Are fish stocks food-limited in the southern Benguela pelagic ecosystem?

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ABSTRACT: Estimates of phytoplankton standing stock from satellite ocean colour measurements are in good agreement with ship observations in the southern Benguela Current system. Monthly variation of phytoplankton biomass was within 50 % of the mean value. Available data on phytoplankton primary production in the system are reviewed and indicates, that an average value of $2.8 \text{ g C m}^{-2} \text{ d}^{-1}$ is appropriate for the productively active area of the system, defined from chlorophyll measurements. Consumer zooplankton and pelagic fish biomass are estimated and used with realistic P/B ratios, growth efficiencies and daily ration requirements to calculate upper and lower production and consumption limits. The estimates agree with independent calculations of pelagic fish production. Combined with zooplankton production estimates, these give consumer production/primary production ecological efficiencies of 5 to 18 % (mean 9.5 %). Considerations of food and spatial suitability within the productively active area (match-mismatch in a pulsed upwelling system) indicate that only some 12 % of total primary production is likely to be utilisable by small pelagic shoal fish, and that a production of some 2 million tonnes wet mass of pelagic shoal fish is the maximum that can be supported in the southern Benguela system. Estimates of the carrying capacity of the spawning area during spring and summer indicate that the maximum spawning biomass which could be supported is little more than 500 000 tonnes wet pelagic fish. Consideration of food requirements and availability suggests that spawning and recruitment areas and times are most likely to limit fish production in the southern Benguela area.

INTRODUCTION

The Benguela Current system, which is bounded by the Agulhas Current retroflexion area south of Cape Agulhas (35° S) and in the north near to Cape Frio (18° S) by interaction with the southward moving Angolan Current, is a highly productive upwelling region. Cushing (1969), in a review of the primary productivity of various upwelling regimes, estimated the total carbon fixation in the Benguela Current to be $274 \times 10^6 \text{ tonnes C yr}^{-1}$ compared to 156×10^6 and $30 \times 10^6 \text{ tonnes C yr}^{-1}$ for the Peruvian/Chilean and Californian upwelling systems, respectively. King & Macleod (1976) inferred that the phytoplankton production in Namibian (South West African) waters is probably sufficient to support the combined biomass of the adult pilchard (*Sardinops ocellata*) and anchovy (*Engraulis capensis*) populations, whereas Longhurst (1971) argued that the South African (i.e. Cape) pil-

chard and anchovy are in a dynamic balance so that their combined biomass equals what can be supported by the planktonic food chain.

South African and Namibian pelagic fisheries have traditionally been managed as separate stocks. Stander and le Roux (1968) concluded that although there was limited interchange of individuals between the Cape and Namibian pilchard populations they were reproductively isolated. Egg and larval surveys off the Cape (Crawford 1981a, b, Shelton & Hutchings 1982), and Namibia (King 1977, Le Clus 1983a, b) likewise suggest that the anchovy populations are reproductively isolated, although recent studies of Grant (unpubl.) have shown that 99.2 % of the total genetic variation was contained within the anchovy populations and only 0.4 % of the gene diversity was due to genetic differences between the Cape and Namibian stocks. Pelagic fishing has traditionally been centred around Walvis Bay in the north and the South Western

Cape in the south, and it is likely that the extensive zone of semi-permanent upwelling between about 25° S and 31° S acts as an effective environmental buffer between the two regions. Boyd and Cruickshank (1983) have shown that a major thermal barrier exists for anchovy between about 24° S and 31° S and for pilchard between about 23° S and 33° S in the summer spawning season. Major and semi-permanent upwelling tongues form the low temperature barrier which separates the preferred habitat into 2 'environmental basins' corresponding to the 2 stocks of each species. These stocks may tend to merge by migration of adults and/or transport of larvae when the stock sizes increase and/or the thermal barrier disappears through reduced upwelling.

The total Cape pelagic catch has remained fairly constant for the past 20 yr, fluctuating around 400 000 tonnes. Although pilchards comprised the bulk of the catch prior to 1965, this species currently contributes only about 50 000 tonnes annually, having been replaced largely by anchovy and to a lesser extent by round herring *Etrumeus teres* (Newman & Crawford 1980, Siegfried & Field 1981, Crawford et al. 1983). Virtual population analysis, dynamic pool and stock production models of Cape pelagic species (Armstrong et al. 1983, Butterworth 1983) indicate that both the anchovy and pilchard stocks are at present probably over-exploited, with the total catch of these 2 main stocks of close to 400 000 being beyond the upper limit of the sustainable yield. If this is so, the steady combined catches of all pelagic species together for two decades seem to suggest that the system is remarkably resilient – in fact MacCall (unpubl.) commented that the Cape pelagic fishery was unusual in that one or other of the pilchard and anchovy populations had not been effectively wiped out.

It has been implied by several South African marine scientists (unpubl.) that food is not a limiting factor for adult pelagic fish in the southern Benguela system, i.e. in the Cape system, south of the Orange River (ca. 29° S). As recently as February 1982 in a Symposium on Benguela Systems Analysis (Benguela Ecology Programme Report No. 1) views were expressed that there was an obvious excess of phytoplankton production in the southern Benguela region. Recently however, in a conference paper on the estimation of primary production from satellite ocean colour imagery, Shannon & Henry (1983) suggested that there was some evidence for food being limiting.

In this paper the question as to whether or not food may be a limiting factor in the pelagic ecosystem will be examined on the basis of recent estimates of the phytoplankton standing stock and primary production and taking into account realistic boundaries for the 'active' area of the system.

METHODS

Estimation of phytoplankton standing stock from ship measurements of chlorophyll a. From August 1977 to August 1978 discrete water samples were collected monthly at 0, 5, 10, 20, 30, 40, 50 and 70 m depths at 120 stations situated around the South Western Cape (Fig. 1). These were analysed for chlorophyll *a* using the spectrophotometric technique (UNESCO 1966). Chlorophyll *a* concentrations in the upper 50 m were integrated using a simple algorithm to give estimates of chlorophyll in units of mg m^{-2} of sea surface at each station. The productively active area was demarcated by considering those stations where the median concentration of chlorophyll *a* during 60 % or more of the surveys was greater than 50 mg m^{-2} . (Chlorophyll *a* concentrations of less than 1 mg m^{-3} as determined routinely by the spectrophotometric technique at the Sea Fisheries Research Institute are not considered to be reliable.) The area so defined is illustrated in Fig. 1. The concentration of chlorophyll *a* at each station within the active area was then assumed to be representative of a surface area of ca. 700 km^2 (actual grid areas which took into account the radial nature of the station network were used in the calculations). The 0 to 50 m depth-integrated chlorophyll *a* values in each station grid area were then multiplied by the grid area and the products added to provide an estimate of the total mass of chlorophyll *a*.

Estimates of total organic carbon were made by assuming a carbon:chlorophyll *a* ratio of 60 for the period September through February and 100 for the period March through August. (Andrews & Hutchings 1980, gave values of 70 and 140 respectively for the Cape Peninsula system, whereas Carter 1983, considered values of 65 and 90 to be appropriate.) Dr. L. Hutchings, (pers. comm.) found a considerable range in ratios during recent plankton dynamics cruises, but he considers a value of 60 to be representative during rapid phytoplankton growth which occurs in summer, and 100 to 120 during the quiescent phase.

