I dedicate this thesis to

Ally

"my best friend"

THE USE OF CAPE GANNETS MORUS CAPENSIS IN MANAGEMENT OF THE PURSE-SEINE FISHERY OF THE WESTERN CAPE

by

ALDO BERRUTI

Sea Fisheries Research Institute

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Supervisor: Prof. G. L. Maclean

CONTENTS

SUMMARY

A large purse-seine fishery is located in the highly productive southern Benguela System off the western Cape. Purse-seine fisheries have been prone to collapse worldwide and management practices have met with limited success. Predators offer potential as biological indicators yielding information on the status of fish stocks. The rationale behind this proposed usage was previously loosely-defined. The premise that some variable of seabird biology is related to some aspect of fish biology about which information is required was critically examined.

The diet of the Cape Gannet was monitored monthly at Lambert's Bay and Malgas Island in the western Cape from 1977 to 1986. Gannets ate shoaling fishes (mainly Cape Anchovy, South African Pilchard and Saury), measuring 29-429 mm Lc, which were available during the day at the surface and hake offal scavenged from demersal trawlers. Comparison with purse-seine fishery catches and the distributional ecology of the fishes suggested that the contributions of epipelagic fishes to the diet of the Cape Gannet were related to their availability and abundance, but that the occurrence of mesopelagic fishes (adult Redeye Roundherring and Onderbaadjie) in the diet of gannets was not related to their availability or abundance. Availability of epipelagic fishes was apparently lowest during late winter and spring; at longer time scales, availability was apparently lowest between 1983 and 1985 during the period from 1978 to 1986. Differences in the diets of breeding and nonbreeding gannets were small.

Gannets from the colony at Lambert's Bay fed primarily north of Cape Columbine. These birds fed in cool inshore waters on juvenile fishes (mainly Cape Anchovy). Gannets from Malgas Island fed primarily south of Cape Columbine. They fed in cool inshore waters on juvenile epipelagic fishes (mainly Cape Anchovy), in warmer waters offshore on large epipelagic fishes (Saury and adult pilchard) or scavenged hake at trawlers offshore. Adult South African Pilchard were preferred prey. Epipelagic prey were selected in preference to mesopelagic fishes and hake.

Significant correlations between the percentage of pilchard in gannet diet and purse-seine fishery catches suggested that gannets were reliable monitors of the trend in pilchard stocks at low biomass levels.

The Saury is a poorly known species and its availability to gannets was reviewed as an example of the indirect use of the diets of predators in understanding the ecology of prey species and functioning of ecosystems.

Future directions for research were suggested. However,

extensive use of data from predators in fisheries management awaits the development of techniques which can use qualitative data. Nevertheless, it was concluded that the species composition and length of prey in gannet diet and the mass of regurgitations and the proportion of birds which regurgitated food were related to the abundance of epipelagic fish prey generally and South African Pilchard in particular.

CHAPTER 1

INTRODUCTION

The harvests of the purse-seine fisheries made up about 22% of the world's total catch of fish in 1983 (FAO 1983). Yet purse-seine fisheries have been prone to collapse world-wide, yielding huge catches for short periods, only to be followed by drastic reductions in catches (Saville 1979; Csirke 1984). Past management practices have been unable to predict or prevent such collapses (Saville 1979; Csirke 1984; Sherman & Alexander 1986). Important purse-seine fisheries are located in eastern-boundary currents, generally highly productive systems characterised by equatorward flow and coastal upwelling (Cushing 1969; Parrish et al. 1983). In these systems, man and natural predators eat the same species of fish (MacCall 1984). Birds have frequently been proposed as indicators of change in environmental conditions (Morrison 1986), and it has been suggested that seabirds offer an alternative, catch-independent method of assessing trends in stock biomasses or other parameters of fish stocks which are useful for managing fishery resources (Crawford & Shelton 1978, 1981; Siegfried & Crawford 1978; Crawford et al. 1983a; Berruti 1985a).

The biology of any species and its interactions with its environment must be well understood before that species can be used to provide specific, management-orientated information. Once this has been achieved, analytical procedures and decision systems which can use data from indicators must be developed to provide specific answers to management problems. These data are frequently qualitative and not amenable to statistical procedures used in fishery management.

This thesis is an investigation of the interaction between the Cape Gannet Morus capensis and pelagic shoaling fish in the southern Benguela System and aims to establish the biological basis on which the use of the Cape Gannet as an indicator of the state of epipelagic fish stocks in this region could be founded. The diet and feeding ecology of the Cape Gannet are investigated, and preliminary attempts are made to use this information to provide advice for the management of the purse-seine fishery of the western Cape.

In order to make a thorough investigation of the topic, extensive co-operation with other scientists was necessary. I received assistance with several chapters. Dr. M.J. Armstrong (Sea Fisheries Research Institute (SFRI)) provided data on research catches for Chapter 8. Data on gannet diet at Algoa Bay were provided by Mr. J. Colclough (Port Elizabeth Museum) for studies in Chapter 9. Drs. P.A Shelton and R.J. Crawford (SFRI) initiated the gannet research programme and were responsible for data collection until January 1981. Other contributions are fully noted in the text and under Acknowledgements.

CHAPTER 2

THE STUDY AREA

2.1 PHYSICAL AND BIOLOGICAL CHARACTERISTICS

The foraging area of Cape Gannets in southern Africa includes both the warm Agulhas Current off the east and south coasts, and the cool Benguela System off the west coast (Fig. 1).

The Benguela System

The Benguela System is one of the world's four major eastern-boundary current regions (Wooster & Reid 1963) where biological production is enhanced by wind-driven upwelling processes (Cushing 1969), and where similar fish species are dominant (Parrish _et al_. 1983). This study is concerned only with the southern Benguela System off South Africa, and does not include the area north of the Orange River. The physical aspects of the system have been the subject of three important recent reviews: Nelson & Hutchings (1983), Parrish _et al_. (1983) and Shannon (1985).

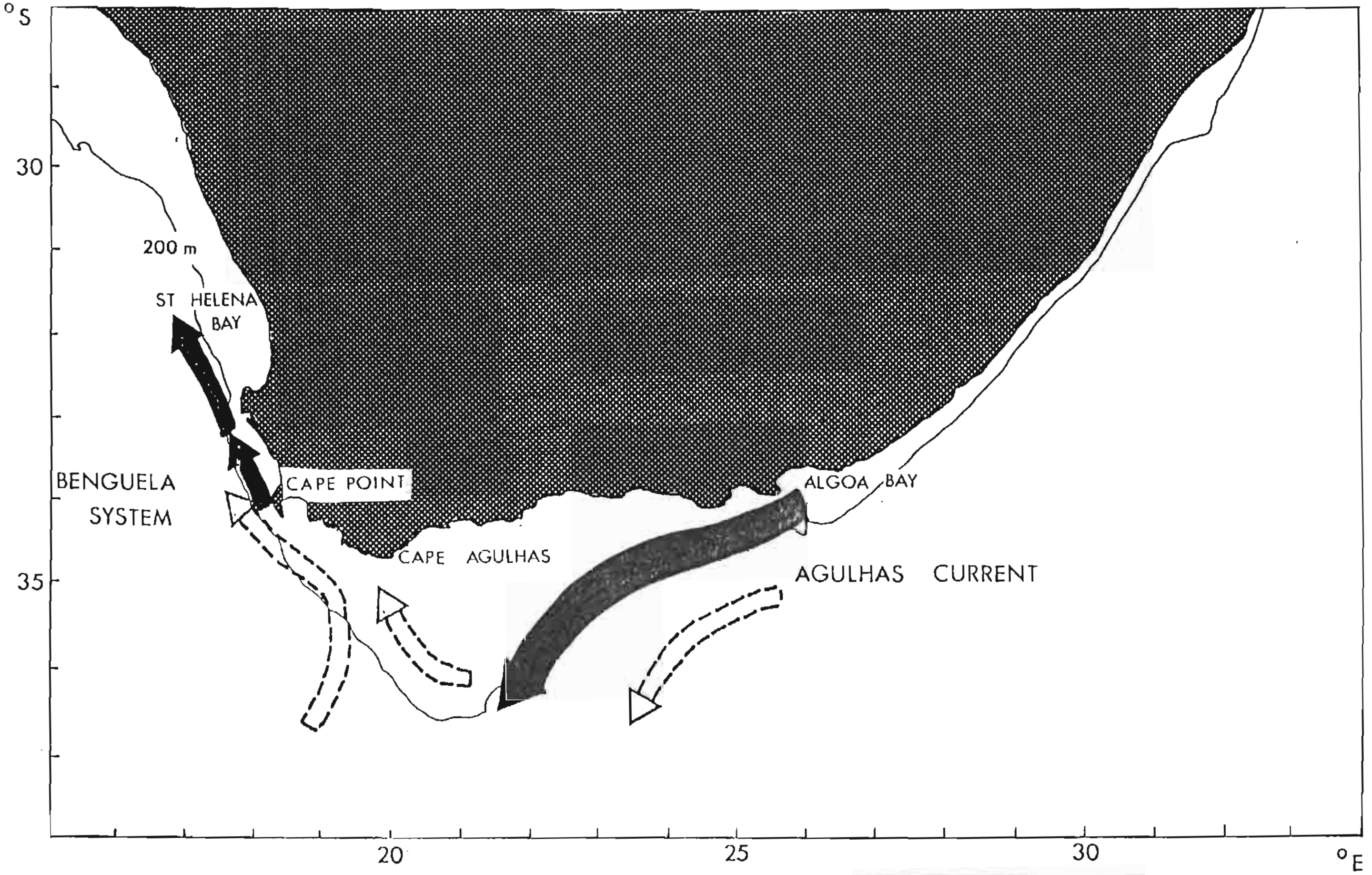


FIGURE 1

South Africa and surrounding waters, showing the direction of surface flow of the Agulhas Current and southern Benguela System and the 200 m depth contour (after Boyd *et al*. 1985). Directions of main (solid arrow) and secondary (dashed arrow) flows are shown.

The cool surface waters of the Benguela System flow equatorward, and are derived by the upwelling of South Atlantic central water from depths generally between 100m and 300m (Shannon 1966). The offshore boundary of this system is mobile, but is loosely associated with the outer shelf-edge break (Shannon 1985). The seasonal strength of upwelling is wind-driven, and hence is closely related to seasonal latitudinal shifts of atmospheric pressure systems and intensification of large-scale pressure gradients (Parrish et al. 1983). Sites of upwelling result from the interaction between these gradients and large-scale topography (Parrish et al. 1983).

Off the western Cape, the most active upwelling centres are located at Hondeklip Bay, Cape Columbine and the Cape Peninsula (Fig. 2) and are associated with narrowings of the continental shelf (Nelson & Hutchings 1983). Upwelling occurs as a narrow coastal strip in the region of Lambert's Bay (Shannon 1985). Submarine canyons cut into the shelf in a southwesterly direction off Cape Columbine and the Cape Peninsula are thought to facilitate upwelling at these localities by funnelling cold, nutrient-rich water into the system (Shannon et al. 1981). Upwelled plumes of cold water extend northwest from these upwelling sites, for distances of up to 200 km in the case of Cape Columbine (Shannon & Anderson 1982). These plumes are separated from oceanic waters by sharp gradients of temperature and salinity and strong equatorward jets may be associated with these frontal systems (Bang &

