*) resources in the Benguela ecosystem in the 1980s are documented. Although fishing had a clear influence on changes in some of the resources, a wide spectrum of organisms, from plankton to top predators, were influenced directly or indirectly by the abiotic environment. Concurrent changes in many of the resources suggest that the same environmental change may impact on more than one. Simultaneous change throughout the Benguela system indicates that environmental forcing sometimes takes place over wide geographic areas. At the northern and southern extremities of the Benguela system, responses to environmental change may be different because processes through which the change is mediated are different.

Verandering wat plaasgevind het in die see-oppervlak- en sommige dieper temperature, oppervlakwinde, strome, plankton en sommige hulpbronne soos skaaldiere (kreef *Jasus lalandii*), weekdiere (tjokka *Loligo vulgaris reynaudii* en perlemoen *Haliotis midae*), vis (ansjovis *Engraulis capensis*, sardyn *Sardinops ocellatus*, Kaapse stokvis *Merluccius* spp., tongvis *Austroglossus pectoralis*, koningklip *Genypterus capensis* en verskeie lynvisspesies) en seevoëls (witmalgas *Morus capensis*) in die Benguela-ekostelsel in die 1980s word gedokumenteer. Ofskoon die vissery 'n duidelike invloed op veranderinge in sommige van die hulpbronne gehad het, is 'n wye spektrum organismes, van plankton tot spitsroofdiere, regstreeks of onregstreeks beïnvloed deur die nie-lewende omgewing. Gelyktydige veranderinge in baie van die hulpbronne dui daarop dat dieselfde omgewingsverandering op meer as een van hulle 'n uitwerking mag hê. Gelyktydige verandering dwarsdeur die Benguelastelsel laat dink dat omgewingsforsering soms oor wye geografiese gebiede plaasvind. By die noorder- en suider- uiteindes van die Benguelastelsel kan die reaksies op omgewingsverandering verskil omdat die prosesse waardeur die verandering teweeggebring word, verskil.

The Benguela upwelling system is inherently highly variable, being pulsed on time-scales from hours to months. Superimposed on this is pronounced variability at the system boundaries on inter- and intra-annual time scales. The Benguela is unique among upwelling systems in that it is bounded on both equatorward and poleward sides by warm-water regimes, the Angola Current and Agulhas Current systems respectively.

Attention was first drawn to interannual variability in the northern Benguela by the major intrusion there of warm water in 1963 (Stander and De Decker 1969), and in the southern Benguela by the anomalous summer and autumn of 1976/77. However, it was the short-lived warm anomaly in the extreme southern part of the Benguela system during the summer of 1982/83 that focused research on the problem of system variability and on associated physical, chemical and biological processes and responses (see the suite of papers in *S. Afr. J. Sci.* **80**(2) of 1984). The 1982/83 anomaly was associated with a major *El Niño*-Southern Oscillation (ENSO) event in the Pacific. Further impetus was given by the 1984 "Benguela *Niño*" (Shannon *et al.* 1986, Boyd *et al.* 1987), which had a considerable impact on living marine resources of the northern Benguela (Boyd *et al.* 1985, Le Clus 1986, 1990, Crawford *et al.* 1990a, b), and by the Agulhas intrusion of 1986 (Shannon *et al.* 1990), which coincided with good year-classes of anchovy in 1986 and 1987.

The 1980s brought a rapid increase in knowledge and understanding of processes in the Benguela ecosystem, stimulated by the multi- and interdisciplinary Benguela Ecology Programme (Siegfried and Field 1981, Payne *et al.* 1987, Shannon *et al.* 1988, this volume). The programme fostered close cooperation between researchers in the public sector and those at universities, museums and the Council for Scientific and Industrial Research (CSIR). It benefited from the acquisition in 1982 of F.R.S. *Africana*, a ship with an advanced hydroacoustic survey capability that improved quantitative resource assessment (Hampton 1987), and by development of mathematical models (e.g. Bergh and Butterworth 1987). Reliable time-series of biomass,

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year-class strength and distribution became available for a number of important resources in the Benguela system, notably Cape anchovy *Engraulis capensis*, allowing meaningful comparison with environmental parameters.

Worldwide, in the latter part of the 1980s, the controversial issue of global environmental change or global warming, better known as the "greenhouse effect", attracted increased attention. In South Africa, a workshop held in 1987 documented long-term trends for various environmental and resource data series (Macdonald and Crawford 1988). Interannual and interdecadal variability in the southern African marine environment was investigated (Boyd *et al. 1987,* Walker 1987, Shannon *et al.* 1988, Taunton-Clark and Shannon 1988, Taunton-Clark 1990). It became clear that, in the 1980s, there was pronounced environmental variability and change in the Benguela system and adjacent regions.

In the same period, there were also substantial changes in the abundance or production of several key living resources in the Benguela system. Examples from the southern Benguela include anchovy, which attained high levels of abundance in 1987 and 1988, but then decreased dramatically in the following two years; South African pilchard *Sardinops ocellatus* (which has recently been shown by Parrish *et al.* [1989] to be the same species as the Californian sardine *S. sagax*, but for consistency with the rest of this volume is still referred to as *S. ocellatus*), which increased in abundance throughout the decade (Cochrane *et al.* 1991); and West Coast rock lobster *Jasus lalandii*, the productivity of which declined sharply towards the end of the 1980s as a result of reduced growth rates.

In this paper, information is collated on changes in the environment and in the resources of the Benguela system during the 1980s. In a preliminary manner, associations between changes in the environment and in the resources are investigated and the role of the environment in influencing biotic changes is considered.

DATA AND METHODS

Sea surface temperature and surface winds

Data on sea surface temperature (SST) and surface winds were provided by The South African Data Centre for Oceanography (SADCO) at Stellenbosch. These data were extracted from the recently updated Voluntary Observing Ship database compiled by the Meteorological Office in Bracknell, United Kingdom, from

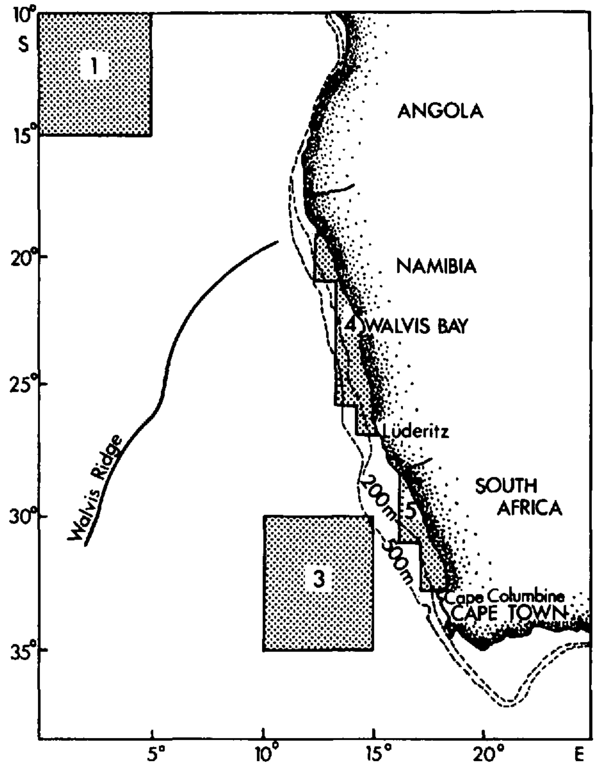


Fig. 1: Map showing the four areas (shaded, 1, 3, 4 and 5) used for analysis of SST and pseudo wind stress. Numbering of the areas is kept the same as for previous analyses reported by Taunton-Clark and Shannon (1988) and Shannon and Taunton-Clark (1989)

Table I: Statistics of current and temperature for serial moorings near Cape Columbine between 12 April 1986 and 28 May 1991. Depth of instruments ranged between 144 and 158 m and sounding between 160 and 179 m. Approximate position was 32°45′S, 17°39′E

Segment	Poleward mean ($cm \cdot s^{-1}$) and bearing(°)		Days per peak on N–S axis	Cross-shelf variance*	Mean temperature (°C) and variance*	
1	6,5	187	8,5	H	8,5	H‡
2	8,2	190	10,0	H	9,0	L
3	6,2	186	9,5	M	†	H
4			No deployment			
5	8,0	198	8,0	L	9,0	L‡
6	9,0	185	10,5	M	8,0	M
7	6,2	195	†	L	9,0	H
8	12,5	195	10,0	M	8,5	L
9	2,5	192	10,0	M	9,5	H‡
10	9,0	193	10,0	L	8,0	L

* H, M, L = High, medium, low variance
† Variation in the longshore too high for useful mean
‡ Exceptional event (see text)

observations made by ships of opportunity.

Information was analysed for four areas in the South-East Atlantic, chosen to represent oceanic and coastal upwelling conditions. The areas are Areas 1, 3, 4 and 5 of Taunton-Clark and Shannon (1988) and Shannon and Taunton-Clark (1989). To facilitate comparison with these earlier papers the same numbers have been retained. The areas (Fig. 1) are:

(1) 10–15°S, 0–5°E, characteristic of the tropical South-East Atlantic;
(3) 30–35°S, 10–15°E, near the Agulhas retroflection zone;
(4) off the Namibian coast between 19 and 27°S;
(5) off the west coast of South Africa between 29 and 33°S.

The numbers of SST observations available for each area during the period 1910–1990 were 85 147, 47 735, 40 337 and 23 498 respectively. Numbers of wind measurements were typically 10 per cent greater. Monthly data density was inadequate during the two world wars, low in the early 1930s, between 1946 and 1948 and after 1989, but was otherwise sufficient.

Mean monthly values of SST and of the equatorward and eastward components of the wind stress, τ_y and τ_x, were calculated for each of the four areas. Throughout this paper, τ more correctly refers to the pseudo wind stress, with dimensions of $m^2 \cdot s^{-2}$. To obtain the correct dimensions would mean multiplying by the drag coefficient and the air density, but these are assumed to have been constant and equal to unity. The components of τ were calculated as follows:

$$\tau_y = 1/N \sum_{i=1}^{N} W_{yi} | W_i | = -1/N \sum_{i=1}^{N} | W_i |^2 \cos \theta_i ,$$

$$\tau_x = 1/N \sum_{i=1}^{N} W_{xi} | W_i | = -1/N \sum_{i=1}^{N} | W_i |^2 \sin \theta_i ,$$

where W_i and θ_i are the wind velocity and direction respectively of the ith observation of a total of N observations in the area being considered. Monthly anomalies were calculated by subtracting the long-term monthly means (1910–1990) from the mean monthly values in each area. Annual anomalies were computed by summation of the monthly anomalies over the calendar years.

Folland *et al.* (1984) and Wright (1986) have examined systematic errors in SST observations made from ships. They concluded that SST before World War II would have experienced evaporative and conductive cooling, arising from the use of uninsulated buckets, relative to the air-sea temperature difference. The corrections for globally averaged SST of 0,25–0,30°C proposed by Folland *et al* (op. cit.) were not applied, but it is clear that years prior to 1940 would have been generally cool, even had the correction been made (see Fig. 4). The high degree of monthly variability in SST, τ_y and τ_x may arise from the uneven distribution of observations in time and space. However, interannual variability and longer trends are largely coherent (see Figs 2 and 4) and probably real.

