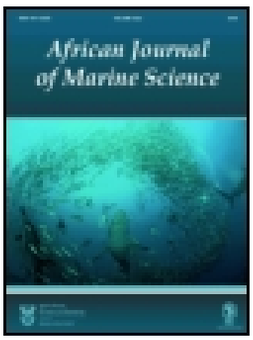

South African Journal of Marine Science

ISSN: 0257-7615 (Print) (Online) Journal homepage: http://www.tandfonline.com/loi/tams19

Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense, perennial upwelling system

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To cite this article: R. J. M. Crawford , R. A. Cruickshank , P. A. Shelton & I. Kruger (1985) Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense, perennial upwelling system, South African Journal of Marine Science, 3:1, 215-228, DOI: 10.2989/025776185784461252

To link to this article: http://dx.doi.org/10.2989/025776185784461252

S. Afr. J. mar. Sci. 3: 215–228
1985

PARTITIONING OF A GOBY RESOURCE AMONGST FOUR AVIAN PREDATORS AND EVIDENCE FOR ALTERED TROPHIC FLOW IN THE PELAGIC COMMUNITY OF AN INTENSE, PERENNIAL UPWELLING SYSTEM

R. J. M. CRAWFORD, R. A. CRUICKSHANK*, P. A. SHELTON* AND I. KRUGER**

Pelagic gobies *Sufflogobius bibarbatus* were numerically the most important prey of jackass penguins *Spheniscus demersus*, Cape cormorants *Phalacrocorax capensis* and bank cormorants *P. neglectus* sampled at islands off the South West African coast during the period 1978–1982. These three seabirds feed on small gobies near the surface and some of them can also dive sufficiently deep to catch larger gobies. Their populations at islands north of Lüderitz, where gobies are abundant, have been increasing. Cape gannets *Morus capensis* feed only on large gobies that are infrequently at the surface, and the gannet population off South West Africa has shown a large decrease since the collapse of the pilchard *Sardinops ocellata* resource in the late 1960s and early 1970s. In the intense perennial upwelling system situated between 22 and 27°S gobies are believed to have partially replaced pilchards during the 1970s. Both pilchards and gobies are able to feed on large diatoms of the genera *Chaetoceros* and *Delphineis*, which dominated the inshore phytoplankton in the early 1970s when biomass levels of both pilchards and gobies were low.

Oseaandikkoppe *Sufflogobius bibarbatus* was getalsgewys die vernaamste prooi van Kaapse pikkewyne *Spheniscus demersus*, trekduikers *Phalacrocorax capensis* en bankduikers *P. neglectus* wat gedurende die tydperk 1978–1982 op eilande teenoor die kus van Suidwes-Afrika bemonster is. Hierdie drie seevoëls vreet klein dikkoppies naby die oppervlak en party van hulle kan ook diep genoeg duik om groter dikkoppe te vang. Hul bevolkings op eilande noord van Lüderitz waar dikkoppe volop is, het vermeerder. Malgasse *Morus capensis* vreet net groot dikkoppe wat af en toe kom na die oppervlak, en die malgasbevolking langs die kus van Suidwes-Afrika het grootliks verminder sedert die ineenstorting van die sardynbron *Sardinops ocellata* in die laat sestiger- en vroeë sewentigerjare. In die intense opwellingstelsel wat deur die jaar tussen suiderbreedtes 22 en 27° voorkom, het dikkoppe sardyne vermoedelik deels vervang gedurende die sewentigerjare. Sardyne sowel as dikkoppe kan leef van groot diatome van die genera *Chaetoceros* en *Delphineis*, wat die aanlandige fitoplankton oorheers het in die vroeë sewentigerjare toe die biomassa van sardyne sowel as dikkoppe op 'n lae vlak was.

The principal upwelling centre of the Benguela Current system is approximately equidistant from its northern and southern boundaries in the vicinity of Lüderitz (26°40'S), and the zone of greatest negative surface temperature anomaly occurs between 23 and 31°S (Shannon 1985 and references therein). This cool water is believed to comprise a major environmental barrier that effectively divides the system in two (Cruickshank 1983a, Boyd and Cruickshank 1983, Shannon op. cit.). In the Lüderitz region southerly coastal winds occur throughout the year, tending to a maximum during the last quarter and a minimum between May and July (Bailey 1979). The southerly winds are favourable to perennial upwelling, with maximum intensity in the austral spring and a minimun in autumn (Stander 1964, Shannon op. cit.).

This paper examines evidence for an altered trophic flow in the pelagic community located between 22°S (just north of Walvis Bay) and Lüderitz. The region supports high primary productivity, and dense concentrations of phytoplankton are generally more widespread than further north (Kruger and Boyd 1984, Fig. 1). Pilchards *Sardinops ocellata* were abundant in both the vicinity of Walvis Bay and further south until the late 1960s (Matthews 1964, Newman 1970, Cram 1977, Fig. 2). In the late 1970s substantial stocks of pelagic gobies *Sufflogobius bibarbatus* were found to occur between Walvis Bay and Lüderitz (Cruickshank *et al.* 1980, Cruickshank 1982, Fig. 3). Large colonies of four species of seabird (Cooper 1981, Cooper *et al.* 1982, Crawford, Shelton, Cooper and Brooke 1983, Shelton *et al.* 1984, Fig. 4) are also located between Walvis Bay and Lüderitz, and immediately to the north and south. Partitioning of the goby resource by these predators is investigated.

METHODS

Historical changes in the species composition of diatoms in the vicinity of Walvis Bay were examined

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Manuscript received: November 1984

