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DIETS OF THE WHITE-CHINNED PETREL AND SOOTY SHEARWATER IN THE SOUTHERN BENGUELA REGION, SOUTH AFRICA[1]

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Abstract. The White-chinned Petrel (*Procellaria aequinoctialis*) and Sooty Shearwater (*Puffinus griseus*) are two of the most abundant pelagic seabirds in the southern Benguela region, off the west coast of South Africa. Stomach samples collected at 3-month intervals during 2 years revealed that White-chinned Petrels fed on trawler offal throughout the year, whereas Sooty Shearwater diets varied temporally between three species of pelagic schoolfish. Crustaceans were minor prey of both species, and squids were eaten only by White-chinned Petrels.

Trawlers influenced the distribution of White-chinned Petrels more than that of Sooty Shearwaters. Dietary differences between the two seabirds result from morphological adaptations related to different foraging methods employed by the birds.

Key words: White-chinned Petrel; Sooty Shearwater; diet; morphology; foraging methods; trawler offal.

INTRODUCTION

The White-chinned Petrel, *Procellaria aequinoctialis*, and Sooty Shearwater, *Puffinus griseus*, (Order: Procellariiformes) are two of the most abundant pelagic seabirds in the Benguela region off the west coast of South Africa (Duffy et al. 1987). White-chinned Petrels breed on the Falkland Islands, other islands in the South Atlantic and South Indian Oceans, and around the coast of New Zealand (Murphy 1936). Sooty Shearwaters breed on islands around Cape Horn, Chile, New Zealand, and Australia (Brown et al. 1981). Between May and September both species disperse from their breeding areas to the continental shelf of the Benguela region (Summerhayes et al. 1974).

This paper reports on my investigation of differences between the diets and distributions of White-chinned Petrels and Sooty Shearwaters at sea in the southern Benguela region from 1984 to 1986. White-chinned Petrel diets have been studied at breeding sites (Imber 1976, Croxall and Prince 1980), but not at sea. Sooty Shearwater diets have been studied at sea (Sealy 1973, Wiens and Scott 1975, Baltz and Morejohn 1977, Ainley and Sanger 1979, Brown et al. 1981, Ogi 1984, Chu 1984, Sanger 1987). However, nothing is known of the diets of either of these seabirds in the Benguela region. Diet separation of seabirds at or near breeding sites has been well-documented (e.g., Ashmole and Ashmole 1968; Sealy 1973; Ainley and Sanger 1979; Croxall and Prince 1980, 1981; Hunt et al. 1981; Harrison et al. 1983), but partitioning of food resources between nonbreeding pelagic seabirds at sea has received less attention (Baltz and Morejohn 1977, Brown et al. 1981).

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METHODS

COLLECTION OF SAMPLES

Complete stomachs were removed from nonbreeding birds shot at sea in the southern Benguela region (32°40′S to 34°30′S; 17°30′E to 18°40′E, Fig. 1). Sampling took place at 3-month intervals throughout 1984, and every 4 months in 1985. Sample sizes are given in Figure 3. Only actively-feeding birds and those resting on the water were shot, as most birds shot while flying had empty stomachs (Duffy and Jackson 1986). Sampling was therefore biased in favor of birds that had recently fed, and feeding frequency could not be estimated from the stomach fullness of birds sampled. Birds were collected from 20 feeding groups and 39 groups of birds resting on the water.

ANALYSIS OF SAMPLES

Stomachs (proventriculi) and gizzards (ventriculi) were removed immediately and preserved separately in 70% ethyl alcohol for 1 to 2 weeks before analysis. These two gastric compartments are separated by a narrow isthmus in Procellariiformes (Ziswiler and Farner 1982). The hard parts of indigestible prey accumulate in the gizzard (Furness 1985).

Prey items were identified to species using fish otoliths, squid beaks, and crustacean exoskeletons. Three methods of analysis were used:

Percentage frequency of occurrence. Both stomach and gizzard contents were used in the analyses. Rates of erosion of hard prey remains in the gizzards of the two species were assumed to be the same. Specimens with empty stomachs were excluded from the analyses.