Estimation of near-surface chlorophyll by satellite imagery. The utility of Nimbus-7 Coastal Zone Colour Scanner (CZCS) satellite ocean colour imagery for estimating near surface concentrations of chlorophyll *a* has been demonstrated by several authors, including Gordon et al. (1980), Clark (1981), Smith & Baker (1982), Shannon et al. (1983) and Walters (1984). Shannon et al. (1983) demonstrated that the accuracy of near surface chlorophyll measurement by CZCS in the Class I type optical waters of the southern Benguela Current system was better than a factor of 2, and they ascribed part of the error to problems associated with discrete shipboard sampling. On the basis of the satellite imagery, these authors suggested that the southern

Fig. 1. Southern Benguela region showing positions of stations occupied monthly during 1977–78, the 3 upwelling zones, and the pilchard and anchovy spawning area. The 'productively active area' (see text for definition) is shaded

Benguela region could be sub-divided into 4 distinct upwelling regimes, viz. southern zone between Cape Point and Cape Agulhas, Cape Peninsula zone, Cape Columbine/St. Helena Bay zone, and Namaqua zone north of 31° 30' S latitude. These sub-divisions are illustrated in Fig. 1.

Relation of surface chlorophyll to phytoplankton standing stock. Surface chlorophyll *a* estimates were related to 0 to 50 m depth-integrated values using separate regressions for each of the 3 upwelling zones and for summer (Nov–Apr) and winter (May–Oct) from a data set of 1400 oceanographic ship stations occupied during 1977–1978 (Table 1). Surface chlorophyll pre-

Table 1. Relation between shipboard surface chlorophyll *a* and 0 to 50 m integrated values in 3 oceanographic areas shown in Fig. 1 (courtesy of S.A. Mostert, Sea Fisheries Research Institute). Linear regressions are of the form $Y = mX + c$, with correlation coefficient (*r*), and number of data pairs (*n*), where $Y = 0$ to 50 m integrated chlorophyll standing stock in mg m^{-2} ; $X =$ surface measurement in mg chl a m^{-3}

Area	Cape Columbine/ St Helena Bay	Cape Peninsula	Cape Point- C. Agulhas
Winter			
m	18.19	21.07	26.32
c	61.63	40.85	35.79
r	0.74	0.79	0.84
n	208	186	153
Summer			
m	21.42	19.39	33.95
c	77.03	62.68	35.35
r	0.72	0.70	0.79
n	157	137	126

dicts 49 to 70 % (r^2 values from Table 1) of the 0 to 50 m depth-integrated chlorophyll in these areas, justifying use of synoptic satellite surface chlorophyll measurements to predict 0 to 50 m phytoplankton standing stocks.

Using contoured surface chlorophyll maps produced by the National Physical Research Laboratory (NPRL) of the SA Council for Scientific and Industrial Research, areas corresponding to 5 chlorophyll *a* concentration ranges (0.1 to 0.3, 0.3 to 1.0, 1 to 3, 3 to 10, > 10 mg m^{-3}) were estimated for the southern, Cape Peninsula, and Cape Columbine/St. Helena Bay zones during different satellite overpass scenes. Mean surface chlorophyll *a* values of 0.2, 0.65, 2.0, 6.5, and 15.0 were assumed to be representative of the respective chlorophyll ranges. The regressions in Table 1 were used to calculate mass of chlorophyll *a* under 1 m^2 of sea for each surface concentration, zone, and season. The total chlorophyll *a* in the upper 50 m of each zone was then calculated by simple multiplication and summation. Organic carbon was estimated as described above.

The productively active area of each zone was taken as that at which the NPRL/CZCS-deduced nearsurface chlorophyll *a* concentration was higher than 0.1 mg m^{-3} in each image. The productively active area of the southern Benguela region on 6 December 1978 is illustrated in Fig. 2. The front is well defined and the similarity between the region of dense chlorophyll in Fig. 2 and the productively active area demarcated in Fig. 1 is evident.

RESULTS AND DISCUSSION

Boundaries of the system

Cushing (1969) assumed the length and width of the southern Benguela Current (Orange River to Cape of Good Hope) to be 700 and 220 km respectively, with a total productive area of 144 000 km^2 . This paper addresses the ecosystem of the main pelagic fish species, so a different, smaller area has been taken to be more appropriate for several reasons. Firstly, the northern boundary of the catch area of the anchovy, pilchard, round herring, mackerel and horse mackerel off South Africa is generally about 31° S (Crawford 1980), a boundary which is consistent with the preferred habitat suggested by the 'environmental basin model' of Boyd and Cruickshank (1983) and the boundary between the Cape Columbine/St. Helena Bay zone and the Namaqua zone, where upwelling is more persistent throughout the year (Shannon et al. 1983). Secondly, the effective southern/eastern boundary of the Benguela system is in the vicinity of Cape Agulhas

Fig. 2. Nimbus-7 CZCS chlorophyll distribution (NASA level-two derived product) on 6 December 1978, illustrating the area of enhanced production extending westwards from Cape Agulhas around the Cape of Good Hope (Cape Point). Approximate chlorophyll concentrations are: west of the well-defined front, $< 0.1 \text{ mg m}^{-3}$; in the frontal zone, 2 to 3 mg m^{-3} ; closer inshore, 3 to 9 mg m^{-3} . Oblique lines are due to missing data

(Harris 1978, Shannon et al. in press) rather than the Cape of Good Hope. Moreover, much of the spawning of the major pelagic fish species, anchovy and pilchard, takes place south and east of the Cape of Good Hope, an area which contributes some 30% of the total

South African pelagic catch (Crawford 1979). The overall extent of the spawning area is about $30\,000 \text{ km}^2$ and encompasses a region of water of optimal temperature for egg survival (16 to 19°C , King et al. 1978) but, as will be seen, lower than average phytoplankton biomass and production.

Table 2 indicates the active areas of the three zones on different satellite overpass scenes which have been analysed on the basis of minimum near-surface chlorophyll concentrations. Estimated total chlorophyll *a* and carbon standing stocks are also given for each zone, with mean values of 11.7 and 7.3 g C m^{-2} for the St. Helena Bay/Cape Columbine and Cape Peninsula zones, respectively.

Table 3 shows results of an extensive data set of more than 1400 ship stations around the South Western Cape at which chlorophyll *a* concentrations were measured at different times of year. Total chlorophyll *a* and carbon standing stocks are estimated for each zone, and mean year-round values calculated showing highest phytoplankton standing stocks in the St. Helena Bay zone, and comparable values off the Cape Peninsula and in the southern zone.

From both satellite and shipboard estimates, the bulk of the phytoplankton biomass appears to be confined to a relatively narrow coastal band, typically less than 70 km wide between Cape Agulhas and Cape Columbine and about 110 km wide between Cape Columbine and the Olifants River. North of 31°S , the productively active zone widens progressively to about 220 km near the Orange River (Shannon et al. 1984). There is good agreement between the estimates of Tables 2 and 3, particularly for the Cape Columbine/St. Helena Bay and Cape Peninsula zones. The combined areas of the 3 zones is of the order of $40\,000 \text{ km}^2$, a number which will be used in subsequent calculations.