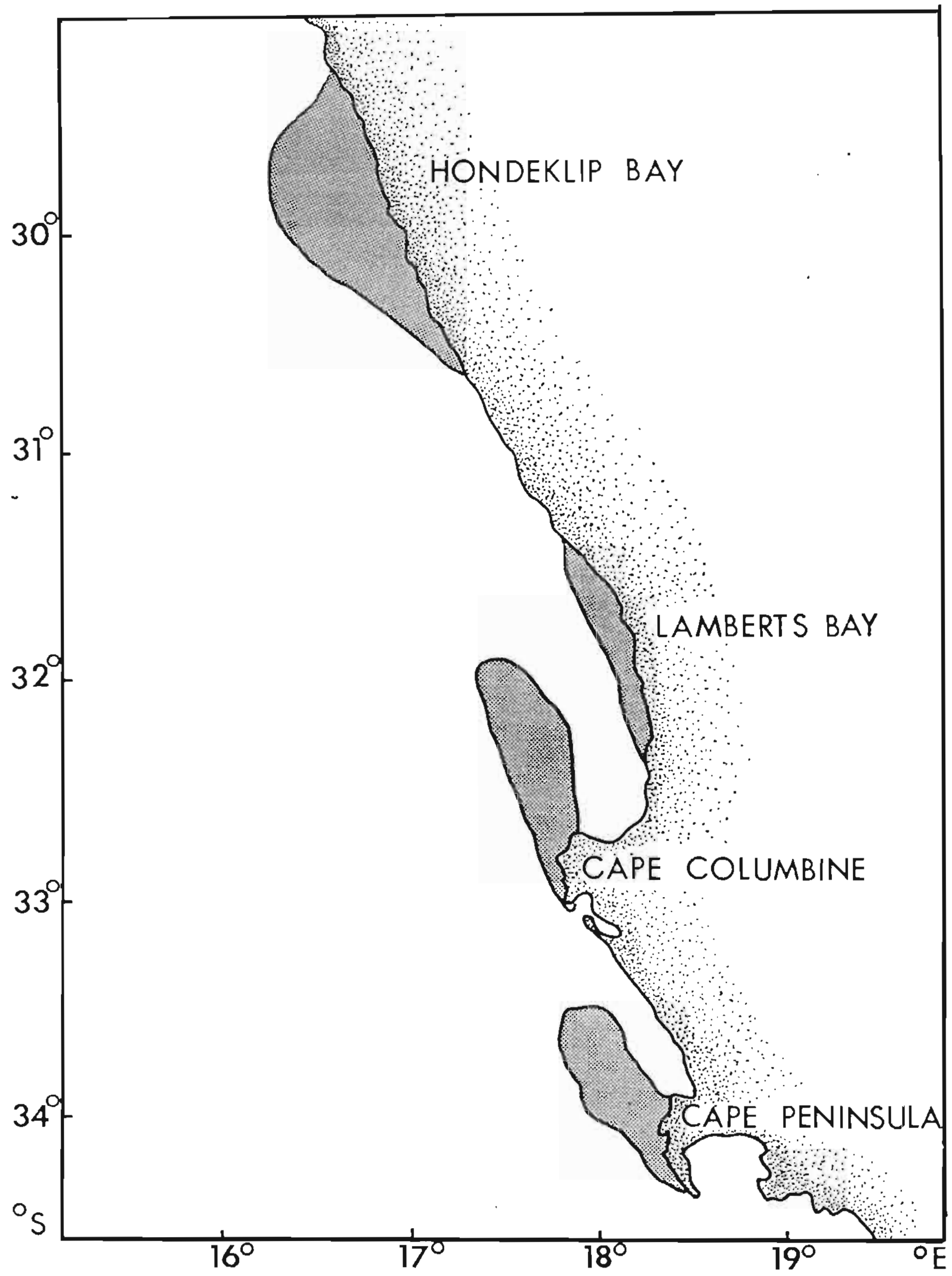


FIGURE 2

The major upwelling sites off southwestern Africa (after Shannon 1985).

Andrews 1974). A frontal jet off the the Cape Peninsula transports eggs and larvae of Cape Anchovy _Engraulis japonicus_ northwards from the spawning grounds which lie southeast of the peninsula (Shelton & Hutchings 1981).

Upwelling is caused by southeasterly winds. Prevailing winds in the southern Benguela System are determined by the South Atlantic high pressure zone (anticyclone), the pressure over the southern African subcontinent and eastward moving cyclones (Nelson & Hutchings 1983; Shannon 1985). The South Atlantic high pressure zone shifts about 4° south in summer, while the pressure over southern Africa changes from low in summer to a weak high in winter (Nelson & Hutchings 1983; Shannon 1985). In summer, eastward-moving fronts pass southern Africa unimpeded, and produce south-easterly winds. These winds are most intense between late September and March with a mid-summer lull (Shannon & Anderson 1982). Upwelling is pulsed with a periodicity of 3-6 days (Nelson & Hutchings 1983; Jury _et al_. 1985), although pulsing is less variable and slower north of Cape Columbine (Shannon 1985). The process is disrupted by downwelling caused by wind reversal (Andrews & Hutchings 1980). Strong thermal fronts between warm oceanic waters and cold upwelled waters are most marked during active upwelling. Summer advection of warmer waters may restrict the surface area of upwelling, and the thermal front may lie close inshore when active upwelling relaxes. The thermal fronts may lose their integrity as surface features when upwelling lulls, and a shallow layer of warm oceanic water may penetrate shorewards causing a strong thermocline (Shelton _et_ _al_. 1985). In winter, the water column is well mixed, and the zone of cool water along the coast is broad. Inshore southward movement of water between Cape Columbine and Cape Point, pulsed over a period of days, has been demonstrated (Holden 1986).

During upwelling, nutrient-rich waters reach the surface near the shore (Chapman & Shannon 1985). Surface water temperatures at the origin of upwelled plumes of water may be as low as $9^{o}C$, and the water warms during transport away from the coast. Dense blooms of phytoplankton colonize the upwelled waters (Olivieri 1983a), followed after a lag by zooplankton growth (Hutchings & Nelson 1985). As a thermocline becomes established, phytoplankton production depletes the nutrients above the thermocline (Olivieri 1983a; Brown & Hutchings 1985; Chapman & Shannon 1985). The plankton of the Benguela System was reviewed by Shannon & Pillar (1986).

There are seasonal trends in chlorophyll concentrations, with lower levels in winter and higher levels in spring following the onset of upwelling (Shannon & Pillar 1986). During summer, production and standing stocks of phytoplankton are variable, but high on average, and high concentrations of phytoplankton are often located offshore in aged, upwelled water (Olivieri 1983b; Brown & Hutchings 1985). Cool mixed water is widely distributed in both the longshore and offshore directions in winter, and is generally associated with relatively low, but uniformly distributed, phytoplankton biomass (Brown & Hutchings 1985). However, nutrient levels and plankton production are consistently high north of Cape Columbine because of perennial upwelling, nutrient regeneration and mixing of the water column in winter (Bailey 1985; Shannon _et al_. 1985). Zooplankton biomasses are highest, but most variable, inshore and are higher in St Helena Bay than on the Agulhas Bank (Pillar 1986). Copepods are least abundant in winter but there is no clear seasonal trend in the biomass of euphausiids (Pillar 1986).

The Agulhas Bank and Agulhas Current

The boundaries of the southern Benguela System are difficult to define because of seasonal changes in the mixing processes. To the south, the Agulhas Bank separates the Benguela System from the Agulhas Current and is an area of mixed water originating from the Atlantic and Indian Oceans (Shannon 1985). In the area between Cape Point and Danger Point, upwelling and stratification is most intense in summer, whereas in winter, the water column is well mixed (Boyd _et al_. 1985).

The warm Agulhas Current flows southwestwards along the eastern coast of South Africa (Fig. 1). It lies close inshore off Natal and meanders are usually small. The current moves offshore to follow the shelf-edge contours further south (Lutjeharms 1981). As the shelf broadens to form the Agulhas Bank, the current moves 350-400 km offshore, and meanders increase. Large rings may form and be advected into the Benguela System, but most of the current turns south and moves east as it meets the West Wind Drift (Lutjeharms 1981). Intrusions of Agulhas water onto the Agulhas Bank may occur. East of Cape Agulhas, winds with an easterly component produce limited upwelling at the capes which point east, especially during summer and autumn (Schumann _et al_. 1982). Cool water wells up along the eastern edge of the Agulhas Bank (Shannon 1966). Mean monthly temperatures less than 20°C do not occur in summer east of Cape Agulhas, while the 21°C isotherm brackets pockets of cooler water against the coast in that region (Christensen 1980). In this region, nutrient upwelling is not as intense as on the west coast. Moderate levels of nutrients occur only in spring; levels in summer are lower because of nutrient depletion in strongly stratified waters (Brown & Hutchings 1985). In summer and late autumn, a subsurface maximum of chlorophyll on the Agulhas Bank is associated with the thermocline (Shannon _et al_. 1984). Eastern and central Agulhas Bank waters are characterized by strong, shallow thermoclines and well developed subsurface maxima in phytoplankton biomass (Carter _et al_. in press). Waters of the western Agulhas Bank are characterized by deeper and less intense thermoclines with less intense subsurface phytoplankton biomass maxima (Carter _et al_. in press). The biomass of zooplankton is lower than off the west coast (Pillar

1986). A wedge of moderate chlorophyll levels associated with cold water derived from coastal and upwelling occurs in the Algoa Bay region (Shannon *et al*. 1984).

Upper trophic levels of the Agulhas Current and Benguela System

In neither system have relationships between the abundance of phytoplankton, of zooplankton and of epipelagic fish been demonstrated over short time and distance scales (Andrews & Hutchings 1980; Hutchings 1981; Shannon *et al*. 1983, 1984; Shannon & Pillar 1986). This is not surprising in terms of the vastly different generation times and mobility of phytoplankton, zooplankton and fish (Hutchings & Nelson 1985). Bergh *et al*. (1985) calculated that 75% of the phytoplankton becomes detritus, because most fish shoals and zooplankton stocks are unable to respond to patchy phytoplankton blooms fast enough to use them fully. Cape Anchovy *Engraulis japonicus*, South African Pilchard *Sardinops ocellatus*, Redeye Roundherring *Etrumeus whiteheadi* and Maasbanker (Cape Horse Mackerel) *Trachurus trachurus* eat mainly zooplankton and to lesser extents, Cape Anchovy and South African Pilchard are herbivores (James in press; A. James unpubl.).
The nomenclature of Smith & Heemstra (1986) has been used for the fish species of southern Africa.

The Benguela System and the Agulhas Bank are generally more patchy (in terms of the distribution of both physical and biological features) and productive in summer. In winter, the productive area is more uniform, well mixed and larger, with a lower production per unit area. Oceanographic features such as upwellings and fronts which in other marine areas are known to concentrate food for seabirds (Brown 1980; Briggs et al. 1984), are primarily summer phenomena. The spatial and temporal variability of plankton decreases north of Cape Columbine. The biomass of plankton decreases from St Helena Bay to the Agulhas Bank (Pillar 1986).

2.2 THE PURSE-SEINE FISHERY OF THE WESTERN CAPE

A multispecies purse-seine fishery is located off the western Cape (Fig. 3). The fishery began in the 1940s, and this brief description is based on information in Du Plessis (1959), Stander & Le Roux (1968), Crawford (1980a & b, 1981a-f), Crawford _et al_. (1983c), Newman & Crawford (1980), Armstrong _et al_. (1983, 1985), Armstrong (1986) and Prosch (1986a,b). South African Pilchard, Cape Anchovy, Maasbanker, Mackerel (Chub Mackerel) _Scomber japonicus_, Redeye Roundherring and Onderbaadjie (Lanternfish) _Lampanyctodes hectoris_ have all provided large catches at some time (Table 1). During the initial stages of the fishery, fishing was localized in St Helena Bay and concentrated on adult South African Pilchard and Maasbanker. In the late 1950s and early 1960s, South African Pilchard increasingly dominated catches as fishing area and effort expanded coincidentally with a series of strong year classes. South African Pilchard catches dropped rapidly in the mid-1960s after recruitment returned to average levels. Catches of South African Pilchard have decreased further from the mid-1960s to 1983, resulting in the imposition of stringent quotas in 1984-1986. Mesh size of purse-seine nets was decreased from 32 mm to 12,7 mm in 1964 to allow exploitation of Cape Anchovy which may have increased at this time after a series of strong year classes. Strong year classes of Mackerel in the mid-1960s produced large catches of this species in the late

