79. Compton A.H. (1924). A general quantum theory of the wavelength of scattered X-rays. *Phys. Rev., Ser. 2*, **24**, 168–176.
80. Klein O. and Nishina Y. (1929). Über die Streuung von Strahlung durch freie Elektronen nach der neuen relativistischen Quantendynamik von Dirac. *Z. Physik* **52**, 853–868.
81. Nishina Y. (1929). Die Polarisation der Comptonstreuung nach der Diracschen Theorie des Elektrons. *Z. Physik* **52**, 869–877.
82. James R.W. (1954). *The Optical Principles of the Diffraction of X-rays.* Bell, London.
83. Evans D.E. and Katzenstein J. (1969). Laser light scattering in laboratory plasmas. *Rep. prog. Phys.* **32**, 207–271.
84. Barkla C.G. (1920). Characteristic Röntgen radiation. *Nobel Lectures in Physics (1901–1921)*, pp. 392–399. Elsevier, Amsterdam (1967).
85. Barkla C.G. (1917). On X-rays and the theory of radiation. *Phil. Trans. R. Soc. Lond.* **217A**, 315–360.
86. Barkla C.G. (1903). Secondary radiation from gases subject to X-rays. *Phil. Mag., Ser. 6*, **5**, 685–698.
87. Barkla C.G. (1904). Energy of secondary Röntgen radiation. *Phil. Mag., Ser. 6*, **7**, 543–560.
88. Crowther J.A. (1907). On the secondary Röntgen radiation from gases and vapours. *Phil. Mag., Ser. 6*, **14**, 653–675.
89. Barkla C.G. (1911). Note on the energy of scattered X-radiation. *Phil. Mag., Ser. 6*, **21**, 648–652.
90. Barkla C.G. (1906). Polarisation in secondary Röntgen radiation. *Proc. Roy. Soc. Lond. A.* **77**, 247–255.
91. Thomson J.J. (1904). On the structure of the atom: an investigation of the stability and periods of oscillation of a number of corpuscles arranged at equal intervals around the circumference of a circle; with application of the results to the theory of atomic structure. *Phil. Mag., Ser. 6*, **7**, 237–265.
92. Kelvin, Lord (1905). Plan of an atom to be capable of storing an electron with enormous energy for radio-activity. *Phil. Mag., Ser. 6*, **10**, 695–698.
93. Kelvin, Lord (1907). An attempt to explain the radioactivity of radium. *Phil. Mag., Ser. 6*, **13**, 313–316.
94. Rutherford E. (1911). The scattering of α and β particles by matter and the structure of the atom. *Phil. Mag., Ser. 6*, **21**, 669–688.
95. Nagaoka H. (1904). Kinetics of a system of particles illustrating the line and the band spectrum and the phenomena of radioactivity. *Phil. Mag., Ser. 6*, **7**, 445–455.
96. Schott G. (1907). On the electron theory of matter and on radiation. *Phil. Mag., Ser. 6*, **13**, 189–213.
97. Larmor J. (1908). William Thomson, Baron Kelvin of Largs (1824–1907). *Proc. R. Soc. Lond. A.* **81**, Appendix, iii–lxxvi.
98. Wien W. (1908). Lord Kelvin. *Ann. Physik* (4) **25**, 1–6.
99. Kelvin, Lord (1900). Nineteenth century clouds over the dynamical theory of heat and light. *Proc. Roy. Inst.* **16**, 363–397.
100. Bohr N. (1913). On the constitution of atoms and molecules. *Phil. Mag., Ser. 6*, **26**, 1–25.
101. Bohr N. (1913). On the constitution of atoms and molecules. Part II — Systems containing only a single nucleus. *Phil. Mag., Ser. 6*, **26**, 476–502.
102. Bohr N. (1913). On the constitution of atoms and molecules. Part III — Systems containing several nuclei. *Phil. Mag., Ser. 6*, **26**, 857–875.
103. Keller A. (1983). *The Infancy of Atomic Physics: Hercules in his Cradle.* Clarendon Press, Oxford.

Snoek and their prey — interrelationships in the Benguela upwelling system

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Snoek, Thyrsites atun, *exhibit well-defined migratory patterns. They occur in the northern part of the Benguela upwelling region during the austral spring and summer, move south in autumn and winter, and return north in spring. The southward movement takes place near the coast, but that towards the north further offshore. The movements are related to seasonal patterns of the availability of prey, and the bulk of the catches of snoek are made in regions supporting large purse-seine fisheries based on prey species. The performances of snoek fisheries have in a number of instances been related to the abundance of prey species or of other predators exploiting the same forage. Indices of the natural mortality rate of anchovies,* Engraulis capensis, *compiled from the diet and handline catches of snoek, exhibit considerable inter-annual variation and are positively related to anchovy biomass. Mortality indices were relatively low immediately before an increase in anchovy biomass.*

Snoek, Thyrsites atun, *vertoon goed ontwikkelde trekpatrone. In die suidelike lente en somer kom hulle in die noordelike deel van die Benguela-opwellingsgebied voor, in die herfs en winter beweeg hulle suidwaarts, en in die lente weer noord. Die suidwaartse trek geskied na aan die kus, maar dié in noordelike rigting verder weg. Hul beweging hang saam met die seisoensbeskikbaarheid van prooi. Die grootste snoekvangste word dan ook gemaak in gebiede waar groot saknetvisserye op die vang van prooispesies staat maak. Die vangste van snoekvisserye is in 'n aantal gevalle in verband gebring met die voorkoms van prooispesies of van ander roofvis wat dieselfde voedselbronne benut. Die indekse vir die normale sterftesyfer van ansjovis,* Engraulis capensis, *wat uit die dieet en handlynvangste van snoek saamgestel is, vertoon heelparty wisselings tussen jare en hou positief met die ansjovisbiomassa verband. Die sterfte-indekse was betreklik laag onmiddellik voor 'n toename in die ansjovisbiomassa.*

Introduction

The snoek, *Thyrsites atun* Euphrasen, is an important fish predator in the Benguela upwelling system.[1-3] Preliminary estimates suggest that snoek consume 300 000 tonnes of anchovies, *Engraulis capensis*, off the west coast of South Africa annually, almost half the loss to natural predators.[4] Off South Africa, snoek are commercially exploited both by inshore handline fishermen[5,6] and by demersal trawlers operating at depths shallower than about 400 m.[7] The handline catch of snoek off the western Cape coast in 1982 (4 085 t) amounted to 85% of the total handline catch for the area and had a landed value of R3.3 million, 80% of the overall value for the fishery.[8] The landed value of snoek caught by South African demersal trawlers in 1982 was R2.3 million.[8] Overall catches of snoek in the Southeast Atlantic rose from 5 462 t in 1972 to 81 676 t in 1978, but then declined to 49 187 t in 1980 (Table 1).