Overall numerical abundance. Total numbers of individual prey items in all stomachs of each species collected during each sampling period were counted, and the proportional contribution of each prey type was calculated. Fish numbers were estimated by counting left and right otoliths in the proventriculus, and the higher count was taken as the number of fish eaten during the most recent meal. To reduce bias resulting from retention of otoliths, only otoliths that showed no signs of wear were counted in analyses of gizzard contents. Whole crustaceans, crustacean heads, and squid buccal masses were counted, and parts of these organisms noted as such. Squid beaks were divided into upper and lower halves, and the higher count taken as the number of squid eaten. Individual prey items could not be counted in the "offal," "squid flesh," and "crustacean remains" categories.

Percentage weight. Once separated into categories, prey items were dried to constant mass at 50°C, and weighed. The contribution of each prey item to the diet was expressed as a percentage of the total dry weight of all prey items from all stomach samples collected. Squid beaks are indigestible and were therefore excluded from the analyses.

Otolith lengths were measured through the graticule eyepiece of a binocular microscope with a 10× objective. Equations describing the relationship between otolith length and fish length were used to calculate caudal lengths of cape anchovy, *Engraulis capensis* (Batchelor and Ross 1984), lantern-fish, *Lampanyctodes hectoris,* and light-fish, *Maurolicus muelleri* (R. Prosch, unpubl. data), and total lengths of cape hake, *Merluccius capensis* or *M. paradoxus* (Botha 1971). No attempt was made to reconstruct original

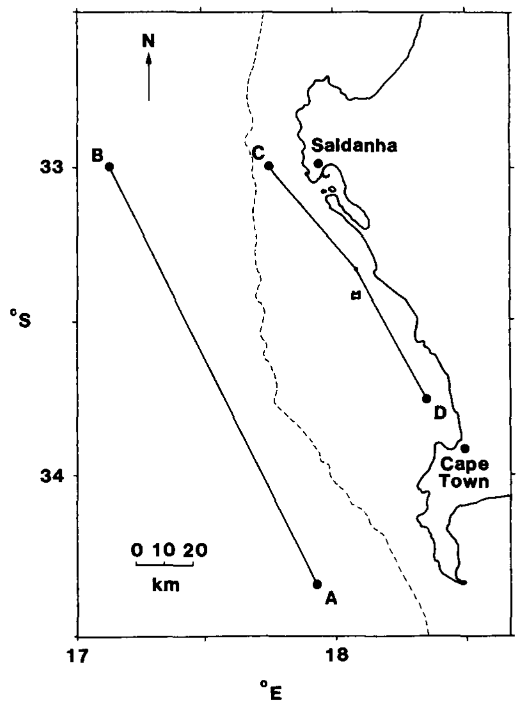

FIGURE 1. Aerial transects (AB and CD) operated between April 1985 and February 1986 in the southern Benguela region. The dashed line indicates the 200-m depth contour.

masses of individual prey from otolith lengths, as differential erosion rates of the otoliths of major prey species of the two seabirds may prevent meaningful dietary comparisons.

The offal category comprised fish heads and intestines scavenged from demersal trawlers operating in the study area. To avoid overestimation of the importance of offal in the diets, fish remains were only placed in this category if otoliths of the commercially exploited cape hake or of *Coelorhynchus fasciatus* (a by-catch species) were present in the stomach or gizzard.

DISTRIBUTION AND FEEDING ASSOCIATIONS

For each collection, position, sea surface temperature, and depth were recorded. Numbers and species of other avian, mammalian, and fish predators were noted. Major prey species were inferred from analyses of the stomach contents of birds shot at each group.