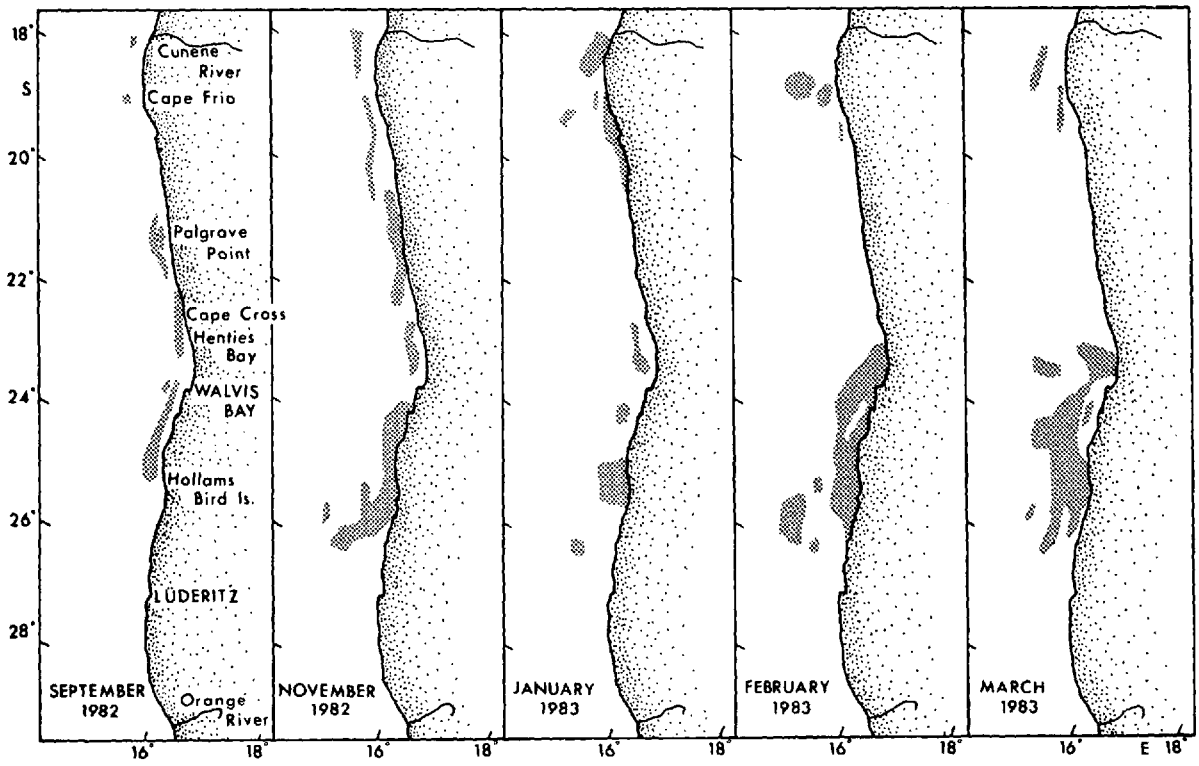

Fig. 1: Areas off South West Africa where phytoplankton concentrations greater than 30 mℓ·haul^{-1} were recorded between September 1982 and March 1983 (after Kruger and Boyd 1984)

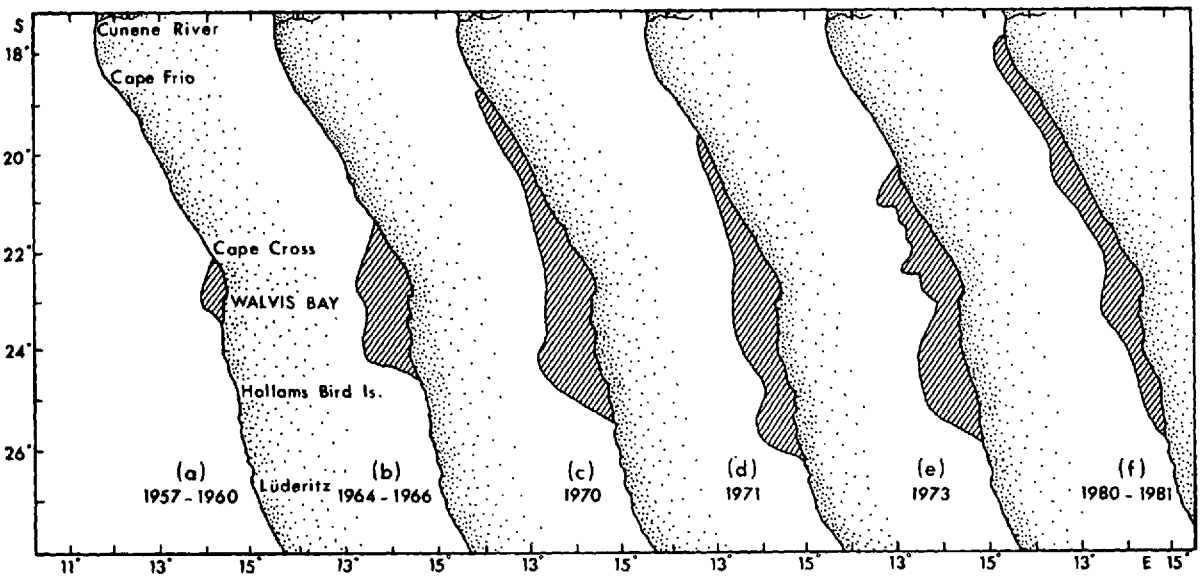

Fig. 2: Areas of purse-seine fishing off South West Africa, 1957–1981 (a - b after Newman [1970], c-e after Cram [1977] and "f" from records of the Sea Fisheries Research Institute)

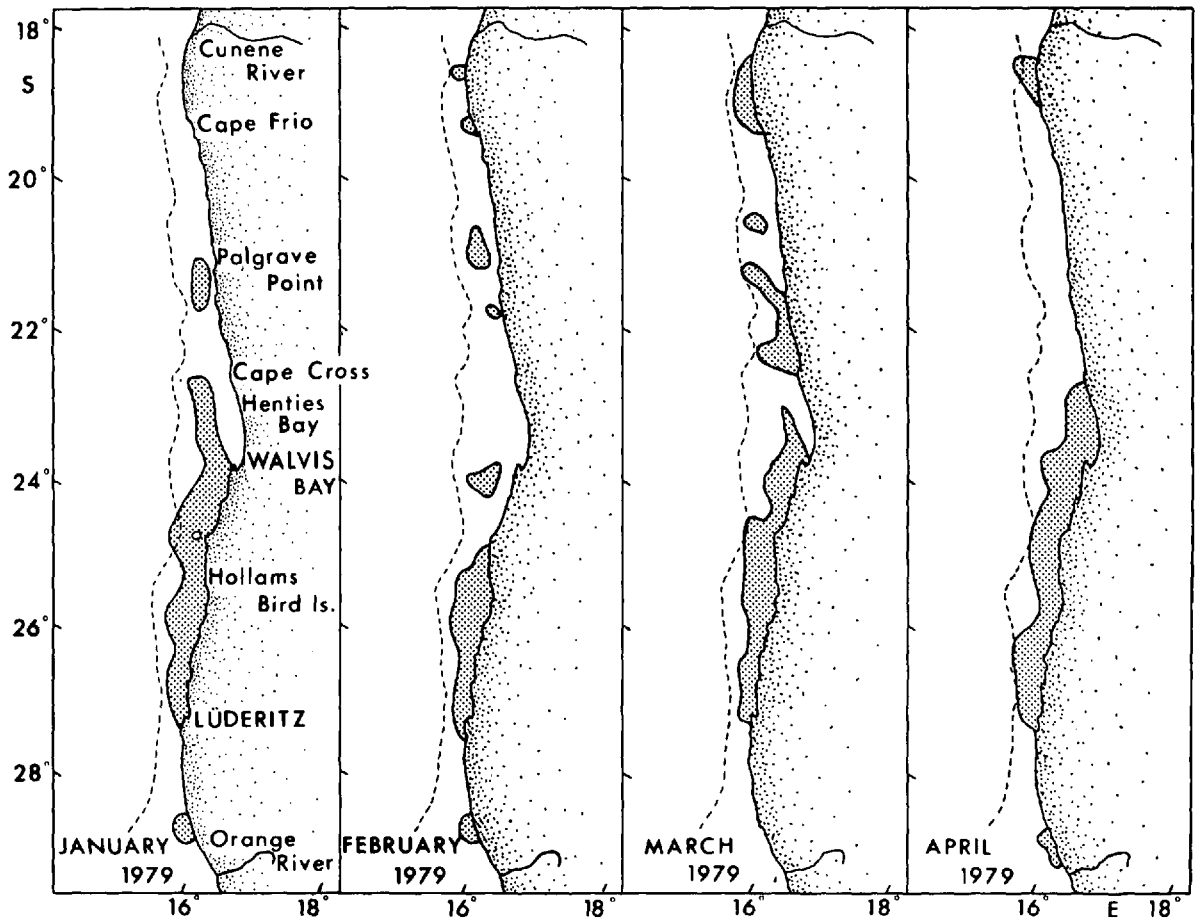

Fig. 3: Distributions of pelagic gobies from acoustic records, January–April 1979 (after Cruickshank *et al.* 1980)