Off Southern Africa, snoek exhibit distinct seasonal patterns of availability in certain areas.[1,2] These patterns are believed to be related to the distribution of prey species.[5] We explore this thesis here in the light of documented information on patterns of availability and distribution of these species, and also review the consequences of trends in the behaviour of prey species for the snoek fisheries. Furthermore, we examine the possibility that predation by snoek may be an important cause of variability amongst prey populations. MacCall[9] has cited Methot[10] as con-

Table 1. Catches (tons) of snoek, *Thyrsites atun*, in the Southeast Atlantic by different countries, 1972 – 1980 (from ICSEAF Statistical Bulletins 2 – 10).

Year	South Africa	Japan	Poland	Portugal	Spain	Romania	USSR	Total
1972	5 462							5 462
1973	7 935	626						8 561
1974	9 777	312						10 089
1975	10 020	7						10 027
1976	16 273	194						16 467
1977	18 724	22	414	142	182			19 484
1978	17 161	17	177	4		6	64 311	81 676
1979	7 104		13				18 601	25 718
1980	11 071	2		3 642			34 472	49 187

Table 2. Catches (tons) of snoek, *Thyrsites atun*, in the different ICSEAF Divisions, 1972 – 1980 (from ICSEAF Statistical Bulletins 2 – 10).

	ICSEAF division											
Year	1.1	1.2	1.3	1.4	1.5	1.6	2.1	2.2	4	8.6	Subarea 1 undefined	Undefined
1972				1 360		2 606						1 496
1973	419	142			2	4 976	26	31		6		2 959
1974	227	28		1 566		8 211	54	3				
1975				1 270	63	6 150	5	2			2 537	
1976				3 221	145	12 602	458	41				
1977			415	3 270	5 690	9 156	808	3			142	
1978	31	454	34 578	31 403	3 021	10 503	1 668	14				4
1979		11	10 865	7 660	1 154	2 542	3 470	16				
1980			19 084	15 388	2 463	4 052	4 556		2			3 642
Total	677	635	64 942	65 138	12 538	60 796	11 045	110	2	6	2 679	8 101
%	.30	.28	28.65	28.74	5.53	26.82	4.87	.05	.00	.00	1.18	3.57

Table 3. Occurrence of anchovies, *Engraulis capensis*, in stomachs of snoek, *Thyrsites atun*, handline catch of snoek off the western Cape, biomass of anchovies and index of consumption of anchovies by snoek, 1958 – 1981.

Year	Number of snoek stomachs containing food	% frequency of occurrence of anchovies in stomachs of snoek[3,11]		Handline-catch of snoek (millions) (updated from Nepgen[5])		Index of consumption of anchovies by snoek	Anchovy biomass (updated from Davies *et al.*[12]) (× 10³ t)	Index of natural mortality rate
		Annual value	3-year moving average	Annual value	3-year moving average			
1958	186	0.8						
1959	48	–						
1960	32	11.5						
1961	33	–		1.94				
1962	6	2.6		1.15				
1963	56	2.0						
1964							310	
1965	44	42.5					310	
1966	83	10.6					290	
1967	95	35.6					343	
1968)	19	10.3					250	
1969)			12.9	1.42	1.49	19.27	290	.07
1970	215	15.5	10.3	1.57	1.44	14.84	323	.05
1971	83	5.1	11.7	1.33	1.27	14.86	283	.05
1972	94	14.5	21.5	.91	1.34	28.79	260	.11
1973	85	45.0	28.6	1.78	1.64	47.01	370	.13
1974	96	26.3	35.7	2.25	2.08	74.31	460	.16
1975				2.22			483	
1976				4.67			500	
1977				2.30			520	
1978				2.39			544	
1979)	1 068	89.0	89.0	1.37	1.48	131.75	610	.22
1980)			89.0	.68	.98	86.78	520	.17
				.88			440	