Bird counts were made from "Albatross" twin-engined coastal patrol aircraft on 19 April, 5 June, 16 July, 20 August, 9 October, and 9 December

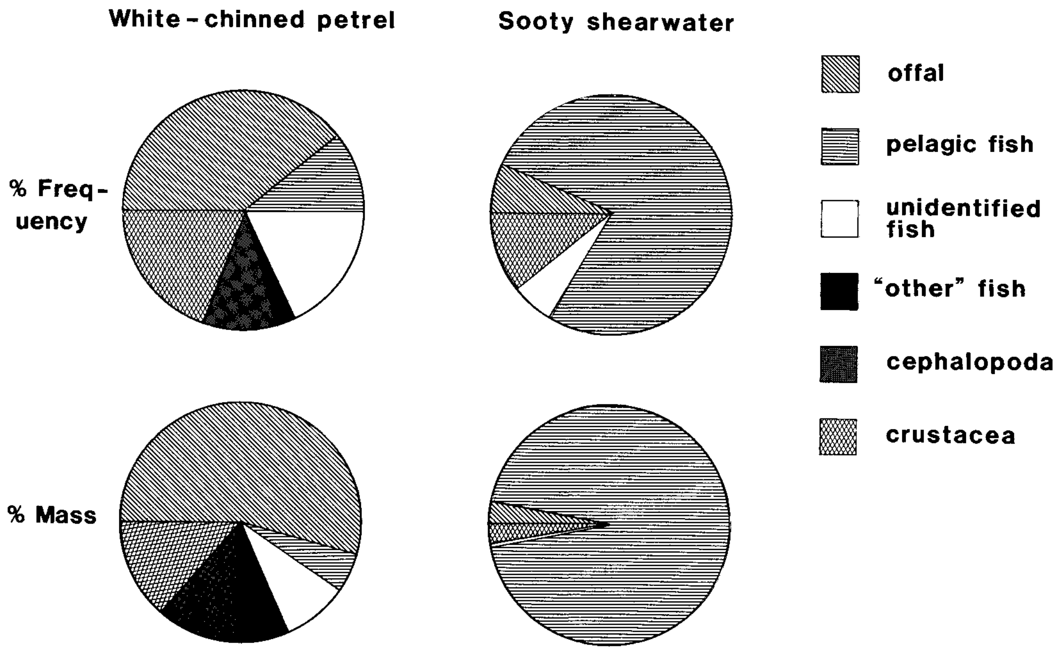

FIGURE 2. Percentage frequency of occurrence and relative importance by dry mass of major prey categories in the stomachs of 106 White-chinned Petrels and 42 Sooty Shearwaters shot in the southern Benguela region, April 1984 to November 1985.

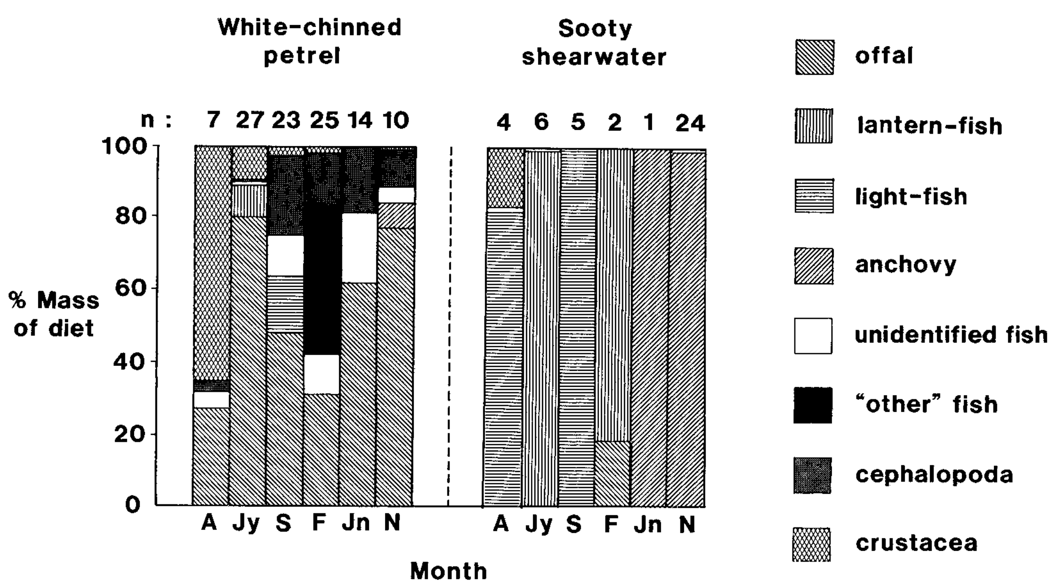

FIGURE 3. Temporal variation in the composition of the diets of White-chinned Petrels and Sooty Shearwaters in the southern Benguela region, April 1984 to November 1985.