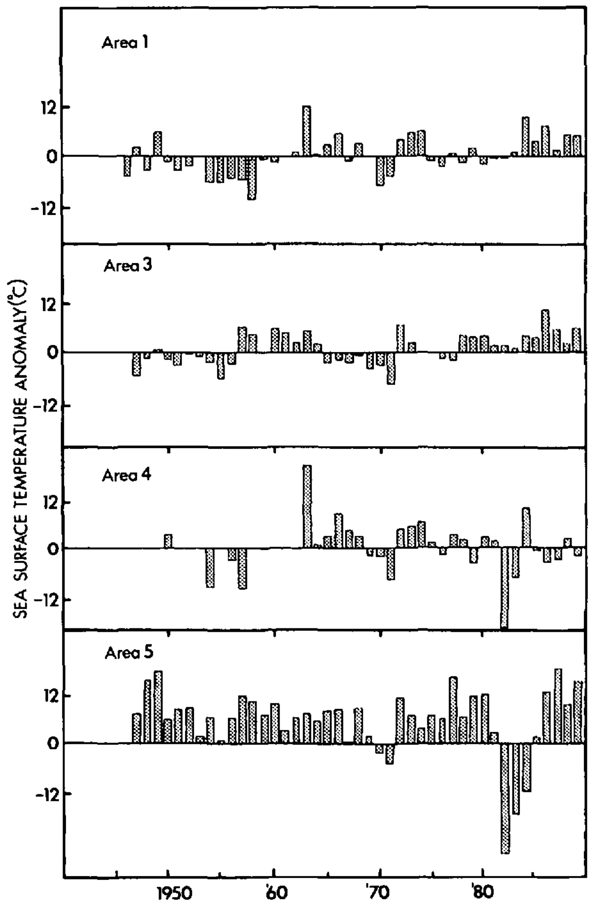


Fig. 2: Annual SST anomalies (summed for 12 calendar months) for Areas 1, 3, 4 and 5, 1947–1989. Note that data density for Areas 4 and 5 was low after 1982, when the record for these two areas is probably insufficient to reflect conditions typical of the shelf zone reliably

It should be noted that the data volumes for the nearshore areas (4 and 5) are lower than for the off-

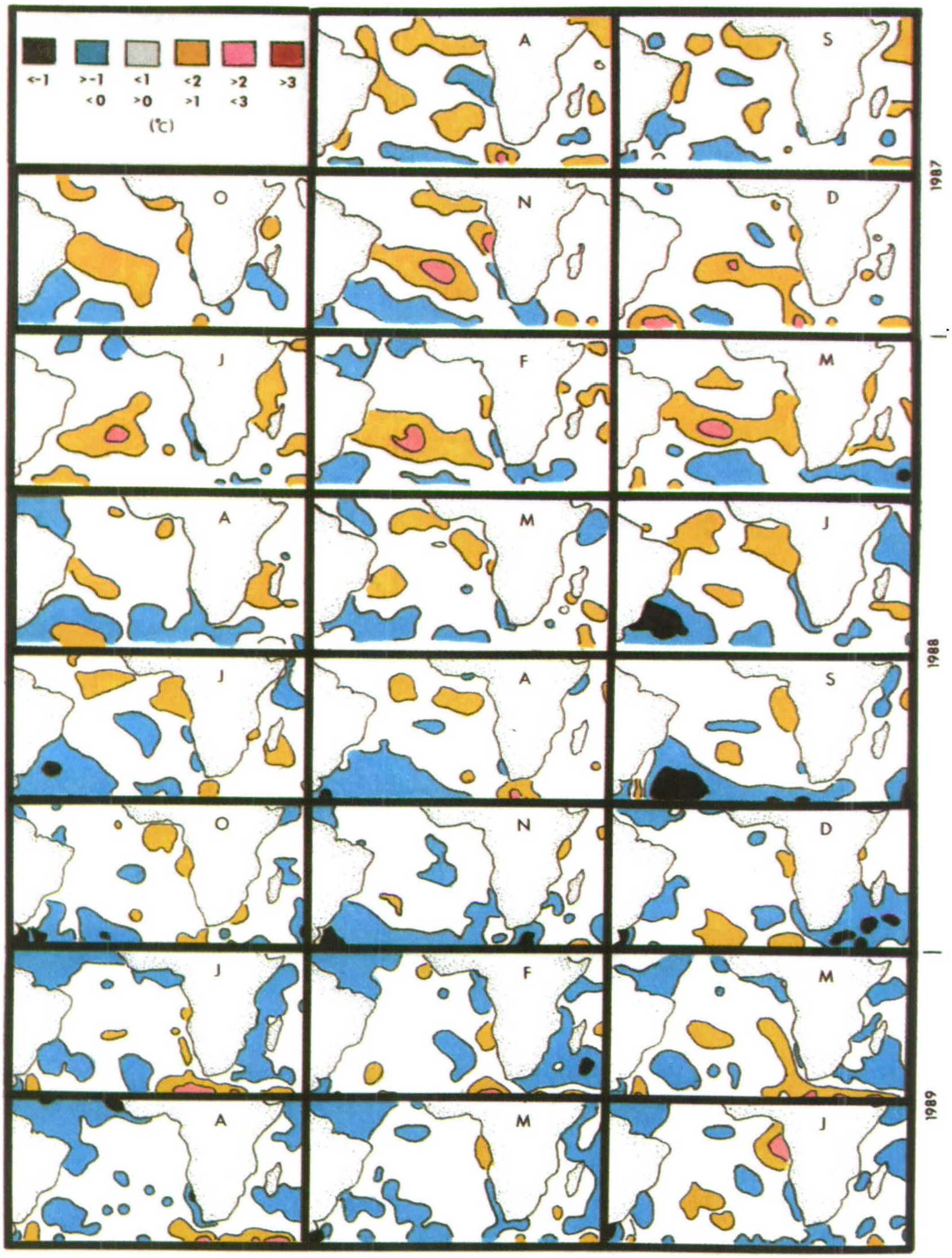
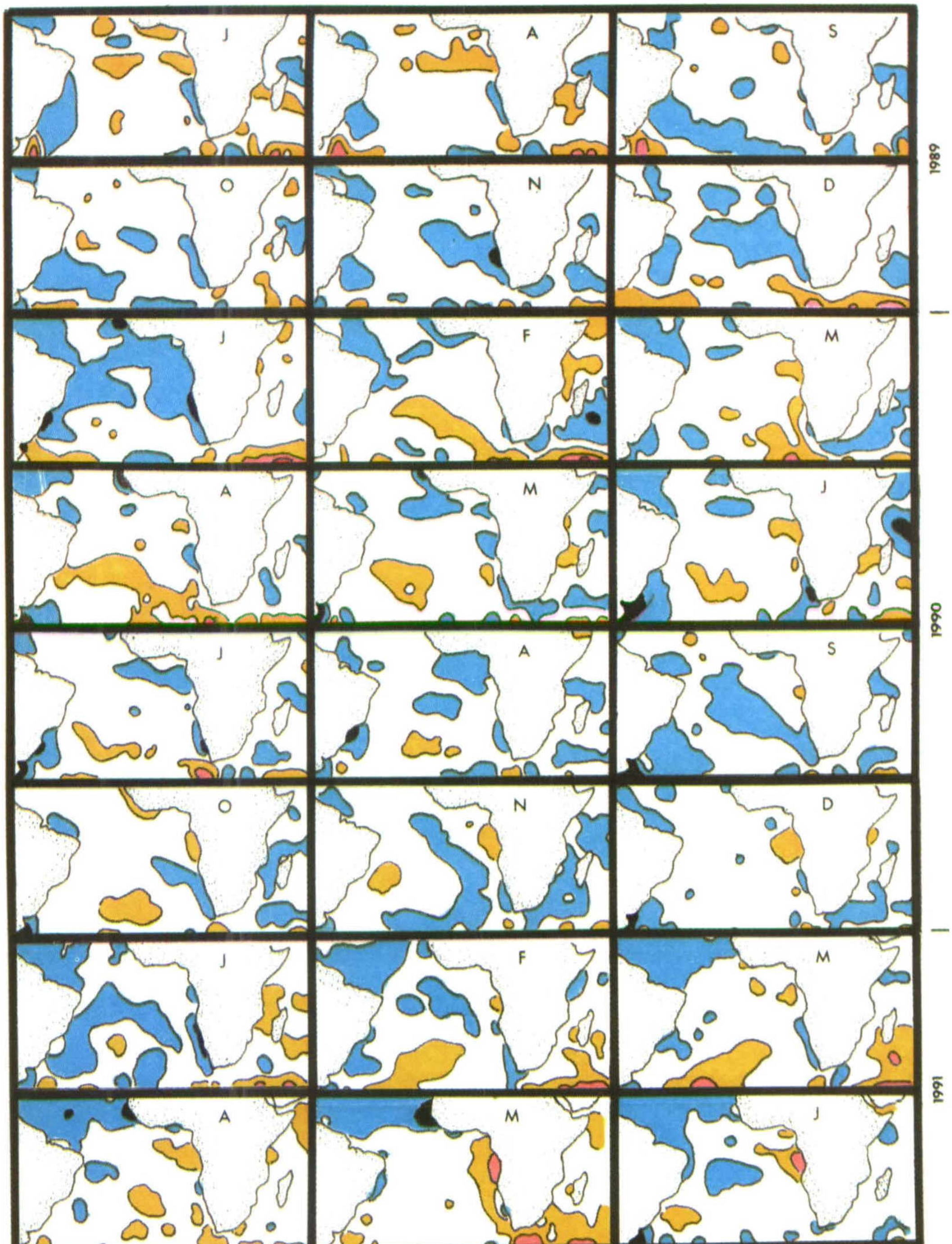


Fig. 3: Monthly SST anomalies in the Atlantic and Indian oceans, 1983–1991 (modified from maps in the Climate Diagnostic Bulletin of the Climate Analysis Center, U.S. Department of Commerce, National Oceanic and



Atmospheric Administration, National Weather Service, National Meteorological Center, edited by V. E. Kousky) shore areas (1 and 3), this being most marked after 1982, monthly means for Areas 4 and 5 commonly being based on fewer than 20 observations. The record for Areas 4 and 5 is probably insufficient to reflect reliably longer-term trends on the shelf zone after 1982.

Hourly estimates of wind speed and direction logged by the keeper of the lighthouse at Cape Columbine (Fig. 1) were processed into monthly accumulated "windrun" or displacement values. Long-term mean monthly values for the equatorward components were computed for the years 1957–1990 and used to generate the monthly departures shown later, in Figure 5.

Current-meter data and subsurface temperature time-series

Since December 1982, the Sea Fisheries Research Institute has maintained a current-meter mooring, almost continuously, west of Cape Columbine. The results of the initial period, until April 1986, have been documented by Holden (1987). Deployments thereafter are detailed in Table I. The use of the Global Positioning Satellite (GPS) and experience in deployments enabled more accurate positioning of moorings to be effected in this latter period. A problem in comparing segments of the series is that small differences in position of the current meter (up to 1 km) may lead to quite different appearances in the time-series.

In all, there are 10 segments after April 1986. In one, from 10 December 1986 to 30 April 1987, no mooring was deployed because of scarcity of manpower and equipment. In all other cases, good data were obtained from depths varying between 144 and 158 m below the surface, in soundings ranging from 160 to 179 m. This corresponded to instrument elevations above the sea floor between 16 and 25 m. In all cases, an Aanderaa RCM4 unit was used, recording at hourly intervals. Data were converted to true north-south and east-west components, assuming a magnetic declination of 24°W. Velocity components were filtered with a Cosine-Lanczos filter to remove tidal and inertial frequencies. This resulted in the loss of 61 hours of data at the beginning and end of each segment, or roughly five days between segments. An hourly temperature series was also obtained from the RCM4 moorings.

Plankton

Information on chlorophyll *a* in the southern Benguela was taken from Brown and Cochrane (1991). Information for 1979 and 1980 has been omitted because of the likelihood of bias in these years resulting from collection of data from water known to be newly upwelled.

Routine collection of zooplankton during surveys to estimate the biomass of recruiting (May) and spawning (November) anchovy was initiated in May 1988. Zooplankton was collected with a vertical Bongo net (57 cm diameter, 200 μm mesh) from the lesser of 200 m or the bottom to the surface, at 10-mile intervals on selected transects. Depth, temperature and flow rates were monitored electronically. In addition, a sample driftnet was deployed for 10 minutes in the upper 15–20 m to collect live copepods for egg-production experiments. Replicate subsamples of zooplankton were counted, enumerating the most important species of copepods and euphausiids to stages, and other groups to genera.

Living marine resources

Time-series of estimates of biomass, year-class strength, growth rates, catches and catch rates for many of the abundant resources in the Benguela ecosystem were collated from published or unpublished literature and records. Sources used are as follows: Cape anchovy (Hampton 1987, IH unpublished information), South African pilchard (Hampton 1987, IH unpublished information, Borchers 1991), Cape hakes *Merluccius capensis* and *M. paradoxus* (Payne *et al.* 1988 and unpublished information, Punt 1991), Agulhas sole *Austroglossus pectoralis* (Badenhorst 1988a, AB unpublished information, Borchers and Punt 1990), kingklip *Genypterus capensis* (Japp 1989, Japp and Punt 1989, Punt 1990), chokka squid *Loligo vulgaris reynaudii* (Augustyn *et al.* 1992), West Coast rock lobster (RMS unpublished information), abalone *Haliotis midae* (Tarr *et al.* 1990, RJQT unpublished information), and various linefish species (A. J. Penney, Sea Fisheries Research Institute, pers. comm.). Information on the diet and abundance of Cape gannets *Morus capensis* was updated from that reported by Berruti (1987) and Crawford *et al.* (1992), as well as from RJMC (unpublished information).