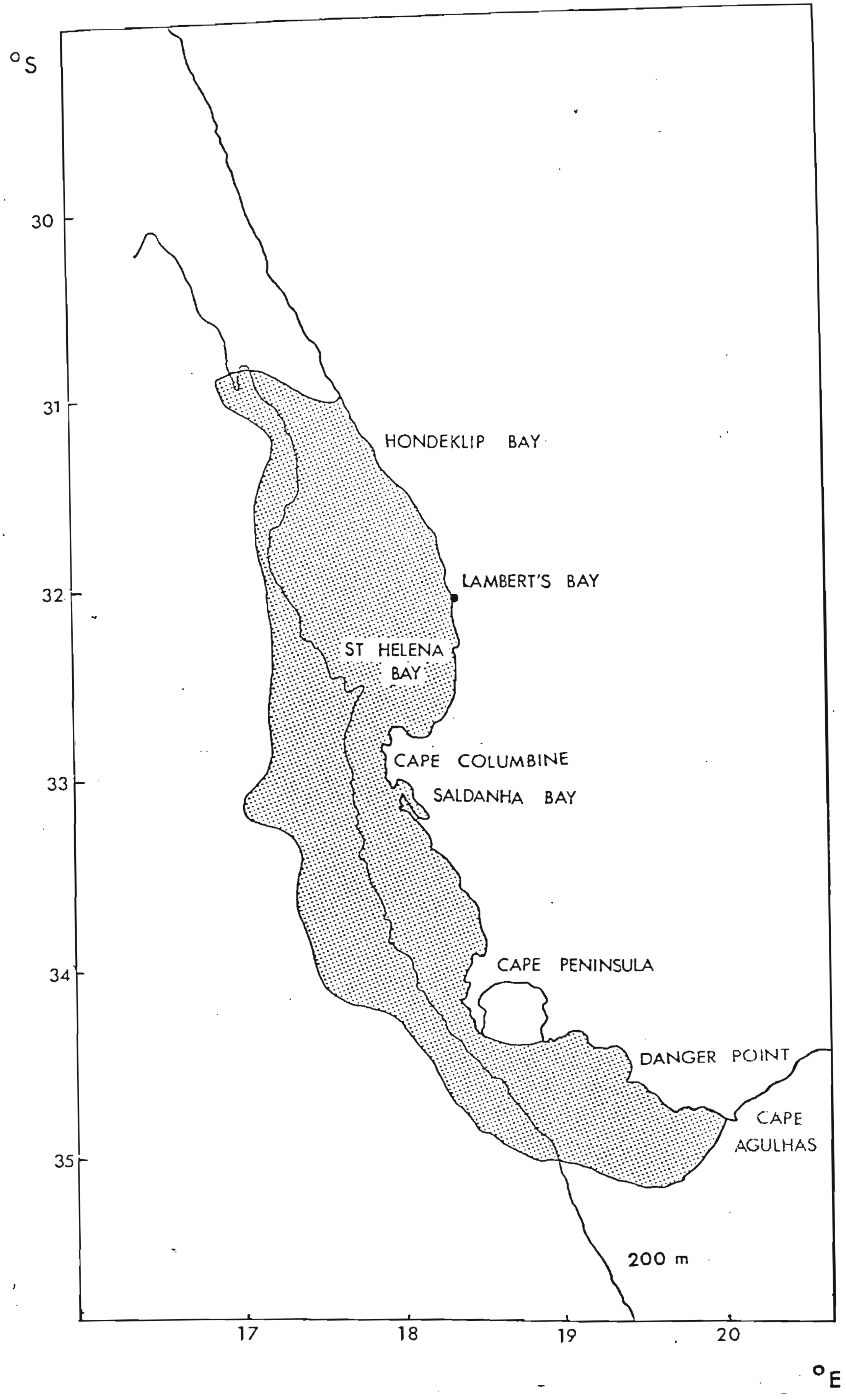


FIGURE 3

Geographical location of the western Cape purse-seine fishery (shaded area) and the 200 m depth contour.

TABLE 1.

SPECIES COMPOSITION OF SOUTH AFRICAN PELAGIC FISHERY LANDINGS IN THOUSANDS OF TONNES FROM 1950 TO 1985

Year	South African Pilchard	Cape Anchovy	Maasbanker	Mackerel	Redeye Roundherring	Onder-baadjie	Total
1950	85	-	50	-	-	-	135
1951	102	-	99	-	-	-	200
1952	170	-	103	-	-	-	273
1953	133	-	85	-	-	-	218
1954	88	-	118	4	-	-	211
1955	122	-	79	20	-	-	221
1956	77	-	46	33	-	-	155
1957	110	-	85	7	-	-	202
1958	194	-	56	22	1	-	273
1959	260	1	18	33	3	-	315
1960	318	-	63	31	-	-	412
1961	402	-	39	50	-	-	491
1962	410	-	67	20	-	-	497
1963	390	-	23	13	-	-	427
1964	256	92	24	50	3	-	426
1965	205	171	55	41	8	-	480
1966	118	144	26	53	15	-	357
1967	70	271	9	128	32	-	509
1968	108	138	1	91	30	-	369
1969	56	149	27	92	23	5	352
1970	62	169	8	78	24	18	358
1971	88	157	2	54	22	2	325
1972	104	236	1	57	21	15	434
1973	69	251	2	59	29	42	451

TABLE 1 (CONTINUED).

Year	South African Pilchard	Cape Anchovy	Maasbanker	Mackerel	Redeye Roundherring	Onder-baadjie	Total
1974	16	350	3	31	1	-	401
1975	89	224	2	69	24	-	407
1976	176	218	-	1	12	-	408
1977	58	236	2	21	35	6	357
1978	97	210	4	2	67	1	380
1979	53	291	4	3	21	9	381
1980	50	316	-	-	14	-	381
1981	46	292	6	-	24	10	379
1982	35	306	1	3	31	1	377
1983	61	240	1	4	69	2	377
1984	27	273	3	1	29	13	346
1985	27	272	1	<1	40	31	376

1960s. By the 1980s, catches of Maasbanker and Mackerel were very small. Since the mid-1960s, Cape Anchovy has dominated the catch. The contributions of Redeye Roundherring and Onderbaadjie became relatively more important; South African Pilchard, Maasbanker and Mackerel have declined. However, catches of Redeye Roundherring and Onderbaadjie were erratic. Redeye Roundherring comprised 18% of the catch in 1978 and 1983. Onderbaadjie comprised 9% and 8% of the catch in 1973 and 1985 respectively, but catches are sporadic and largely confined to St Helena Bay and an area off Cape Columbine. Adult South African Pilchard are commercially more valuable than Cape Anchovy as the major fishery target because of its canning potential as a high-quality food, whereas Cape Anchovy is reduced to fishmeal and oil (Armstrong 1986).

The pelagic fishery is subject to several restrictions, one of the more important being quotas for catches of individual species or the fishery as a whole (Newman _et al_. 1979; Crawford 1981f; Sea Fisheries Research Institute (SFRI) unpubl.). Scientific research has sought to estimate the maximum sustainable yield without damaging the structure and functioning of the ecosystem as a basis for quota determination (Newman _et al_. 1974; Crawford 1979; Armstrong _et al_. 1983). However, the biological characteristics of epipelagic shoaling fishes pose problems for yield estimation using catch-based statistics (Butterworth 1980, 1983; Armstrong _et al_. 1985; Hampton in press). Off South Africa, movements and distribution of epipelagic species show seasonal patterns which are size-related (Crawford 1980a). Short-lived epipelagic fish species are characterized by varying annual recruitment strength of year classes (Newman & Crawford 1980; Crawford et al. 1980b, 1983b; Parrish et al. 1981), although recruitment is relatively stable in most years (Lasker 1978; Crawford 1981b). Populations are spread over large areas; numbers of age-classes of highly variable biomass are restricted and shoaling distributions highly clumped. These characteristics present severe problems for catch-based stock assessments and for direct surveys of abundance. Virtual Population Analysis is a retrospective method which estimates fish populations after a time-lag equal to the interval between the year of first appearance of a new cohort or year-class and the year in when the last fish of that cohort are caught, and suffers from a number of shortcomings (Ulltang 1976; Butterworth 1983; Armstrong et al. 1985). In South African waters, much of the adult Cape Anchovy population lies outside the fishing area, thereby invalidating the use of Virtual Population Analysis (Armstrong et al. 1985; Hampton in press). Catch-per-unit-effort (CPUE) statistics are essentially estimates of fish density (Csirke 1980). Fish shoal size may remain constant despite changes in population size (Radovich 1979), and therefore CPUE and catchability are very unlikely to be independent of stock size. Such independence is a basic assumption of stock production models (Francis 1980). Catchability is likely to increase as stock size drops, as fish still form shoals which can be caught even at low total biomass.

In the period 1983 to 1986, epipelagic fish stock assessments in South Africa relied on direct surveys (Hampton _et_ _al_. 1985), as large variances and biases are associated with catch-based statistics, particularly at low stock biomasses (Butterworth 1980, 1983; Armstrong _et_ _al_. 1985). The size of the adult Cape Anchovy population was assessed annually from egg and hydroacoustic surveys and that of the recruits by hydroacoustic survey (Hampton _et_ _al_. 1985; Hampton in press). Coeffecients of variation in the order of 20-30% are associated with these estimates (Hampton in press), but potential biases are fewer and regarded as less important than in catch-based statistics (M. J. Armstrong _pers_. _comm_.). The application of hydroacoustic survey was extended to South African Pilchard and Redeye Roundherring in 1986, but has yet to be extended to Onderbaadjie, the only other species which has contributed at least 10% of the total catch since 1983 (SFRI unpubl.). Estimates of the size of adult stock do not allow prediction of recruitment strength in any given year except on a probabilistic estimate. All direct surveys are reliant on correct timing of surveys, correct calibrations of acoustic gear and adequate sampling to avoid bias. Direct surveys are less reliable at low population biomasses (Armstrong _et_ _al_. 1985) and are susceptible to bias (Mais 1974; Cram & Hampton 1976). Direct surveys do not include shallow waters, which may be used extensively by epipelagic fish (Hewitt & Brewer 1983). Clearly, while direct surveys have improved the assessment of the abundance South African pelagic fish, difficulties remain.

There are difficulties with all methods of assessing pelagic fish abundance, and the simultaneous use of several techniques is desirable. Therefore, the use of the interaction between seabirds and pelagic fish is worthy of investigation.

2.3 THE CAPE GANNET

This section briefly reviews the biology of the Cape gannet, the species selected for study, concentrating on its distribution and breeding biology. The reasons for the selection of the gannet as a study species are given in Chapter 4, following a review of research into the use of seabirds as indicators of fish stocks.

The Cape Gannet is a member of the family Sulidae, which comprises nine species of boobies and gannets. The family has been studied intensively, notably by Nelson (1978a), who reviewed the taxonomy, distribution, numbers, breeding biology and behaviour of each species. Whether the gannets and boobies constitute one genus _Sula_, or two genera, _Morus_ (the gannets) and _Sula_ (the boobies) (Nelson 1978a), and whether the three gannets (Cape, North Atlantic and Australian Gannets) comprise three distinct species, perhaps within a superspecies, or three subspecies (Jarvis 1972; Nelson 1978a) are controversial matters. Thus the Cape Gannet has variously been referred to as _Sula capensis_, _Morus capensis_ and _Sula bassana capensis_. The debate lies beyond the scope of this thesis; and the name _Morus capensis_, used by the List Committee of the Southern African Ornithological Society (Clancey 1980) and Maclean (1985) has been adopted.

Gannets and boobies are plunge-divers (Ashmole 1971), varying in mass from 900 g for the Redfooted Booby *Sula sula* to 3120 g for the North Atlantic Gannet *Morus bassana* (Nelson 1978a). Fish is by far the most important item of diet for all species. The gannets breed in temperate areas and feed in cold highly productive waters. The boobies are tropical or subtropical in breeding distribution and feed in warm oceanic waters, with the exception of the Peruvian Booby *Sula variegata* which feeds in the cold waters of the Humboldt Current and extends southwards along the coast of Chile (Nelson 1978a; Harrison 1983).

The Cape Gannet *Morus capensis* (Lichtenstein) breeds on six islands off southern Africa: Mercury, Ichaboe, Possession, Malgas, Bird (Lambert's Bay) and Bird (Algoa Bay) Islands (Crawford *et al*. 1983c) (Fig. 4). Population counts for the period 1978-1985 are given in Table 2. All these colonies are located in the Benguela System except Bird Island (Algoa Bay), which is located in the Agulhas Current. There are three colonies off South Africa: Malgas and Bird (Lambert's Bay) Islands in the western Cape and Bird Island (Algoa Bay) in the eastern Cape (Fig. 4). In 1984, 1985 and 1986, gannets occupied Dyer Island (Fig. 4) during the breeding season and a single egg was laid in 1985 (Berruti 1985b, unpubl.; R.J.M Crawford (SFRI) *pers*. *comm*.).