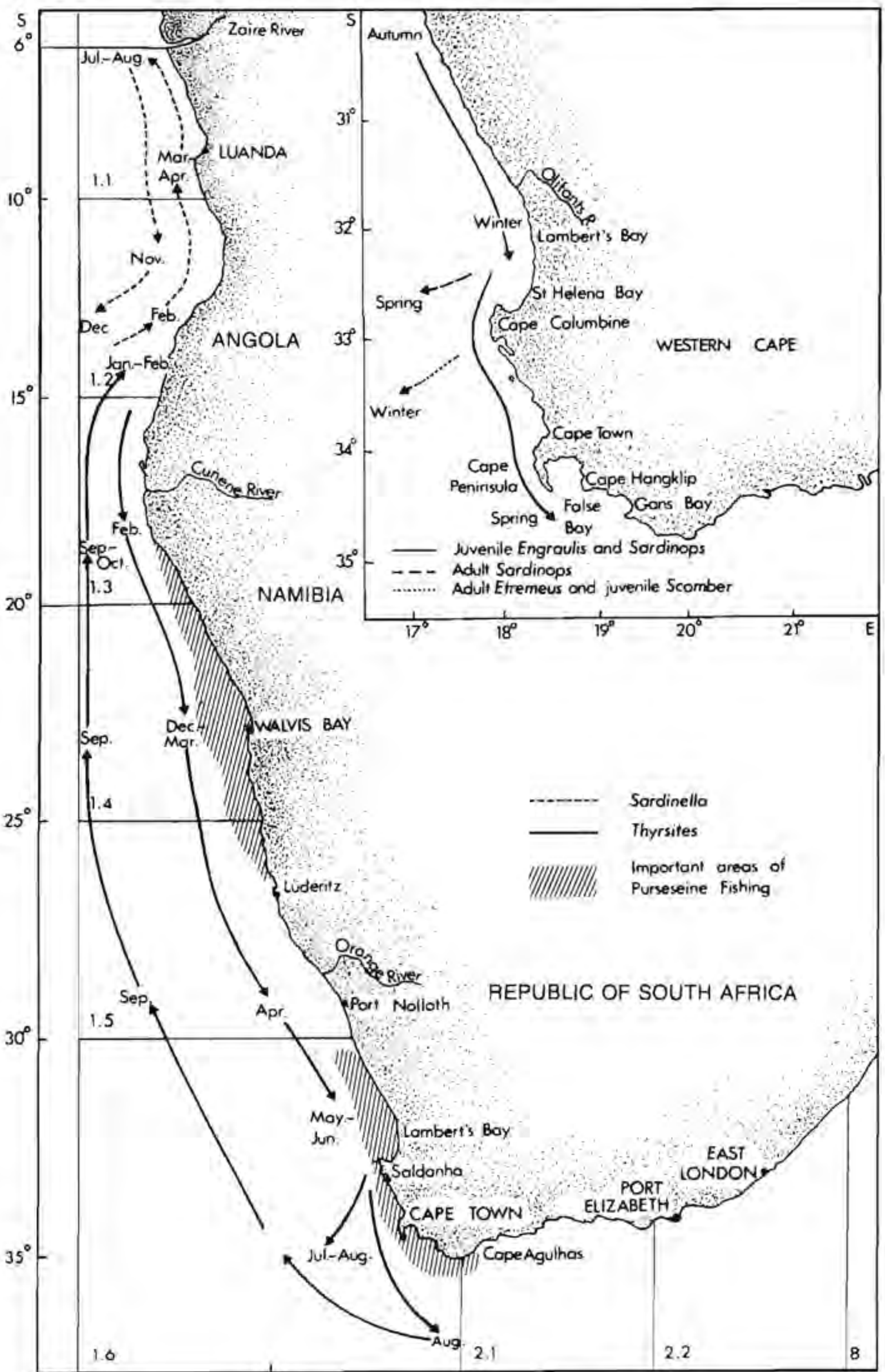

Fig. 1. Map of the Southeast Atlantic, showing the ICSEAF divisions, the main areas of purse-seine operations off South Africa and Namibia,[31] seasonal patterns of availability of snoek *Thyrsites atun* (modified from Davies[1]) and migrations of *Sardinella* spp.[18] Inset depicts aspects of movements of *Engraulis capensis, Sardinops ocellata, Etrumeus teres* and *Scomber japonicus* in the southern Benguela region (modified from Crawford[22]).

cluding that a high biomass of anchovies, *E. mordax*, off California in the mid-1970s was not simply the product of strong recruitment, but rather was due to a substantial decrease in the natural mortality rate.

Methods

Information on the seasonal distribution of catches of snoek in Divisions 1.1 to 1.5 of the convention area of the International Commission for the Southeast Atlantic Fisheries (ICSEAF) was extracted from ICSEAF Statistical Bulletins 2 to 10 covering the years 1972 – 1980. The information was scanty and was pooled for the entire period. No comparable information was available from the ICSEAF Statistical Bulletins for Division 1.6, but records of monthly catches of snoek by South African trawlers operating in ICSEAF Divisions 1.6 and 2.1 were available for the period 1979 – 1982.[27] Annual catches recorded in each of the ICSEAF divisions for the period 1971 – 1980 were extracted from the ICSEAF Statistical Bulletins.

An index of the annual consumption of anchovies by snoek was computed as the product of the frequency of occurrence of anchovies in the diet of, and the annual landing of, snoek caught by handline off the western Cape. The frequency of occurrence of prey items in the stomachs of snoek sampled mostly in the vicinity of the Cape Peninsula (Fig. 1) was recorded for the period 1958 – 1974, except for 1964,[3] and in the stomachs of snoek sampled in False Bay, which is bounded on one side by the Cape Peninsula, in 1979 and 1980.[11] Sampling methods during the two studies were similar.[30] The numbers of stomachs that were examined and contained food ranged from six to 1 068 per annum with a mean of 140.[3,11] To obviate the low sampling frequency of some years, three-year moving averages (two-year averages for years at the extremities of sampling periods) were employed in this study. Information on the handline catches of snoek off the western Cape[5] was treated similarly. The consumption index is based on the assumptions that the numbers of snoek preying on the western Cape anchovy population in any year are reflected