VARIABILITY IN THE ENVIRONMENT

Sea surface temperature

Annual SST anomalies for four areas for the period 1947–1990 are illustrated in Figure 2. Warming is evident for Areas 1 and 3, which represent the oceanic or offshore waters. Both areas were generally cool in the mid 1950s and warm in the 1980s. No clear trend is apparent for Areas 4 and 5, the coastal waters of Namibia and South Africa respectively. However, there is considerable interannual variability, e.g. the Benguela *Niño* of 1963 is the highest SST anomaly on record in Area 4, followed by the 1984 Benguela *Niño*. Variability prior to 1986 has been discussed previously (Taunton-Clark and Shannon 1988, Shannon and Taunton-Clark 1989).

During the 1980s there were several important oceanographic features, namely:

(i) below-average SST in the two shelf areas (4 and 5) during 1982 and 1983 (Walker 1987);
(ii) subsequent warming in each of the four areas;
(iii) the 1984 Benguela *Niño*, evident in both northern areas (1 and 4), that followed the cool period in the shelf waters of Area 4;
(iv) the warm anomaly of 1986, that coincided with pronounced intrusion of Agulhas water in the same year, evident especially in Area 5;
(v) an onset of cooling in 1987 (Anon. 1991), i.e. reversal of the warming trend (Agenbag and Shannon 1987, Shannon and Agenbag 1990), with influx of Subantarctic water into the southern Benguela in early 1987. This cooling trend is not apparent for Area 5 on Figure 2 but, as mentioned above, data density for this area is poor after 1982;
(vi) a brief period of warming early in 1989, caused in the southern Benguela by a short-lived intrusion of warm water (Anon. 1991);
(vii) sustained cooling of shelf waters off western southern Africa from autumn 1989, with consistent negative anomalies recorded in shelf waters (Areas 4 and 5) from April 1989 to April 1991. For Area 5, this is clearly apparent in Figure 3, which is based on the NOAA/CAC Diagnostic Bulletin Series. Offshore temperatures (Areas 1 and 3) remained about 0,4°C above average in 1989.

There seems to have been a sudden change in much of the South Atlantic and South Indian oceans around 1988/89. The warm phase that persisted throughout much of the 1980s was terminated (Fig. 3). Exceptional climatic anomalies were later reported for the tropical Atlantic in the second quarter of 1991 (Demarcq and Marec 1991). It is worth noting that low shelf temperatures off western southern Africa in 1981 and 1982 immediately preceded the onset of the 1982/83 ENSO.

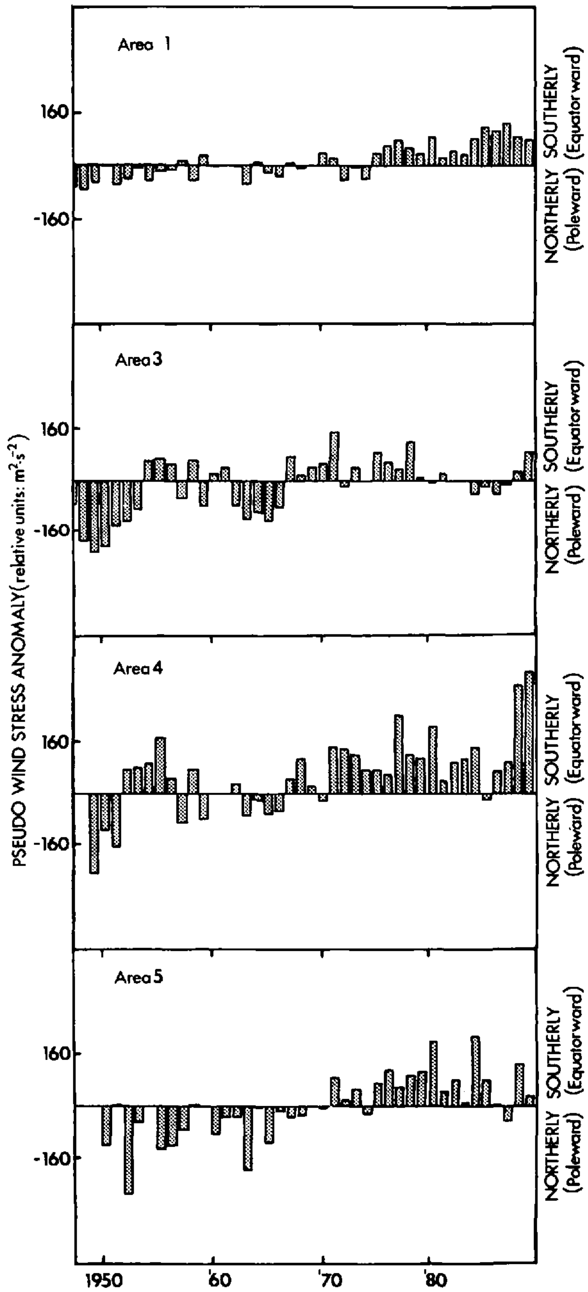


Fig. 4: Annual averaged anomalies of equatorward pseudo wind stress for Areas 1, 3, 4 and 5, 1948–1989. Note that data density for Areas 4 and 5 was low after 1982, when the record for these two areas is probably insufficient to reflect conditions typical of the shelf zone reliably

Winds

Annual averaged anomalies of equatorward pseudo wind stress, representing the southerly, upwelling-favourable component, in Areas 1, 3, 4 and 5 over the past 40 years are shown in Figure 4. Part of the record has been discussed previously (Taunton-Clark and Shannon 1988, Taunton-Clark 1990). During the 1950s, 1960s and 1970s, there was a trend towards increased equatorward wind stress (τ_y). After 1975, markedly stronger equatorward winds prevailed. There was a reduction in τ_y in the 1980s in some

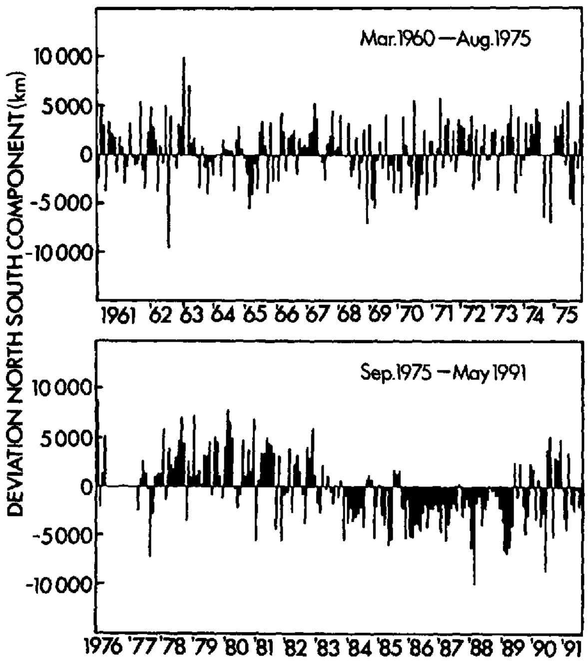


Fig. 5: Deviation from the monthly mean of the equatorward wind component at Cape Columbine lighthouse, 1960–1991

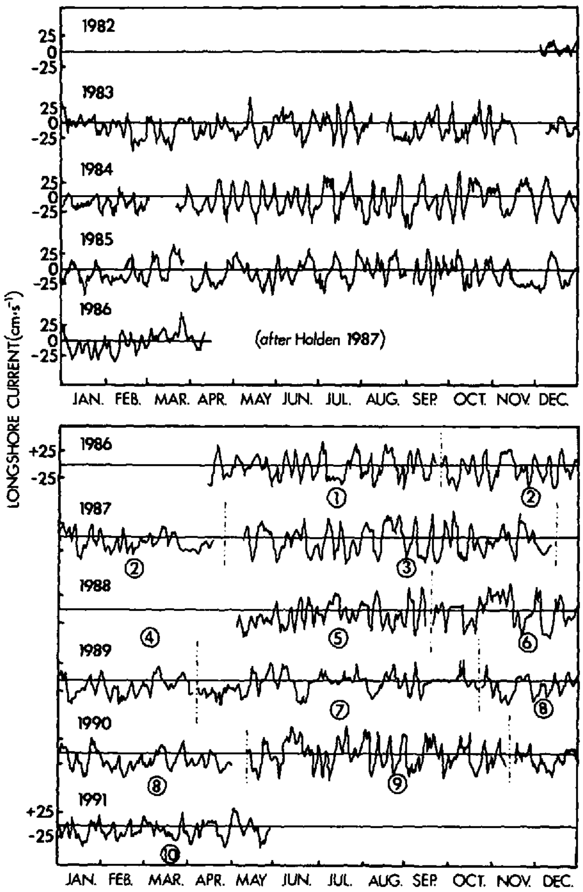


Fig. 6: Time-series of north-south currents at a depth of about 150 m below the surface off Cape Columbine, 1982–1991. Information until April 1986 has been reported by Holden (1987)

areas. In the southern offshore area (3), this resulted in negative anomalies between 1983 and 1987. In coastal areas, minima occurred in 1985 off Namibia and 1987 off South Africa. From the commencement of the period there was an increase in easterly winds (not shown), consistent with a southward shift in the mean position of the South Atlantic Anticyclone and stronger south-easterly trades, reported by Taunton-Clark and Kamstra (1988). In the southern region, this trend was reversed by slightly enhanced westerly winds after 1979 in Area 3 and after 1984 in Area 5 (not shown).

Winds at selected coastal monitoring sites show changes during the past decade more clearly. The deviations from the monthly means of the equatorward wind component at Cape Columbine between 1960 and 1991 are shown in Figure 5. Prior to about 1976 the deviations appear to be random. However, in 1977/78 there was an increase in the S–N component which persisted until the summer of 1982/83 (the date of a major Pacific ENSO). Equatorward winds then entered an extended low phase, and only picked up again in 1989, i.e. at about the time of the onset of the recent period of cooling of shelf waters.

During 1982/83, the principal wind axis at both Cape Town and Port Elizabeth shifted by about 25° (Schumann in prep.). The shift persisted until at least 1987. The change would have increased the influence of westerly winds, and this would have had a substantial impact on Ekman transport in the southern Benguela. It would also have resulted in reduced coastal upwelling and an onshore movement of the surface expression of the oceanic thermal front.

Currents

Records of currents off Cape Columbine are available from late 1982 (Fig. 6). The mooring site is situated where the shelf narrows polewards. Energy in longshore currents, either remotely forced by the wind and propagating polewards as free waves, or generated locally, is focused onto the narrow (25 km wide) shelf.