Table 2. Phytoplankton standing stock in the upper 50 m in 3 zones of the southern Benguela Current region, estimated from Nimbus-7 CZCS imagery, 1978/79

Zone	Date	Active area ($\text{km}^2 \times 100$)	Chlorophyll <i>a</i> (tonnes)	Organic carbon (tonnes $\times 10^3$)	Organic carbon per unit area (gC m^{-2})	Mean per area (gC m^{-2})
Cape Columbine/ St Helena Bay	19 Feb 1979	185	2635	158	8.5	11.7
	6 Apr 1979	146	2835	283	19.3	
	9 May 1979	215	1791	179	8.3	
	22 Aug 1979	113	1200	120	10.6	
Cape Peninsula	19 Feb 1979	102	1321	79	7.7	7.3
	6 Apr 1979	39	441	44	11.3	
	9 May 1979	169	856	86	5.1	
	22 Aug 1979	71	366	37	5.2	
Southern	24 Nov 1978	46	759	46	10.0	—
	6 Feb 1979	83	2848	171	20.6	

Table 3. Phytoplankton standing stock in the upper 50 m in 3 zones of the southern Benguela Current region, calculated from ship measurements of chlorophyll *a* during 1977 and 1978

Month, year	Cape Columbine/St Helena Bay (active area = 17,200 km ²)		Cape Peninsula (active area = 11,800 km ²)		Southern (active area = 9,800 km ²)	
	Chl <i>a</i> (tonnes)	Org. carbon (tonnes × 10 ³)	Chl <i>a</i> (tonnes)	Org. carbon (tonnes × 10 ³)	Chl <i>a</i> (tonnes)	Org. carbon (tonnes × 10 ³)
Aug, 1977	1439	144	544	54	584	58
Sep, 1977	2917	175	1581	45	709	43
Oct, 1977	4502	270	1880	113	983	59
Nov/Dec, 1977	3594	216	1248	75	1188	71
Jan, 1978	3675	220	3298	198	2376	143
Feb, 1978	2495	150	1465	88	1245	78
Mar, 1978	2621	262	984	98	1375	137
Apr, 1978	2792	279	1432	143	1229	123
May, 1978	4637	464	942	94	1416	142
Jun, 1978	2410	241	756	76	1077	108
Aug, 1978	2492	249	1022	102	886	89
Mean per unit area (g m ⁻²)	0.177	14.1	0.117	8.6	0.122	9.7

Phytoplankton standing stock

The phytoplankton standing stock expressed in tonnes of carbon and tonnes of chlorophyll *a* in the upper 50 m in each of the zones estimated from CZCS imagery and ship data has been given in Tables 2 and 3 respectively. Good agreement between the 2 techniques is an indication that satellite ocean colour imagery holds considerable potential for the study of upwelling systems, particularly for monitoring changes. The results indicate that the phytoplankton standing stock in the system is relatively constant, ranging from a minimum of 256 000 tonnes C during August 1977 to 700 000 tonnes C during May 1978, with a mean value of 437 000 tonnes C (± 135 SD). Expressed per unit area, the mean standing stock was highest in the Cape Columbine/St. Helena Bay zone (14 g C m⁻²) and slightly less (9 to 10 g C m⁻²) in the Cape Peninsula and southern zones. These values should be compared with the measurements of Brown (1983 a) during four studies of plankton dynamics in the southern Benguela region (9 to 15 g C m⁻²) and the mean value given by Andrews and Hutchings (1980) of 11.2 g C m⁻² along their upwelling monitoring line off the Cape Peninsula.

Phytoplankton primary production

The available data on phytoplankton primary production per unit area in the euphotic zone in the southern Benguela Current region are summarised in Table 4. Some comments on these values are necessary. Firstly, most of the observations were made dur-

ing the main upwelling season between September and April, and relatively few data points are available for winter. Secondly, many of the observations were made close inshore either in bays (Mostert pers. comm., Henry et al. 1977, Henry 1979), in a kelp bed (Carter 1983), or at the base of an upwelling plume (Brown 1980). Thirdly, the results of Brown (1983a) were from cruises which were located and timed specifically to study the dynamics of plankton, viz. seeding, blooming, grazing and decay in the Cape Peninsula subsystem. In view of the foregoing, many of the results may be atypical of the whole system. Brown's (1983a) results are nevertheless probably the most appropriate for the system during periods of active upwelling and growth, and represent an impressive data set. Her values of phytoplankton net primary production have been adjusted by -10 % to allow nighttime respiration and the unknown degree of over-estimation inherent in ¹⁴C-uptake experiments. The mean production to standing stock ratio is about 0.25 d⁻¹ (Brown 1983a), indicating a turnover time of some 4 d.

From the phytoplankton standing stock estimates in Table 3, and assuming a turnover rate (P/B) of 0.25 d⁻¹, the primary production in the active zones of the system can be estimated (Table 5). From this table and the published data it seems probable that the mean primary production of the active area of the subsystems ranges from about 1.5 g C m⁻² d⁻¹ for the Cape Peninsula zone during winter, to close to 4 g C m⁻² d⁻¹ during summer in the Cape Columbine/St. Helena Bay zone. Our best estimate of the annual average production of the southern Benguela system is therefore 2.8 g C m⁻² d⁻¹, which is equivalent to 110 × 10³ tonnes C

Table 4. Summary of available data on phytoplankton primary production in the southern Benguela region (standard deviations in brackets)

Area	Season	Technique used	Number of observations	Primary production		Source
				Range of values (gC m ⁻² d ⁻¹)	Mean (gC m ⁻² d ⁻¹)	
Cape west coast	Summer	C ¹⁴	4	0.7–3.6*	2.2 (± 1.2)*	Steeman Nielsen & Jensen (1957)
Saldanha Bay	Year	O ₂ /P:B	10	0.9–3.3	1.7 (± 0.6)	Henry et al. (1977)
Oudekraal/Table Bay/	Winter	C ¹⁴	9	0.3–2.4	0.8 (± 0.7)	Henry (1979)
St Helena Bay	Spring/Summer	C ¹⁴	17	0.5–11	5.1 (± 2.6)	
Oudekraal	Spring-autumn	O ₂	35		2.4 (± 2.4)	Brown (1980)
	Winter	O ₂	10		1.9 (± 1.4)	
Table Bay (Robben Is.)	Spring-autumn	O ₂	13		4.0 (± 2.8)	
Southern Agulhas Bank	Summer	C ¹⁴	2		0.1	Allanson et al. (1981)
Southern zone, offshore	Summer	C ¹⁴	1		0.2	
Oudekraal (inshore, 20 m depth)	Year	O ₂	29	0.6–4.2 ⁺	2.6 (± 1.76) ⁺	Carter (1982, 83)
Cape Peninsula system	Spring	C ¹⁴	12	1.3–10.8 ⁺	4.0 (± 2.4) ⁺	Brown (1983a)
Cape Peninsula to Cape Columbine	Late summer	C ¹⁴	25	1.1–5.4 ⁺	2.9 (± 1.4) ⁺	
	Summer	C ¹⁴	12	1.6–11.7 ⁺	3.5 (± 2.8) ⁺	
Agulhas Bank Spawning Area	Late spring	C ¹⁴	5	.31–2.5 ⁺	1.07 (± 0.9) ⁺	Brown (1983b)
Cape Columbine/St Helena Bay	Summer	C ¹⁴ /CZCS	N/A	2–4	approx 4	Shannon & Henry (1983)
Cape Peninsula system	Summer	C ¹⁴ /CZCS	N/A	2–4	approx 3	
Southern zone	Summer	C ¹⁴ /CZCS	N/A	2–4	approx 2–4	
Saldanha Bay	Winter	O ₂	1		1.9	Mostert (pers. comm.)
	Spring/Summer	O ₂	4	3.6–10	6.3 (± 2.8)	

* Results corrected in accordance with Steeman Nielsen (1964)

⁺ Results adjusted for night respiration (see text)

d⁻¹ or 40 × 10⁶ tonnes C yr⁻¹. This is considerably less than the productivity of the whole Benguela area, estimated by Cushing (1969) to be 274 × 10⁶ tonnes C yr⁻¹, but ours is confined to the southern part of the system and is based on the productively active area in which most of the small pelagic shoal fish occur.