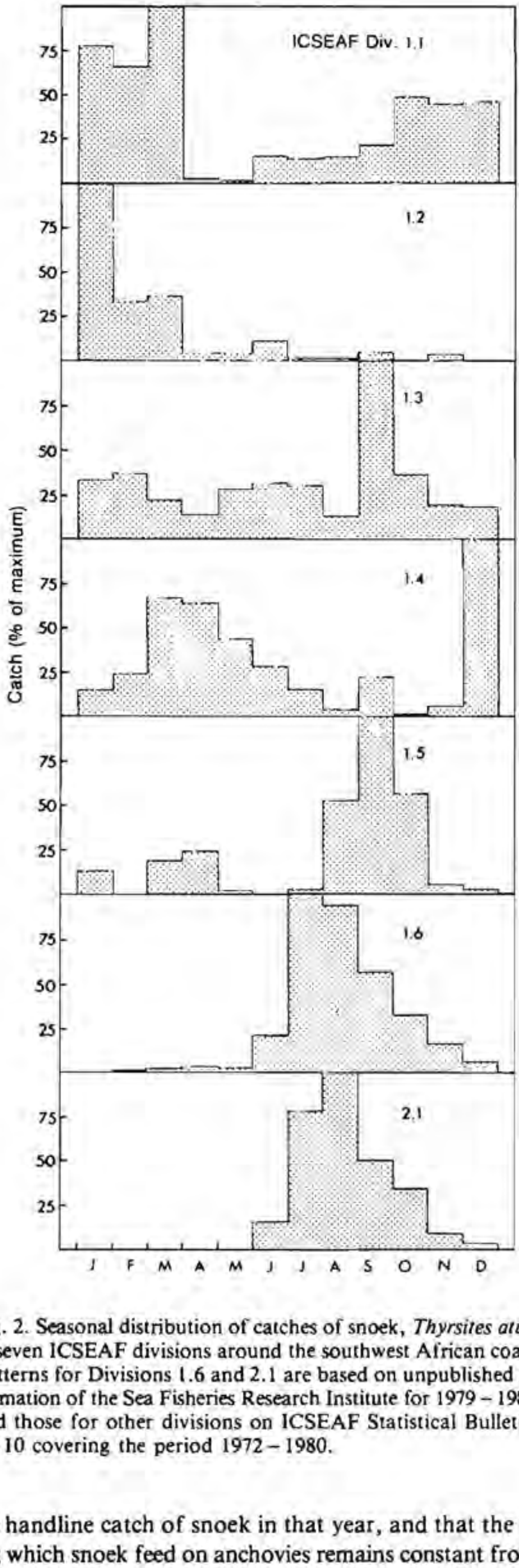

Fig. 2. Seasonal distribution of catches of snoek, *Thyrsites atun*, in seven ICSEAF divisions around the southwest African coast. Patterns for Divisions 1.6 and 2.1 are based on unpublished information of the Sea Fisheries Research Institute for 1979 – 1982, and those for other divisions on ICSEAF Statistical Bulletins 2 – 10 covering the period 1972 – 1980.

by the handline catch of snoek in that year, and that the period during which snoek feed on anchovies remains constant from year to year.

An index of the annual mortality rate of anchovies caused by snoek was derived by dividing the consumption rate by the virtual population (VPA) estimate of anchovy biomass for the appropriate year. The VPA estimates used were based on the assumption of a constant natural mortality rate of 0.8.[12]

Results

The seasonal distributions of catches in the six divisions of ICSEAF Subarea 1 are illustrated in Fig. 2. Snoek were caught in the three northern divisions mainly from spring to early autumn (September – March). Almost 60% of the catches from Division 1.4 were made between February and June, 26% in December, and only small amounts in intervening months. The December catch was attributable mainly to a harvest of 11 938 t reported by the USSR for December 1980. Virtually all catches from Division 1.5 were made in late autumn or from late winter to early spring. Demersal catches by South African trawlers operating in Divisions 1.6 and 2.1 were highest in winter and early spring. Catches from Division 2.1 peaked later (August) than those from Division 1.6 (July).

Divisions 1.3 and 1.4 each accounted for about 30% of the catches of snoek in the Southeast Atlantic for the period 1972 – 1980 (Table 2). Division 1.6 contributed 27% and no other division more than six per cent. Snoek were not caught on the two northern grounds except during 1972 – 73 and 1978 – 79.

The index of the natural mortality rate for anchovies derived from the diet and handline catches of snoek revealed considerable inter-annual variation, there being a steady increase during the 1970s (Table 3). The highest index (1979) was more than four time greater than the smallest (1970, 1971). The mortality index was positively related ($r^2 = 0.81$) to anchovy biomass (Fig. 3), as was the index of consumption of anvhovies by snoek ($r^2 = 0.94$).

Discussion

Influence of prey availability on distribution of snoek

Seasonal patterns of availability of snoek to inshore handline fishermen operating along the west coast of Southern Africa have been described by several authors.[1,2,5,13] From November to January snoek are caught in inshore waters off Namibia, but in autumn they migrate south and during April and May are exploited by handline boats in the vicinity of Port Nolloth.[1] Snoek continue to move south and in late autumn and winter are caught off St Helena Bay and the Cape Peninsula.[1,2] Historically, the availability of snoek to handline fishermen along the western Cape coast decreased sharply after July.[1] However, more recently snoek have been relatively abundant east of the Cape Peninsula from June to October.[5] From 1965 to 1977 the bulk of the handline catch of snoek at Gans Bay was made in June and July.[6] Snoek were not permitted to be caught with handlines from August or October to November inclusive between the 1940s and 1980.[13,14]

All 19 recoveries of snoek tagged near Walvis Bay in November and December 1934 indicated a southward movement.[2] Fourteen of these fish were recovered off South Africa, twelve between April and June.[2] Nepgen[5] reports the results of a tagging study conducted off the western Cape in 1973 and 1974. No long-distance movements were evident, the 18 recoveries all being off the western Cape. The majority (15 or 83%) were recovered between May and August, mostly in July.[5]

The above patterns conform well with southward movements of snoek that may be inferred from the seasonal distributions

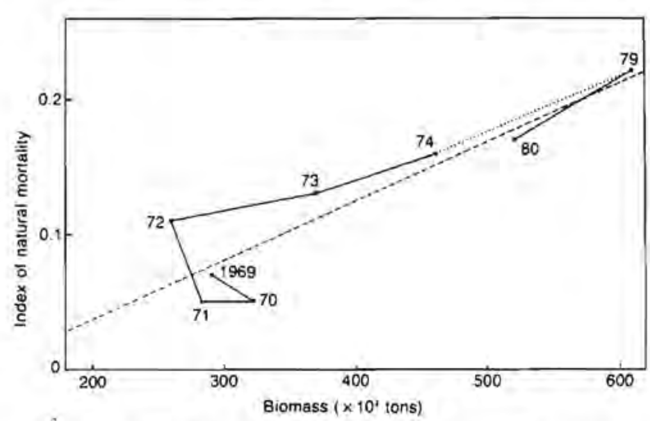

Fig. 3. The relationship between the biomass of anchovies, *Engraulis capensis*, off the western Cape[12] and an index of mortality calculated as being attributable to predation by snoek, *Thyrsites atun*.