by analysing the published information of Hart and Currie (1960) and Kollmer (1963), relating to 1950 and 1959–1960 respectively. Unpublished records of the Sea Fisheries Research Institute were used for the periods 1970–1973 and 1981–1983. Station grids and extent of coverage differed among the four surveys, but an attempt was made to retain comparability by selecting stations falling within a similar area. The resultant area extended from *c.* 18°30'S to *c.* 23°30'S and from the coast to about 60 nautical miles offshore. It included stations WS967 - WS972, WS979 - WS982, WS1074 - WS1079 and WS1096 - WS1099 of Hart and Currie (op. cit.), the entire "Routine Area" of Kollmer (op. cit.), the northern extent of which was *c.* 21°45'S, Stations CC31 - CC36, CC41 - CC46, CC51 - CC56, CC61 - CC66 and CC71 - CC76 for the period 1970–1973, and Stations 4602 - 4608, 5802 - 5808 and 7002 - 7008 for the period 1981–1983.

On the first three surveys an N50V net was deployed, but in the 1980s Nansen Pettersson bottles were used. Although the sampling gear differed, the relative proportions of dominant diatoms encountered is unlikely to have been seriously affected. The vertical hauls sampled from near the bottom or from 100 m to the surface in 1950 (Hart and Currie 1960), but from 50 m to the surface in later surveys (Kollmer 1963, Kruger in preparation). Kruger and Cruickshank (1982) have shown that most of the phytoplankton off South West Africa occurs in the top 50 m of the water column, so again the different starting depths for the tows should not severely influence comparability of results. The mesh size used by Hart and Currie (op. cit.) and Kollmer (op.

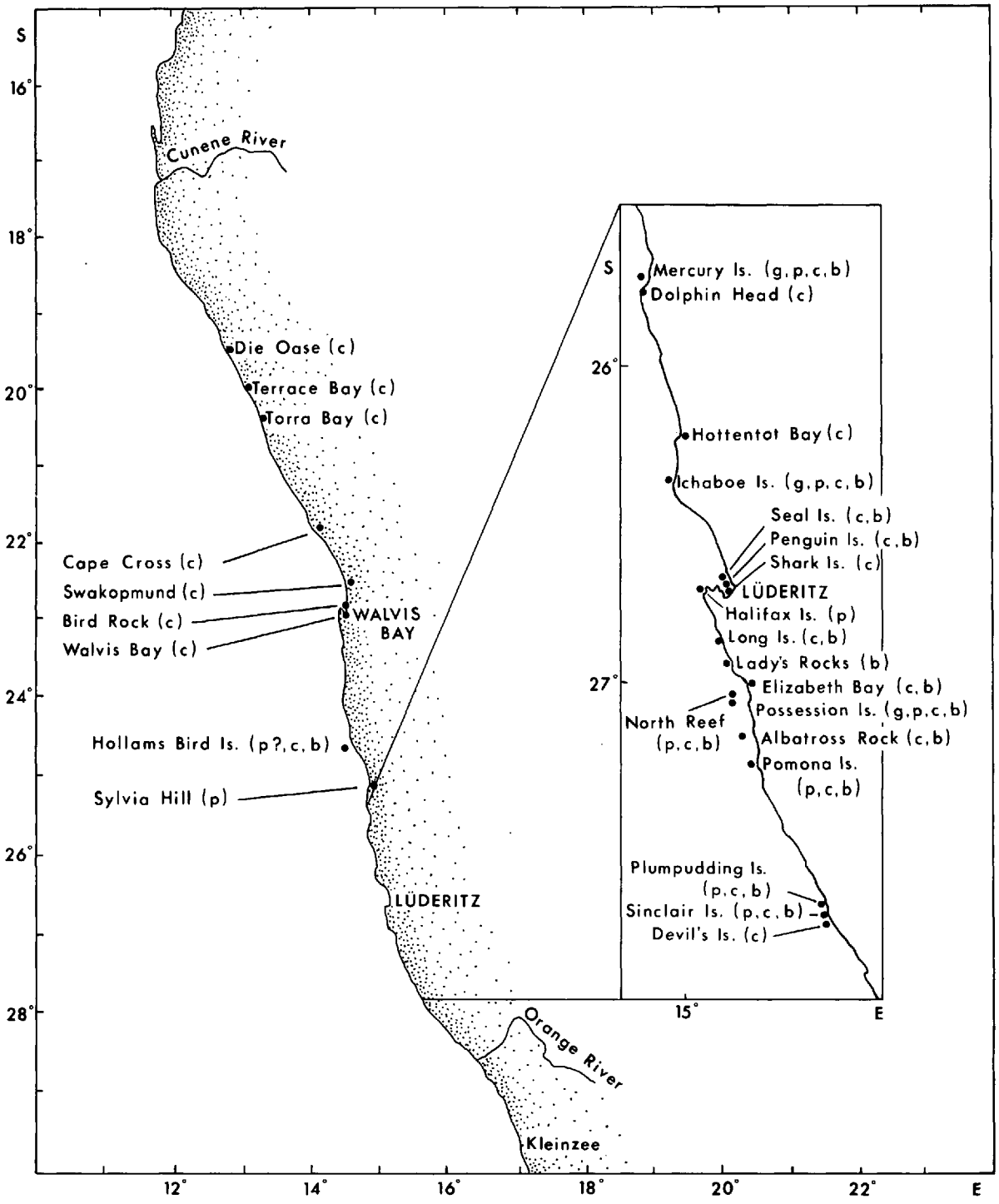

Fig. 4: Extant breeding colonies of Cape gannets (g), jackass penguins (p), Cape cormorants (c) and bank cormorants (b) off South West Africa (based on Cooper 1981, Cooper and Smith 1982, Cooper *et al.* 1982, Crawford, Shelton, Cooper and Brooke 1983 and Shelton *et al.* 1984)