Table 5. Estimates of phytoplankton primary production from standing stock, assuming a constant P:B ratio of 0.25 d⁻¹

Zone	Primary production (g C m ⁻² d ⁻¹)		
	Winter (Jun–Aug)	Rest of year (Sep–May)	Year
Cape Columbine/ St Helena Bay	3.1	3.7	3.5
Cape Peninsula	1.6	2.4	2.2
Southern	2.2	2.5	2.4
Total 'active' system	2.4	3.0	2.8

Standing stock, production, and consumption of zooplankton

According to Andrews and Hutchings (1980) the zooplankton standing stock (obtained with 200 µm mesh nets) in the Cape Peninsula zone varies between average summer values of about 3.5 g dry material m⁻² and average winter values of about 1.5 g dry material m⁻² (corresponding to 1.5 and 0.6 g C m⁻²). More recent estimates by Olivieri & Hutchings (1983) (using 200 µm mesh nets) gave the zooplankton biomass in the range 24 to 81 g wet weight m⁻², which corresponds to about 1 to 4 g C m⁻² if the wet weight: carbon ratio is taken to be 17; this can be compared with a value of 3.6 g C m⁻² given for the region by Cushing (1969). Andrews & Hutchings (1980) found that the zooplankton, expressed as carbon, averaged 12 % of the phytoplankton standing stock, whereas a compari-

son of the data of Brown (1983a) and Olivieri & Hutchings (1983) suggests a higher ratio, closer to 20 %. Estimates of biomass are summarised in Table 6, the mean of the upper and lower zooplankton biomass estimates being 74 000 metric tonnes in the active upwelling area.

Zooplankton production can be estimated from mean turnover times (B/P ratios). Zooplankton in the southern Benguela region have been estimated to have a generation time of 15 to 35 d (Hutchings, 1979). However, this estimate does not take into account the fast turnover of nauplius and other juvenile stages and, in the Peruvian upwelling system, B/P ratios of about 5 to 10 d have been estimated from energy budget measurements (Shushkina et al. 1978, Sorokin & Mikheev 1979). Similar turnover times are given by Conover (1974). Since these studies accounted for all zooplankton components, a mean turnover time of 7.5 d has been adopted, comparing closely with the mean B/P of

7.13 for micro- and meso-zooplankton at 8 stations in the Peruvian upwelling system (Sorokin & Mikheev 1979). This gives an estimated annual zooplankton production of 3.6×10^6 tonnes carbon or 9 % of primary production.

Zooplankton food requirements have been calculated from estimates of growth efficiency. Gross growth efficiency, K_1 (production/consumption) in copepods, is usually in the range 28 to 50 % (Corner & Davies 1971, Conover 1978, Mann 1982). These values have been used in Table 6 to estimate zooplankton food requirements, with a mean requirement of 9×10^6 tonnes yr^{-1} , suggesting that on average, zooplankton graze about 20 % of the phytoplankton production. This should be compared with experimental measurements of 31 to 76 % (mean 46 %) of daily phytoplankton production being grazed in plumes of upwelled water (Olivieri & Hutchings 1983). Viewed another way, the zooplankton carbon requirements amount to

Table 6. Estimates of production and consumption of major components in the southern Benguela system. All values expressed in thousands of metric tonnes of carbon for active upwelling area of 40,000 km². For plankton components, the wet mass : carbon ratio is taken to be 17 : 1 (Cushing 1969, Platt & Irwin 1973), while fish wet mass : carbon ratio is taken to be 8 : 1 (see text). Other assumptions on which calculations are based are given in brackets; estimated phytoplankton consumption by fish based on the assumption that their diet is 67 % phytoplankton. Phytoplankton biomass (B_p) and turnover rates (B/P ratios) are given

PRODUCERS	Mean biomass	Annual production	Annual consumption	Annual phytoplankton consumption
Phytoplankton (from Table 3)				
low (9 gC m ⁻²)	350	25,000 (P/B = .2 d ⁻¹)	—	—
high (14 gC m ⁻²)	560	62,000 (P/B = .3 d ⁻¹)	—	—
mean (B_p)	450	40,000 (P/B = .25 d ⁻¹)	—	—
CONSUMERS				
Zooplankton				
low	55 (12 % of B_p)	2,000 (B/P = 10 d)	4,000 ($K_1 = 0.5$)	4,000
high	92 (20 % of B_p)	6,700 (B/P = 5 d)	22,400 ($K_1 = 0.3$)	22,400
mean	74 (16 % of B_p)	3,600 (B/P = 7.5 d)	9,000 ($K_1 = 0.4$)	9,000
Surface shoal fish				
low	75	75 (B/P = 1 yr)	770 (6 % of body wt d ⁻¹)	520
high	325	650 (B/P = 0.5 yr)	6,700 (12 % of body wt d ⁻¹)	4,500
Level A (pilchard predominant)	225	225 (B/P = 1 yr)	2,700 (7 % of body wt d ⁻¹)	1,800
Level B (anchovy predominant)	100	200 (B/P = 0.5 yr)	1,700 (10 % of body wt d ⁻¹)	1,150
Food requirement in active area for pilchard-dominated system: 9,000 + 2,700 = 11,700 tonnes carbon (or 28 % of primary production)				
Upper food requirement in active area: 22,400 + 6,700 = 29,100 tonnes carbon (or 69 % of primary production)				

19 to 66 % of zooplankton carbon standing stock per day, with a mean of 33 % per day.

Standing stock, production, and consumption of pelagic fish

Fig. 3 gives Virtual Population Analysis (VPA) estimates of pelagic fish biomass in the southern Benguela region since the fishery began in 1950 (based on data in Crawford et al. 1983). The estimates prior to 1964, when small-mesh nets were introduced to catch anchovy, are based on the assumed contribution of 300 000 tonnes (wet) of anchovy and round herring. Guano records confirm the trend (Crawford & Shelton 1978), except that the biomass trough and peak of the mid- and late-1950's are not as marked. Recent work

suggests that the trough and peak may be artefacts of the VPA (Bergh pers. comm.), although egg surveys contradict this (Crawford et al. 1983). It is apparent that the biomass of pelagic fish supported before the steep increase in pilchard catches and subsequent introduction of small-meshed nets, was about 1.8×10^6 tonnes (wet) (Level A), and that this fell to about 0.8×10^6 tonnes (Level B) when anchovy became the dominant stock. The highest guano yield since records were first kept in the 1890's was nearly twice the 1960 yield (Crawford & Shelton 1978), suggesting the approximate magnitude of the largest biomass of pelagic fish before exploitation, and placing our upper estimate in perspective.