There is little sexual dimorphism in the Cape Gannet. Jarvis (1971a) reported that males were slightly larger than females in linear dimensions, with females being slightly heavier on average

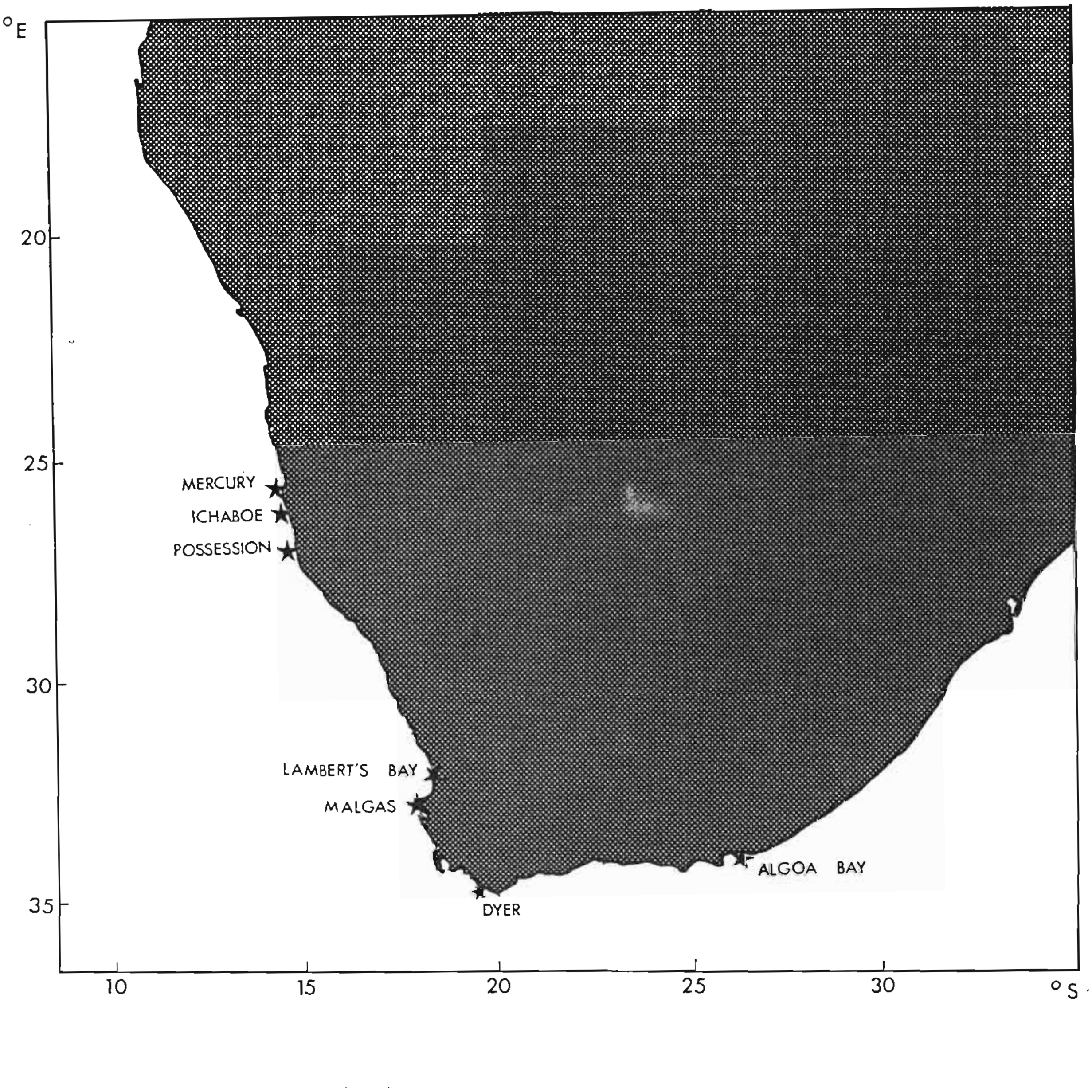


FIGURE 4

The location of Cape Gannet breeding colonies in southern Africa.

TABLE 2.

BREEDING POPULATIONS (UNCORRECTED COUNTS OF INDIVIDUALS ON AERIAL PHOTOGRAPHS) AT CAPE GANNET COLONIES, 1978-1985

	Island					
Year	Mercury	Ichaboe	Possession	Lambert's Bay	Malgas	Bird (Algoa)
1978	2754	80447	5505	6895	32169	57981
1980		32077	2962	8007	29949	56459
1981	1871		3937	9158		51262
1982	2107	47418	3442	6351	29130	57559
1983	1861	42986	3113	10716	25630	
1984	2108	48635		10985	36410	
1985	1576	44168	2351	10089	28924	59719

(2670 g and 2619 g for 53 females and 61 males respectively). This is similar to other gannets (Nelson 1978b; Cramp & Simmons 1977). Fledglings are greyish speckled with white, but can be greyish white below. Adult plumage is attained in 2-4 years (Jarvis 1971a; pers. obs.). Age of first breeding is 2-4 years (Jarvis 1971a; pers. obs.). Adults show a high degree of nest and site fidelity (J. Colclough, Port Elizabeth Museum, unpubl.).

The Cape Gannet breeds in dense colonies on flat islands, except at Mercury Island, where it occupies flat ledges on a steeply sloping island (Duffy & La Cock 1985). Nest densities vary from 2,3-8,6 nests/m^2 (Jarvis 1971a; Crawford et al. 1983c). At Malgas Island and Lambert's Bay, reoccupation of nest sites and nestbuilding begin in earnest in August. Although thousands of birds may be present at colonies throughout the nonbreeding period, numbers are highly variable between May and July (Rand 1959; pers. obs.). Egg laying occurs from September to December, with a peak from September to mid-October at Malgas Island, and in October at Lambert's Bay (Rand 1959; pers. obs.). The nest is built almost entirely of guano and mud. The clutch is one egg, very rarely two, re-laying often following 2-4 weeks later if the egg is lost (Jarvis 1971a, 1974). The egg is relatively small at 3,9 % of female body mass (Nelson 1978b). The egg is incubated with the webs of the feet, an unusual incubation pattern apparently restricted to the Pelecaniformes.

The incubation period is 42-46 days, and the nestling period 93-105 days (Jarvis 1971a). Male and female take turns in incubating the egg in shifts averaging 41 hours (Jarvis 1971a). The chick is guarded by both parents alternately for much of the nestling period, average shifts decreasing from 29 hours in length in the first 20 days to 10 hours at ages of 80-100+ days (Jarvis 1971a). Periods of parental non-attendance are variable, presumably in relation to food supply and average 7-12 hours at different stages of the nestling period (Jarvis 1971a). The average adult foraging trip is 23 hours (Jarvis 1971a). Chicks reach a mean peak mass of about 3190 g at 80 days of age, and the mean mass thereafter recedes to about 2890 g. Chicks depart in February and March, either by swimming or flying. The mass of chicks at nest departure is variable and post-departure mortality is related to mass (Jarvis 1971a). There is no post-nestling parental care, and post-departure mortality is high but undetermined. Mortality in the first year is estimated at 76% for the Australian Gannet (Robertson quoted in Jarvis 1971a) and 80% in the North Atlantic Gannet (Nelson 1966a).

During the nonbreeding season (winter), Cape Gannets, particularly juvenile birds, migrate northwards to east and west Africa (Broekhuysen _et al_. 1961; Crawford _et al_. 1983c), many following the annual "sardine run" into Natal waters, usually in June-July. Adults and juveniles roost at sea. Juveniles do not return to breeding islands until they are at least 2-3 years old (Rand 1959; pers. obs.).

Cape Gannets feed during the day, leaving the colony after sunrise, and usually returning before sundown unless roosting at sea (Rand 1959). In southern Africa, the Cape Gannet eats epipelagic shoaling fish caught by plunge-diving in continental shelf waters, and on fish and offal discarded from demersal trawlers (Crawford & Shelton 1981). Although gannets apparently catch prey using the momentum of their dives, birds have been observed to swim underwater with half-opened wings (Nelson 1978b; G. Brill, SFRI, pers. obs.). Dives are usually made from a height of 5-30 m, and last from 2-8 s (pers. obs.), but birds sometimes catch prey at the surface in very shallow dives lasting less than 1 s. The major dietary items of Cape Gannets are Cape Anchovy, South African Pilchard, Saury _Scomberesox saurus_, Shallow-water Hake _Merluccius capensis_ and Deep-water Hake _Merluccius paradoxus_, and to a lesser extent, Redeye Roundherring, Mackerel, Maasbanker, Snoek _Thyrsites atun_, Southern Mullet (Harder) _Liza richardsoni_, Onderbaadjie and Pelagic Goby _Sufflogobius bibarbatus_ (Davies 1955, 1956, 1958; Rand 1959; Matthews 1961; Crawford & Shelton 1978, 1981; Batchelor 1982; Matthews & Berruti 1983; Batchelor & Ross 1984; Cooper 1984; Crawford _et al_. 1985).

The Cape Gannet has been intensively studied in South Africa. The major publications are listed here; Cooper & Brooke (1981) list virtually all publications referring to the Cape

Gannet prior to 1981. Important early contributions were by Broekhuysen _et al_. (1961), who investigated distribution and movements, Davies (1955, 1956, 1958) and Matthews (1961) who concentrated on the diet of the Cape Gannet. Rand (1959) examined population numbers, diet and feeding at sea. Jarvis (1971a, 1971b, 1972, 1974) studied the breeding ecology and ethology of the population at Bird Island, Lambert's Bay and its interaction with man. Recent papers by Crawford & Shelton (1978, 1981) related changes in the population size and guano harvests to changes in fish populations; Cooper (1978) who estimated chick energy requirements; Crawford _et al_. (1983c) who reviewed population changes, breeding distribution and migration. Early work by Courtenay-Latimer (1954), including information on diet of the population at Algoa Bay is questionable. For example, Courtenay-Latimer (1954) gives a weekly description of changes in chick development over 33 weeks (231 days) when the nestling period is 93-105 days (Jarvis 1971a; Maclean 1985; pers. obs.). Jarvis (1971a) noted that "practically all her observations are in disagreement with my findings at Lambert's Bay and it seems unlikely that differences of this nature could be caused by geographic position". Therefore, this work will not be referred to again in this thesis. Since 1978, the diet of the Algoa Bay population has been studied in relation to population changes (Batchelor 1982; Batchelor & Ross 1984; Randall & Ross 1979; J. Colclough in prep.).

All the gannets have been well studied, the North Atlantic Gannet Morus bassana in the eastern Atlantic by Nelson (1964, 1966a, b, 1978a, b and other references) who concentrated on population changes, breeding ecology and behaviour. In the western Atlantic, Montevecchi & Porter (1980), Montevecchi et al. 1984, Ricklefs et al. (1985) and several other authors have concentrated on the energetics of reproduction. Until recently, few data were available on the food of the North Atlantic gannet (Wanless 1984; Kirkham et al. 1985). In New Zealand, studies on the Australian Gannet Morus serrator include diet, distribution, population numbers and dispersal (Wodzicki 1955, 1967a, b; Wodzicki & Moreland 1966; Wodzicki et al. 1984) and breeding biology (Warham 1958; Wingham 1984a, b).

Nelson (1978b) regarded the North Atlantic Gannet as the most specialized of the three gannet populations, descended from Cape Gannets overshooting on northward migration. He suggested that the Cape Gannet, in turn, may have descended from Australian Gannets overshooting on westward migration. Australian Gannets have been recorded at Marion Island (Brown & Oatley 1982) and South Africa (Cassidy 1983), but a Cape Gannet has been found breeding with an Australian Gannet in Australia (Venn 1982).

CHAPTER 3

BIRDS AS INDICATOR SPECIES: THE USE OF SEABIRDS IN FISHERIES MANAGEMENT

INTRODUCTION

Monitoring aspects of birds' biology to indicate environmental or biological change in ecosystems is frequently proposed (Morrison 1986). Bird species used in this way have been termed "indicator species". Morrison (1986) reviewed the use of bird populations as indicators of environmental change, and found their use as indicators tenuous and inappropriate in most cases. However, birds have been used successfully to show deleterious effects of pesticides and other contaminants in food webs (Risebrough 1986; Furness & Monaghan 1986). Every organism responds to its environment, but demonstration of such responses does not qualify a species to fill a useful role as an indicator, unless the causal links between the response and the causative agents are known (Morrison 1986). The monitoring of a seabird species to conserve or manage that species does not constitute the use of an indicator species *per se*, unless the information from the monitoring programme is applied to other components of the biota or environment about which information is required. Such monitoring may be goal-orientated and specifically related to a management problem as in the fisheries context (Berruti 1985a), or can indicate perturbations not specifically investigated, such as the impact of the Sahelian drought on migratory birds in general indicated by the crash in Whitethroat Sylvia communis population (Winstanley et al. 1974).

SEABIRDS AS INDICATORS

Seabirds have been proposed as goal-orientated indicators useful for ecosystem or fisheries managers (Crawford & Shelton 1978; Ainley 1980; Brown 1980; Anderson & Gress 1984; Bengtson 1984; Berruti 1985a; Duffy et al. in press). However, this use of seabirds is not generally accepted: Morrison (1986) did not mention their use, nor are they mentioned in recent reviews of pelagic fisheries management (Saville 1979; Csirke 1984; Sherman & Alexander 1986). Furness & Monaghan (1986) suggested that certain seabirds might prove to be useful in providing cheap, "early-warning" systems of recruitment failure or stock depletion, but noted that this use had not yet been established. However, seabird monitoring is an integral part of proposals to manage the Antarctic ecosystem (SCAR/SCOR 1982; Bengtson 1984).

If the resource is to be managed at the ecosystem level, then maintenance of predator and prey stocks are equally considered. Predator-prey interactions may be monitored although neither predator nor prey are commercially exploited, but because they represents flows of energy through trophic pathways considered of importance in the system as a whole. For example, monitoring of sub-Antarctic populations of Wandering Albatrosses _Diomedea exulans_, which feed mainly on squid, may suggest changes in the abundance of squid prey and hence ecosystem function (SCAR/SCOR 1982). Management action is concerned with ecosystem integrity and more attention is likely to be focussed on the predator during the monitoring programme and in the management response. In situations where information is required about a single exploited species, the predator is monitored to provide insight into the status of that exploited prey population. Management action is concerned with prey stocks and not with predator stocks except insofar as they provide data on prey. In both instances, a detailed understanding of the functional relationships between the predator and prey is required as these relationships are the basis for the monitoring programme.