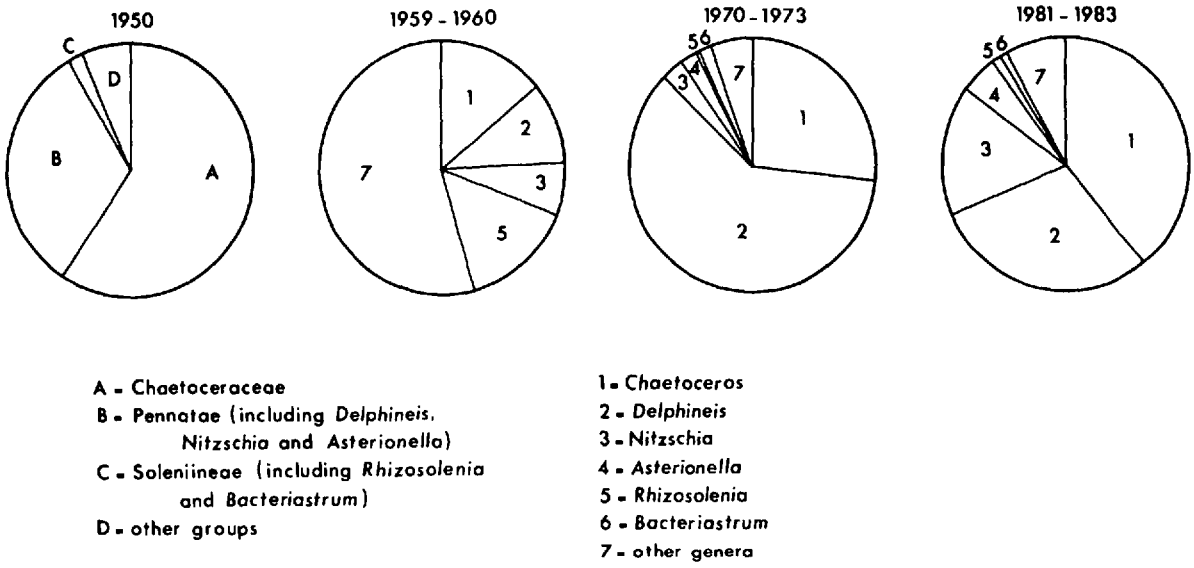

Fig. 5: Relative abundance of diatom taxa in the inshore region between c. 18°30' and 23°30'S in 1950, 1959-1960, 1970-1973 and 1981-1983 (1950 after Hart and Currie [1960]and1959-1960 after Kollmer [1963])

cit.) was 40 - 50 μm, but that in the 1970s was 80 μm (Kruger op. cit.). Most phytoplankters, with the exception of nanoplankton, would have been caught by both meshes. In the 1980s bottle samples were obtained at 0, 10, 20, 30 and 50 m at each station. Equal volumes from each were then combined to produce a composite sample for the depth range 0 - 50 m, which was used for analysis.

For the 1970s and 1980s only information for January, June and October was used, because these were the months most regularly sampled. The same months were extracted from Kollmer's (1963) analysis, but Hart and Currie (1960) only sampled in March and September–October. For each time period an overall picture was obtained by giving equal weight to the mean values for each month.

Counts were made of the organisms in the stomachs of 10 gobies of different size classes caught in the area between 23 and 25°S during the period 1979–1981.

Over the period 1972–1981 the caudal lengths (L_c) of 1 127 274 gobies occurring in catches of purse-seiners operating off South West Africa (Namibia) were measured for comparison with the size of gobies taken by seabirds. Further, the L_c of 2 977 gobies caught in Bongo nets (mesh size 300 - 1 000 μm) during egg and larva surveys, such as that described by Cruickshank *et al.* (1980), conducted off South West Africa between 1978 and 1980, was determined.

Between 1978 and 1982 food of the four seabirds was collected sporadically during research visits to the islands off South West Africa, and by Mr B. H. Smith at Ichaboe Island. Virtually all of the birds studied were adults at nests. Gannets and cormorants were made to regurgitate their stomach contents by pointing their heads downwards into a receiving container while gently massaging their abdomen. A stomach pump similar to that described by Randall (1983) was used to collect the stomach contents of penguins. For Cape gannets 116 samples were collected at Mercury Island, 967 at Ichaboe Island and 345 at Possession Island during the months November–April. Jackass penguins were sampled at Mercury (50), Ichaboe (43), Halifax (21) and Possession (45) islands during January and February; Cape cormorants were studied at Mercury (71), Ichaboe (255), North Long (1) and Possession (1) islands in the months November–March; bank cormorants were only sampled at Ichaboe Island (41) between March and July. The stomach contents were preserved in formalin and later sorted in the laboratory, where undamaged gobies were measured to the nearest millimetre below (L_c). Numerical frequency of occurrence was the method employed to express the findings.

Differences in the sizes of gobies eaten by the four seabirds were examined by grouping gobies into three size categories (0–39, 40–79 and 80–119 mm) and applying χ^2 contingency tables.

Table I: Analysis of stomach contents of ten gobies from the region between Walvis Bay and Lüderitz, January 1979–February 1981

Species	Frequency of occurrence (%)	Total number present	Proportion of total counted (%)
Chaetoceros spp.	30	20	0,28
Delphineis karstenii (= *Fragilaria karstenii*)	90	6 455	89,39
Nitzschia seriata	10	15	0,21
Coscinodiscus spp.	60	60	0,83
Actinocyclus ehrenbergii	30	15	0,21
Radiolaria spp.	20	6	0,08
Navicula spp.	10	5	0,07
Helicostomella subulata	10	5	0,07
Thalassiosira decipiens	10	5	0,07
Peridinium triquetrum	10	5	0,07
Diplopsalis lenticula	10	5	0,07
Coccolithophorid spp.	20	25	0,35
Blue-green algae	10	100	1,38
Phytoplankton subtotal	90	6 721	93,08
Copepod spp. (adults & nauplii)	50	50	0,69
Nyctiphanes capensis	60	32	0,44
Calanoid spp.	50	15	0,21
Clausocalanus sp.	10	1	0,01
Cirripedia spp. (larvae + nauplii)	40	20	0,28
Bivalve spp.	10	1	0,01
Euchaeta sp.	10	1	0,01
Unidentified zooplankton remains	10	380	5,26
Zooplankton subtotal	80	500	6,92
Total plankton	90	7 221	100,00
Fish remains (e.g. scales)	80*	214*	—
Small protozoan cells	100*	262 495*	—