The estimates given in Table 6 are based on the data of Fig. 3, taking a wet fish: carbon ratio of 8, based on a wet: dry mass ratio for pilchard, anchovy and round herring of 3.7 (Shannon 1972, also Schneider & Hunt 1982), and a mean dry mass: carbon ratio of 2.2 (Vinogradov 1953, Schneider & Hunt 1982). This compares with the value of 10 used by Gulland (1970). The turnover time (B/P ratio) of fish is likely to vary with the age structure of the fish populations, a heavily fished young population having a shorter turnover time than one consisting mainly of older fish. Pilchard, having a maximum lifespan of some 9 yr, are likely to have an annual B/P ratio of about 1 yr when heavily fished, whereas for short-lived anchovy populations the ratio is .3 to .5 (D. Butterworth pers. comm.). Application of these turnover times gives the production estimates in Table 6, showing similar values for Level A, dominated by pilchard and Level B, dominated by anchovy, in spite of the different biomass levels. These production estimates are consistent with estimates of natural predation on anchovies and pilchards and the catch records (D. Duffy and M. Bergh pers. comm.). On the other hand, the upper and lower limits of production are extreme since B/P ratios are likely to compensate, and not magnify, changes in population biomass.

The ecological efficiency (secondary production/mean primary production) calculated from Table 6 has a mean value of 9.5 %, with lower and upper values of 5 and 18 %, respectively. As elsewhere in this paper, we make the simplifying assumption that all macro-zooplankton are secondary producers, and have combined all fish and macro-zooplankton production to calculate secondary production. The ecological efficiency is considerably lower than that assumed for upwelling systems by Ryther (1969) and others (e.g. Steele 1974).

Fish consumption rates are normally in the range 6 to 12 % of body weight d^{-1} , and even higher for active predatory fish (Conover 1978). Using these values, the biomass estimates have been multiplied to give lower and upper annual fish consumption estimates, with

Fig. 3. Landings of pilchard *Sardinops ocellata* and anchovy *Engraulis capensis* in South Africa, with virtual population analysis (VPA) estimates of the combined biomass of pilchard, anchovy, horse mackerel *Trachurus trachurus*, mackerel *Scomber japonicus*, and round-herring *Etrumeus teres* since the fishery commenced in 1950 (dashed line). An assumed biomass of 300 000 tonnes for anchovy and round-herring has been added to the VPA total for the other species before 1964 when no catches of those 2 species were made. Guano production is also shown. Levels A and B respectively indicate the best estimates of total pelagic fish biomass before and since 1964, when small-mesh nets were introduced; carbon equivalents of the biomass are also given. (Data from Crawford et al. 1983)

best estimates based on a requirement of 7 % of pilchard and 10 % of anchovy body weight per day (Hatanaka & Takahashi 1960, Sirotenko & Danilevski 1977, Mikhman & Tomanovich 1977, Brownell pers. comm.).

Total consumption estimates for pelagic shoal fish (Table 6) indicate that fish consume 20 to 30 % as much carbon as the zooplankton. Level A (pilchard-dominated system) and Level B (anchovy-dominated) require some 7 and 4 % of primary production respectively, with lower and upper limits of 2 and 17 % primary production. These values should be compared with an estimate by Smith & Eppley (1982) which indicated that the ration for anchovies off California was 18 % of the primary production during 1966.

Relatively little research has been undertaken on the diet of pelagic fish in South African waters. However, the early work of Davies (1957) on the feeding of adult pilchards indicated that the fish are omnivorous, taking phytoplankton and zooplankton in the ratio of about 2:1. Robinson's (1966) preliminary work on the South African anchovy showed a similar preponderance of phytoplankton in the diet. The most comprehensive study on the feeding of pilchard and anchovy was the work done by King & Macleod (1976) in South West Africa. Their findings were that phytoplankton contributed more to the diet of adults of both species, forming 77 and 70 % respectively of the food of anchovies longer than 8 cm and pilchards longer than 10 cm. However, juveniles feed largely on zooplankton. From this it appears that a diet of 2/3 phytoplankton would be realistic (although a young population would take a greater proportion of zooplankton), and phytoplankton requirements are indicated on this basis in Table 6.

Taking the carbon requirements of pelagic fish (Level A) to be about 3 million tonnes annually, it appears that some 2 million tonnes of phytoplankton carbon is consumed (or 6 % of residual primary production after feeding the zooplankton). On the other hand, about 1 million tonnes of zooplankton carbon or 28 % of zooplankton production is estimated to be required by fish. Thus it appears that fish growth is more likely to be limited by zooplankton production than by phytoplankton production.

Using the highest estimates of carbon consumption requirements of zooplankton and fish, 66 % of phytoplankton production would be utilized, with a best estimate of some 27 %, leaving a balance of 44 to 73 % of phytoplankton production unaccounted for. There are obvious simplifications and omissions from this balance sheet, the most obvious being the exclusion of bacterial and microzooplankton components which are clearly important in an area of high primary production (Azam et al. 1983, Linley et al. 1983). Another omission

is the ultimate dependence of midwater fish (such as myctophids and horse mackerel, *Trachurus* sp. and important demersal hake, *Merluccius* spp.) stocks which both tend to occur on the outer shelf and slope (Botha 1971), on the primary production which we have shown to be greatest on the inner and mid-shelf. The area of enhanced fish production extends beyond the productively active area defined from chlorophyll data here, presumably through the transport of detritus onto the outer shelf, much as described for the Peruvian system by Walsh (1983), to feed zooplankton, midwater fish, and demersal fish there. This corresponds to the findings of Mills & Fournier (1979) in that pelagic fish are most productive in the area of highest primary productivity, and demersal fish dominate in less productive areas. It differs in that the upwelling situations both in Peru (Walsh 1983) and the Benguela system (this paper) have enhanced primary production and pelagic fish production on the shelf, with demersal fish dominating on the slope. On the other hand, the Scotian shelf is dominated by demersal fish, with increased primary and pelagic fish production at a front over the slope (Mills & Fournier 1979).

Spawning area

The spawning area extends considerably beyond the productively active area, and is characterised by a smaller standing stock of phytoplankton, which is largely subsurface away from the shore (P. Brown and L. Hutchings, pers. comm.), making satellite-based chlorophyll estimates unreliable. Only 5 production measurements are available (Table 4), so the mean estimate of $1 \text{ g C m}^{-2} \text{ d}^{-1}$ must be regarded as very provisional. For the spawning area of about $30\,000 \text{ km}^2$, it suggests total primary production of the order of 5.4×10^6 tonnes carbon for the 6 mo spawning season and area. An upper estimate based on integrated chlorophyll measurements, and assuming a turnover time of 4 d, gives a daily production rate of $1.5 \text{ g C m}^{-2} \text{ d}^{-1}$ and a seasonal estimate of some 8×10^6 tonnes carbon.

Table 7 gives the estimated consumption requirements of zooplankton and pelagic fish in the spawning area and season calculated in the same way as for Table 6. The mean zooplankton requirement is some 35 % of primary production. Estimates of the biomass of spawning fish are taken from Armstrong et al. (1983) and Butterworth (1983 and pers. comm.), with consumption estimates based on slightly higher than average estimates of daily ration requirements during the protracted serial spawning period. The respective Level A (pilchard-dominated) and Level B (anchovy-dominated) consumption estimates amount to some 24

Table 7. Estimates of consumption of major components in the southern Benguela spawning area. All values are expressed in thousands of metric tonnes of carbon for the spawning area of 30,000 km² and a 180-d spawning season. For the plankton components, the wet mass : carbon ratio is taken to be 17:1 (Cushing 1969, Platt & Irwin 1973), while fish wet mass : carbon ratio is taken to be 8:1 (see text). Other assumptions on which calculations are based are given in brackets

	Mean biomass	Season's consumption	% of primary production
CONSUMERS			
Zooplankton			
low	–	900	16
high	–	2,900	53
mean	–	1,900	35
Spawning shoal fish			
low	26	180 (8 % d ⁻¹)	3
high	177	1,800 (12 % d ⁻¹)	33
Level A (pilchard predominant)	150	1,270 (10 % d ⁻¹)	24
Level B (anchovy predominant)	70	710 (12 % d ⁻¹)	13
Low food requirement in spawning area: 900 + 180 = 1,080 × 10 ³ tonnes carbon (or 20 % of primary production)			
Upper food requirement in spawning area: 2,900 + 1,800 = 4,700 × 10 ³ tonnes carbon (or 87 % of primary production)			

to 13 % of primary production, or about 36 and 20 % of primary production after subtracting the mean zooplankton requirement. These are much larger proportions of primary production than calculated for the whole productively active area, suggesting that food in the spawning area may be limiting.