Seabirds may be used to establish a specific aspect of fish biology (e.g. number of year classes of fish or trend in prey abundance) required for fishery management, primarily for stock assessment. Examples are the use of seabird diet to show whether in a direct survey all populations of target species were encountered and all year classes encountered in specific areas (Sunada _et al_. 1981; Chapter 8), and the use seabirds to monitor trends in regional recruitment of Cape Anchovy (Duffy *et al*. in prep.). Alternatively, information from seabirds may help to elucidate aspects of the ecology of the prey, particularly distribution and movements. This information may be used to test assumptions on which research strategies and management practices depend, such as the distribution of various age classes of prey species (Hatch 1984; Croxall *et al*. 1985; Duffy *et al*. 1985; Armstrong *et al*. in press). This review concentrates on the status of research into the use of seabirds in the narrower context of the assessment and management of marine fisheries, comprising one or several species.

This review on the use of seabirds in fisheries management is based on the premise that selected variables of seabird biology are closely related to some aspect of fish biology or the structure and functioning of the ecosystem about which information is required for fisheries management. The types of fisheries for which seabirds may be useful indicators are considered first, then the aspects of prey biology for which data is required. Discussion then moves to the choice of seabird species and of the variables of their biology selected for monitoring, and finishes with a discussion of the relationships between seabird variables and aspects of fisheries biology and the use of seabirds in the management of the purse-seine fishery of the western Cape.

FISHERIES FOR WHICH SEABIRDS MAY BE USEFUL INDICATORS

Seabirds have been suggested as indicators of the state of epipelagic shoaling fishes such as those in the Benguela System (Crawford & Shelton 1978; Berruti 1985b; Duffy *et al*. in press), Northern Anchovy *Engraulis mordax* off California (Sunada *et al*. 1981; Anderson & Gress 1984), Capelin *Mallotus villosus* in the North Atlantic (Brown & Nettleship 1984), and Herring *Clupea harengus* in the North Sea (Hislop & Harris 1985) and for shoaling crustaceans such as krill *Euphausia superba* in the Southern Ocean (SCAR/SCOR 1982; Bengtson 1984). Seabirds are clearly inappropriate as indicators of aspects of the biology of adult demersal and large predatory fishes which they are unable to catch. However, juveniles of predatory and demersal fishes may be surface-shoaling (Cram & Schulein 1974) and therefore become available to seabirds. Thus Cape Gannets catch juvenile Snoek with caudal lengths of 90-360 mm, and have provided the only long time-series on juvenile Snoek occurrence and abundance in the western Cape for the period 1978-1986 (Dudley pers. comm.); Cape Cormorants eat juvenile hake at Lambert's Bay (pers. obs.); and Swift Terns eat juvenile hake in Namibia (Walter 1984). Snoek and hake are the major contributors to the handline- and demersal fisheries respectively in the western Cape (Chalmers 1976). However, demersal fisheries usually exploit species with a large number of year classes and are effectively managed with catch-based techniques.

PREY PARAMETERS TO BE MONITORED

Prey parameters to be monitored are determined by the goals of management, and therefore, the information required from seabirds will be decided by existing assessment practices. Some of these parameters for such assessment practices required are listed in Table 3 and ultimately, are concerned with estimating the abundance of fishes. It is possible that alternative techniques which are able to use qualitative information from predators may be developed later and could conceivably constitute a new approach to the management of pelagic shoaling fish.

The type of information required depends on the characteristics of the exploited species and the nature of management procedures. The management of the pelagic fish stocks off the western Cape will be used to show the potential contribution of seabirds to management advice. The abundance of fishes is determined by hydroacoustic surveys (Hampton _et_ _al_. 1985; Hampton in press) which assume a random sampling of the area, or subarea, inhabited by the stock. Potential errors are allocated variances, sometimes arbitrarily. However, bias also exists, because hydroacoustic searches do not survey shallow waters, where fish may occur (Hewitt & Brewer 1983) or the uppermost few metres of the ocean (Croxall _et_ _al_. 1985) and they assume there is no ship-avoidance by target species (Cram & Hampton 1976). The target species might break up into tiny shoals at some stage of the

TABLE 3.

SELECTED PARAMETERS OF SEABIRD BIOLOGY WHICH MAY PROVIDE INFORMATION ON SELECTED ASPECTS OF FISH BIOLOGY

	Aspect of fish biology					
Parameter	Abundance	Distribution	Mortality	Condition	Age/ Length	Spawning
Reproduction						
Breeding success	X					
Incub./brood shift	X					
Timing of egglaying	X					
Yolk formation	X					
Feeding						
Meal size	X					
Species composition	X	X				
Age/length of prey	X	X	X	X	X	X
Foraging range	X	X				X
Foraging trip	X	X				X
Condition/chick growth						
Adult weight	X					
Chick growth rate	X					
Fledging weight	X					
Population dynamics						
Population size	X		X			
Guano harvest	X					
Adult survival	X					
Chick survival	X					
First breeding (age)	X					
Prop. of nonbreeders	X					

daily or life cycle (Cram & Hampton 1976). Small shoals are less acoustically visible and are generally not targets for research catches because they are small. Seabird diet, combined with a knowledge of feeding area, can indicate whether all populations and age classes of the target species have been sampled (Sunada et al. 1981; Croxall et al. 1985). Spawner biomass estimates based on egg surveys assume the proportion of spawning fish caught reflects their representation in the population as a whole and a mean value of the number of spawnings per female (Parker 1980). The examination of prey from seabird diet could be used as a test of the length of the spawning season, extent of spawning area and the proportion of spawning fish in the population.

It appears unlikely, however, that seabird data alone will provide absolute estimates of the size of fish stocks. However, seabirds may be used to monitor trends in the timing and recruitment of fish stocks (Duffy et al. in prep.). Seabirds potentially offer a role in situations where direct measurement of fish stocks is difficult or logitically impossible. For example, the direct estimation of the size of the South African Pilchard stock between 1984 and 1986 was difficult, because of high variances associated with estimation of a small population and a highly clumped distribution. The Cape Gannet may prove to be a better integrator of the trends in the abundance of South African Pilchard in this situation (Chapter 9).

CHOICE OF SEABIRD

The choice of species of seabird as a potential indicator is governed by several factors (SCAR/SCOR 1982; Bengtson 1984; Berruti 1985a).

Firstly, at least some of the populations of the seabird should eat a large amount of the species for which information is needed, but it need not be dominant in the diet. The numbers of breeding Western Gulls Larus occidentalis and the proportion of Northern Anchovy in their diet were correlated with the amount of Northern Anchovy seen by commercial spotter pilots, although the proportion of Northern Anchovy varied between 18% and 42% of the diet (Hunt & Butler 1980). The size of the prey is important because seabirds may eat the target species at a size smaller than that which commercial fisheries take and at different stages of its life cycle and migration, allowing for the possibility of predictive advice for prey stocks.

Secondly, the species should be easily studied, because the low cost of seabird monitoring is a primary motivation for using them. The species should be tolerant of human disturbance and easily accessible on a regular, predictable basis. It should be colonial or available in large numbers to allow collection of large sample sizes.

Thirdly, the monitored variables should be easily and simply measured. In particular, the diet should be easily sampled and the prey in stomach contents relatively undigested. Collection of data on the condition and stage of gonad maturation of fish are possible only if the prey are largely undigested. The condition of fish obtained by various methods from different seabirds species varies greatly (Ashmole & Ashmole 1967).

Fourthly, the seabird should be widely distributed and its range should include a major part of the fishery area, in order to demonstrate changes in prey biology over a wide geographical range. The availability of several populations for study allows a comparative assessment of the variability of the response to changes in the biology of the prey. It is possible that long-term study of one population may not provide data on a range of responses if there is little variability in the population parameters of the prey species.

Fifthly, the species should be well studied, to provide the necessary baseline and background data for interpretation and comparison. By choice of the appropriate indicator species, it will be possible to distinguish between near-shore and pelagic conditions, or focus upon particular parts of oceanic systems or marine food webs (Ricklefs _et_ _al_. 1984). Choice of seabird is dependent on the type of information required.

SEABIRD PARAMETERS TO BE MONITORED

The choice of variables is governed by several factors. Firstly, the selected variable should be closely related to that aspect of fish biology for which information is required, but relatively insensitive to natural fluctuations in physical environmental conditions at that scale of measurement, providing that physical change does not also act directly on the fish populations. The sensitivity of such variables to changes in the fish parameters should be tested by means of models. Thus, MacCall (1984), using a simulation model, cautioned against the use of absolute population size of seabirds as an index of the abundance of the forage base, a result confirmed for Peruvian guano birds which responded to an increase in nesting space independent of prey abundance (Duffy 1983a).

Secondly, each variable of the seabird which is related to an aspect of seabird biology is influenced by that aspect over a period of time. Different variables of seabirds are influenced by aspects of fish biology over different lengths of time. Each variable can be regarded as an integration of that particular aspect of fish biology for a particular duration of time. Some variables may be measured only at at set times of year, particularly those relating to breeding, or accessibility to the seabird population during breeding (Table 4). For example, the proportion of fish species by mass, number and frequency of occurrence in a number of the stomach contents of birds taken on one day at any

TABLE 4.

SAMPLING INTERVALS, INTEGRATION TIME AND LENGTH OF TIME SERIES REQUIRED FOR PARAMETERS OF CAPE GANNET BIOLOGY SELECTED FOR MONITORING

Variable	Sampling interval	Integration time	Time series required
Reproduction			
Breeding success	within season/year-to-year	months	5-10 years
Incubation/ brood shift	within season	days	5-10 years
Timing of egg-laying	within season/year-to-year	days/months	5-10 years
Yolk formation	within season/year-to-year	days	5-10 years
Feeding			
Meal size	daily	days	3-5 years
Species composition	daily	days	3-5 years
Age/length composition	daily	days	3-5 years
Foraging range	within season	days	3-10 years
Foraging trip	daily/within season	days	3-10 years
Condition and chick growth			
Adult mass	within season/year-to-year	days/months	5-10 years
Chick growth	within season/year-to-year	months	5-10 years
Fledging mass	within season/year-to-year	months	5-10 years
Population dynamics			
Population size	years	months/years	>10 years
Guano harvest	years	years	>10 years
Adult survival	years	years	>10 years
Chick survival	years	months/years	>10 years
Age at first breeding	years	years	>10 years
Prop. of nonbreeders	yeasr	months/years	>10 years

time of year is an integration of all fish available to that population on that day at any time of year. However, the timing of egg-laying may reflect the biomass of fish available in the few weeks before breeding only (August and September in the case of the Cape Gannet).

Thirdly, the variables should be rapidly determined; a major motivation for using seabirds is to provide immediate warnings of drastic changes in prey stocks, particularly recruitment failure.

Fourthly, the variables should be cheaply determined to offer an inexpensive alternative to the high cost of ship-based research.

Fifthly, time series of guano harvests and population counts exist for periods before the collection of catch-based data. These time series (e.g. guano harvests), the accumulation of fish scales in anaerobic sediments (Soutar & Isaacs 1974; Shackleton in press) and other predator indices such as Snoek harvests (Crawford & Shelton 1981) provide the only historical information on fish abundance.

Seabird variables available for the monitoring of fisheries comprise the spectrum of responses by seabirds to changes in their food supply. These variables fall into overlapping groups: reproductive biology, chick growth and feeding, diet and feeding ecology, population dynamics and adult condition. A review of this enormous subject lies beyond the scope of this work.

If necessary, a monitoring programme should consist of a number of variables representing different durations of time spaced throughout the period over which the fish parameter can be estimated. Variables pertaining to chick growth and feeding and reproductive biology can be measured only in the breeding season, which in some seabirds is protracted. In practice, many of the other variables are most easily determined during the breeding season when the birds stay near the breeding island and are under maximal stress to harvest food for reproductive activities.

Most of the variables listed in Table 3 are likely to be proximately linked to fish availability, but only diet analysis and foraging range can be used to determine the age composition (especially of spawning fishes), distribution and migration, condition and stage of gonad maturation and timing and area of spawning of fishes available to the birds. The diet of seabirds has been suggested as a technique for sampling fish within certain size ranges (Ashmole & Ashmole 1968; Sunada _et al_. 1981; Chu 1984; Vermeer & Westrheim 1984; Berruti 1985a). Proper interpretation of seabird data is dependent on determination of the foraging range of the seabird. The degree of correlation between the breeding success of Brown Pelican _Pelecanus occidentalis_ and the abundance of Northern Anchovy varied with the scale of the estimated foraging range (Anderson _et al_. 1982). Diet composition has been shown in many seabirds to vary locally (Harrison _et al_. 1983; Schneider & Hunt 1984; Chapter 5).