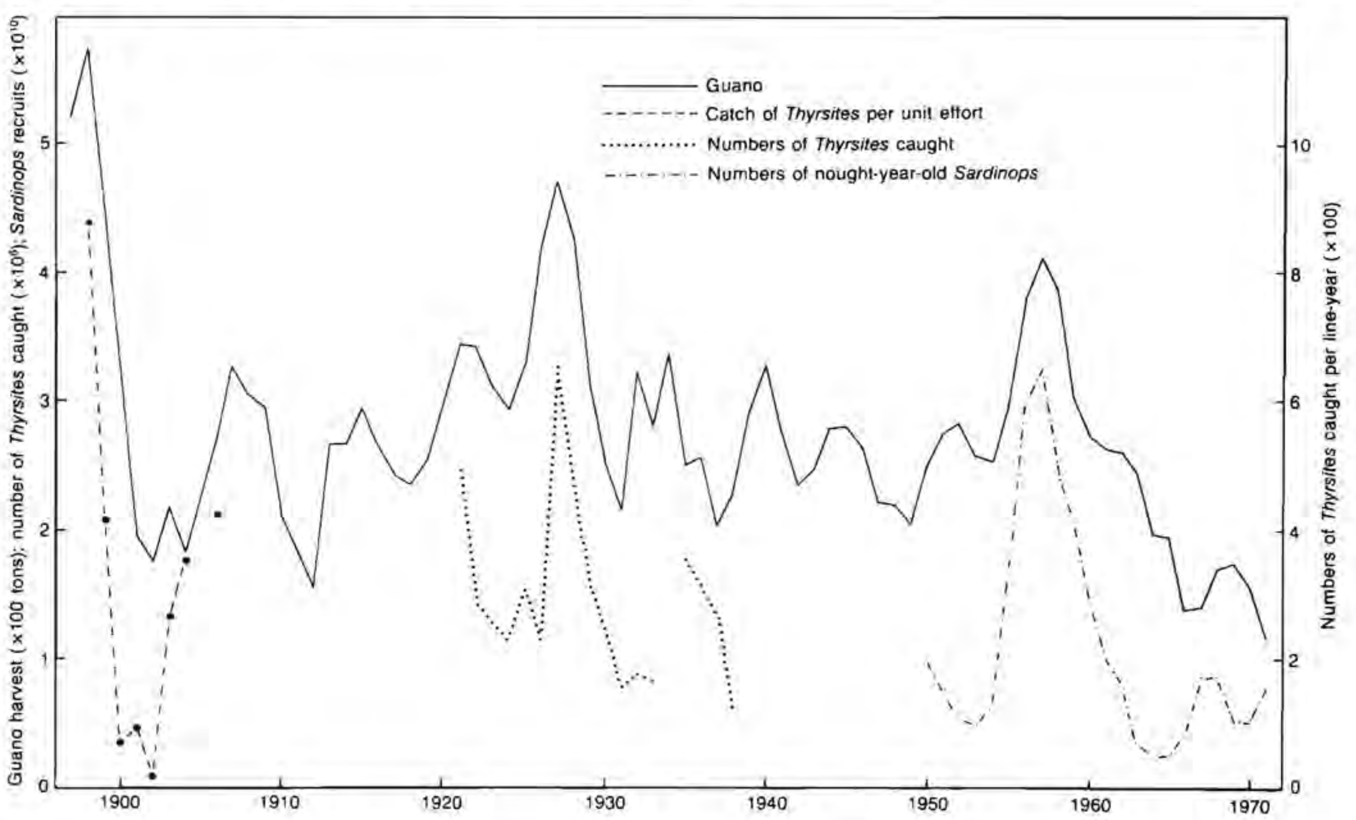

Fig. 4. Trends in the guano harvest at Lambert's Bay and in catch rates of snoek *T. atun* and year class strength of pilchards, *Sardinops ocellata*, off the western Cape, 1897 – 1972 (from Crawford *et al.*[31]).

of catches in the different ICSEAF divisions (Figs 1 and 2), if the reasonable[15] assumption is made that catches are not influenced to any great extent by changes in the deployment of fishing effort. During spring and summer snoek are caught mainly in the northern Benguela region (Divisions 1.1, 1.2 and 1.3). Catches improve in the central region (Divisions 1.4 and 1.5) in autumn, and peak in the south (Divisions 1.6 and 2.1) in winter. As suggested by Davies,[1] a return northward movement appears to take place from August to October (Fig. 2). Snoek move away from the western Cape coast at the end of winter, and its believed that the northward movement occurs in offshore waters.[1]

The food of snoek caught inshore along the western Cape by handlines is to a large extent made up of small shoaling pelagic fishes.[3,11] The main pelagic resources of the northern Benguela region are those of horsemackerel, *Trachurus* spp., and sardinellas, *Sardinella* spp., in Divisions 1.1, 1.2 and 1.3, and of anchovies and pilchards, *Sardinops ocellata*, in Division 1.3.[16,17] Seasonal trends in the distribution of sardinellas have been described by Baptista.[18] In winter the most rewarding catches of sardinellas are made off the Congo, Zaire and northern Angola. In spring and summer, however, there is a southward shift in the distribution of sardinellas, catches off southern Angola improving but those north of the Zaire river decreasing (Fig. 1). One-year-old pilchards occur off northern Namibia in summer.[19,20,39] The presence of snoek in the northern ICSEAF divisions corresponds with both this availability of juvenile pilchards and the southward shift in the distribution of sardinellas.

The inshore availability of snoek in Division 1.4 between November and January[1] coincides with a likely onshore, post-spawning movement of the older age classes of the Namibian pilchard stock in the same vicinity.[21]

Further south, the appearance of snoek near Port Nolloth during April and May[1] corresponds with recruitment to the western Cape purse-seine fishery in the same region of shoals of juvenile anchovies and pilchards.[22] On the basis of tagging and genetic studies pilchard and anchovy stocks off the western Cape are regarded as distinct from those off Namibia.[23,24]

Off the western Cape, juvenile anchovies and pilchards migrate southwards through St Helena Bay, and are encountered in the waters east of Cape Point in winter and spring.[22] Snoek apparently follow these migrations (Fig. 1), being caught off St Helena Bay and the Cape Peninsula during late autumn and winter[1,2] and east of Cape Point from winter to spring.[5,6]