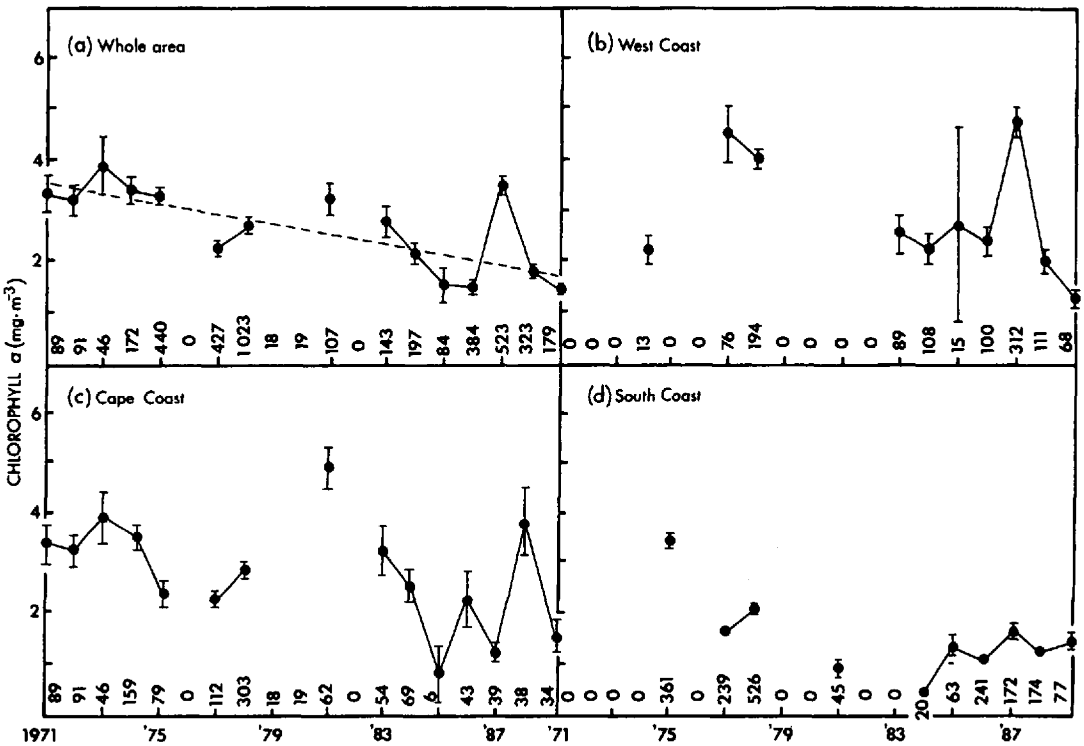


Fig. 7: Time-series of annual averaged surface concentrations of chlorophyll *a* for three areas off South Africa and for the region as a whole, modified from Brown and Cochrane (1991). Numbers above the *x* axis denote the number of data points for each month

This results in large-amplitude swings in current speed, from approximately 35 to –35 $cm \cdot s^{-1}$, superimposed on an ambient poleward flow that ranges between 3 and 12 $cm \cdot s^{-1}$. The spectral energy in the longshore flow is concentrated around a 10-day period, with weaker peaks between $2\frac{1}{2}$ and 4 days. The cross-shelf current averages out to zero, but a number of events of strong onshore flow and weaker offshore flow were observed.

Some statistical details for each of the 10 segments spanning the period 1986–1991 are presented in Table I. A ‡ in the temperature column indicates that one or more events with depressions of a few degrees Centigrade were observed. These events lasted one or two days. They were preceded by onshore flow about two days earlier. An event in Segment 1 in mid 1986 caused a depression of 5°C and was associated with the Agulhas intrusion of 1986, when there was a warm ring adjacent to the shelf-edge (Shannon *et al.* 1990). Two events in Segment 9 in 1990 had depressions of 2°C that developed over 30 days. These were associated with weak onshore flow over the same periods.

There were two prominent features of longer duration. Periods of two months of below-average reversals of flow, uncharacteristic of the Columbine record, occurred during the period June–September 1989 (Segment 7, Fig. 6). There was an unusually low mean poleward flow of 2,5 $cm \cdot s^{-1}$ and warmer (9,5°C) water from May to November 1990 (Segment 9, Table I). This followed a period of stronger than average poleward flow (12,5 $cm \cdot s^{-1}$) during summer and autumn 1989/90.

Shipboard measurements of currents made with an acoustic doppler current profiler are at present too short to infer trends. Nevertheless, the northward flow recorded inshore off western South Africa during May 1990 contrasts with the more normal southward flow as observed, for example, in May 1991.

PLANKTON

Phytoplankton

Mean annual concentrations of chlorophyll *a* for the period 1971–1989 are shown in Figure 7. Although

Table II: Decrease in the occurrence of *Calanus agulhensis* in live-net tows on the west coast of South Africa, 1988–1991

Date	July 1988	June 1989	February 1990	May 1990	May 1991
Total number of stations	54	54	36	35	44
Number of positive stations	32	20	7	9	4
Percentage positive	59%	37%	19%	26%	9%

there appears to be a decreasing trend over the 20-year period, data are highly patchy and the trend is not statistically significant.

Zooplankton

There was a decrease in the abundance of female *Calanus agulhensis* in live-net tows made off western South Africa between 1988 and 1991 (Table II). The species, characteristic of water over the Agulhas Bank (De Decker *et al.* 1991), was fairly common in plankton net hauls on the west coast of South Africa during 1987/88, but scarcer on the inner and mid shelf after 1989. It was also scarce inshore off the Cape Peninsula in the 1960s. The recent decline in abundance of *C. agulhensis* off western South Africa reflects the cooling there that followed warming in the mid 1980s. It is indicative of less penetration of Agulhas Bank water around the Cape of Good Hope onto the shelf of the West Coast.

The euphausiid *Nyctiphanes capensis* was apparently common around the South-Western Cape in the period 1954–1956 (Nepgen 1957). It has since been scarce, and the euphausiid community of the region has been dominated by *Euphausia lucens* (Pillar *et al.* 1989).

Data collected during cruises in May of 1988, 1989 and 1990 suggest that copepod biomass was higher in 1989, when there was a weak anchovy year-class, than in 1988, when there was a strong year-class. Zooplankton production was low over most of the shelf during 1988, because extensive parts of the inner shelf were dominated by small plankton cells. Even in St Helena Bay, where large cells dominated, zooplankton production was low because adults were depleted by size-selective grazing by anchovy, although the survivors were producing eggs at near maximal rates (Painting and Huggett 1989). On the spawning grounds of anchovy over the Agulhas Bank, the concentration of copepods was low in November 1988, in sharp contrast with the situation in November 1990, when copepods were plentiful there.

Off Namibia, abundance of phytoplankton and zooplankton was reduced during the Benguela *Niños* of 1963 and 1984 (Stander and De Decker 1969, Boyd *et al.* 1985).

CHANGES IN THE LIVING MARINE RESOURCES

Anchovy

Prior to the start of direct (hydroacoustic) surveys in 1984, assessments of biomass and year-class strength of anchovy were based on Virtual Population Analysis (VPA), which for a short-lived species is particularly unreliable. From the early 1970s until 1984, large fluctuations in the abundance of anchovy in the southern Benguela were not apparent, both catches and catch rates being relatively stable (Crawford *et al.* 1987). Off Namibia, catches of anchovy from 1978 to 1983 were 200 000 tons or more, except in 1982 when they only reached some 80 000 tons. They then plummeted to a mere 14 000 tons in 1984, following formation of a poor cohort after the 1984 Benguela *Niño* (Boyd *et al.* 1985), and remained low in 1985 and 1986.

Direct surveys indicate that strong year-classes of anchovy were formed in the southern Benguela in 1986 and 1987, and that biomass was high (Fig. 8). There was then a sharp decline in year-class strength in 1989 and 1990, leading to a greatly reduced spawner biomass. The year-class of 1991, as measured in May 1991, was somewhat stronger again. The area occupied by adult anchovy was considerably smaller in November 1989 than in November 1987 (Fig. 9). Catches of anchovy off both South Africa and Namibia peaked in 1987 and then decreased, more rapidly off Namibia (Fig. 10). In 1989 and 1990 there was a reduced contribution of anchovy to the diet of the Cape gannets off western South Africa, anchovy being replaced in the diet by pilchard (Fig. 11). After 1987, there was a sharp decrease in the quantity of oil produced per ton of fish reduced to meal at plants processing South Africa's purse-seine catch (F. H. Schülein, Sea Fisheries Research Institute, pers. comm.). This suggests that the fish being processed by the reduction plants (predominantly anchovy) were in poor condition. In the 1988/89 anchovy spawning season, there was a large increase in the proportion of female anchovy

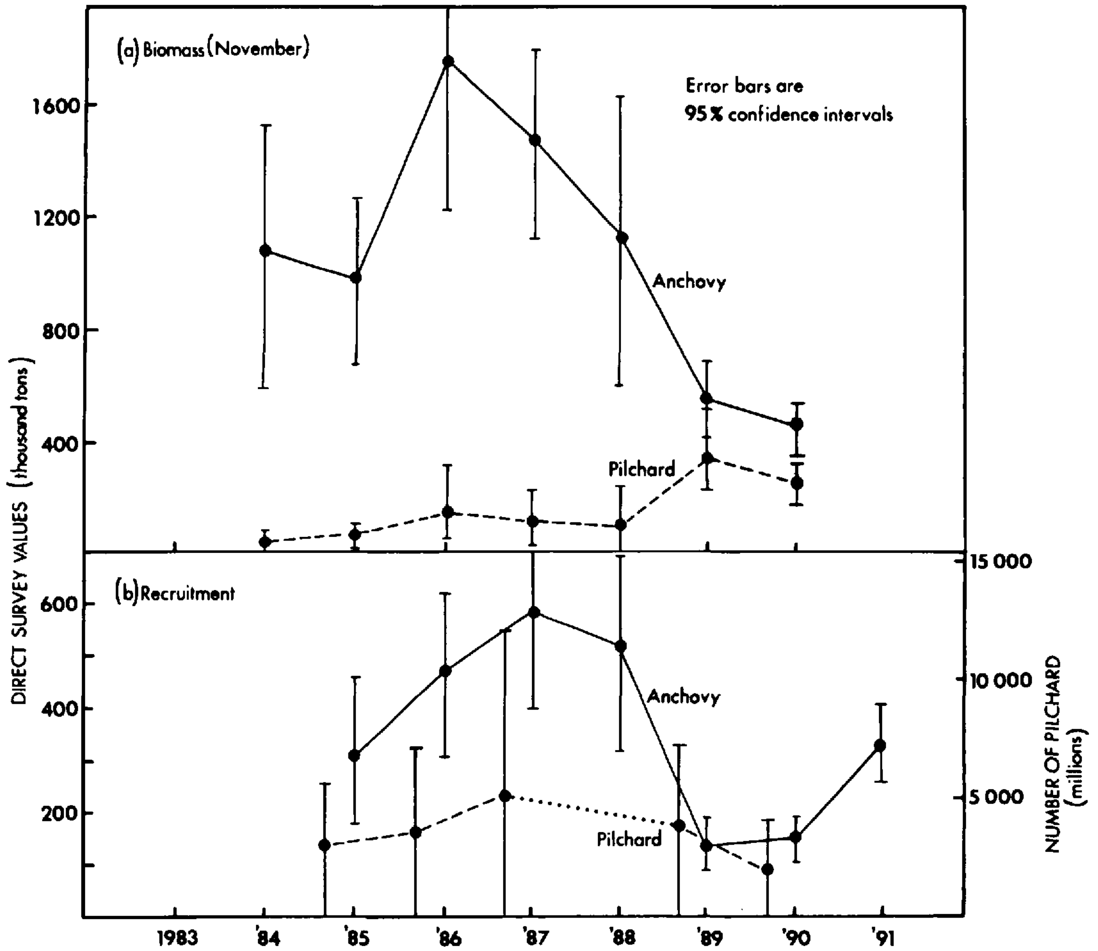


Fig. 8: Acoustic estimates of (a) spawner biomass of pilchard and anchovy, and (b) biomass of nought-year-old anchovy and numbers of nought-year-old pilchard off South Africa, 1984–1991 (after Borchers 1991)

with reabsorbed eggs. Oocyte atresia is typically 1 per cent, but it was 18 per cent in November 1988 (Y. C. Melo, Sea Fisheries Research Institute, pers. comm.).