*Excluded from totals

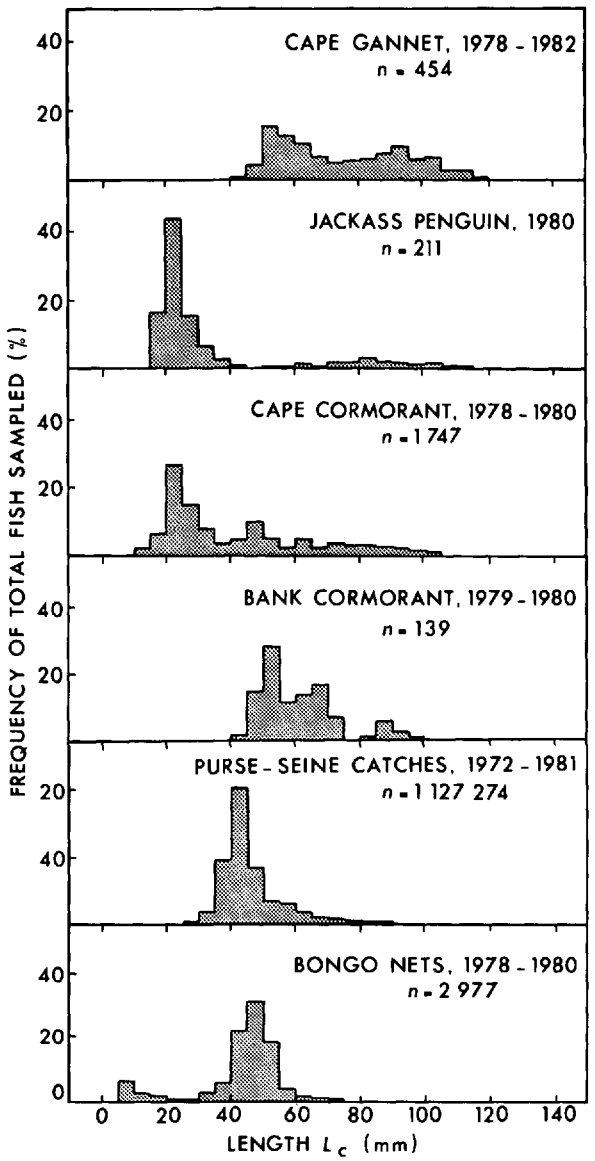

Fig. 6: Size distribution of gobies in the diets of Cape gannets, jackass penguins, Cape cormorants and bank cormorants, and in the catches of purse-seine and Bongo nets off South West Africa, 1972–1981

RESULTS

The relative contributions of various diatom taxa to counts of phytoplankton off South West Africa between *c.* 18°30'S and 23°30'S and from the coast to about 60 miles offshore are illustrated for the four periods 1950, 1959–1960, 1970–1973 and 1981–1983 in Figure 5.

In 1950 the Chaetoceraceae and "Pennatae" [sic] of Hart and Currie (1960), including the genera *Chaetoceros* (Chaetoceraceae) and *Delphineis (Fragilaria), Asterionella* and *Nitzschia* ("Pennatae"), accounted for 91,5 per cent of the diatom count. The Chaetoceraceae alone accounted for almost 60 per cent.

In 1959–1960 *Chaetoceros* spp. and *Delphineis karstenii* accounted for 24,4 per cent of the overall count, compared with 87,4 per cent in 1970–1973 and 68,6 per cent in 1981–1983. Kollmer (1963) provided information only for ". . . some big-celled or chain-forming species . . .", but he gave no details for 54,2 per cent of the counts for 1959–1960.

Table II: Diets of Cape gannets *Morus capensis*, jackass penguins *Spheniscus demersus*, Cape cormorants *Phalacrocorax capensis* and bank cormorants *P. neglectus* off South West Africa at different time intervals, 1957–1982

Avian predator	Cape gannet			Jackass penguin		Cape cormorant			Bank cormorant
Date of study	1957–1958	1958–1959	1978–1982	1957–1958	1980	1957–1958	1958–1959	1978–1980	1979–1980
Source of information	Matthews (1961)	Matthews & Berruti (1983)	This study	Matthews (1961)	This study	Matthews (1961)	Matthews & Berruti (1983)	This study	This study
Study area	Walvis Bay vicinity	Walvis Bay vicinity	Mercury, Ichaboe & Possession islands	Walvis Bay vicinity	Mercury, Ichaboe, Halifax & Possession islands	Walvis Bay vicinity	Walvis Bay vicinity	Mercury, Ichaboe, North Long & Possession islands	Ichaboe Island
Number of birds examined	155	240	1 437	19	114	210	250	328	41
Food item	Contribution to total of all food items examined (% by numbers)								
Pilchard *Sardinops ocellata*	85	99	< 1	83	—	76	76	< 1	—
Anchovy *Engraulis capensis*	—	—	53	—	< 1	—	2	16	—
Horse mackerel *Trachurus trachurus*	10	1	< 1	6	—	18	14	< 1	—
Chub mackerel *Scomber japonicus*	—	< 1	< 1	—	—	—	—	—	—
Snoek *Thyrsites atun*	—	< 1	2	—	< 1	—	—	< 1	—
Goby *Sufflogobius bibarbatus*	—	—	17	—	56	—	—	80	95
Saury *Scomberesox saurus*	—	—	14	—	< 1	—	—	< 1	—
Harder *Liza richardsoni*	—	< 1	< 1	—	—	—	< 1	—	—
Hake *Merluccius* spp.	—	—	6	—	4	< 1	—	3	5
Sole *Austroglossus microlepis*	—	—	< 1	—	—	—	< 1	1	—
Other teleosts	5	—	4	—	< 1	1	< 1	< 1	—
Cephalopods	—	—	< 1	11	40	1	—	< 1	—
Crustaceans and polychaetes	—	—	< 1	—	< 1	3	7	< 1	< 1

The diet of gobies sampled in 1979–1981 (Table I) contained numerically 93,08 per cent phytoplankton (mostly diatoms) and 6,92 per cent zooplankton. However, some small protozoan species were also abundant numerically. Zooplankton was present in 80 per cent of the stomachs examined and phytoplankton in 90 per cent. *Delphineis* (= *Fragilaria*) *karstenii* was the most abundant phytoplankton species and euphausiids and copepods were the dominant zooplankton groups.

Most gobies sampled from purse-seine catches ranged between 45 and 60 mm long, fish longer than 75 mm contributing less than 5 per cent (Fig. 6). Gobies caught by Bongo nets were seldom longer than 60 mm, most falling in the range 40–55 mm. Very few of L_c 20–30 mm were sampled (Fig. 6).

From 1978 to 1982 pilchards were of little consequence, and gobies numerically the most important prey, in the stomach contents of jackass penguins, Cape cormorants and bank cormorants sampled at islands off the South West African coast (Table II). Gobies were also eaten by Cape gannets. They were particularly prominent in the bird diets at islands north of Lüderitz (Mercury and Ichaboe), but less so at those further south (Halifax and Possession) — see Table III.

Table III: Diets of Cape gannets *Morus capensis*, jackass penguins *Spheniscus demersus*, Cape cormorants *Phalacrocorax capensis* and bank cormorants *P. neglectus* at different islands off South West Africa, 1978–1982

Avian predator	Cape gannet			Jackass penguin				Cape cormorant		Bank cormorant
Island	Mercury	Ichaboe	Possession	Mercury	Ichaboe	Halifax	Possession	Mercury*	Ichaboe	Ichaboe
Period of study	November 1978 – February 1982	November 1978 – February 1981	December 1978 – February 1982	February 1980	February 1980	January 1980	January 1980	November 1978 – February 1980	November 1978 – March 1980	May 1979 – March 1980
Number of birds examined	116	967	345	50	43	21	45	71	225	41
Food item	Contribution to total of all food items examined (% by numbers)									
Pilchard *Sardinops ocellata*	< 1	< 1	< 1	—	—	—	—	—	< 1	—
Anchovy *Engraulis capensis*	69	36	77	—	< 1	—	< 1	—	23	—
Horse mackerel *Trachurus trachurus*	4	1	< 1	—	—	—	—	—	< 1	—
Chub mackerel *Scomber japonicus*	1	< 1	< 1	—	—	—	—	—	—	—
Snoek *Thyrsites atun*	5	3	< 1	—	—	—	< 1	—	< 1	—
Goby *Sufflogobius bibarbatus*	10	28	< 1	73	37	—	3	96	72	95
Saury *Scomberesox saurus*	4	19	7	—	< 1	—	1	—	< 1	—
Mullet *Liza richardsoni*	< 1	< 1	< 1	—	—	—	—	—	—	—
Hake *Merluccius* spp.	5	9	3	< 1	19	—	—	—	4	5
Sole *Austroglossus microlepis*	< 1	< 1	—	—	—	—	—	4	—	—
Other teleosts	< 1	1	11	—	—	1	< 1	—	< 1	—
Cephalopods	< 1	1	< 1	26	44	99	93	< 1	< 1	—
Crustaceans and polychaetes	—	< 1	—	< 1	< 1	—	< 1	—	< 1	< 1