1985, and on 12 February 1986. The aircraft flew at an altitude of 125 m, at an average speed of 260 km·hr^{-1} while two observers counted all birds seen within two continuous 100-m-wide strips on opposite sides of the aircraft. All trips were made on the same flight path with an offshore leg of 168 km (Fig. 1, AB) and an inshore leg of 101 km (Fig. 1, CD). When trawlers were sighted, the aircraft deviated to fly a separate transect passing within 5 km of each ship. The regular flight path was then resumed by the most direct route. The total length of transects completed along the regular flight path therefore varied between trips. Data from transects in the proximity of trawlers were analyzed separately from data collected along the regular flight path. The 5-km limit was chosen to encompass the theoretical radii within which White-chinned Petrels (3.8 km) and Sooty Shearwaters (0.6 km) are attracted to ships (Ryan and Moloney, unpubl.). The radii of attraction were calculated using ship-based estimates of relative densities of each species at and between demersal trawl stations (Ryan and Moloney, unpubl.).

RESULTS

DIET

A total of 129 White-chinned Petrels and 60 Sooty Shearwaters were shot, yielding 106 and 42 stomach samples respectively, and 120 and 48 gizzard samples. Some stomachs and/or gizzards were empty. The results of analyses of these samples are presented in Tables 1 and 2. Eighteen prey types were identified.

Fish. Fish was the most important prey item by percentage frequency of occurrence, numerical abundance, and percentage mass in the stomachs of both White-chinned Petrels and Sooty Shearwaters (Fig. 2), but there was little overlap between the two birds in the species of fish eaten. The number of White-chinned Petrel stomachs containing cape hake, rat-tail, and offal was significantly higher than the corresponding figure for Sooty Shearwaters ($\chi^2 = 18.09$, $P < 0.001$, df = 1). Trawler offal (cape hake and rat-tail remains are included in this category) was the dominant food by mass of White-chinned Petrels (Fig. 2). Small pelagic fish formed the bulk of Sooty Shearwater diets by mass. Significantly more Sooty Shearwater than White-chinned Petrel stomachs contained lantern-fish, light-fish, and cape anchovy ($\chi^2 = 26.21$, $P < 0.001$, df = 1). Larger pelagic fish such as redeye round-herring, *Etrumeus terres,* and maasbanker, *Trachurus capensis* ("other fish" category, Fig. 2), occurred infrequently in White-chinned Petrel stomachs, and were not found in the stomachs of Sooty Shearwaters.

The mean total length of cape hake eaten by White-chinned Petrels was 190.6 mm (SD = 96.5, range = 71.3–352.0, $n = 7$). Hake otoliths found in the stomachs of Sooty Shearwaters were badly broken, and could not be measured. Cape hake of the size eaten by White-chinned Petrels swarm in surface waters (Cram and Schulein 1974), where they are vulnerable to birds. However, intact vertebral columns of hake were never found in stomach samples which contained hake heads. Heads and intestines of hake are discarded from trawlers (FitzPatrick Institute, unpubl. data), so it is likely that such fish heads were taken by birds scavenging behind trawlers. Rat-tail have never been recorded in surface waters.

Anchovy, light-fish, and lantern-fish otoliths from the gizzards of both bird species were significantly shorter than otoliths from the birds' stomachs (*t*-test of paired means, $t_7 = 4.66$, $P < 0.01$, $n = 8$). Such erosion of otoliths in the gizzards indicates that gizzard contents should not be used in analyses of the relative importance of prey by reconstructed mass in diet studies of members of the Procellariiformes. Otoliths in the birds' gizzards had probably been retained for longer periods than the otoliths found in their stomachs. This is supported by evidence for retention of squid beaks in seabird stomachs (Furness et al. 1984).