Pilchard

Stocks of pilchard collapsed off South Africa in the mid 1960s and off Namibia in the early 1970s. Estimates of biomass from VPA suggest pre-collapse maxima of the order of a million tons in the south and 10 million tons in the north, compared with post-collapse levels in the early 1980s of around 0,05 million tons and 0,2 million tons respectively (Crawford *et al.* 1987). By the mid 1980s, fishermen were anticipating a recovery in the pilchard resource off South Africa, a perception partly supported by the four-fold increase in the contribution of the species to the diet of Cape gannets between the early 1980s and 1985 (Fig. 11, Berruti 1987). Although hydroacoustic estimates of pilchard biomass showed little increase (only 54 000 tons in 1985, Fig. 8), the precision of these estimates is low because of the low stock levels (Borchers 1991). In contrast, there is no reason to suspect a similar poor precision of the index of pilchard in the diet of Cape gannets (Berruti 1987), suggesting that the gannet diets gave an earlier indication of rising stock levels than the hydroacoustic surveys. By 1987, pilchard was

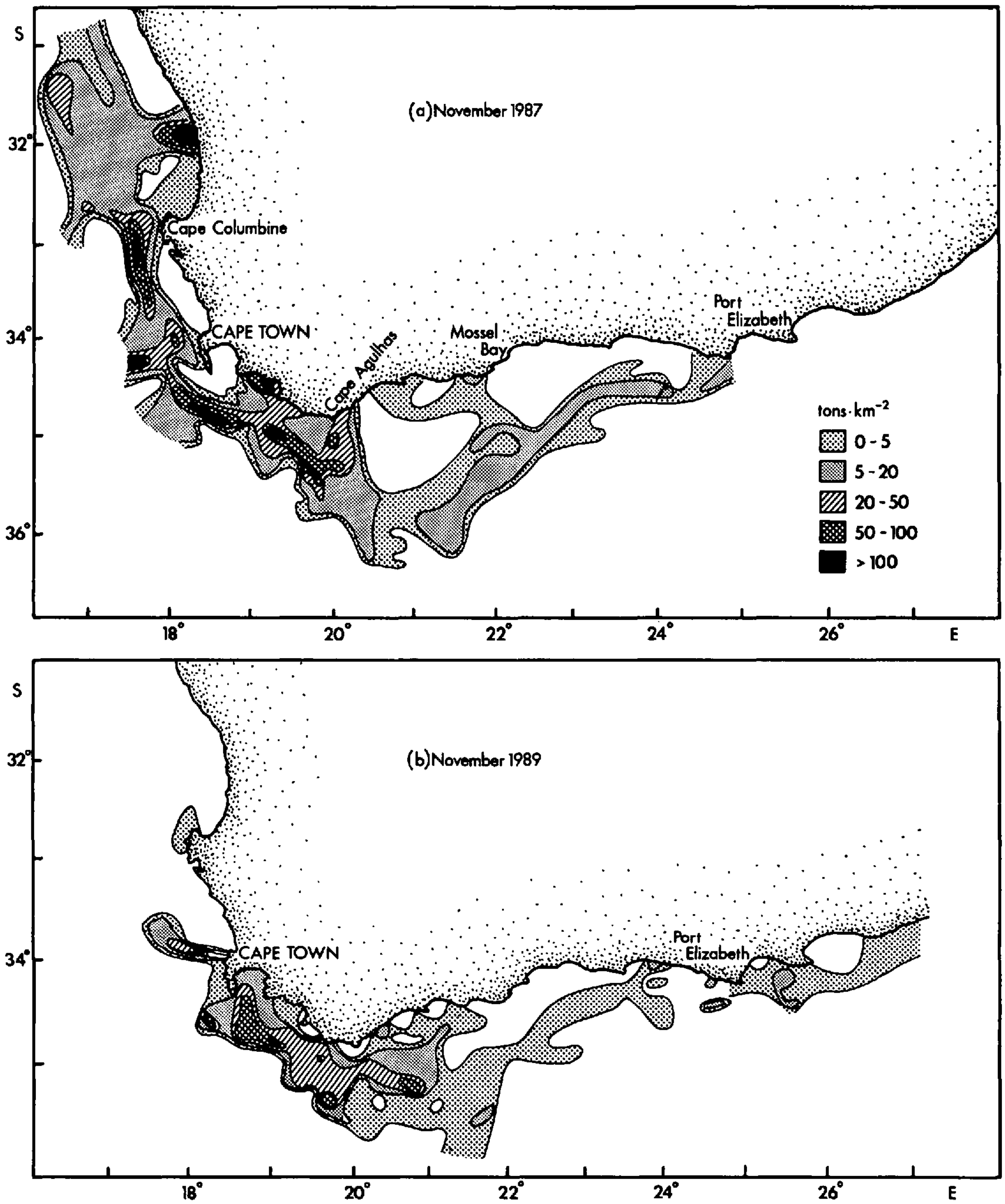


Fig. 9: Distribution of adult anchovy in the southern Benguela region in (a) November 1987 and (b) November 1989

constituting more than 40 per cent of gannet diet in the southern Benguela, and by 1989 and 1990 in excess of 50 per cent, indicating a partial recovery of the stock. Of course, this trend may have been partly influenced by the reduced availability of anchovy to gannets in 1989 and 1990. However, the recovery of the pilchard

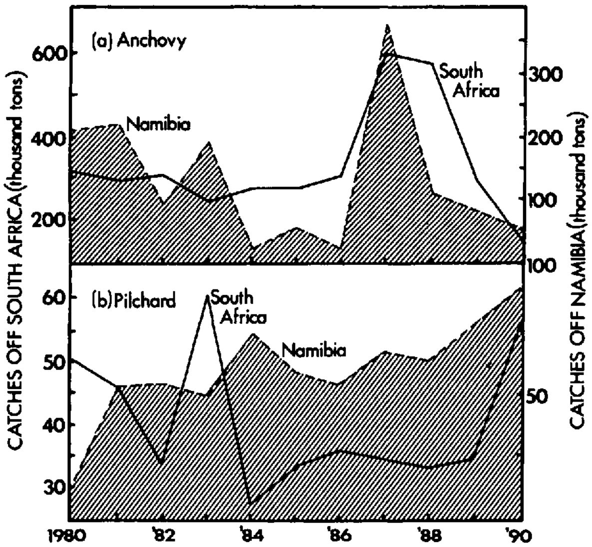


Fig. 10: Annual landings of (a) anchovy and (b) pilchard by Namibia and South Africa, 1980–1990

resources in recent years is borne out by the hydro-acoustic estimates (Fig. 8). A good year-class in 1988 is indicated from a maximum likelihood VPA model (Fig. 12, Borchers 1991), and much of the recovery can be attributed to this year-class. In the 1980s there was a partial increase in the Namibian catch of pilchard, following very poor catches from 1978 to 1980 (Fig. 10). However, Namibian catches still remained well below those taken in the 1960s and mid 1970s.

Cape hakes

Survey estimates of the biomass of Cape hakes off South Africa's west and south coasts have been of the order of 650 000 tons since 1983 (Payne *et al.* 1988 and unpublished information, Punt 1991). However, there has been substantial variability in the biomass estimates from the individual research surveys, which have large standard errors. Nevertheless, the short time-series (not shown) suggests that biomass has indeed been increasing. The increase is supported by improvements in catch rate (*cpue*) on both the west

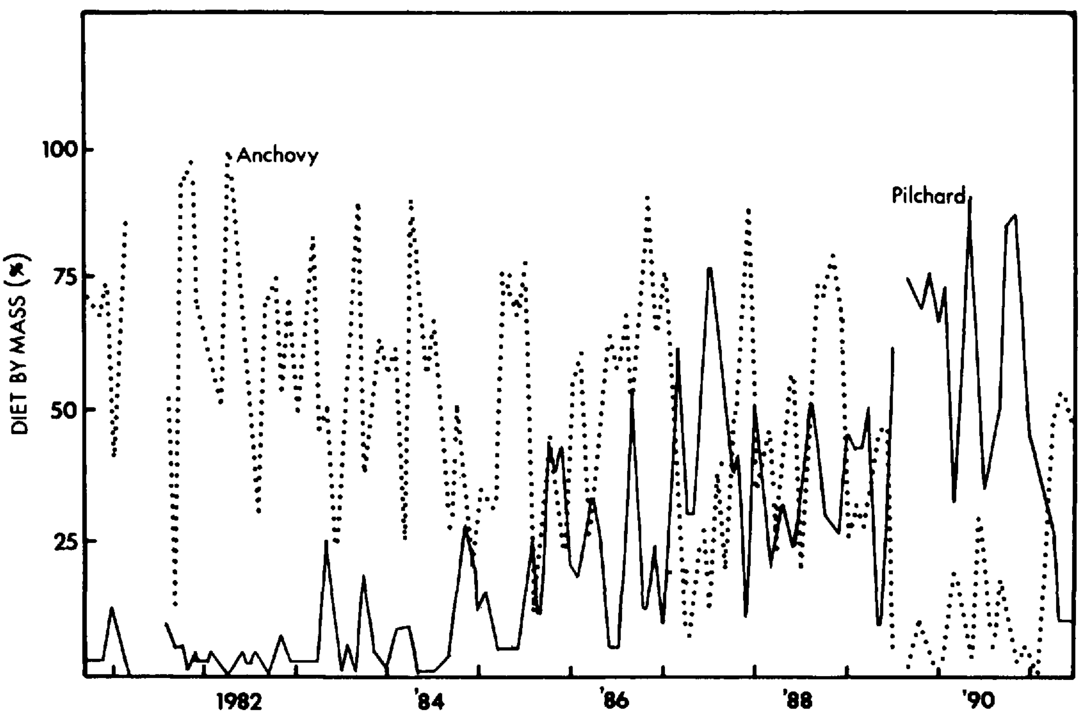


Fig. 11: Monthly trends in the contribution of anchovy and pilchard to the diet of Cape gannets off western South Africa, 1980–1991

Fig. 12: Estimates of year-class strength of pilchard in the southern Benguela from a maximum likelihood VPA model, 1983–1990

Table III: Catch and catch rates of Cape hakes off South Africa, 1955–1990

Year	West Coast		South Coast	
	Catch ('000t)	Catch rate (tons·day^{-1})	Catch ('000t)	Catch rate (tons·h^{-1})
1955	115,4	17,31		
1956	118,2	15,64		
1957	126,4	16,47		
1958	130,7	16,26		
1959	146,0	16,26		
1960	159,9	17,31		
1961	148,7	12,09		
1962	147,6	14,11		
1963	169,5	13,97		
1964	162,3	14,60		
1965	203,0	10,84		
1966	195,0	10,63		
1967	176,7	10,01	17,3	1,28
1968	143,6	10,01	31,3	1,28
1969	165,1	8,62	41,7	1,28
1970	142,5	7,23	27,8	1,22
1971	202,0	7,09	34,5	1,14
1972	243,9	4,90	51,3	0,64
1973	157,7	4,97	77,3	0,56
1974	123,0	4,65	100,9	0,54
1975	89,6	4,66	73,8	0,37
1976	143,8	5,35	57,6	0,40
1977	102,3	4,84	40,4	0,42
1978	101,1	5,90	38,8	0,41
1979	92,7	6,13	53,8	0,46
1980	101,5	5,48	47,5	0,44
1981	100,6	5,81	35,1	0,40
1982	85,9	5,87	46,8	0,51
1983	73,6	6,49	41,1	0,48
1984	88,4	6,67	43,1	0,55
1985	99,5	7,29	56,2	0,67
1986	109,0	6,93	51,1	0,63
1987	104,0	6,46	41,8	0,55
1988	90,1	6,88	44,9	0,54
1989	84,8	7,18	51,7	0,51
1990	78,7	7,29	58,2	0,60

and south coasts of South Africa of the order of 40–50 per cent since the mid 1970s (Table III), and by VPA estimates of biomass (Fig. 13). The average annual catch of Cape hakes in South African waters was some 135 000 tons during the 1980s.

Research surveys and reports from the fishing industry indicated a relative absence of two-year-old fish during 1991, suggesting that either the 1989 year-class was smaller than normal or the stock had shifted northwards into Namibian waters in 1991.

Agulhas sole

Agulhas sole are caught in the mixed-species, bottom trawl fishery on South Africa's south coast (Payne and Badenhorst 1989). Catches in the 1980s fluctuated between a maximum of 1 026 tons in 1981 and a minimum of 682 tons in 1983. Catch rates were high in the early 1980s, in 1989 and 1990, but poor in the middle of the decade (Fig. 14). Biomass is estimated to be of the order of 3 000 tons (Badenhorst 1988a, Borchers and Punt 1990).

Kingklip

Kingklip contribute a small, but important, by-catch in the hake-directed bottom-trawl fishery. Historical records show that kingklip catches constituted 2–3 per cent of the total landings by bottom trawlers off South Africa between 1932 and 1983, though rarely exceeding 3 per cent (Japp 1989). In this period, the greatest portion of the kingklip catch was made on the West Coast (Fig. 15). Catches from 1932 increased steadily, along with increased hake-directed fishing effort. From 1970 to 1983, total catches of kingklip caught by trawl fluctuated between 2 700 and 5 300 tons. The peak in trawl catches of kingklip in 1973 coincided with large-scale fishing for hake by foreign fleets at the time, shortly before declaration of the 200-mile fishing zone by South Africa in 1977.

Introduction in 1983 of an experimental longline fishery, targeting on kingklip, had a serious impact on kingklip stocks (Fig. 15). Catches of kingklip immediately increased sharply, the greatest rise being on the South Coast, where the longline fleet targeted almost entirely on spawning aggregations at the eastern edge of the Agulhas Bank (Badenhorst 1988b, Japp 1988, 1989). After the mid 1980s, catches of kingklip by both trawl and longline fleets decreased rapidly.