Aspects of breeding biology readily reflect food availability over relatively short periods of time (Table 3). Clutch size, timing of egg-laying, egg size, chick growth rates and breeding success in seabirds have been related to food availability (Anderson _et al_. 1980; Hunt & Butler 1980; Batchelor 1982; Gaston & Nettleship 1982; Duffy 1983). Egg harvests of Jackass Penguins and breeding success of Peruvian guano birds have been used as an indication of historical fish abundance (Siegfried & Crawford 1978; Duffy 1983).

Female condition is a primary determinant of clutch size, laying date and occurrence of breeding (Drent & Daan 1980). Adult mass is likely to be an indication of fish availability throughout the year.

Aspects of population dynamics tend to reflect food availability over long periods of time (Table 4). Numbers of birds at colonies and breeding success, have been used to indicate shorter-term fish abundance (Hunt & Butler 1980; Gaston & Nettleship 1982). Guano and egg harvests, population sizes and changes in sizes of breeding colonies have provided historical insight into fluctuations in fish abundance (Crawford & Shelton 1978, 1981; Siegfried & Crawford 1978).

Ricklefs et al. (1984) stated that growth of seabird chicks can provide a valuable index of seasonal and long-term variation in their prey. The Bluefooted Booby Sula nebouxii has a 9-10-month breeding season providing a long monitoring period. By choosing the appropriate indicator species, it will be possible to distinguish between near-shore and pelagic conditions, or to focus upon particular parts of oceanic systems or food webs.

Growth of seabird chicks can vary temporally and geographically and may be sensitive to the local availability of marine food resources (Hunt 1972; Dunn 1975; Hunt & Hunt 1976; Nelson 1978a; Lloyd 1979; Summers & Drent 1979; Birkhead & Nettleship 1981; Ricklefs et al. 1984).

Seabirds may respond directly to changes in the physical environment. For example, the feeding of seabirds is directly affected by short-term changes in the weather (Dunn 1973; Birkhead 1976; Mendelsohn 1981). Storms can reduce breeding success (Wingham 1984b). Man can directly affect the monitored variables of seabirds e.g. egg harvests reduced Jackass Penguin population size at Dassen Island (Siegfried & Crawford 1981) and an oil spill in 1983 reduced the number of breeding pairs and increased adult mortality of Cape Gannets at Malgas Island (pers. obs.). The monitored variable should not be significantly affected by factors other than the aspect of fish biology being investigated.

RELATIONSHIPS BETWEEN SEABIRD AND FISHERY PARAMETERS

A major stumbling block to interpretation of data from seabirds is a lack of detailed understanding of prey selectivity by seabirds. Holling (1959) distinguished four principal types of response by predators to changes in prey density. His type 3 curve, which is sigmoid in shape and which described most of the responses he investigated has also been regarded by others (Anderson & Gress 1984; Beddington 1984, 1986) as applicable to marine predator-prey interactions. Clearly, the functional response of seabirds cannot be determined with accuracy because of the lack of information on the size of the prey resource. Nevertheless, it is clear that all four functional responses described by Holling (1959) share a period of linearity or near-linearity with respect to changes in prey density, followed by a plateau or very small change as prey density increases still further. Thus, if it has been shown that the monitored response of the seabird shows large variation, it is reasonable to assume a linear or near-linear response as prey density increases from low to moderate levels and is followed by a period of little or no change as prey density increase from high to superabundant levels. It is difficult to determine whether lower threshold values exist and where upper and lower threshold values for changes in rates of response to changes in prey density lie. The response is also likely to be affected by the presence of alternative prey (Holling 1959).

Time series of variables of seabird biology may show presence or absence of, qualitative changes or quantified trends in aspects of fish biology. Complementary evidence from several monitored variables in the absence of measures of fish stocks may confirm presence or absence of fish, or the direction of trend in aspects of fish biology at various time and distance scales. A time series of seabird variables, measured simultaneously with and calibrated against catch-based statistics, could produce good correlations. Only then can rapid, quantified inferences on aspects of fish stocks be made from bird variables alone, ahead of the lag in processing of catch-based statistics, which cannot currently provide timeous warning of recruitment failure. Even more desirable would be time series of bird variables calibrated against catch-independent direct assessments (e.g. aerial and acoustic surveys), which may be less prone to sampling bias. However, the lack of correlation with the results from direct surveys will not necessarily invalidate the use of seabird data, as direct surveys are subject to considerable bias and variance. Information from biological indicators is generally lacking in quantitative data (Zonneveld 1983). In fact, the lack of techniques which can use qualitative or quantitative data generated by seabirds points to the need to develop alternative systems

(Bradbury _et al_. 1986; Starfield & Bleloch 1986).

THE USE OF SEABIRDS IN FISHERY MANAGEMENT IN SOUTH AFRICA

Assessments of epipelagic fish stocks in the southern Benguela have used catch-based techniques and results from hydroacoustic and egg surveys (Davies _et al_. 1981; Armstrong _et al_. 1983; Hampton _et al_. 1985).

Because the use of catch-based statistics is generally unable to provide timely warning of fluctuations in recruitment (Butterworth 1980), attention has turned to the possible use of seabirds as a catch-independent means of assessing the state of pelagic fish populations (Newman & Crawford 1980). Long time series of guano yields, scraped for use as fertilizers, were used by Crawford & Shelton (1978) to demonstrate significant correlations between guano yields and catches, catch rates and VPA estimates of the abundance of South African Pilchard at several localities, and between guano yields and catches and catch rates of Snoek (a predator of South African Pilchard). As the South African Pilchard was the major prey of the three guano-producing seabirds, the Cape Gannet, the Jackass Penguin and the Cape Cormorant (Rand 1959, 1960a, b), Crawford & Shelton (1978) made the reasonable assumption that food supply controlled guano production and suggested that there were large fluctuations in fish populations before the advent of fishing. They suggested that guano harvests could be used as an index of the state of fish resources. However, as guano is deposited in the year before collection, it cannot provide a timely warning. Therefore Crawford & Shelton (1978) suggested that, as guano yields reflect bird numbers, a more timely assessment could be made by counting seabirds present in breeding seasons, especially as guano harvesting was terminated at many islands in Southern Africa in the 1970s and 1980s. Crawford & Shelton (1981) showed close relationships between seabird numbers and fish populations, but lacked sufficient time-series of population counts to undertake statistical tests. This work was hampered by the fact that the biomasses of South African Pilchard were estimated by Virtual Population Analysis, since subjected to heavy criticism (Butterworth 1980, 1983; Armstrong _et al_. 1985, Hampton in press).

Siegfried & Crawford (1978) found significant correlations between the guano yield and the number of Jackass Penguin eggs collected at Dassen Island. The number of eggs is a function of population size. They noted that if food supply could be shown to be the factor controlling guano yields, the possibility existed of correlating guano yields with environmental factors. If such correlations were established, they would provide a means of forecasting the availability of commercially important stocks.

Crawford _et al_. (1983b) compared the number of Cape Cormorants entering St Helena Bay with indices of the availability and abundance of South African Pilchard and found congruent trends. They noted that the biology of the Cape Cormorant was better suited to take advantage of short-term (months) variability than that of the Cape Gannet and Jackass Penguin and suggested that colony location, timing of breeding, clutch size and breeding success varied with prey abundance.

Duffy et al. (in prep.) proposed the use of an index based on a comparison of the diets of the Cape Gannet and Jackass Penguin for monitoring the strength of Cape Anchovy recruitment. Duffy et al. (1985) used data from Jackass Penguins to test hypotheses about Cape Anchovy distribution. Armstrong et al. (in press) used data from Cape Gannets to investigate the migration and distribution of South African Pilchard in South African waters.

From 1984 to 1986, scientific advice on the management of the South African purse-seine fishery included information on the proportion of South African Pilchard in the gannet diet (Chapter 9) and on the timing and strength of Cape Anchovy recruitment (SFRI unpublished). However, the full use of seabirds as indicators awaits the acceptance of alternative systems of analysis (Bradbury et al. 1985; Starfield & Bleloch 1986) which accept qualitative data.

CHAPTER 4

SELECTION OF THE CAPE GANNET AS AN INDICATOR SPECIES AND OF DIET AS THE MONITORED RESPONSE TO CHANGES IN ABUNDANCE AND DISTRIBUTION OF PELAGIC FISH STOCKS

INTRODUCTION

Chapter 3 listed criteria of indicator species, and variables of seabird biology which respond to changes in fish stocks. The choice of the Cape Gannet as study species and the selection of diet as the monitored variable are discussed in this chapter.

Firstly the indicator species should consume significant quantities of the target species: Cape Anchovy, South African Pilchard, Redeye Roundherring and Onderbaadjie. In South African waters, several seabirds eat these species: Cape Gannet (Davies 1955, 1956, 1958; Rand 1959; Crawford & Shelton 1981; Batchelor 1982; Batchelor & Ross 1984), Jackass Penguin _Spheniscus demersus_ (Davies 1955, 1956, 1958; Rand 1960a; Randall _et al_.1981a & b; Randall 1983; Wilson 1985a & b), Cape Cormorant _Phalacrocorax capensis_ (Davies 1955, 1956, 1958; Rand 1960b; Crawford & Shelton 1981), Swift Tern _Sterna bergii_ (Walter _et al_. in press), and Sooty Shearwater _Puffinus griseus_ (Jackson in prep.).

The Sooty Shearwater is a nonbreeding pelagic visitor to South African waters. Therefore, responses in its reproductive biology cannot be monitored. Its pelagic feeding ecology can be investigated with great difficulty and expense and would entail extensive collection of specimens. The Sooty Shearwater and other pelagic seabird visitors which eat commercially important species are not suitable for fisheries monitoring in South Africa, because of the limited range of data which can be obtained and because of logistical difficulties in their collection.

The resident seabirds are more easily studied because they are confined to breeding colonies at some stage of the year, and provide the possibility of investigating aspects of breeding biology.

The Swift Tern is the most abundant of the terns breeding in South Africa. Swift Terns breed from February to October (Maclean 1985). There are apparently three breeding areas in the southern Benguela System and Agulhas Current; one located on one of the Saldanha Bay islands, one on Robben Island, and one on the Algoa Bay islands (Randall *et al*. 1981a). However, breeding is not invariably located on an easily accessible island and the terns are present at breeding colonies only for about 2-4 months. Swift Terns are not very tolerant of human disturbance, and some aspects of reproductive biology (e.g. breeding success) would be difficult to monitor, and might be heavily influenced by monitoring procedures. Swift Terns catch prey by plunge-diving, taking prey within 1 m of the surface (Duffy 1982). While it is possible to identify prey carried in the beak by parents to the chick, it would be difficult to obtain large numbers of prey for length-frequency determination. Terns regurgitated pellets of undigested remains, which contained otoliths identifiable to the species level (Walter 1984). However, regurgitated otoliths are eroded, making estimation of prey lengths impossible and differential digestion could eliminate small otoliths altering species composition (Duffy & Laurenson 1983; Walter 1984). Collection of pellets from nonbreeding Swift Terns may be difficult because roosting flocks may comprise several gull and tern species. Swift Terns have only recently been studied in detail in South Africa (W. Suter in prep.).

The Jackass Penguin breeds at twelve colonies in the southern Benguela (Shelton _et al_. 1984; pers. obs.) and at six in Algoa Bay (Randall _et al_. 1981a). Although its numbers have decreased markedly over the last few decades, two new colonies have been established in recent years at Robben Island and Stony Point (Shelton _et al_. 1984). The Jackass Penguin is readily and predictably available at breeding sites (Wilson 1985a). The breeding season covers most of the year, with little breeding during the period November-January in the Benguela (Wilson 1985a) and October-December in Algoa Bay (Randall 1983). Penguins show distinctly different peaks of breeding at different islands (Wilson 1985a). Birds are available throughout the year and variables related to breeding can be measured during most of year. The penguin is the only seabird considered here that breeds during the southward winter migration of juvenile Cape Anchovy. The prolonged breeding season and a clutch size of two eggs allows more variability in adjustment of breeding effort to food availability than in the Cape Gannet. Its restricted foraging range during the breeding season (Broni 1985) allows more localized investigation of aspects of fish biology. Although the Jackass Penguin can dive to 130 m, most foraging occurs within 10 m of the surface (Wilson & Bain in press). The Jackass Penguin is tolerant of human disturbance, but diet must be sampled with the water-offloading technique (Randall & Davidson 1981; Wilson 1984), and the condition of prey obtained in this way is often poor (pers. obs.). The Jackass Penguin eats Cape Anchovy smaller than that taken by the commercial fishery, which allows the possibility of predicting abundance of Cape Anchovy before their recruitment to the fishery (Duffy et al. in prep.). The Jackass Penguin is a well studied species (Rand 1960a; Frost et al. 1976; Cooper 1977, 1978, 1980; Crawford & Shelton 1981; Randall 1983; Shelton et al. 1984; Broni 1985; Wilson 1985a, b). The feeding ecology of the Jackass Penguin has been the focus of intensive study by the Percy FitzPatrick Institute of African Ornithology (Wilson 1985a & b; Broni 1985; Duffy et al. 1985).