*In an independent study at Mercury Island in 1978 (Cooper 1985), the regurgitations of 19 Cape cormorants contained 939 gobies and one anchovy

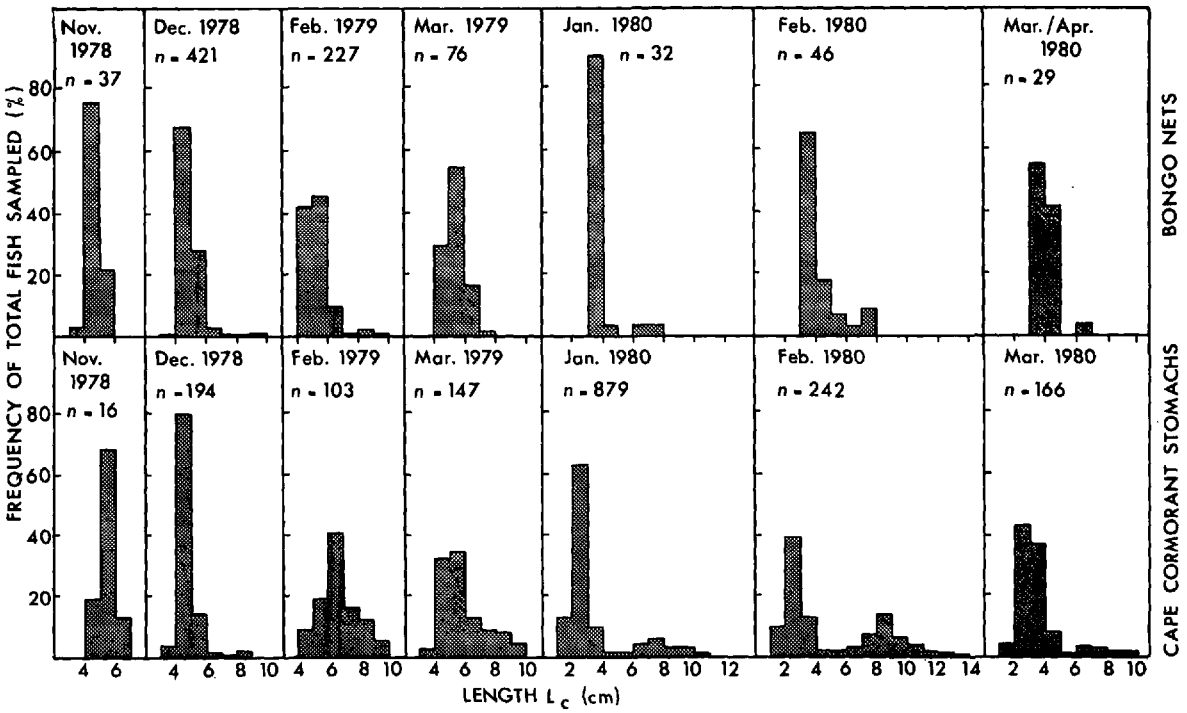

Fig. 7: Size distribution of gobies in the catches of Bongo nets and the diet of Cape cormorants in particular months, November 1978–April 1980

No gobies smaller than 40 mm L_c were found in the stomach contents of Cape gannets; 44 per cent of those measured were between 50 and 70 mm, and 35 per cent longer than 85 mm (Fig. 6). Jackass penguins and Cape cormorants fed on a wide range of length classes, but gobies less than 35 mm dominated the diets of both (Fig. 6). Cape cormorants consumed reasonable numbers of gobies of *c.* 45 mm, but few fish of this size category were found in the stomach contents of penguins. However, penguins ate small amounts of gobies of *c.* 80 mm long. Limited information suggests that gobies eaten by bank cormorants fell primarily within the length range 45–70 mm (Fig. 6). The overall mode for Cape gannets and bank cormorants was between 50 and 55 mm and that for jackass penguins and Cape cormorants between 20 and 25 mm.

Results of χ^2 contingency tests showed significant differences in the sizes of gobies eaten by the four seabirds (Table IV). The most disparate pairings were the gannet and Cape cormorant and the gannet and penguin. The most similar were the penguin and Cape cormorant and the gannet and bank cormorant.

There was inter-annual variation in the size of gobies in stomach contents of Cape cormorants (Fig. 7). Fish between 40 and 65 mm dominated the diet between November 1978 and March 1979, but these size classes were scarce and fish of smaller and greater length relatively more abundant in February and March 1980. In December 1978 and March 1979 the sizes of gobies caught by Bongo nets were similar to those eaten by Cape cormorants, but in 1980 Cape cormorants tended to feed on smaller fish than those sampled by this gear (Fig. 7).

Table IV: Results of χ^2 contingency tests comparing the size composition of gobies in the diets of six seabird pairings

Species 1	Species 2	χ^2	d.f.	*P*
Cape gannet	Cape cormorant	743	2	< 0,001
Cape gannet	Jackass penguin	431	2	< 0,001
Cape cormorant	Bank cormorant	221	2	< 0,001
Jackass penguin	Bank cormorant	175	2	< 0,001
Cape gannet	Bank cormorant	51	2	< 0,001
Jackass penguin	Cape cormorant	15	2	< 0,001

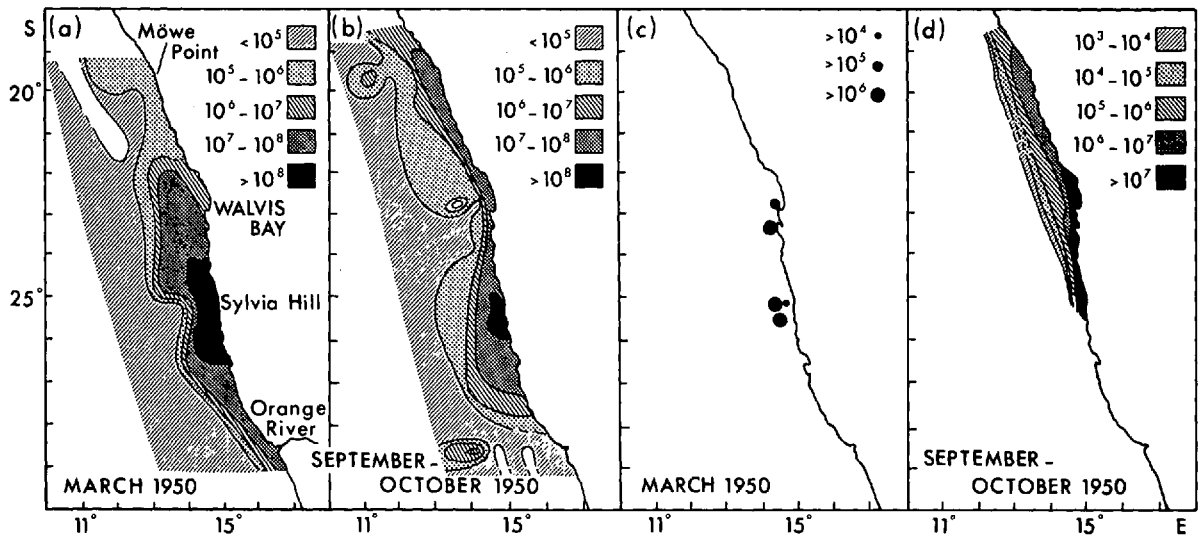

Fig. 8: Distributions of (a) and (b) *Chaetoceros* spp. and (c) and (d) *Delphinais karstenii* off South West Africa, March and September-October 1950 (after Hart and Currie 1960)