Kingklip biomass prior to fishing (early this century) is estimated to have been about 133 000 tons (Japp and

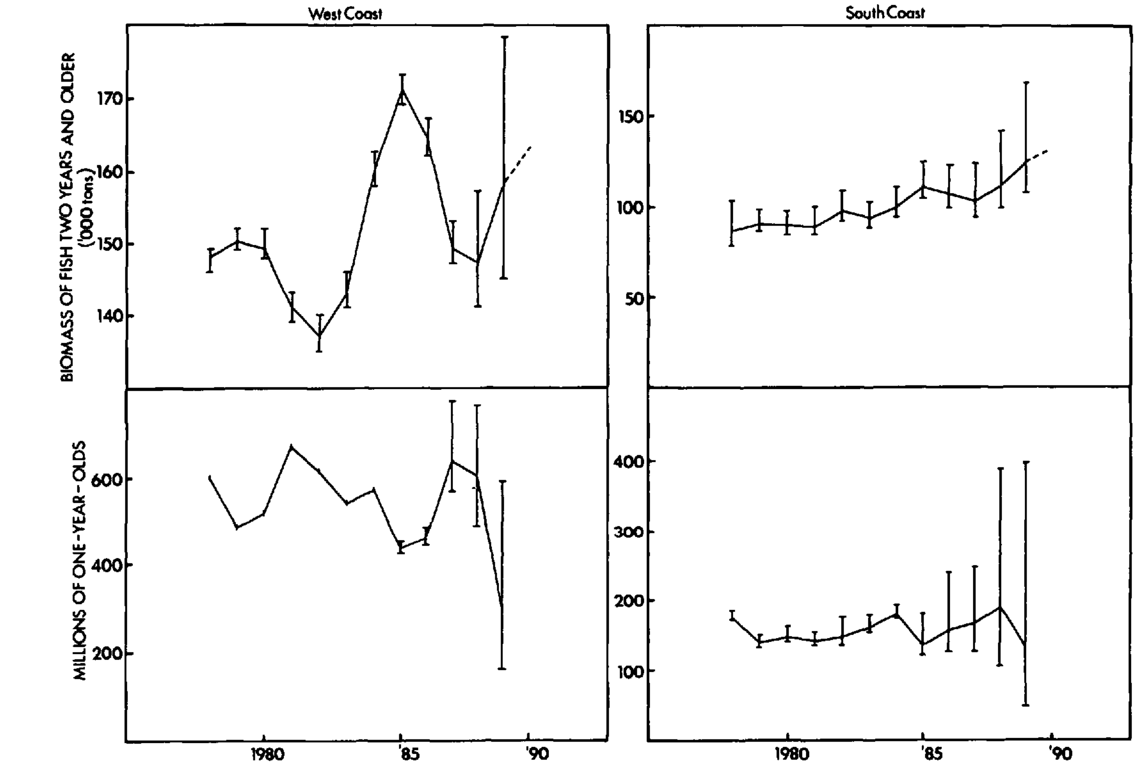


Fig. 13: Estimates of biomass of fish aged two and older and numbers of fish aged one for Cape hakes in two regions off South Africa from VPA, 1978–1989 (after Punt 1991)

Punt 1989, Punt 1990). However, this figure had been reduced by about 60 per cent by the advent of longlining and, within eight years of commencement of longlining, to 18 per cent of the pristine level. The decline of the kingklip resource can be attributed to overfishing of the kingklip spawner stock in the south and to a subsequent reduction in the number of kingklip recruiting to the trawl fishery, rather than to environmental perturbations. The effect of the extremely heavy fishing pressure on the kingklip spawner stock over the eastern Agulhas Bank on recruitment to both the Agulhas and Benguela systems illustrates the likely interdependence of kingklip and possibly certain other demersal species in the two systems.

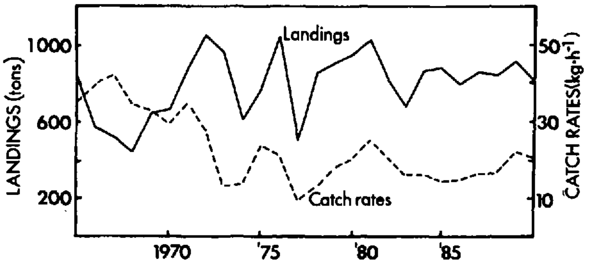


Fig. 14: Landings and catch rates of Agulhas sole off South Africa, 1965–1990

Squid

The chokka squid is the only squid species of commercial significance off South Africa. Nowadays, it is fished mainly by jigging on the spawning grounds off the Eastern Cape, but it has also been taken traditionally as a by-catch in foreign and South African bottom trawls over most of the shelf out to a water depth of about 300 m. Trends in catches of the main sectors of the fishery are shown in Figure 16. The jig fishery for squid developed rapidly in the mid 1980s and is now

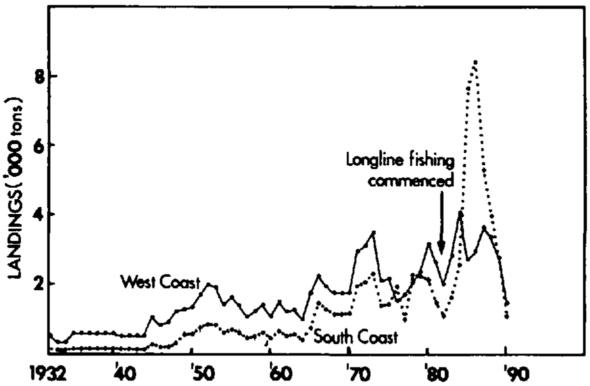


Fig. 15: Landings of kingklip from the west and south coasts of South Africa, 1932–1990

dominant, whereas catches by the trawl fisheries have been declining gradually since the late 1970s. After stable catches in the jig fishery from 1985 to 1987, there was a sharp peak in 1988 and 1989, followed by a return to earlier levels in 1990 (Fig. 16a). Catch rates in both trawl and jig fisheries declined after 1985 as the jig fishery developed, but then increased to a lesser peak in 1989 (Fig. 16b) before declining again. The trends in catch rates reflect those of the catches.

Biomass indices obtained from stratified, random sampling on trawl surveys off southern South Africa confirmed the peak in abundance in 1989 and the subsequent decline, but did not correlate well with trends in catch and catch rates (Fig. 16c). This is perhaps because the surveys were not all conducted at the same time of the year and were not really targeted at squid.

It can probably be said safely that chokka squid biomass was high in the late 1970s and early 1980s, decreased after 1984, rose to a peak in 1988/89 and then decreased to average or lower levels.

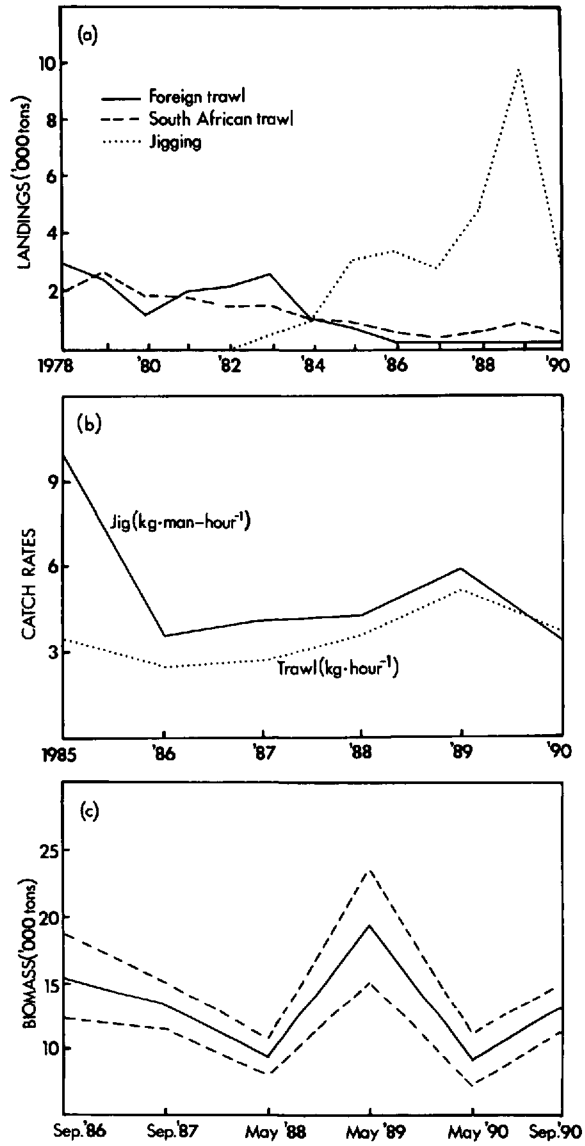


Fig. 16: Trends in the fishery for chokka squid off South Africa, 1978–1990 — (a) landings, (b) catch rates and (c) estimates of biomass

West Coast rock lobster

Prior to 1980, the fishery for West Coast rock lobster was managed by regulating catching season, fishing effort, fishing area and minimum legal size. Following a sharp decline in catches in the late 1970s, total allowable catches (*TAC*s) were applied from 1980 to eight fishing grounds off the South African west coast (Pollock 1986). The *TAC*s helped stabilize annual catches during the 1980s at between 3 000 and 4 000 tons. After the introduction of separate *TAC*s for the eight grounds, catch rates in most areas improved until the 1988/89 fishing season (Fig. 17). However, catch rates then fell and, in both 1989/90 and 1990/91, the *TAC*s were not filled. In 1990/91, landings only totalled 2 935 tons (77% of the *TAC* of 3 790 tons), and considerable effort was needed to achieve this level. Catch rates in fact declined sharply in all fishing grounds along South Africa's west coast during 1990/91, most

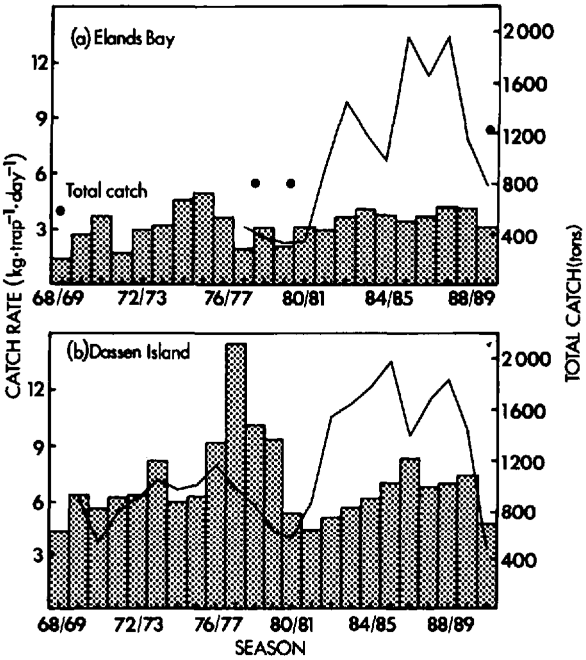


Fig. 17: Catches (histograms) and catch rates (solid lines) of West Coast rock lobster at (a) Elands Bay and (b) Dassen Island, 1968/69–1990/91. Seasons in which an outbreak of *Gonyaulax catanella* was recorded are indicated

noticeably off Elands Bay and at Dassen Island (Fig. 17). However, the decrease in catches was not limited to South African waters, however, a similar situation prevailing in the Namibian fishery off Lüderitz (Fig. 18).

The recent decrease in catches and catch rates in South African waters has been attributed to reduced rates of growth (Fig. 19). Fewer animals grew to legal size, thereby reducing production to the fishery. Available evidence suggests that food was the limiting factor. Ribbed mussels *Aulacomya ater* and shallow-water black mussels *Choromytilus meridionalis* are important items in the diet of West Coast rock lobster. Diving surveys indicated a marked decline in the biomass of *A. ater* at Dassen Island and of *C. meridionalis* at Elands Bay (DEP unpublished information).