The Cape Cormorant is the most abundant of the breeding seabirds considered here (Crawford & Shelton 1981) and has bred at 33 localities in South Africa (Cooper et al. 1982). The bird is usually available in large numbers during the breeding season, which lasts from September to March with a peak between September and October (Maclean 1985). However, the timing, location and number of birds breeding in the western Cape is variable (pers. obs.). It is the least tolerant to human disturbance of the four breeding species discussed here (Crawford et al. 1983a), but appears to have become accustomed to human presence at Lambert's Bay (pers. obs.) and other localities (Berry 1976). Desertions of breeding colonies, attributed to food shortages, occur frequently (Crawford et al. 1980a, 1986). The maximum clutch size is five eggs (Berry 1976). The species has greater scope for adjustment of breeding effort than the other three breeding species. The Cape Cormorant seldom feeds far offshore (Siegfried et al. 1975; Cooper 1984), and may forage singly but usually in flocks which may number several thousand (Duffy et al. 1984). Prey is caught by pursuit diving to depths estimated as at least 15 m (Duffy 1982). The prey is usually smaller than that taken by the gannets (Crawford & Shelton 1981). Cape Cormorants regurgitate pellets of undigested food remains, including otoliths, which can be used to identify prey remains but not for age or length determinations as otoliths are eroded by digestion (Duffy & Laurenson 1983). When Cape Cormorants regurgitate relatively fresh stomach contents, Hartlaub's *Larus hartlaubi* and Kelp Gulls *L. dominicanus* usually scavenge the regurgitations before they can be collected (pers. obs.). The Cape Cormorant is less well known than the Jackass Penguin and Cape Gannet, but has been studied by Rand (1960b); Berry (1976); Cooper et al. (1982). Crawford et al.(1983a) suggested that the colony location, timing of breeding, clutch size and breeding success of the Cape Cormorant varied with prey abundance, but noted its intolerance of human activities.

The Cape Gannet breeds at three colonies in South Africa (Crawford et al. 1983c), although a new colony may be in the process of establishment at Dyer Island (Berruti 1985b). It is readily and predictably available throughout the year in large numbers at its breeding colonies, which are readily accessible (Rand 1959). Its diet is easily sampled (Batchelor & Ross 1984) and it is tolerant of human disturbance (pers. obs.). Timing and location of breeding are highly predictable (pers. obs.) and birds show high site and mate fidelity (J. Colclough pers. comm.). The Cape Gannet has a large foraging range (Chapter 7) and is a well studied species (Davies 1955, 1956, 1958; Rand 1959; Jarvis 1971a, b, 1972, 1974; Cooper 1978, 1984; Crawford & Shelton 1981; Batchelor 1982; Batchelor & Ross 1984). It is currently being studied on Bird Island, Algoa Bay (J. Colclough, Port Elizabeth Museum in prep.).

Relevant biological characteristics of three major candidate species for monitoring are summarised in Table 5. The Cape Gannet has been selected as the major study species for the following reasons: (a) the diet can be easily sampled throughout the year on a predictable basis (b) diet samples are relatively undigested (c) it has a high tolerance of human disturbance (d) its biology is well-known and (e) baseline diet data and an intensive research programme into the Jackass Penguin already exist. Nevertheless, a comparison of variables of different seabird species which select different ranges of prey size caught by different foraging techniques at varying distances from breeding islands will provide complementary information (Duffy et al. 1984; Ricklefs et al. 1984; Berruti 1985a).

The variables selected for monitoring (species and length composition of prey, regurgitation mass, proportion of birds regurgitating food) relate to diet. The major reasons for selection of diet are: (a) a time series of data exists, (b) diet can be determined throughout the year allowing year-round monitoring (c) diet provides information on a wide range of fish parameters (Table 6) and (d) dietary parameters are linked without time lag to availability of prey. Additionally, short-term variability of diet is under investigation at Algoa Bay (J. Colclough, Port Elizabeth Museum, unpubl.).

Aspects of population dynamics can be affected by various

TABLE 5.

BIOLOGICAL CHARACTERISTICS OF THE CAPE GANNET, CAPE CORMORANT AND JACKASS PENGUIN IN THE SOUTHERN BENGUELA SYSTEM

Biological characteristic	Cape Gannet	Cape Cormorant	Jackass Penguin
Breeding biology			
no. of breeding stations	2[1]	variable	12[2]
breeding season	Sep-Apr	Aug-Apr	Jan-Oct
predictability of breeding	very high	moderate	high
clutch size	1	2-5	1-2
fidelity to breeding station	very high	low?	high
Feeding ecology			
foraging method	plunge-diving	pursuit-diving	underwater pursuit
foraging range (breeding birds)	hundreds of km	100 km ?	50 km ?
state of prey digestion in diet samples	fresh to moderate	very advanced[3]	moderate
ease of diet sampling	simple	simple to moderate[3]	moderate
tolerance of disturbance	very high	low	high
ease of census	easy	easy	difficult

1. A third colony may become established at Dyer Island.
2. Includes two small mainland colonies.
3. Pellets only. Stomach samples difficult to obtain.

TABLE 6.

SELECTED VARIABLES OF THE BIOLOGY OF THE CAPE GANNET AND OF ASPECTS OF PELAGIC FISH BIOLOGY

	Aspect of fish biology				
Variable	Available biomass	Distribution	Natural mortality	Age	Spawning
Feeding ecology					
prey species composition	x	x	x		x
prey age/length composition	x	x	x	x	x
prey condition, maturity	x	x		x	x
foraging range	x	x			x
Breeding biology					
timing of egg-laying	x				
duration of yolk formation	x				
incubation, brood shifts	x				
chick feeding frequency	x				
chick meal size	x				
chick growth rate	x				
nest departure mass (chick)	x				
breeding success	x				
Adult condition					
body mass	x				
Population dynamics					
proportion of non-breeders	x				
adult survival	x				
postfledging mortality	x	x			
guano harvest	x				
proportion of 2 & 3 year olds	x				
population size	x		x		

factors independent of food abundance, such as pesticides, oil spills, storms and direct human interference. In addition, many variables of population changes may be related to food changes 2-3 years previously; for example, adult and chick survival, recruitment of adults and population size, and as such constitute *post-hoc* determinations of changes that have already been detected. However, catastrophic changes (e.g. Schreiber & Schreiber 1984; Duffy et al. 1984) are still useful, indicating marked declines of food supply. Chick growth and condition, and aspects of reproductive biology are clearly related to food availability, but can only be determined over a limited period of time which does not coincide with the major southward migration of Anchovy. Time series of data and historical data were not available for these variables. Logistical difficulties exist in the collection of sufficiently large sample sizes. Adult condition can be monitored throughout the year, but cannot be interpreted independently of diet data. It is necessary but time-consuming to establish sex and breeding status because body mass is likely to be linked to these factors. Clearly, diet parameters were the most suitable for monitoring changes in epipelagic fish stocks.

CHAPTER 5

THE DIET OF THE CAPE GANNET

INTRODUCTION

The species composition, length of prey and other parameters such as regurgitation mass in the existing time series of regurgitations from Cape Gannets must be described at monthly and annual time scales at each colony to provide a baseline against which changes can be assessed. Previous dietary studies of the Cape Gannet have shown temporal and geographical variation in these parameters. Gannet diet was studied in the southwestern Cape in the early 1950s by Davies (1955, 1956, 1958) and Rand (1959a) and in 1978-1979 by Crawford & Shelton (1981). Batchelor (1982) and Batchelor & Ross (1984) reported on gannet diet at Algoa Bay between 1978 and 1981. Matthews (1961) and Matthews & Berruti (1983) reported on the diet of gannets off Walvis Bay in the late 1950s. Crawford & Shelton (1981) and Crawford _et_ _al_. (1985) presented data on gannet diet off southern Namibia during 1978-1982. The present study is the most extensive, comprising 8 465 regurgitations collected monthly over eight years, and includes the data for the southwestern Cape used by Crawford & Shelton (1981).

Most of the epipelagic prey species show regular, seasonal patterns of longshore abundance (Crawford 1980). Substantial changes in biomass and strength of year classes at annual and decadal time scales seem to be characteristic of epipelagic fish species in the Benguela System (Shelton & Armstrong 1984; Shelton et al. 1985). In this chapter, the species composition, length of prey, regurgitation mass and proportion of birds handled which regurgitated food at Lambert's Bay and at Malgas Island are related to known seasonal, annual and decadal patterns of fish migration and abundance. This chapter also constitutes a preliminary investigation of the hypothesis that seabird diet changes in relation to the availability of prey.

METHODS

Breeding and nonbreeding gannets at the edge of the colonies were caught with a crook attached to the end of a long pole (Nelson 1978b), immediately after they returned from foraging trips. The birds were inverted over a bucket, into which they usually regurgitated their stomach contents. Gannets may regurgitate two boluses of food, the second being more highly digested. However, in most instances, only one bolus was collected as birds were released immediately after regurgitating the first bolus. The number of birds which did not regurgitate was recorded. Most samples were collected between 16h00 and 18h30. Initially the sample was preserved in 4% formalin, and then sorted in the laboratory, days later. After March 1982, samples were sorted immediately in the field. Samples preserved in formalin were first drained of liquid. The sample was weighed, then sorted into species components. There were very few problems with identification of prey to species as nearly all samples comprised well known species, and were not highly digested. The mass and/or volume of each species was determined. The number of fishes present was determined by the number of caudal fins or heads of each species, whichever was greater. Heads were sometimes more easily counted in well-digested regurgitations of small fishes, especially Onderbaadjie. The remains of hake usually consisted of heads or tails and occasionally livers, but whole fish were seldom found. During 1978 and early 1979, volume but not mass was measured. From March 1979 to 1982, mass and volume were measured, but only mass after March 1982. As 1 g of fish has a volume of 1 ml (Table 7), earlier measures of volume were regarded as directly comparable with later measures of mass. For all whole fishes, the caudal (standard) length (Lc) (from the tip of the snout to the base of the peduncle) was measured (Fig. 5).

Dietary samples were collected monthly at each colony. At Lambert's Bay, 3 647 regurgitations were collected between September 1978 and August 1986 (Table 8). At Malgas Island, 4 818 regurgitations were collected between September 1978 and August 1986 (Table 9). If there were fewer than 10 regurgitations in any month, they were excluded from further analysis. Thus, 25 regurgitations from Lambert's Bay (April, May and July 1978, July 1979

TABLE 7.

THE DENSITY (G/ML) OF PELAGIC FISH SPECIES, MEASURED USING FISH IN REGURGITATED SAMPLES FROM CAPE GANNETS

Species	Mass (g)	Volume (ml)	Number	Density (g/ml)
Cape Anchovy	29 198	27 993	2 360	1,043
Hake spp.	17 290	17 146	40	1,008
Saury	12 243	11 841	173	1,034
South African Pilchard	3 002	2 980	23	1,007
Snoek	1 437	1 445	8	0,995
Redeye Roundherring	1 878	1 841	31	1,020
Lightfish	1 818	1 745	1 135	1,045
Mackerel	571	570	2	1,002
Maasbanker	470	469	30	1,002
Southern Mullet	318	305	3	1,043
Onderbaadjie	40	36	17	1,111