It is likely that the spawning area under present circumstances (anchovy-dominated, Level B) has been overestimated (Fig. 1 and Crawford et al. 1980), whereas prior to 1963 when pilchard were dominant (Level A) spawning extended northwards along the Cape west coast and the area has probably been underestimated. If the spawning areas have been over and underestimated respectively by 1/3, then in both cases spawning shoal fish consume some 17 to 18 % of primary production, suggesting a possible limitation by primary production at that level.

Is food limiting for pelagic fish?

Approaching the problem another way, what are the critical factors likely to be? Firstly, the distribution of fish and plankton patches is such that only a small

area, say 25 %, is available and suitable to fish at any time. For example, the whole Cape Peninsula area, nearly one third of the southern Benguela system and through which fish migrate rapidly on their way to the southern spawning grounds, has erratic, pulsed upwelling and patchy plankton. Secondly, only a fraction of the production is likely to be of suitable quality and size for fish feeding, say 50 %. Taking these factors into account suggests that the pelagic fish are only able to utilize 25 × 50 % = 12.5 % of primary production, and that if their requirements exceed this, food may limit fish growth.

Assuming the estimates of Table 6, and Case A (predominantly pilchard system), a standing stock of 250 thousand tonnes (carbon) of fish is likely to require some 3 million tonnes of food carbon annually. The food available would be 40 million tonnes of primary production less 22 million tonnes consumed by zooplankton plus 6.7 million tonnes of zooplankton production, a total of some 25 million tonnes of carbon. Thus the average requirements over a year would be 12 % of the available food supply. This may explain why the pelagic fish biomass has an evident upper limit of around 1.8 million tonnes (225 000 tonnes carbon). Recent studies by Crawford et al. (1980) have shown that there is an indication of density dependence in the southern Benguela system, the length at sexual maturity of pilchards having decreased with the stock decline in the 1960's, suggesting that pilchards were limited by food supply prior to the decline. According to these calculations, therefore, a predominantly pilchard fish standing stock would have been limited by its food supply in the southern Benguela region.

Shelton & Armstrong (1983) have also presented evidence of density-dependence in the anchovy population, the length at sexual maturity of anchovies having increased with their apparent biomass increase in the early 1970's, suggesting that anchovy too are limited by resources at peak biomass levels. Thus although the biomass supported at Level A appears to have been twice that at Level B, the productivity was about the same (Table 6). Under Level B circumstances the proportion of zooplankton in fish diets may be considerably larger than when the system is dominated by older pilchards, for Bergh (1983) points out that the present heavily exploited pelagic stocks consist mainly of young fish under 10 cm in length, which have very limited capacity for filtering phytoplankton (King & Macleod 1976), and whose diet is largely zooplankton. The dependence on zooplankton, effectively increasing the length of the food chain, may not necessarily result in less efficient fish production (Kerr & Martin 1970). This is consistent with the roughly equal productivity of Levels A and B (Table 6).

Furthermore, the annual peak in fish biomass occurs when young fish recruit to the fishery and biomass is then some 50 % above the annual mean (Butterworth 1983). At this time the recruits are growing rapidly and likely to need some 12 % of body weight in zooplankton food per day (King & Macleod 1976, Brownell pers. comm.). Thus at the recruitment stage, which is limited to the St. Helena Bay/Columbine zone (or some 44 % of the total productively active area), pelagic fish require large amounts of food in the form of zooplankton, which may then be limiting.

CONCLUSION

For a substantially larger pelagic fish biomass to be supported by the system it would require either a larger system area, wider distribution over the area under consideration, or more efficient feeding on the food supply. The total geographic range of both anchovies and pilchards is known to be considerably greater than the bounds of the system considered in this paper – for example the Natal 'sardine run' (Heydorn 1978) and the work of Batchelor (1982) on the feeding of gannets on anchovies in Algoa Bay. What is not known, however, is what the contribution of these areas is to the pelagic fish biomass and production. Another factor which should be considered is that low but significant phytoplankton production does take place seawards of the 'productively active' area, e.g. the estimate of $0.2 \text{ g C m}^{-2} \text{ d}^{-1}$ in the offshore region during summer by Allanson et al. (1981) (Table 4).

The fact that the system has yielded about 400 000 tonnes of pelagic fish consistently each year for the past 2 decades does seem to imply considerable resilience or buffering against environmental perturbations. In this respect it is tempting to speculate that this may be due to the fact that during upwelling favourable years when the phytoplankton and zooplankton production is probably maximal, the reduced temperatures may *decrease* the size of the preferred fish habitat and conversely during periods of reduced upwelling the favourable habitat may *increase* in area – the latter may result in, for example, the region between the Olifants and Orange Rivers (immediately north of the active area under consideration) becoming a favourable area for anchovy and pilchard.

If food in the systems is limiting then this might suggest that the decrease in pilchard biomass during the 1960s was in part precipitated by the period of reduced upwelling in 1964–1969 (Nelson & Hutchings 1983). In South West Africa an analogous example was documented by Stander & De Decker (1969), who found that reduced food availability and higher temperatures resulted in a reduction of spawning, catch and

oil yield of pilchards during an environmental anomaly in 1963. An expected result of food scarcity would be for larger shoals to break up into smaller shoals increase foraging efficiency – a common belief of local fishermen (W. van Essen pers. comm.), but this may well be at the expense of increased predation. In this respect it is worth noting that Wilson (1983) has observed that penguins feed successfully when no large shoals of fish are present in the area.

The results of this study suggest that the productively active, preferred habitat of the southern Benguela Current system can support probably no more than a total production of 2 million tonnes wet pelagic fish per annum during average environmental conditions. Likewise, it appears likely that a biomass of 2 million tonnes of pelagic fish is near to the maximum carrying capacity of the system. When the system changed from one dominated by pilchards to one dominated by anchovies, the fish biomass was halved but the production remained similar. Indications are that the spawning and recruitment times and areas may be crucial, particularly since the juvenile fish feed on zooplankton and form a large annual biomass peak. Longhurst (1971) stated that '... in some way the populations of the two (i.e. pilchards and anchovies) are in a dynamic balance so that their combined biomass equals what can be supported by the planktonic food chain'. The present study supports his statement if one substitutes 'production' for 'biomass'.

Acknowledgements. We thank R. Crawford for criticizing the manuscript, our colleagues D. Butterworth, L. Hutchings, P. Brown, C. Brownell, M. Bergh, P. Shelton and D. Duffy, for valuable discussions, and D. Gianakouras and S. Tolosana for help in preparing the manuscript. The work was undertaken as part of the Benguela Ecology Programme and was given financial support by the SA National Committee for Oceanographic Research.