Abalone

Similar to the situation in the rock-lobster fishery, abalone had been managed by a minimum size limit, control of catch and effort, closed areas and closed

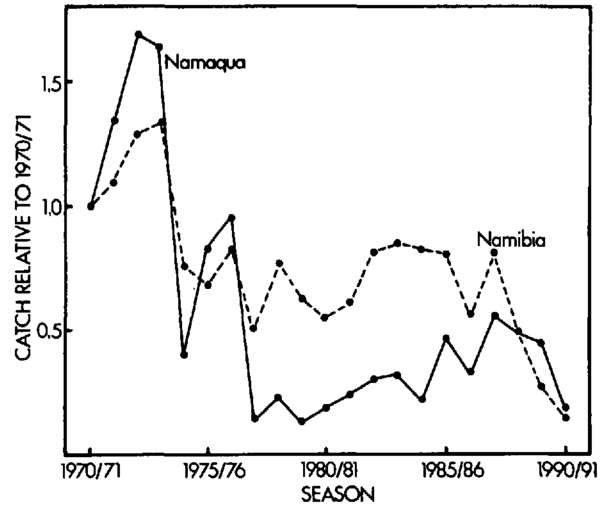


Fig. 18: Catches relative to the 1970/71 season of West Coast rock lobster in Namibia and in the Namaqua area off South Africa, 1970/71–1990/91

seasons. In 1986/87, *TAC*s were introduced in the seven areas that constitute South Africa's commercial fishing grounds. Most fishing takes place between Quoin Point and Cape Hangklip, and total annual landings have fluctuated around 600 tons during the 1980s. In spite of the public denuding some highly accessible areas of animals of legal size, and in spite of a spate of illegal catching, there has been no noticeable decrease in the stock of animals of legal size.

East of the Cape Peninsula, larval settlement is regular, with no obvious interannual differences apparent from available data. West of the Cape Peninsula, however, settlement is sporadic. At Robben Island there was no settlement in 1988, 1989 or 1990, whereas settlement did take place in 1987 and in 1991.

Linefish

Many factors govern the catches of linefish, so to attempt to link time-series of catch statistics to changes in the environment is not currently possible. However, catches off western South Africa of four sought-after species, elf *Pomatomus saltatrix*, kob *Argyrosomus hololepidotus*, geelbek *Atractoscion aequidens* and yellowtail *Seriola lalandii*, were all low during the period 1986–1989, in sharp contrast to the high catches of anchovy in 1987 and 1988 (Fig. 20). Catches of all four species increased again in 1990, which, as stated above, was a poor year for anchovy.

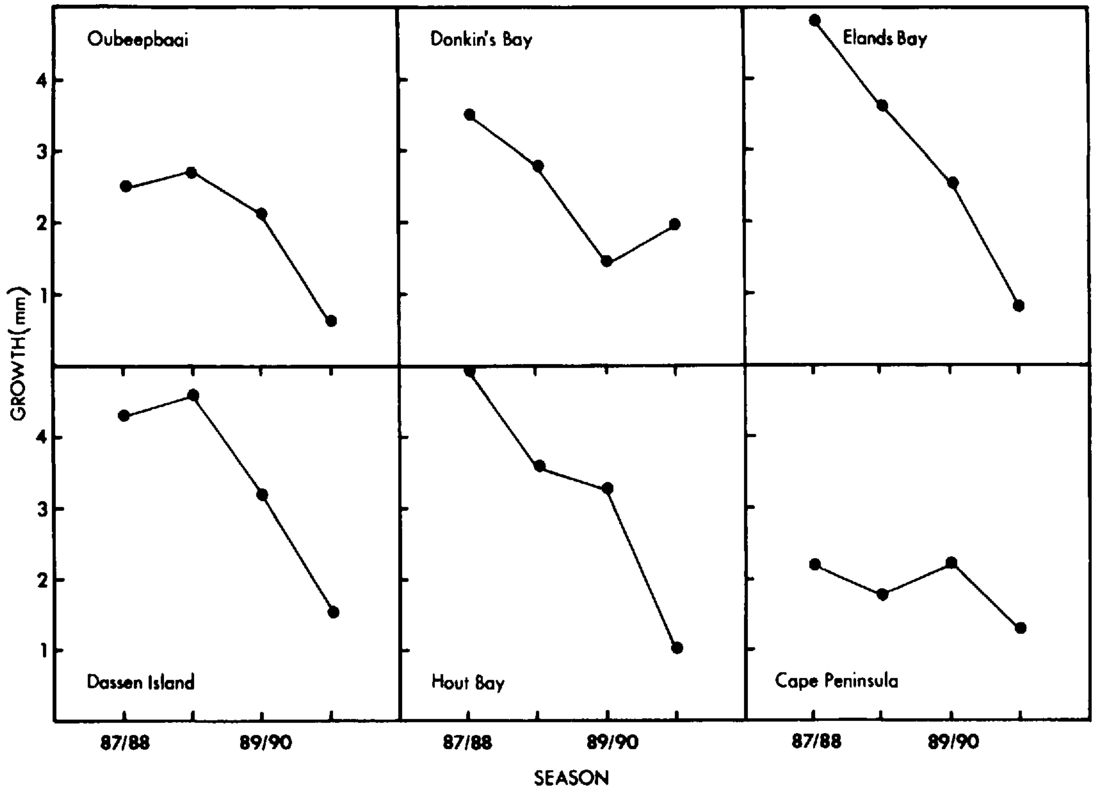


Fig. 19: Growth rates of sublegal male West Coast rock lobster in six areas in the southern Benguela, 1987/88–1990/91

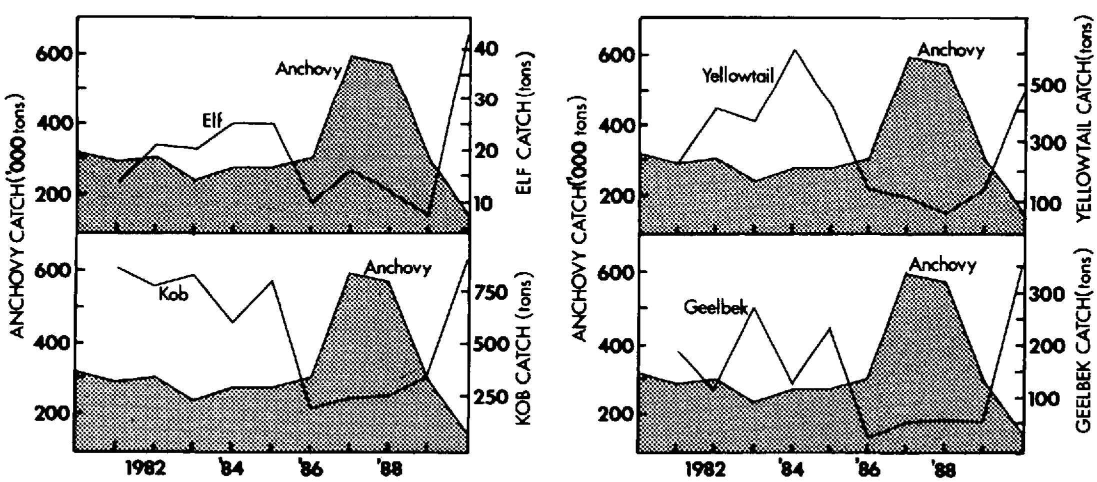


Fig. 20: Trends in the catches of four fish species caught by line off South Africa, contrasted with the catch of anchovy, 1980–1990

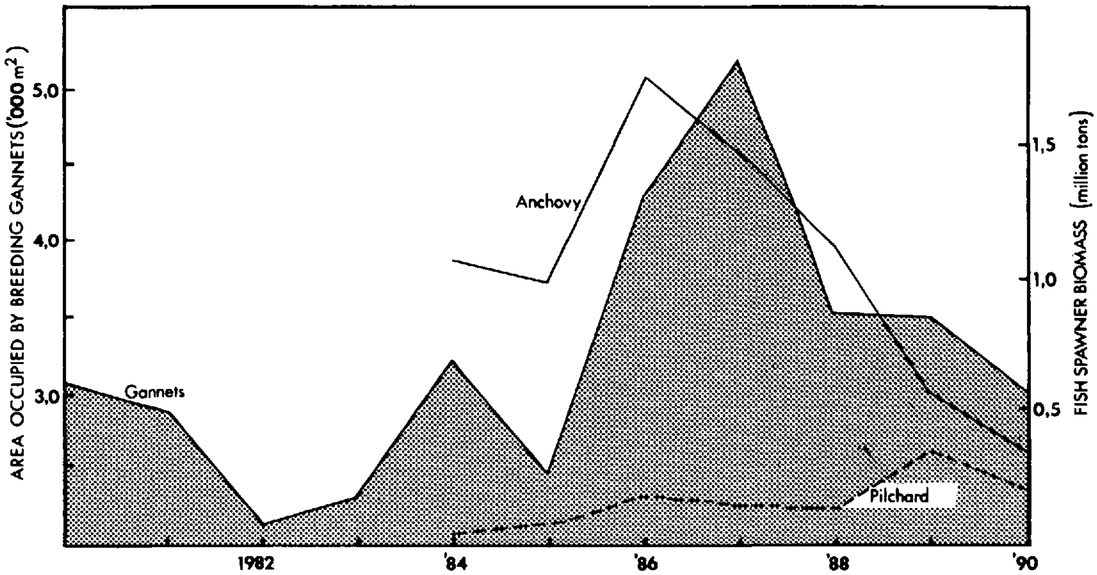


Fig. 21: Area occupied by breeding gannets at Lambert's Bay, 1980–1990, contrasted with trends in the spawner biomass of anchovy and pilchard off South Africa

Seabirds

Seabirds appear to have been substantially influenced by the large fluctuations in abundance of prey species, especially of pilchard and anchovy. Numbers of Cape gannets breeding at Lambert's Bay increased markedly during 1986 and 1987, when the anchovy biomass was high, but thereafter decreased towards levels experienced in the early 1980s (Fig. 21). For most of the 1980s anchovy was an important item in the diet of Cape gannets, but its contribution fell in 1989 and 1990 coincident with weak anchovy year-classes in those years (see Fig. 8). In 1989, there was a relatively high abundance of pilchard, but in 1990, when the combined biomass of anchovy and pilchard off western South Africa was low, the numbers of gannets breeding decreased at both gannetries off South Africa's west coast — Lambert's Bay and Malgas Island. Malgas Island was proclaimed part of the West Coast National Park in 1985 and there was no scraping of seabird guano there between 1986 and 1990. This permitted gannets to initiate breeding earlier than formerly, because availability of old nests obviates the necessity to construct new ones, a factor which may have influenced breeding success (Crawford and Cochrane 1990). However, at Lambert's Bay, where the management strategy was unaltered and guano was collected on an annual basis until 1990, the trend in numbers of breeders (Fig. 21) is likely to have been primarily influenced by altered availability of food.

Three other seabirds that breed off western South Africa also prey heavily on anchovy, i.e. Cape cormorant *Phalacrocorax capensis*, African penguin *Spheniscus demersus* and swift tern *Sterna bergii* (Crawford and Shelton 1978, 1981, Walter *et al.* 1987a, b). For all three, the numbers of birds that attempted nesting decreased sharply after the severe decrease in abundance of anchovy in 1989. The mean number of Cape cormorants breeding at seven islands fell from 87 000 to 27 000 pairs (Crawford *et al.* 1992); the mean number of African penguins nesting at Dyer Island, the world's most populous colony for the species, fell from 18 000 to 6 000 pairs (Shelton *et al.* 1984, Crawford *et al.* 1990c, RJMC unpublished information); the mean number of swift terns breeding off western South Africa fell from 3 800 to 1 600 pairs (Cooper *et al.* 1990, RJMC unpublished information).