The movement of snoek away from the coast of the western Cape at the end of winter[1,2] may also relate to the availability of prey. Until the pilchard resource of the western Cape was depleted in the early 1960s, the older age classes were available to purse-seiners in the vicinity of St Helena Bay from late summer to early winter,[25] but towards the end of winter moved offshore to spawn.[22] Adult roundherrings, *Etrumeus teres*, similarly move away from the coast to spawn.[22] In the same region the abundance of euphausiids increases markedly from early spring, particularly offshore.[26] Roundherrings form a large part of the diet of snoek trawled off the western Cape between winter and early summer, as do euphausiids in spring.[27] In winter, juveniles of another predator, the chubmackerel, *Scomber japonicus*, move away from the western Cape,[22] roundherrings and euphausiids being important in their diet.[28]

Snoek spawn off the western Cape from July to October,[1,2,5] their condition deteriorating in these months.[5,14] Their movement in winter to offshore waters is believed to be a spawning migration.[2] It is noteworthy that both predator and prey species undertake similar spawning migrations.

The biomass of pelagic fish populations off the western Cape reaches a maximum in autumn and winter,[29] following the recruitment of juveniles.[22] Thereafter there is a rapid decrease in prey abundance,[29] which may prompt the return northward migration of snoek. Off Namibia adult pilchards are believed to move away from the coast to spawn in later winter and early spring,[21] so there would be an offshore availability of prey further north. The northward flowing Benguela Current is also expected to transport the spawning products of snoek in a northerly direction.

From the foregoing it is evident that the migrations and seasonal occurrence of snoek along the Southern African coast are strongly influenced by the availability of prey, although spawning is also an important consideration. It is especially noteworthy that 90% of the overall catch of snoek in the Southeast Atlantic from 1972 to 1980 was taken in the ICSEAF divisions sustaining the large Namibian (Divisions 1.3 and 1.4) and South African (Divisions 1.6 and 2.1) purse-seine fisheries (Fig. 1). Only six per cent was taken from the intervening Division 1.5 (Table 2), supporting the hypothesis that the Benguela upwelling region comprises at least two (northern and southern) subsystems.[31]

Influence of prey abundance on trends in the snoek fisheries

Three large increases in the availability of snoek to handline fishermen off the western Cape since the 1890s have each been related to the abundance of prey or of other predators of small shoaling pelagic fishes.[31,32] Catch rates of snoek were high during the late 1890s, as were handline catches of snoek in the late 1920s.[5,32] Both these periods coincided with large peaks in the amount of guano collected from the seabird island at Lambert's Bay (Fig. 4), there being significant correlations between the indices for snoek and guano ($r = 0.804$, $P < 0.02$, $n = 7$ and $r = 0.739$, $P < 0.001$, $n = 18$ respectively). The guano is deposited by seabirds which prey primarily on small, shoaling pelagic fishes[32] and the island at Lambert's Bay is situated at the centre of the recruitment grounds for anchovies, pilchards, roundherrings and horsemackerel off the western Cape.[22] A third large peak in the production of guano at Lambert's Bay during the 1950s has been correlated ($r = 0.783$, $P < 0.001$, $n = 20$) with an eruption in the recruitment of pilchards off the western Cape at this time.[32] Unfortunately there are no records of the performance of the snoek fishery during the 1950s,[5] but snoek are reported to have been exceptionally abundant (J.P. Matthews *in litt.*).

The biomass of the western Cape anchovy population doubled as a result of favourable recruitment during the mid-1970s.[12] Handline catches of snoek off the western Cape closely followed ($r = 0.708$, $P < 0.02$ $n = 10$) VPA estimates of anchovy biomass from 1969 to 1978.[31] The relationship broke down in subsequent years (Fig. 5), but the catch of snoek off Southern Africa quadrupled between 1977 and 1978 (Table 1), halving stock size.[40] Handline catches of snoek were exceptionally good in 1976 (Fig. 5) and may have resulted from an unusually high availability of snoek to fishermen in that year. Purse-seine catches of pilchards off the western Cape were greater in 1976 than in any year since 1965 and 2½ times the mean for the period 1969 – 1982.[31]

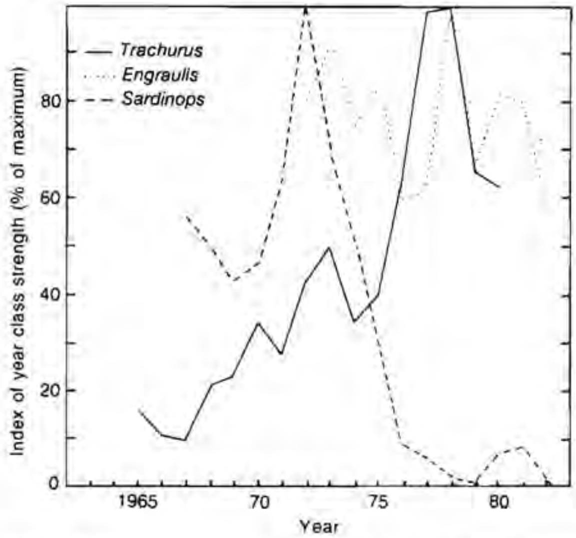

Fig. 6. Relative year class strength of pilchards, *S. ocellata*, anchovies, *E. capensis*, and horsemackerel, *Trachurus trachurus*, off Namibia, 1965 – 1982 (from Crawford *et al.*[31]).

Nepgen[5] highlighted the increased availability of snoek to handline fishermen operating east of Cape Point from 1973 and ascribed it to a greater abundance of anchovies and pilchards in that vicinity. In the region between Cape Hangklip and Cape Agulhas there have also been large increases recently in the abundance of two other predators of anchovies and pilchards, jackass penguins, *Spheniscus demersus*, and Cape cormorants, *Phalacrocorax capensis*.[33,34] A third seabird predator, the Cape gannet, *Morus capensis*, has increased in numbers off the southern Cape,[35] and the fishing effort of the western Cape purse-seine fishery deployed east of Cape Point has grown substantially since 1974.[36]

In the northern Benguela region powerful year classes of pelagic or mesopelagic stocks were formed during 1972 – 73 and 1977 – 78 (Fig. 6), and it is interesting that a northward extension in the distribution of snoek catches followed in both instances (Table 2). One-year-old pilchards occur off northern Namibia and along the Angolan coast as far north as the southern portion of ICSEAF Division 1.1.[19,20,39]

Thus trends in the performances of snoek fisheries have in a number of instances reflected variations in the abundance of prey species. It may be concluded that successful snoek fisheries depend on prey populations being maintained at reasonable levels.