LITERATURE CITED

- Allanson, B. R., Hart, R. C., Lutjeharms, J. R. E. (1981). Observations on the nutrients, chlorophyll and primary production of the Southern Ocean south of Africa. *S. Afr. J. Antarct. Res.* 10: 3–14
- Andrews, W. R. H., Hutchings, L. (1980). Upwelling in the southern Benguela Current. *Prog. Oceanogr.* 9: 1–81
- Armstrong, M. J., Shelton, P. A., Prosch, R. M., Grant, W. S. (1983). Stock assessment and population dynamics of anchovy and pilchard in ICSEAF Division 1.6 in 1982. *Colln scient. Pap. int. Commn S. E. Atl. Fish.* 10: 7–25
- Azam, F., Fenchel, T., Field, J. G., Gray, J. S., Meyer-Reil, L. A., Thingstad, F. (1983). The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* 10: 257–263
- Batchelor, A. L. (1982). The diet of Cape gannets, *Sula capensis*, breeding on Bird Island, Algoa Bay. M. Sc. thesis, University of Port Elizabeth, South Africa
- Bergh, M. O. (1983). Modelling in the Benguela ecosystem with emphasis on pilchard and anchovy biomass esti-

- mates. M. Sc. thesis, University of Cape Town, South Africa
- Botha, L. (1971). Growth and otolith morphology of the Cape hakes *Merluccius capensis* Cast. and *M. paradoxus* Franca. Investl Rep. Div. Sea Fish. S. Afr. 97: 1–32
- Boyd, A. J., Cruickshack, R. A. (1983). An environmental basin model for west coast pelagic fish distribution. S. Afr. J. Sci. 79: 150–151
- Brown, P. C. (1980). Phytoplankton production studies in the coastal waters off the Cape Peninsula, South Africa. M. Sc. thesis, University of Cape Town, South Africa
- Brown, P. C. (1983a). Phytoplankton development in newly upwelling water. Proceedings 5th National Oceanographic Symposium, Grahamstown, S. Afr., 24–28 January 1983. Abstract in S. Afr. J. Sci. 79: 144
- Brown, P. C. (1983b). First look at phytoplankton production on the Agulhas Bank. 1st Ann. Congr. Phycol. Soc. southern Africa, Johannesburg, Jan. 1983. Abstract in S. Afr. J. Sci. 79: 382
- Butterworth, D. S. (1983). Assessment and management of pelagic stocks in the southern Benguela region. In: Sharp, G. D., Csirke, J. (ed.) Proceedings of FAO-IOC Expert consultation to examine changes in abundance and species composition of neritic fish stocks. San Jose, Costa Rica, 18–29 April 1983. FAO Fish. Rep. 291: 329–405
- Carter, R. A. (1982). Phytoplankton biomass and production in a southern Benguela kelp bed system. Mar. Ecol. Prog. Ser. 8: 9–14
- Carter, R. A. (1983). The role of phytoplankton and micronekton in carbon flow through a southern Benguela kelp bed. Ph. D. thesis. University Cape of Town, South Africa
- Clark, D. K. (1981). Phytoplankton pigment algorithms for the Nimbus-7 CZCS. In: Gower, J. F. R. (ed.) Oceanography from space. Plenum Press, New York, p. 227–237
- Conover, R. J. (1974). Production in marine plankton communities. Proc. 1st Internatnl Congr. Ecol. Centre for Agric. Publish. Documentn, Wageningen, Netherlands, p. 159–163
- Conover, R. J. (1978). Feeding interactions in the pelagic zone. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173: 66–76
- Corner, E. D. S., Davies, A. G. (1971). Plankton as a factor in the nitrogen and phosphorus cycles in the sea. Adv. mar. Biol. 9: 101–204
- Crawford, R. J. M. (1979). Implications of recruitment, distribution and availability of stocks for management of South Africa's western Cape purse-seine fishery. Ph. D. thesis, University of Cape Town, South Africa
- Crawford, R. J. M. (1980). Seasonal patterns in South Africa's Western Cape purse-seine fishery. J. Fish Biol. 16: 649–664
- Crawford, R. J. M. (1981a). Distribution, availability and movements of pilchard *Sardinops ocellata* off South Africa, 1964–1976. Fish. Bull. S. Afr. 14: 1–46
- Crawford, R. J. M. (1981b). Distribution, availability and movements of anchovy *Engraulis capensis* off South Africa, 1964–1970. Fish. Bull. S. Afr. 14: 51–94
- Crawford, R. J. M., Shelton, P. A. (1978). Pelagic fish and seabird interrelationships off the coast of South West and South Africa. Biol. Conserv. 14: 85–109
- Crawford, R. J. M., Shelton, P. A., Hutchings, L. (1980). Implications of availability, distribution and movements of pilchard (*Sardinops ocellata*) and anchovy (*Engraulis capensis*) for assessment and management of the South African purse-seine fishery. Rapp. P.-v. Réun. Cons. int. Explor. Mer 177: 355–373
- Crawford, R. J. M., Shelton, P. A., Hutchings, L. (1983). Aspects of the variability of some neritic stocks in the southern Benguela system. In: Sharp, G. D., Csirke, J. (ed.) Proceedings of FAO-IOC Expert consultation to examine changes in abundance and species composition of neritic fish stocks. San Jose, Costa Rica, 18–29 April 1983. FAO Fish. Rep. 291: 407–448
- Cushing, D. H. (1969). Upwelling and fish production. FAO Fisheries Technical Paper No 84: 1–40
- Davies, D. H. (1957). The South African pilchard (*Sardinops ocellata*); preliminary report on feeding off the west coast, 1953–1956. Investl Rep. Div. Fish. 30: 1–40
- Gordon, H. R., Clark, D. K., Mueller, J. L., Hovis, W. A. (1980). Phytoplankton pigments from the Nimbus-7 coastal zone color scanner. Science 210: 63–66
- Gulland, J. A. (1970). Food chain studies and some problems in world fisheries. In: Steele, J. H. (ed.) Marine food chains. Oliver and Boyd, Edinburgh
- Harris, T. F. W. (1978). Review of coastal currents in southern African waters. S. Afr. National Scientific Programmes Report No 30: 1–103
- Hatanaka, M. A., Takahashi, M. (1960). Studies on the amounts of anchovy consumed by the mackerel. Tohoku J. Agric. Res. 11 (1): 83–100
- Henry, J. L. (1979). Radiocarbon productivity measurements off the Cape west coast. 4th S. Afr. Natl Oceanogr. Symp., July 1979, Cape Town, S 189 (abstract). CSIR, Pretoria, South African
- Henry, J. L., Mostert, S. A., Christie, N. D. (1977). Phytoplankton production in Langebaan Lagoon and Saldanha Bay. Trans. R. Soc. S. Afr. 42: 383–398
- Heydorn, A. E. F. (1978). The ecology of the Agulhas Current region: an assessment of biological responses to environmental parameters in the south-west Indian Ocean. Trans. R. Soc. Afr. 43: 151–190
- Hutchings, L. (1979). Plankton of the Cape Peninsula upwelling system. Ph. D. thesis, University Cape Town, South Africa
- Kerr, S. R., Martin, N. V. (1970). Trophic dynamics of lake trout production systems. In: Steele, J. H. (ed.) Marine food chains. Oliver and Boyd, Edinburgh, p. 365–376
- King, D. P. F. (1977). Distribution and relative abundance of eggs the South West African pilchard *Sardinops ocellata* and anchovy *Engraulis capensis*, 1971/72. Fish. Bull. S. Afr. 9: 23–31
- King, D. P. F., Macleod, P. R. (1976). Comparison of the food and the filtering mechanism of pilchard *Sardinops ocellata* and anchovy *Engraulis capensis* off South West Africa 1971–1972. Investl Rep. Sea Fish. Brch S. Afr. 111: 1–29
- King, D. P. F., Robertson, A. A., Shelton, P. A. (1978). Laboratory observations on the early development of the anchovy *Engraulis capensis* from the Cape Peninsula. Fish. Bull. S. Afr. 10: 37–45
- Le Clus, F. (1983a). Observations on the egg production of pilchard and anchovy off South West Africa in 1981/82. Colln scient. Pap. int. Commn S. E. Atl. Fish. 10: 139–145
- Le Clus, F. (1983b). Anchovy spawning off Namibia. S. Afr. J. Sci. 79: 143
- Linley, E. A. S., Newell, R. C., Lucas, M. I. (1983). Quantitative relationships between phytoplankton, bacteria and heterotrophic microflagellates in shelf waters. Mar. Ecol. Prog. Ser. 12: 77–89
- Longhurst, A. R. (1971). The clupeoid resources of tropical seas. Oceanogr. mar. Biol. A. Rev. 9: 349–385
- Mann, K. H. (1982). Ecology of coastal waters: a systems approach. Blackwell, Oxford
- Mikhman, A. H., Tomanovich, L. V. (1977). The feeding of the Azov anchovy, *Engraulis maeoticus*. J. Ichthyol. 17 (2): 240–244