Cephalopods. The remains of squid flesh were found only in the stomachs of White-chinned Petrels. The importance of squid by percentage frequency of occurrence and percentage weight may be overrepresented in Table 1, because of the less digestible nature of this prey (Wilson et al. 1985, Jackson and Ryan 1986). Even if overrepresented, squid is unimportant in the diet of the White-chinned Petrel in the southern Benguela region.

Many more squid beaks were present in the gizzards of the birds than in their stomachs (Tables 1 and 2). More than 98% of the squid beaks present in the gizzards of the birds were very worn, and could have been ingested 50 days or more before sampling took place (Furness et al. 1984).

Crustaceans. Crustaceans were relatively un-

TABLE 1. Incidence of prey items by % frequency of occurrence, numerical abundance, and % dry weight in the stomachs (proventriculi) of 106 White-chinned Petrels and 42 Sooty Shearwaters in the southern Benguela region.

	White-chinned Petrel			Sooty Shearwater		
Prey item	% Frequency of occurrence	% Total no. of prey items	% Total dry weight	% Frequency of occurrence	% Total no. of prey items	% Total dry weight
Fish						
Cape hake *Merluccius capensis*	6.1	1.3	2.7	0	0	0
Rat-tail *Coelorhynchus fasciatus*	20.3	13.1	12.8	8.3	2.4	3.0
Offal	19.5	–	35.7	0	–	0
Unidentified fish	20.7	11.3	8.8	7.7	1.1	0.1
Lantern-fish *Lampanyctodes hectoris*	8.2	17.6	1.6	31.1	30.7	30.3
Light-fish *Maurolicus muelleri*	3.6	6.5	2.7	29.2	24.0	30.3
Cape anchovy *Engraulis capensis*	1.7	0.9	1.2	29.2	32.2	33.3
Maasbanker *Trachurus trachurus*	1.9	0.4	0	0	0	0
Red-eye round-herring *Etrumeus teres*	0.7	1.3	6.9	0	0	0
Crustacea						
Stomatopoda *Squilla armata*	15.7	13.9	12.7	8.3	7.4	3.0
Crab megalopid larvae	0.7	0.1	0	2.1	0.6	0
Euphausidae *Euphausia lucens*	1.5	5.1	0	3.3	0.1	0
Amphipoda	0.7	3.9	0	0.7	0.2	0
Unidentified crustacean remains	5.6	–	0.5	0	–	0
Cephalopoda						
Sepiidae (flesh)	12.2	–	11.4	0	–	0
Beaks	13.6	24.7	–	4.2	1.2	–
Gastropoda	0	0	0	0.7	0.2	0
Salps	0	0	0	0.7	0.2	0

important in the diets of both White-chinned Petrels and Sooty Shearwaters according to percentage mass and percentage frequency of occurrence. Stomatopods, *Squilla armata,* were taken more frequently than other crustaceans by White-chinned Petrels. Large numbers of euphausids, *Euphausia lucens,* were present in the stomachs of White-chinned Petrels collected at a surface swarm of these crustaceans in September 1984.

The gizzards of both White-chinned Petrels and Sooty Shearwaters contained only unidentifiable exoskeletal fragments of crustaceans.

TEMPORAL VARIATION IN DIET

Offal was the major food of White-chinned Petrels throughout the year, while the diet of the Sooty Shearwater varied temporally between lantern-fish, light-fish, and cape anchovy (Fig. 3).

DISTRIBUTION AND FEEDING ASSOCIATIONS

The mean densities (birds per km^2) of White-chinned Petrels, calculated from aerial transects passing within 5 km of trawlers operating in the study area during 1985 and 1986, were significantly higher than densities further away from trawlers (Mann-Whitney *U*-test with tied ranks, $U_{(1)4,7} = 24.5$, $P < 0.05$). Sooty Shearwater densities were not affected by the proximity of trawlers ($U_{(1)4,7} = 13.5$, $P > 0.1$). White-chinned Petrel densities were highest offshore of the 200-m depth contour and Sooty Shearwater densities were highest inshore of the contour (Table 3), but the differences were not significant.