DISCUSSION

Partitioning of the goby resource by the four avian predators

Small gobies, of the size caught by Bongo nets, purse-seiners and most frequently by jackass penguins and Cape cormorants, have a light colouration typical of pelagic fish, whereas larger gobies have a darker colouration more characteristic of fish species living close to the sea bottom (RAC personal observation). Cape gannets feed by plunging and submerge for less than six seconds (Duffy *et al.* 1984), but are known to scavenge hakes *Merluccius* spp. and other fish from demersal trawlers (Sinclair 1978, Batchelor 1982, Batchelor and Ross 1984, Cooper 1984). Off South West Africa, demersal trawlers bring large gobies to the surface where they either escape through the meshes of the net or are discarded over the side (RAC personal observation), and in the present study stomachs of gannets often contained species, such as hake, West Coast sole *Austroglossus microlepis*, gurnard *Chelidonichthys* spp. and rattails (Coryphaenoididae), that are commonly caught by bottom trawl (Botha 1980). It is possible that the large gobies (> 80 mm) eaten by Cape gannets were scavenged from demersal trawlers. These large gobies would otherwise most likely be available to gannets because of their depth in the water column during the day and possibly also because of their cryptic colouration.

Cape gannets fed frequently on gobies of 45–70 mm L_c (Fig. 6), a length range at the upper end of the spectrum of fish caught by purse-seine and Bongo nets. In each of four studies conducted off southern Africa during the period 1953–1979, the mean length of prey taken by Cape gannets was greater than that taken by jackass penguins and Cape cormorants (Davies 1955, 1956, Matthews 1961, Crawford and Shelton 1981). Gannets tend to forage further offshore than the other two species (Cooper 1984). Gobies shorter than about 50 mm are presumably available to gannets but energetically unrewarding to exploit for a bird of mean mass as high as the gannet's 2,6 kg. In contrast, the mean mass of Cape cormorants is only 1,2 kg (Maclean 1985). Gobies have a low fat content at 1,5 per cent by weight but up to 15,7 per cent crude protein (Cruickshank 1982), making them less rewarding energetically than other pelagic fish.

Despite relatively small numbers measured, the similarity for some months in sizes of goby taken by Cape cormorants and those caught by Bongo nets (Fig. 7), which sampled to a depth of about 50 m, suggests that Cape cormorants feed on whatever gobies are available in the pelagic zone. Gobies of *c.* 80 mm were seldom eaten by Cape cormorants, though this size group formed a minor secondary peak in the diet of jackass penguins, a species able to submerge for longer periods and to forage at greater depths (Duffy *et al.* 1984).

Predation by jackass penguins and Cape cormorants was heaviest on gobies less than 35 mm L_c. The slightly larger size of fish in purse-seine and Bongo catches (35–55 mm) may have resulted from these nets sampling beyond the normal foraging range of penguins and Cape cormorants, which generally is within 10–15 km of the mainland (Siegfried, Frost *et al.* 1975, Siegfried, Williams *et al.* 1975, Cooper 1984). Gobies may also have grown in the interval between the months (November–March) in which penguins and Cape cormorants were sampled and those (February–April and July–September) in which purse-seine fishing was conducted (Butterworth 1983).

Feeding of the Cape cormorant appears to be morphologically adapted to capturing small and active prey, whereas the bank cormorant is a generalized feeder and takes both a larger meal size and mean size of prey than the Cape cormorant (Burger 1978). In support of this observation, the gobies eaten by bank cormorants during this study were considerably larger than the modal size of gobies found in the stomach contents of Cape cormorants, and also that in stomachs of penguins (Fig. 6). Similarly, at Mercury Island in November 1978, bank cormorants ate significantly larger gobies than did Cape cormorants (Cooper 1985).

Bank cormorants are bottom feeders, diving for a mean of 45 seconds (Cooper 1984). The gobies they select appear to be generally unavailable to penguins and Cape cormorants. Larger gobies are probably most often at depths in the water column beyond the normal foraging range of the last two species, but apparently they do occur irregularly in the pelagic zone, possibly offshore, because gobies of similar size are taken by Cape gannets, and on occasion by purse-seine and Bongo nets (Fig. 6).

Altered trophic flow in the Walvis Bay — Lüderitz region

Off South West Africa, diatoms of the genera *Delphineis* and *Chaetoceros* were dominant in the stomach contents of adult pilchards during 1971–1972 (King and Macleod 1976) and of larval, juvenile and adult gobies during 1972–1974 (O'Toole 1978). Barber and Haedrich (1969) found *Delphineis karstenii* and *Coscinodiscus* spp. to dominate the diet of juvenile gobies, and Ryther (1969) also drew attention to the importance of the large, chain-forming *Delphineis* in the food of gobies. D'Arcangues (1977), however, found mainly copepods and euphausiids in the stomachs of the juvenile and adult gobies that she studied. The present study (Table I) has confirmed that *D. karstenii*, *Chaetoceros* spp. and *Coscinodiscus* spp. continue to be prominent in the stomach contents of gobies off South West Africa. The distribution of these diatoms has been documented by Hart and Currie (1960), whose findings are reproduced in Figure 8. It is evident that both *D. karstenii* and *Chaetoceros* spp. are most abundant in the region between 22°S (just north of Walvis Bay) and Lüderitz (26°40'S). From Figure 1 it is also evident that this is generally the region of highest phytoplankton concentration.

Prior to 1970 the bulk of the purse-seine catches off South West Africa, which were dominated by pilchard (Crawford, Shelton and Hutchings 1983), were made between *c.* 22 and 25°S (Fig. 2). The pilchard resource off South West Africa collapsed from an estimated biomass of 6,8 million metric tons during the years 1963–1966 (Newman 1970) to 1,4 million tons by 1971 and 0,05 million tons by 1979 (Butterworth 1983). Distributions of purse-seine catches (Cram 1977, Cruickshank 1983a, b, Fig. 2), and of eggs of pilchards (Matthews 1964, King 1977, Le Clus and Kruger 1982) suggest that this collapse was accompanied by a contraction in the range of pilchard towards the north.