- Mills, E. L., Fournier, R. O. (1979). Fish production and the marine ecosystems of the Scotian Shelf, Eastern Canada. *Mar. Biol.* 54: 101–108
- Nelson, G., Hutchings, L. (1983). The Benguela upwelling area. *Prog. Oceanogr.* 12: 333–356
- Newman, G. G., Crawford, R. J. M. (1980). Population biology and management of mixed – species pelagic stocks off South Africa. *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 177: 279–291
- Olivieri, E. T., Hutchings, L. (1983). Zooplankton grazing in the southern Benguela. *Proc. 5th National Oceanographic Symposium*, Grahamstown, S. Afr., January 1983. Abstract in *S. Afr. J. Sci.* 79: 145
- Platt, T., Irwin, B. (1973). Caloric content of phytoplankton. *Limnol. Oceanogr.* 18: 306–309
- Robinson, G. A. (1966). A preliminary report on certain aspects of the biology of the South African anchovy, *Engraulis capensis* (Gilchrist). M. Sc. thesis, University of Stellenbosch, South Africa
- Ryther, J. H. (1969). Phytosynthesis and fish production in the sea. *Science* 171: 72–76
- Schneider, D., Hunt, G. L. (1982). Carbon flux to seabirds in waters with different mixing regimes in the south Bering Sea. *Mar. Biol.* 67: 337–344
- Shannon, L. V. (1972). Marine alpha-radioactivity off southern Africa. 1. Gross alpha-activity, radiation dose, alpha-spectrum and variations in alpha-activity of marine life. *Investl Rep. Div. Sea Fish. S. Afr.* 98: 1–80
- Shannon, L. V., Henry, J. L. (1983). Phytoplankton primary production in the Benguela Current from ship and satellite measurements. *Proc. 5th National Oceanographic Symposium*, Grahamstown, S. Afr., January 1983. Abstract in *S. Afr. J. Sci.* 79: 144
- Shannon, L. V., Mostert, S. A., Walters, N. M., Anderson, F. P. (1983). Chlorophyll concentrations in the southern Benguela Current region as determined by satellite (Nimbus7 Coastal zone colour scanner). *J. Plankton Res.* 5: 565–583
- Shannon, L. V., Hutchings, L., Bailey, G. W., Shelton, P. A. (1984). The 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., Armstrong, M. J. (1983). Variations in the parent stock and recruitment of pilchard and anchovy populations in the southern Benguela system. In: Sharp, G. D., Csirke, J. (ed.) *Proceedings of FAO-IOC Expert consultation to examine changes in abundance and species composition of neritic fish stocks*. San Jose, Costa Rica, 18–29 April 1983. *FAO Fish. Rep.* 291: 1113–1133
- Shelton, P. A., Hutchings, L. (1982). Transport of anchovy *Engraulis capensis* Gilchrist, eggs and early larvae by a frontal jet current. *J. Cons. int. Explor. Mer* 40: 185–198
- Shushkina, E. A., Vinogradov, M. Y., Sorokin, Y. I., Lebedeva, L. P., Mikheyev, V. N. (1978). The peculiarities of functioning of plankton communities in the Peruvian upwelling. *Oceanology* 18: 579–589
- Siegfried, W. R., Field, J. G. (ed.) (1981). A description of the Benguela Ecology Programme. *S. Afr. National Scientific Programmes Report* 54: 1–39
- Sirotenko, M. D., Danilevski, N. N. (1977). Quantitative indices of the feeding of the Black Sea anchovy, *Engraulis encrassicholus ponticus*. *J. Ichthyol.* 17: 610–617
- Smith, P. E., Eppley, R. W. (1982). Primary production and the anchovy populations in the southern Californian Bight: a comparison of time series. *Limnol. Oceanogr.* 27: 1–17
- Smith, R. C., Baker, K. S. (1982). Oceanic chlorophyll concentrations as determined by satellite (Nimbus-7 coastal zone color scanner). *Mar. Biol.* 66: 269–279
- Sorokin, Y. I., Mikheev, V. N. (1979). On characteristics of the Peruvian upwelling system. *Hydrobiologia* 62: 165–189
- Stander, G. H., De Decker, A. H. B. (1969). Some physical and biological aspects of an oceanographic anomaly off South West Africa in 1963. *Investl Rep. Div. Sea Fish. S. Afr.* 81: 1–46
- Stander, G. H., le Roux, P. J. (1968). Notes on fluctuations of the commercial catch of the South African pilchard (*Sardinops ocellata*), 1950–1965. *Investl Rep. Div. Sea Fish. S. Afr.* 65: 1–14
- Steele, J. H. (1974). *The structure of marine ecosystems*. Blackwell Scientific Publications, Oxford
- Steeman Nielsen, E., Jensen, E. A. (1957). Primary oceanic production. The autotrophic production of organic matter in the oceans. *Galathea Rep. Denmark* 1: 49–136
- Steeman Nielsen, E. (1964). On the determination of the activity in C^{14} ampoules. *ICES C. M.* 1964, Plankton Committee Doc. 105: 1–2
- UNESCO (1966). Determination of photosynthetic pigments in sea water. *Monographs of Oceanographic Methodology* 1: 1–69
- Vinogradov, A. P. (1953). The elementary chemical composition of marine organisms. *Mem. Sears Fdn mar. Res.* 2
- Walsh, J. J. (1983). Death in the sea: enigmatic phytoplankton losses. *Prog. Oceanogr.* 12: 1–86
- Walters, N. M. (1984). Verification of the utility of the coastal zone colour scanner in portraying pigment concentrations along the Cape west Coast. *S. Afr. J. Physics* (in press)
- Wilson, R. (1983). Aspects of the marine ecology of the jackass penguin (*Spheniscus demersus*). M. Sc. thesis, University of Cape Town, South Africa