Of the 19 feeding groups sampled, 16 occurred in water 14 to 19°C, in the zone of maximum productivity between freshly upwelled water (9 to 11°C) and the offshore divergence (>19°C) (Bang 1971). Marine mammals occurred in association with nine out of 13 groups of feeding White-chinned Petrels, and with seven out of 13 groups in which Sooty Shearwaters were present. The species of marine mammals and predatory fish associated with seabird feeding groups were common, *Delphinus delphis,* and dusky, *Lagenorhynchus obscurus,* dolphins, brydes whale, *Balaenoptera edeni,* cape fur seal, *Arctocephalus pusillus,* and tuna, *Thunnus* spp.

TABLE 2. Incidence of prey items by percentage frequency of occurrence and numerical abundance of prey items in the gizzards (ventriculi) of 120 White-chinned Petrels and 48 Sooty Shearwaters in the southern Benguela region.

Prey item	White-chinned Petrel		Sooty Shearwater	
	% Frequency of occurrence	% Total no. of prey items	% Frequency of occurrence	% Total no. of prey items
Fish				
Cape hake *Merluccius capensis*	16.8	0.8	0	0
Rat-tail *Coelorhynchus fasciatus*	14.9	1.0	15.3	0.7
Offal	0.6	—	0	—
Unidentified fish	7.0	0.2	0.7	0.1
Lantern-fish *Lampanyctodes hectoris*	12.9	2.4	29.0	21.2
Light-fish *Maurolicus muelleri*	5.1	0.4	41.7	27.4
Cape anchovy *Engraulis capensis*	2.3	0.1	8.9	2.0
Crustacea				
Stomatopoda *Squilla armata*	7.8	0	4.2	0.2
Unidentified crustacean remains	1.2	—	0	—
Cephalopoda				
Beaks	76.9	95.1	60.7	40.2

DISCUSSION

MORPHOLOGY, FEEDING TECHNIQUES AND DIET

Morphological differences between Sooty Shearwaters and White-chinned Petrels are correlated with different foraging techniques which apparently preclude dietary overlap between the two species in the southern Benguela region. White-chinned Petrels scavenged fish discarded behind trawlers while Sooty Shearwaters exploited schools of small fish near the surface. Kuroda (1954) found that the skeletal proportions and body shape of Sooty Shearwaters confer diving abilities superior to those of larger petrels such as White-chinned Petrels. Sooty Shearwaters are

TABLE 3. Relative density (no. birds per km^2) of White-chinned Petrels and Sooty Shearwaters, based on counts made from aircraft (Fig. 1). — = no data. In April and June, trawlers were in close proximity for the entire offshore leg, hence no data was collected for the "further than 5 km from trawlers" category for these months. Where several values are given, each is from a discrete transect.

Month	Transects within 5 km of trawlers			Transects further than 5 km from trawlers		
	Total transect length (km)	White-chinned Petrel density	Sooty Shearwater density	Total transect length (km)	White-chinned Petrel density	Sooty Shearwater density
Inshore of the 200-m contour						
February	—	—	—	106.0	0.1	0
April	224.6	1.2; 0.3; 1.0; 1.8	2.7; 0; 0; 0	68.3	0.3	0.6
June	—	—	—	106.0	0.3	0.6
July	46.5	12.0	6.0	101.0	0.5	4.6
August	—	—	—	76.3	0	0.9
October	—	—	—	101.0	0	0
December	—	—	—	54.1	0	0
Offshore of the 200-m contour						
February	—	—	—	163.3	0	0
April	16.0	0	0	—	—	—
June	206.7	14.9; 118.2; 3.6	0; 0; 0.9	—	—	—
July	89.9	190.9; 12.4	0; 0	72.3	6.1	0.4
August	—	—	—	138.7	1.3	0.2
October	—	—	—	152.6	0.5	0.2
December	87.6	0.7	0	85.1	0.1	0.1