DISCUSSION

From the aforegoing it is clear that there were substantial changes in the Benguela ecosystem during the 1980s. Much of the observed variability could have been reasonably expected in an upwelling system such

Table IV: Main features of variability in indices of the Benguela environment and of resour

Parameter	Comment per year					
	1980	1981	1982	1983	1984	1985
Sea surface temperature	Decade characterized by general warming trend		Shelf very cold in both south and north	Shelf cold, except in extreme south	Benguela *Niño* in north	
Winds	Decade characterized by above-average equatorward wind stress (τ_y) in north			Start of period of reduced τ_y in south		
Currents					Influx of Angola Current and oceanic water in north	
Plankton	Possible decline in phytoplankton abundance in south over decade. Toxic red-water outbreaks at start and end of decade					
Anchovy	Prior to 1984, biomass data unreliable				Poor catches off Namibia	Poor catches off Namibia
Pilchard	Stocks recovered gradually over the decade			Good year-class in south	Weak year-class in south	
Hakes	Slow recovery of stocks off western and southern South Africa over decade	Above average abundance of one-year-olds off western South Africa				Low abundance of one-year-olds off western South Africa
Agulhas sole	Catches and catch rates over decade display no obvious trends					
Kingklip	Stock size estimated at 0,4 × pristine level		Longline fishery increases catches			
Chokka squid	High biomass					Rapid development of jig fishery in mid 1980s
Abalone	No obvious trends during decade, but larval settlement on West Coast sporadic					
West Coast rock lobster	Catch rates low at start of decade			Apparent improvement in catch rates		
Linefish						
Seabirds	Gradual switch over decade in diet of Cape gannets from anchovy to pilchard					

undance (in the southern Benguela except where indicated to the contrary), 1980–1991

Comment per year					
1986	1987	1988	1989	1990	1991
Agulhas intrusion in south	Subantarctic water instrusion in south, followed by warming		Initial warming, followed by cooling of shelf waters	Shelf cool	Shelf cool until autumn
		Increase in τ_y offshore in south	Termination of period of reduced τ_y on shelf in south		
Agulhas intrusion in south: interaction between Agulhas and shelf water			Anomalous: below-average reversals in flow at 150 m off Cape Columbine (winter-spring). Interaction between Agulhas ring and upwelling filament	Very low net poleward flow off Cape Columbine (winter/spring)	
		Calanus agulhensis abundant off western South Africa. Copepod abundance low on Agulhas Bank in spawning season	*C. agulhensis* less abundant off western South Africa. Copepods more abundant on Agulhas Bank in spawning season	*C. agulhensis* continues to decrease off western South Africa. Copepods abundant during spawning season	*C. agulhensis* scarce off western South Africa
Poor catches off Namibia. High spawner biomass and good year-class off South Africa	Powerful year-class in south; good catches throughout Benguela	Good year-class and reasonable spawner stock in south. Poor catches off Namibia	Poor year-class in south leads to reduced spawner biomass. Poor catches off Namibia	Poor year-class and low spawner biomass in south. Poor catches off Namibia	Improved year-class; possible recovery of stock
		Good year-class in south			Stock recovering in north
Low abundance of one-year-olds off western South Africa	High abundance of one-year-olds off western South Africa				
Peak longline catch	Catches by longline decrease for first time			Stock size estimated at 0,18 × pristine level. Longlining phased out	
Declining biomass and trawl catches		Good catches in jig fishery	Excellent catches in jig fishery		
	Settlement of larvae at Robben Island	No settlement of larvae at Robben Island	No settlement of larvae at Robben Island	No settlement of larvae at Robben Island	Settlement of larvae at Robben Island
			Catch rates declining; growth rates decreasing	Catch rates low: very slow growth	
Catches of elf, yellowtail, kob and geelbek below average	Below-average catches of same four species	Below-average catches of same four species	Below-average catches of same four species	Good catches of same four species	
Good breeding by Cape gannets on West Coast	Good breeding by Cape gannets on West Coast		Area occupied by breeding gannets at Lambert's Bay smaller than average. Anchovy scarce in diet	Area occupied by breeding gannets at Lambert's Bay smaller than average. Anchovy scarce in diet	

as the Benguela, which has warm-water regimes at both poleward and equatorward boundaries, and which is subject to pulsing on a wide spectrum of spatial and temporal scales. There is, of course, no proof that variability during the 1980s was greater than that of preceding decades. More reliable information for both the environment and the resources have resulted from improved technology and better assessment techniques. They have permitted change in the 1980s to be documented more rigorously than in earlier years.

A synthetic documentation of this change, from that in the environment, through change in the plankton and in the fish resources, to change in populations of top predators, has been the primary objective of this paper. Linkages between the various data series presented await rigorous statistical analysis, but this is intended for the future. In the interim, a summary is presented in Table IV of some of the main events that occurred.

A few tentative conclusions may be drawn about the association between some of the changes, but it is also necessary to list a few of the principal features which emerge from examination of the available data:

(i) The 1984 Benguela *Niño*, which followed an extended cold period on the shelf, had an adverse effect on the anchovy resource off Namibia. This has been well documented by several authors (Boyd *et al.* 1985, Le Clus 1986, 1990, Crawford *et al.* 1990a, b). The impact of the intrusion of water from the Angola Current and the tropical oceanic region appears to have been limited to the northern part of the Benguela system, in contrast to the 1963 perturbation.

(ii) The warming that took place in the southern Benguela during the mid 1980s and peaked in 1986, with the intrusion of Agulhas Current water to the shelf off western South Africa, was associated with above-average recruitment of anchovy to the fisheries off both South Africa and Namibia. For the South African fishery, this can be attributed to powerful year-classes being formed in 1986 and 1987 (Fig. 8). Off Namibia, it is probable that the good catches of 1987 were bolstered by recruitment from the south (Hewitson 1988, Cruickshank *et al.* 1989). This theory is borne out by the low catches off Namibia in other years between 1984 and 1990 (Fig. 10). The period of warming coincided with a period of reduced equatorward wind stress in the southern coastal regions and increased influence of westerly winds (Schumann in prep.). This would tend to reduce advective loss of eggs, larvae and small fish from the southern Benguela system. Therefore, it seems likely that the good year-classes of anchovy resulted from entrainment of biota inshore and reduced advective loss offshore. Others have already concluded that transport has an important influence on the strength of anchovy year-classes off South Africa (Duncombe Rae *et al.* 1992). The powerful year-classes of 1986 and 1987 resulted in a large increase in anchovy biomass (Fig. 8). This, in turn, primed the food chain and led to improved breeding by southern Africa's two major producers of seabird guano, Cape gannets (Fig. 21) and Cape cormorants (Crawford *et al.* 1992).

(iii) The weak anchovy year-class formed off South Africa in 1989 was associated with poor feeding conditions during the latter part of 1988 in the spawning area on the western Agulhas Bank, and with less favourable transport to the nursery grounds off western South Africa. In November 1988, fish on the western Agulhas Bank were "starving" and had the potential to consume all available zooplankton production (Peterson *et al.* 1992). A progressive decrease in the volume of Agulhas Bank water rounding the Cape of Good Hope after 1988 is evident from the decreased abundance of *C. agulhensis* west of the Cape Peninsula (Table II). There was increased equatorward wind stress in 1988/89, intensified upwelling, and consequently increased Ekman transport of coastal water offshore. This would have increased advective loss of ichthyoplankton. Advective loss may have been further exacerbated during autumn/winter 1989 through the drawing off of shelf water by a large Agulhas ring that interacted with a Benguela filament (Duncombe Rae *et al.* 1992). Pilchard predation on anchovy eggs during the 1988/89 spawning season, and the presence of unusually warm water low in chlorophyll *a* near St Helena Bay early in 1989, may both have had a detrimental effect on anchovy spawning success (Anon. 1991). In 1989, growth of zero-group anchovy was slow, suggesting that food was limiting in nursery grounds west of the Cape Peninsula (Waldron *et al.* 1992).

(iv) A relatively good year-class of pilchard was estimated to have been formed off South Africa in 1988 (Fig. 12) during a period of cooling in the southern Benguela. It was followed by a reasonable year-class in 1989, one attributable to pilchard spawning earlier than anchovy in the 1988/89 spawning season, during the latter part of which food became limiting (Anon. 1991).

(v) A high abundance of one-year-old hake in 1982 and 1987 off western South Africa (Fig. 13) coincided with cool conditions in the southern

Benguela (Walker 1987, Anon. 1991), whereas there was reduced abundance in the warmer mid 1980s. This is consistent with the findings of the empirical study of Shannon *et al.* (1988). Off southern Namibia, survey estimates of the biomass of Cape hakes in summer are higher than survey estimates in winter when summer sea surface temperatures are anomalously warm, but the same does not apply in other years (Macpherson *et al.* 1991). This suggests some relationship between density of hakes and SST. Density may influence the mortality of young hake attributable to predation by older hake (Shannon *et al.* op. cit.).

(vi) The rapid decline in abundance of kingklip, a long-lived demersal species, was clearly the result of excessively heavy fishing pressure on spawning fish.

(vii) Changes in the abundance or availability of chokka squid appear related to both fishing pressure and the environment. Catch rates decreased after the onset of jigging, but were again high in 1989. Reduced catches in 1990 were associated with increased advection of warm water into the bays off southern South Africa (Anon. 1991).

(viii) Towards the end of the 1980s there was a sharp decline in production of rock lobster throughout the Benguela system (Figs 17, 18). In the southern Benguela, the decreased production resulted from reduced growth rates. Off Namibia, it has been attributed to overexploitation and changes in availability related to fluctuations in the levels of oxygen depletion of bottom waters (B. M. Tomalin, Sea Fisheries, Namibia, pers. comm.). There is relatively little meridional migration of rock lobster, and it seems improbable that fishing would have impacted all fishing zones of the species at the same time. It seems more likely that the resource has responded to some large-scale change in the environment. In the south, the reduced rates of growth were probably caused by a reduced biomass of ribbed mussels. This may have resulted from toxic red-water blooms (see Fig. 17), or storms, or the silting over of reefs from recent flooding of rivers off western South Africa. It is unlikely that the rapid increase in biomass of the exotic Mediterranean black mussel *Mytilus galloprovincialis* during the 1980s (Griffiths *et al.* 1992) had any adverse impact on ribbed mussels or on the feeding of rock lobster. It is possible that changes in production of rock lobster may be associated with changes in primary production in the Benguela system, which would influence production of ribbed mussels. Primary production was low off South Africa's west coast in 1988 and 1989 (Fig. 7).

(ix) Settlement of abalone larvae off South Africa's west coast has been sporadic and probably influenced by interannual changes in advection.

CONCLUDING REMARKS

Populations of epipelagic species, in particular shorter-lived species such as anchovy and chokka squid, appear highly susceptible to environmental influence. Longer-lived demersal and benthic animals are to some extent buffered by the existence of a larger number of age-classes. However, year-classes of these longer-lived species have also varied widely (Fig. 13), and the environment does appear to have influenced their distribution (Macpherson *et al.* 1991). For the long-lived West Coast rock lobster, growth rates of sublegal animals can change by a factor of four (Fig. 19), with a marked impact on recruitment of animals to the fishable population. Even the relatively long-lived seabirds respond almost instantaneously to an altered abundance of prey. Therefore, a broad spectrum of species in the Benguela ecosystem, from plankton to top predators, appears to be influenced by change in the abiotic environment, directly or indirectly.

Many of the changes took place at much the same time. For example, landings of four important linefish species are inversely related to those of anchovy (Fig. 20). Towards the end of the 1980s, there were decreases in the year-class strength of anchovy off South Africa, in growth rates of West Coast rock lobster and in settlement of abalone off South Africa's west coast. There was also change in the zooplankton community off western South Africa. This suggests that environmental change sometimes impacts a wide range of resources.

Although the northern and southern parts of the Benguela system may function as quasi-independent systems much of the time, because of independent intrusions of warm water from the Angolan and Agulhas currents respectively, some change in the 1980s was common to both. For example, the high abundance of anchovy off Namibia in 1987 probably originated in the south. Also, pilchard abundance increased off both South Africa and Namibia in the 1980s and, towards the end of the 1980s, productivity of West Coast rock lobster decreased throughout the Benguela. It appears that some environmental change influences resources over a wide geographic range.

Although both extremities of the Benguela system are bounded by warm water, responses of epipelagic fish species in the north and south to major incursions of warm water are sometimes different. In the north, production of plankton and of eggs of anchovy and pilchard are greatly decreased during Benguela *Niños* on account of warm, nutrient-poor water occupying the entire coastal zone (Boyd *et al.* 1985, 1987). Nevertheless, good year-classes of pilchard may be formed (Crawford *et al.* 1990a). In the south, influx of water from the Agulhas Bank and the Agulhas Current may facilitate formation of good anchovy year-classes. Such intrusions do not appear to impact the abundance of food for small fish off South Africa's west coast because the intrusions do not invade the coastal region over an entire season. However, they may facilitate transport of ichthyoplankton and small fish from spawning to nursery grounds and reduce advective loss of these organisms offshore. An exception would be when the incursion of Agulhas water takes the form of a deep ring adjacent to the shelf and draws water and associated biological material offshore (Duncombe Rae *et al.* 1992). Therefore, whereas Benguela *Niños* may limit both phytoplankton and zooplankton production off Namibia, Agulhas intrusions do not seem to do this on the west coast of South Africa. Different responses to change by resources in different areas clearly make it important to understand the processes through which change is mediated.

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