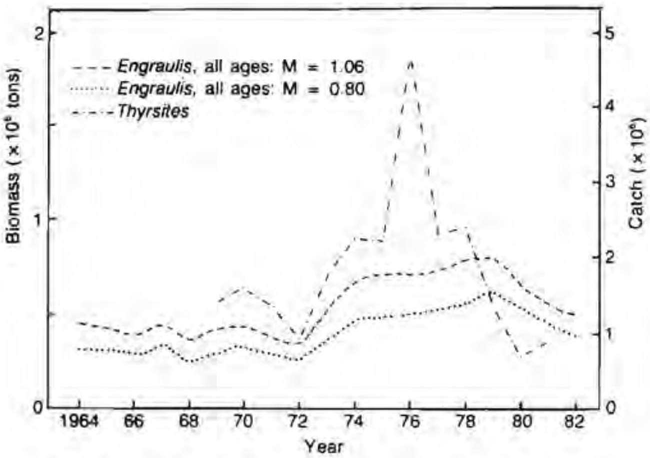

Fig. 5. Trends in the biomass of anchovies *E. capensis*, and handline catches of snoek, *T. atun*, off the western Cape, 1964 – 1982 (from Crawford *et al.*[31]).

Influence of predation by snoek on prey variability

Snoek is believed to be the most important predator on the western Cape anchovy resource, currently accounting for almost half the loss to natural predators.[4] The regular seasonal occurrence of snoek at different localities along the coast of Southern Africa[12,5,6] lends confidence to the assumption that the period during which snoek prey on anchovies off the western Cape remains relatively constant from year to year. Similarly, the close relationship between handline catches of snoek and VPA estimates of anchovy biomass (Fig. 5) suggests that in most years the handline catch of snoek is a valid measure of the numbers of snoek preying on anchovy. If these assumptions are correct, the mortality indices for anchovies estimated to result from predation by snoek reveal considerable inter-annual variation (Table 3, Fig. 3). Such variation would invalidate previous uses of constant natural mortality rates in VPA to estimate trends in the abundance of anchovies.

Available information suggests that the mortality rate inflicted by snoek on anchovies was greater when the biomass levels of anchovies were high (Fig. 3). As biomass was computed assuming constant natural mortality,[12] it is unlikely that Fig. 3 reflects the real situation. The relationship should probably be skewed downward to the right, decreasing the variability of the mortality index but enhancing discrepancies between high and low biomass levels. Off the western Cape, therefore, the biomass of anchovies in recent years probably approximated that of pilchards prior to the collapse of the pilchard resource more closely than was initially thought. The possibility of the replacement of pilchards by anchovies off the western Cape has been discussed more fully by Crawford *et al.*[31] There is evidence that food availability may be limiting the productivity of the mixed-species pelagic resource in the southern Benguela region.[37] For Californian waters, Daan[38] concluded that, in view of the time lag between the initial decrease of the sardine, *S. caerulea*, and a subsequent increase of anchovies, the sardine stock had not collapsed as a result of direct competition from anchovies.

Off the western Cape the anchovy biomass peaked in 1979, 20 years after the highest pilchard biomass was recorded and 13 years after the pilchard biomass had decreased to less than 12% of its maximum value. The delay in replacement may be attributable to an increased natural mortality rate for all small shoaling pelagic fishes following the collapse of the pilchard stock.[31] This would have been especially likely if inshore availability of snoek increased during the late 1950s, following a major eruption of the pilchard population (Fig. 4). Anchovies became considerably more important in the diet of snoek immediately after the collapse of the pilchard resource.[3] Unfortunately, data are insufficient to permit computation of the mortality indices for anchovies as a result of predation by snoek during the early and mid-1960s. However, it is noteworthy that mortality indices were relatively low during the period (1969 – 1972) immediately prior to the increase of the anchovy resource (Figs 3 and 5). We support MacCall's[9] conclusion that changes in natural mortality rate may be an important cause of variability of pelagic fish stocks.