proficient swimmers, diving to depths of 10 m (Brown et al. 1978). White-chinned Petrels have lower wing-loadings (0.78 $g \cdot cm^2$, $n = 4$) than Sooty Shearwaters (1.12 $g \cdot cm^2$, $n = 23$) (Warham 1977). High wing-loading is characteristic of seabirds adapted for diving (Warham 1977), because wings that are large in relation to body size increase drag on swimming birds. White-chinned Petrels are thus more suited to gliding than diving, whereas Sooty Shearwaters must expend more energy in flapping flight but are able to maneuver well under water. Consequently, Sooty Shearwaters feed by "pursuit plunging" (Brown et al. 1978) and White-chinned Petrels by "surface-seizing" (Imber 1976). Dive times for the two species reflect the difference in foraging techniques: Sooty Shearwaters foraging behind trawlers stay submerged for longer ($\bar{x} = 6.0$ sec, SD = 3.6, $n = 61$) than White-chinned Petrels ($\bar{x} = 2.2$ sec, SD = 1.7, $n = 150$) (FitzPatrick Institute, unpubl. data). Because of their ability to dive to greater depths, Sooty Shearwaters presumably are more efficient predators of fish such as cape anchovy, light-fish, and lantern-fish than are White-chinned Petrels.

Bill structure also influences seabird feeding techniques. White-chinned Petrels have large, heavy bills, better suited to tearing up large chunks of offal than are the slender, forceps-like bills of Sooty Shearwaters. Brown et al. (1981) considered that differences in bill size permitted diet separation between Sooty Shearwaters and Greater Shearwaters, *Puffinus gravis,* off eastern Canada, where Sooty Shearwaters eat softer-bodied prey than do their heavier-billed congenerics. Chu (1984), Ogi (1984), and Sanger (1987) found that Sooty Shearwaters ate primarily fish rather than squid. Squid muscle tissue is harder to tear and ingest than fish flesh, due to interlacing collagen fibres (Bone et al. 1981). *Procellaria* petrels off the coast of New Zealand and White-chinned Petrels off South Georgia are primarily squid-eaters (Imber 1976, Croxall and Prince 1980). The strong bills of this genus may have evolved for seizing and ingesting food such as squid, but now enable White-chinned Petrels to exploit trawler offal in the southern Benguela region.

DISTRIBUTION, FEEDING ASSOCIATIONS AND DIET

Most foraging by procellariiforms is limited to the upper 10 m of the water column. Although anchovy school near the surface during the day, myctophids, such as lantern-fish and light-fish are mesopelagic, supposedly only rising to feed near the surface at night (Holton 1969, Hulley 1986). Seabird predation on myctophids during the day is thus unexpected in the light of available knowledge of myctophid behavior in the southern Benguela. In two groups of actively feeding White-chinned Petrels and Sooty Shearwaters sampled when lantern-fish was the major prey item, more than 100 seals were feeding in association with the birds. Seals, dolphins, or predatory fish, such as tuna, *Thunnus* spp., may drive shoals of small fish to the surface, where the fish can be exploited by seabirds (e.g., Ashmole and Ashmole 1967). Diurnal predation by aerial seabirds on myctophids is probably only possible in the presence of other marine predators, whereas the anchovy's occasional surface-schooling behavior exposes it to seabird predation, independently of marine mammals and predatory fish.

White-chinned Petrels are more frequently associated with cetaceans in the southern ocean than any other seabirds (Enticott 1986). A natural tendency to exploit the feeding activity of whales may account for the propensity of White-chinned Petrels to scavenge behind fishing vessels (e.g., Murphy 1936, Summerhayes et al. 1974). Trawlers operate offshore, whereas concentrations of cape anchovy, lantern-fish, and light-fish usually occur inshore of the 300-m depth contour (Crawford 1980, 1981; Hulley 1986). The distribution of White-chinned Petrels and Sooty Shearwaters in the southern Benguela is probably influenced by the local availability of the different food sources exploited by the two seabirds.

CONCLUSION

Ecological segregation between White-chinned Petrels and Sooty Shearwaters in the southern Benguela region appears to result from differential use of an artificial food source. Sooty Shearwaters prey opportunistically on surface schools of pelagic fish, catching their prey independently of man's fishing activities, but may exploit the same surface shoals of pelagic fish as the purse-seine fishery. In contrast, White-chinned Petrels take few pelagic fish but scavenge offal from demersal trawlers. Preadaptations for a squid diet and scavenging habits may increase the efficiency and readiness with which White-chinned Petrels exploit trawler offal.

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