Following the collapse of the pilchard resource it seems likely that much of especially the primary production would have become available to other consumers occurring south of 22°S, particularly those able to utilize chain-forming diatoms such as *Delphineis karstenii* and *Chaetoceros* spp. Indeed, during the early 1970s, immediately after a five-fold reduction in the biomass of pilchard (Crawford, Shelton and Hutchings 1983), the dominance of diatoms of the genera *Delphineis* and *Chaetoceros* in the inshore phytoplankton near Walvis Bay was considerably more pronounced than in 1959–1960 or 1981–1983 (Fig. 5).

Comparison with 1950 is difficult, because months of sampling were not the same and Hart and Currie (1960) provided information only for species groups. Those groups ("Pennatae" [sic] and Chaetoceraceae) containing the genera *Delphineis* and *Chaetoceros* dominated the diatom flora of 1950. Interestingly, guano production off South West Africa, which may be used as an index of pelagic fish abundance (Crawford and Shelton 1978), showed a marked trough during the late 1940s and early 1950s (Crawford, Shelton and Hutchings 1983), suggesting that biomass of pilchard may also have been low at that time.

During the years 1978–1981, acoustic surveys indicated that gobies were abundant inshore between 22°S and Lüderitz (Cruickshank *et al.* 1980, Cruickshank 1982, Fig. 3). It appears likely that the species

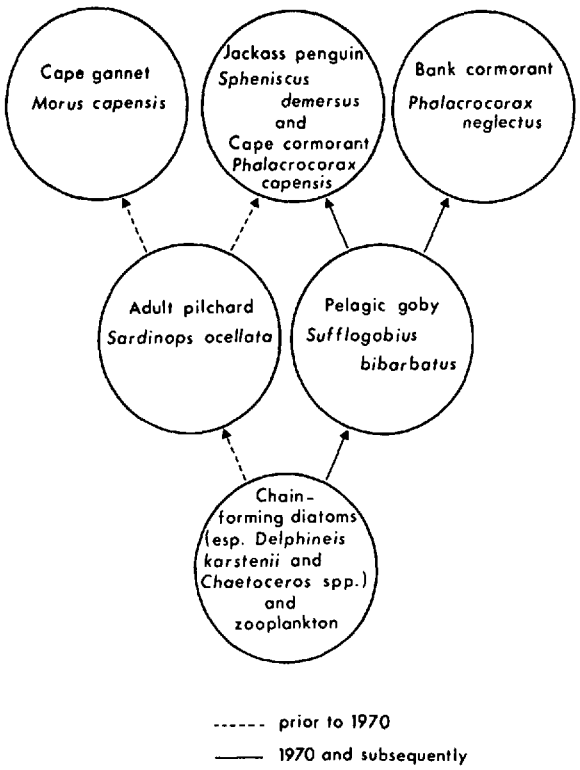

Fig. 9: Likely alteration in trophic flow thought to have occurred in the intense perennial upwelling region north of Lüderitz

at least partially replaced the pilchard in these waters.

In the years 1957–1959, pilchard dominated the diet of Cape gannets, jackass penguins and Cape cormorants sampled near Walvis Bay (Matthews 1961, Matthews and Berruti 1983, Table II). Gobies were absent from the stomach contents and were first reported from waters off South West Africa only in the 1960s (Barber and Haedrich 1969). In spite of small-meshed (11-mm stretched mesh) nets being used by purse-seiners initially from 1963 and extensively from 1968 (Cram 1977, Schülein *et al.* 1978, Butterworth 1983), gobies were not recorded in purse-seine catches until 1972. The species has contributed a by-catch in all subsequent years, leading previous authors (O'Toole 1978, Cooper 1981) to suggest that its population size had increased. During the periods 1972–1974 and 1978–1981, pelagic gobies formed 53 and 59 per cent respectively of all small fish caught incidentally in Bongo nets on egg and larva surveys off South West Africa (O'Toole 1976, Cruickshank 1982). During 1972–1974 they contributed 61 per cent of all larvae collected (O'Toole 1978).

Since the 1950s, when the South West African pilchard stock was still at a high level (Newman 1970), numbers of gannets have decreased markedly at all three breeding localities off South West Africa (Crawford, Shelton, Cooper and Brooke 1983). Conversely, at islands north of Lüderitz, there have been large increases in numbers of penguins (Shelton *et al.* 1984), Cape cormorants (Cooper *et al.* 1982) and bank cormorants (Cooper 1981). These increases may be attributed to the ability of penguins and cormorants to utilize efficiently the large resource of small gobies occurring in the pelagic zone, or to dive sufficiently deep to exploit gobies of a bigger size (Table II). Cape gannets do neither, but feed on gobies only when larger fish that are not normally available are occasionally brought to the surface naturally or by demersal trawlers.

During 1978–1982, gobies were seldom eaten by seabirds at Halifax and Possession islands (Table III), supporting the findings of acoustic surveys that gobies are generally scarce south of Lüderitz (Cruickshank *et al.* 1980, Cruickshank 1982, Fig. 3). At all breeding localities off South West Africa south of Lüderitz, penguin numbers have decreased (Shelton *et al.* 1984). Penguins being flightless have a limited foraging range, especially during breeding (Frost *et al.* 1976). The decreases in numbers of penguins south of Lüderitz have probably resulted from a poor availability of food.

Gobies have not been intensively sought by commercial purse-seiners, so virtually their entire production has been available to predators. In addition to seabirds, Cape fur seals *Arctocephalus pusillus* have proliferated in the Lüderitz vicinity in recent years (Butterworth *et al.* in press). In 1977 gobies were the most important food of seals sampled between Cape Cross and Lüderitz (Shaughnessy 1980).

The probable change in trophic flow in the intense perennial upwelling system located between Walvis Bay and Lüderitz that resulted from collapse of the pilchard resource is illustrated in Figure 9. The pilchards traditionally located south of Walvis Bay were the larger, older schools (Schülein 1971, Cram 1977), and the short food chain may have been partially responsible for the large biomasses (*c.* 7 million tons) recorded during the 1960s (Newman 1970). The nearest this stock size has been approached by a fish resource in the South-East Atlantic is the *c.* 4 million tons for horse mackerel *Trachurus trachurus* off northern South West Africa during the early 1980s (Babayan *et al.* 1983).

Large gannet colonies historically thrived on the abundant pilchard resource (Crawford, Shelton,

Cooper and Brooke 1983). The severe pilchard decline appears to have triggered an expansion of the goby population, in turn leading to greatly increased numbers of bank cormorants. Penguins and Cape cormorants have been able to forage effectively on both pilchards and gobies, but gannets have not been as effective in foraging for gobies and consequently populations of this species have declined.

ACKNOWLEDGEMENTS

We are grateful to Mr B. H. Smith, the headman of Ichaboe Island, and technical staff of the Sea Fisheries Research Institute for assistance with collection and analysis of samples. The help of the captains and crew of the Institute's research vessels, used for transport to the islands and for the survey cruises, is also gratefully acknowledged. Messrs A. L. Batchelor, A. Berruti and J. Cooper and Dr L. V. Shannon are thanked for commenting on the draft manuscript.

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