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1. Davies D.H. (1954). The South African pilchard (*Sardinops ocellata*). Development, occurrence and distribution of eggs and larvae, 1950 – 51. *Investl Rep. Div. Fish. S. Afr.* **15**, 1 – 28.
2. de Jager B.v.D. (1955). The South African pilchard (*Sardinops ocellata*). The development of the snoek (*Thyrsites atun*) a fish predator of the pilchard. *Investl Rep. Div. Fish. S. Afr.* **19**, 1 – 11.
3. Nepgen C.S. de V. (1979). The food of the snoek *Thyrsites atun*. *Fish. Bull. S. Afr.* **11**, 39 – 42.
4. Anon. (1983). Final report of the scientific committee of enquiry into the exploitation of pelagic fish resources of South Africa and South West Africa, Cape Town.
5. Nepgen C.S. de V. (1979). Trends in the line fishery for snoek *Thyrsites atun* off the south-western Cape, and in size composition, length-weight relationship and condition. *Fish. Bull. S. Afr.* **12**, 35 – 43.
6. Crawford R.J.M. and Crous H.B. (1982). Trends in commercial handline catches of red fishes along the southern Cape coast, Republic of South Africa. *Koedoe* **25**, 13 – 31.
7. Botha L. (1980). *The biology of the Cape hakes* Merluccius capensis *Cast. and* M. paradoxus *Franca in the Cape of Good Hope area.* PhD thesis, University of Stellenbosch.
8. Anon. (1983). Statistical summary 1982. Republic of South Africa fisheries. *Internal Rep. Sea Fish. Res. Inst. S. Afr.*, 1 – 14.
9. MacCall A.D. (1983). Variability of pelagic fish stocks off California. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Stocks, San Jose, Costa Rica, 18 – 29 April 1983*, edit. G.D. Sharp and J. Csirke. *FAO Fish. Rep.* **291**(2), 101 – 112.
10. Methot R. (1982). Age-specific abundance and mortality of northern anchovy. *Admin. Rep. SW. Fish. Centre USA, LJ-82-31.*
11. Nepgen C.S. de V. (1982). Diet of predatory and reef fish in False Bay and possible effects of pelagic purse-seining on their food supply. *Fish. Bull. S. Afr.* **16**, 75 – 93.
12. Davies S.L., Newman G.G. and Shelton P.A. (1981). A review of the South African multispecies pelagic fishery in ICSEAF Division 1.6 in 1980. *Colln scient. Pap. int. Commn SE. Atl. Fish.* 51 – 74.
13. Van Wyk G.F. (1944). South African fish products. Part VIII. Composition of the flesh of Cape fishes. *J. Soc. chem. Ind., Lond.*, **63**, 367 – 371.
14. Nepgen C.S. de V. (1975). The closed season for snoeking. *S. Afr. Shipp. News Fishg. Ind. Rev.* **30**(11), 57.
15. Crawford R.J.M. and De Villiers G. (1984). Chub mackerel *Scomber japonicus* in the south-east Atlantic — its seasonal distribution and evidence of a powerful 1977 year-class. *S. Afr. J. mar. Sci.* **2**, 49 – 61.
16. Newman G.G. (1977). The living marine resources of the southeast Atlantic. *FAO Fish. Tech. Pap.* **178**, 1 – 59.
17. le Clus F. and Melo Y.C. (1983). Virtual population analysis of the anchovy stock off South West Africa: 1972 – 1982. *Colln scient. Pap. int. Commn SE. Atl. Fish.* **10**, 103 – 109.
18. Baptista S.R. da F. (1977). The distribution and movements of the sardinellas (*Sardinella aurita* Val. and *Sardinella eba* Val.) off the Angolan coast. *Colln scient. Pap. int. Commn SE. Atl. Fish.* **4**, 21 – 24.
19. Schülein F.H. (1971). *Rekruteringstudies oor die Suidwes-Afrikaanse sardyn,* Sardinops ocellata, *1954 – 1968.* MSc thesis, University of Stellenbosch.
20. Schülein F.H. (1973). Recruitment studies on the South West African pilchard, 1958 – 1972. *Abstracts of the South African National Oceanographic Symposium, Cape Town, 6 – 10 August 1973*, 29.
21. Matthews J.P. (1964). The pilchard of South West Africa (*Sardinops ocellata*). Sexual development, condition factor and reproduction. *Investl Rep. mar. Res. Lab. SW. Afr.* **10**, 1 – 96.
22. Crawford R.J.M. (1980). Seasonal patterns in South Africa's Western Cape purse-seine fishery. *J. Fish. Biol.* **16**, 649 – 664.
23. Newman G.G. (1970). Migration of the pilchard *Sardinops ocellata* in Southern Africa. *Investl Rep. Div. Sea Fish. S. Afr.* **86**, 1 – 6.
24. Armstrong M.J. *et al.* (1983). Stock assessment and population dynamics of anchovy and pilchard in ICSEAF Divisions 1.6 in 1982. *Colln scient. Pap. int. Commn SE. Atl. Fish.* **10**, 7 – 25.
25. Crawford R.J.M. (1981). Distribution, availability and movements of pilchard *Sardinops ocellata* off South Africa, 1964 – 1976. *Fish. Bull. S. Afr.* **14**, 1 – 46.
26. Nepgen C.S. de V. (1957). The South African pilchard (*Sardinops ocellata*) and maasbanker (*Trachurus trachurus*). The euphausiids of the west coast of South Africa. *Investl Rep. Div. Fish. S. Afr.* **28**, 1 – 30.
27. Sea Fisheries Research Institute, Cape Town, unpublished records.
28. Baird D. (1978). Food of the mackerel *Scomber japonicus* from Western Cape waters. *Fish. Bull. S. Afr.* **10**, 62 – 68.
29. Butterworth D.S. (1983). Assessment and management of pelagic stocks in the southern Benguela region. In ref. 9, pp. 329 – 405.
30. C.S. de V. Nepgen, personal communication.
31. Crawford R.J.M., Shelton P.A. and Hutchings L. (1983). Aspects of variability of some neritic stocks in the southern Benguela system. In ref. 9, pp. 407 – 448.
32. Crawford R.J.M. and Shelton P.A. (1978). Pelagic fish and seabird interrelationships off the coasts of South West and South Africa. *Biol. Conserv.* **14**, 85 – 109.
33. Crawford R.J.M. and Shelton P.A. (1981). Population trends for some southern African seabirds related to fish availability. In *Proceedings of the Symposium on Birds of the Sea and Shore, University of Cape Town, 19 – 21 November 1979*, edit. J. Cooper, African Seabird Group, Cape Town, 15 – 41.
34. Cooper J. *et al.* (1982). Distribution, population size and conservation of the Cape cormorant *Phalacrocorax capensis*. *Fish. Bull. S. Afr.* **16**, 121 – 143.
35. Crawford R.J.M. *et al.* (1983). Distribution, population size and conservation of the Cape gannet *Morus capensis*. *S. Afr. J. mar. Sci.* **1**, 153 – 174.
36. Crawford R.J.M. (1981). Catch per standard-boat-day and deployment of effort in the South African purse-seine fishery, 1964 – 1976. *Investl Rep. Sea Fish. Inst. S. Afr.* **122**, 1 – 24.
37. Shannon L.V. and Field J.G. (in press). Are fish stocks food limited in the southern Benguela pelagic ecosystem? *Mar. Ecol. — Prog. Ser.*
38. Daan N. (1980). A review of replacement of depleted stocks by other species and the mechanisms underlying such replacement. *Rapp. P.-v. Reun. Cons. int. Explor. Mer* **177**, 405 – 421.
39. Thomas R.M. (in prep.). Age composition of South West African pilchard, 1970 – 1983.
40. Crawford R.J.M. (in prep.). A preliminary assessment of the snoek *Thyrsites atun* fishery in the Southeast Atlantic.