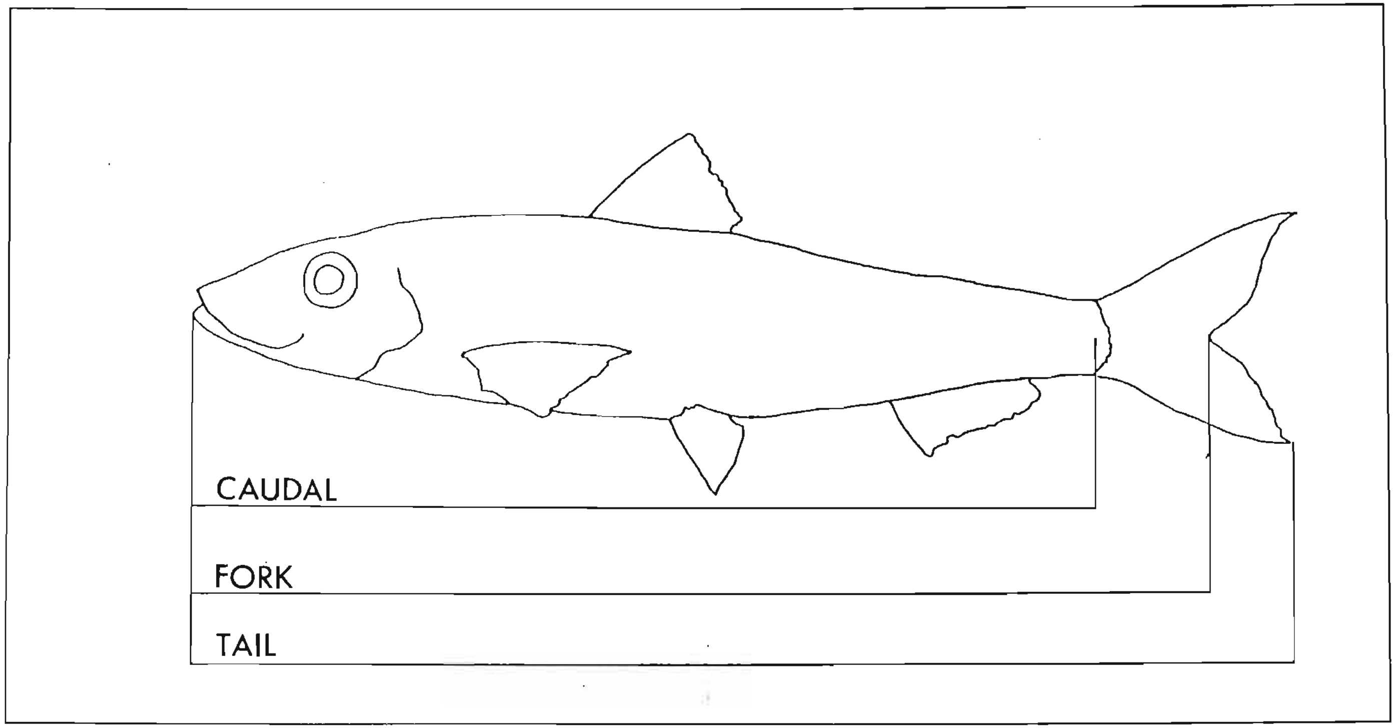


FIGURE 5

Diagram showing caudal, fork and total length measurements of fish.

TABLE 8.

THE NUMBER OF REGURGITATIONS OBTAINED MONTHLY FROM CAPE GANNETS AT LAMBERT'S BAY, DECEMBER 1977 TO AUGUST 1986

YEAR	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN	SD
1977												60		
1978	30	50	42	5	3	29	7	50	19	49	49	45	31,7	18,8
1979	49	50	50	50	50	17	9	39	35	50	50	50	41,6	14,4
1980	46	49	48	51	14	10	30	50	49	47	54	48	41,3	14,9
1981	50	39	1	50	31	49	0	10	13	50	30	13	30,5	18,6
1982	50	50	51	25	20	10	11	20	15	15	20	15	25,2	15,7
1983	18	13	15	16	17	18	13	12	15	15	128	17	24,8	32,6
1984	15	15	30	20	15	15	30	16	24	92	100	40	34,3	29,9
1985	30	41	35	30	40	45	25	40	34	40	75	60	41,3	13,9
1986	102	53	39	46	51	30	31	20					46,5	25,1
Mean	43,3	40,0	34,6	32,6	26,8	24,8	19,5	28,6	44,8	44,8	63,3	38,7		
S.D.	25,9	15,4	16,9	17,3	17,1	14,5	10,5	16,1	24,2	24,2	36,1	18,9		

TABLE 9.

THE NUMBER OF REGURGITATIONS OBTAINED MONTHLY FROM CAPE GANNETS AT MALGAS ISLAND, SEPTEMBER 1978-AUGUST 1986

YEAR	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN	SD
1978									50	50	42	49	47,8	3,9
1979	46	44	40	31	30	40	26	25	21	51	50	50	37,8	10,8
1980	48	47	46	38	13	-	30	12	48	48	35	284	59,0	75,8
1981	301	180	21	-	10	-	48	28	30	49	21	113	80,1	93,7
1982	251	10	34	16	20	39	30	31	28	95	65	60	56,6	65,7
1983	79	24	30	32	24	30	30	16	30	16	125	50	40,5	31,6
1984	80	30	30	20	22	30	30	40	45	34	26	30	34,8	15,8
1985	50	65	45	28	32	60	60	45	60	60	96	45	53,8	17,7
1986	60	75	60	75	15	75	90	45					61,9	23,3
Mean	114,4	59,4	38,3	34,3	20,8	45,7	43,0	30,3	39,0	50,4	57,5	85,1		
S.D.	101,5	53,1	12,2	19,4	7,9	18,1	22,3	12,5	13,6	22,5	36,3	84,0		

and March 1981) were excluded. The mean monthly sample size (including months with fewer than 10 regurgitations) varied from 24,8 (SD ±32,6) to 41,6 (SD±14,4) annually at Lambert's Bay, and from 34,8 (SD±15,8) to 69,3 (SD±89,0) annually at Malgas Island. During the nonbreeding season fewer adults are present. The lowest mean monthly sample sizes were 19,5 (SD±10,5) for July at Lambert's Bay and 20,8 (SD±7,9) for May at Malgas Island (Tables 8 & 9). No samples were collected in July 1981 at Lambert's Bay and in June 1980, April and June 1981 at Malgas Island (Tables 8 & 9).

Species were considered individually in the analysis if they contributed more than 5% of gannet diet by numerical abundance or mass or volume or frequency of occurrence at either Lambert's Bay or Malgas Island in any one year (Cape Anchovy, South African Pilchard, Saury, hake (including both _M_. _paradoxus_ and _M_. _capensis_), Snoek, Maasbanker, Mackerel, Onderbaadjie, Lightfish and Redeye Roundherring) or if they were of commercial importance (Southern Mullet and Squid). Squid include both _Loligo_ _vulgaris_ and _Lolliguncula_ sp. Other organisms were grouped into one of three categories (Offal, Unidentified and Other). Three species obtained as discards from demersal trawlers contributed to the Offal category: Buttersnoek (Ribbonfish) _Lepidopus_ _caudatus_, Jacopever _Helicolenus_ _dactylopterus_ and Grenadiers (Rattails) _Coelorhyncus_ spp. Fourteen species were included in the "Other" category. Of these, two were seen by the author: Flying Fish

Exocoetidae, and Cape Gurnard *Chelidonichthys capensis*. The remaining species require confirmation: Elephantfish (St Josephs Shark) *Callorhinchus capensis*, Atlantic Bonito (Katonkel) *Sarda sarda*, Monkfish *Lophius upsicephalus*, Cape Silverside *Atherina breviceps*, Dolphinfish *Coryphaena hippurus*, Mantis Shrimp *Squilla armata*, Steentjie *Spondyliosoma emarginatum*, Beaked Sandfish *Gonorhyncus gonorhyncus*, Cape Sandlance *Gymnammodytes capensis*, Pelagic Goby and Ladder Dragonet *Paracallionymus costatus*.

The composition of the diet was determined according to Hyslop (1980): numerical abundance (frequency) (N) is the number of individuals of each species from all stomachs; mass (M) is the mass of each species from all stomachs; volume (V) is the volume of each species from all stomachs; frequency of occurrence (F) is the number of stomachs containing a particular species. The mean species composition of each month (mean monthly composition) between 1977 and 1986 by numerical abundance, mass or volume and frequency of occurrence was calculated from the monthly percentages, thus weighting each month equally. The annual species compositions by numerical abundance, mass or volume and frequency of occurrence were calculated from monthly percentages in each year, thus weighting each month equally. The ranking method of Ashmole & Ashmole (1967) was used to combine these three measures to achieve a single ranking of prey importance, using data from Batchelor (1982) for Bird Island, Algoa Bay. Harrison *et al*. (1983) found that this ranking method differed little from the method used by Pinkas _et al_. (1971); Duffy & Jackson (1986) recommend its use.

Monthly length compositions for Cape Anchovy, South African Pilchard and Saury at Lambert's Bay and Malgas Island were derived by summing all available length frequencies for those species, and for all fishes together by summing all available length frequencies in each month. Separate length-frequency distributions were obtained for Cape Anchovy, South African Pilchard, Saury, Snoek, Onderbaadjie, Southern Mullet, Maasbanker, Mackerel and Redeye Roundherring by combining all available length frequencies. A length-frequency distribution was obtained for all fishes by summing all available length frequencies. Length-frequency distributions of fishes at the two localities were compared using the Kolmogorov-Smirnov test (Tate & Clelland 1957).

The mean (± one standard deviation (SD)) monthly proportions of gannets handled which regurgitated food were calculated by taking the mean of all percentages for particular months, thus weighting each month equally. The mean (±SD) annual proportions of gannets handled which regurgitated food were calculated by taking the mean of all monthly percentages for a particular year, thus weighting each month equally. The significance of differences in proportions recorded at the two colonies for the same time period were examined with the Mann-Whitney test (Conover 1971). For this test, all proportions recorded in the given time period and not the means were used. The mean (±SD) monthly and annual regurgitation masses were calculated in similar fashion. Mean regurgitation mass was calculated for all regurgitations and separately for all regurgitations excluding those containing hake or Offal. The differences between mean regurgitation masses at the two colonies were tested for the same time periods with the Students t-test.

The previous studies of gannet diet which provide historical and geographical comparisons with this study are listed in Table 10, which gives location, date, method of sampling, sample size and publications arising from the data sets.

The species composition and length frequency of catches by the purse-seine and demersal fisheries are monitored by the Sea Fisheries Research Institute (SFRI). The species composition and landed mass of all purse-seine fishery catches were recorded in 10' (about 18,5 km or 10 nautical miles) by 10' squares, which can then be aggregated into larger pool areas. Caudal lengths of fishes were obtained from samples taken from purse-seine catches. The catches between 1978 and 1984 were allocated to areas either north or south of Cape Columbine, which correspond roughly to the foraging areas of gannets from Lambert's Bay and Malgas Island respectively (Chapter 7).

The locality, number of net hauls, mass and species composi-

TABLE 10.

PREVIOUS STUDIES OF THE DIET OF CAPE GANNETS

Date	Area	No. of samples	Method of collection	Publications
1953-1955	St Helena Bay	289	Shooting at sea	Davies 1955, 1956, 1958
1954-1956	mainly Cape Columbine to Cape Hangklip	257	Shooting at sea	Rand 1959a
1957-1958	Walvis Bay area	155	Shooting at sea	Matthews 1961
1958-1959	Walvis Bay area	240	Shooting at sea	Matthews & Berruti 1983
1978-1979	Lambert's Bay & Malgas Island	1 224	Regurgitations at colony	Crawford & Shelton 1981
1978-1979	Mercury, Ichaboe & Possession Islands	256	Regurgitations at colony	Crawford & Shelton 1981
1978-1981	Bird Island, Algoa Bay	2 031	Regurgitations at colony	Batchelor 1982 Batchelor & Ross 1984
1977-1978	Malgas Island		Regurgitations at colony	Cooper 1984
1978-1982	Mercury, Ichaboe & Possession Islands[1]	1 437	Regurgitations at colony	Crawford *et al.* 1985
1977-1986	Lambert's Bay[1]	3 500	Regurgitations at colony	This study
1978-1986	Malgas Island[1]	4 500	Regurgitations at colony	This study

[1] Includes 1978-1979 data from Crawford & Shelton (1981).

tion of fishes landed by demersal trawlers in each 30' by 30' block covering the fishing ground between 200 m and 600 m off South Africa are monitored by the SFRI. These data were used to investigate seasonal use of trawling grounds by summing the total catch of hake in each block in March, June, September and December 1985. The mass of offal from hake (heads and viscera dumped at sea) is, on average, 46% of the landed mass of hake (B. Rose, SFRI, pers. comm). Offal, trash fish and an indeterminate amount of small hake are not used by the industry.

RESULTS

Species composition

The mean monthly species composition (by numerical abundance, mass/volume and frequency of occurrence) of gannet diet at Lambert's Bay from December 1977 to August 1986 and at Malgas Island from September 1978 to August 1986 is given in Tables 11-16. The smaller species (Cape Anchovy and Onderbaadjie) were relatively more important when measured by numerical abundance, whereas the larger species (hake, Saury and Snoek) and adults of other species (South African Pilchard and Redeye Roundherring) were relatively more important when considered by mass or volume.

TABLE 11.

THE MEAN MONTHLY SPECIES COMPOSITION (% NUMBERICAL ABUNDANCE - SEE METHODS) OF THE DIET OF THE CAPE GANNET AT LAMBERT'S BAY, DECEMBER 1977-AUGUST 1986

Species		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
Cape Anchovy	Mean	60,4	80,6	73,2	96,1	93,3	91,5	95,4	91,6	81,6	84,3	66,0	58,7	81,1
	SD	30,7	21,5	24,9	4,1	13,2	10,8	4,8	9,7	29,9	16,8	27,0	36,2	13,6
South African Pilchard	Mean	4,9	3,5	4,0	2,7	5,4	2,6	0,4	2,0	2,2	4,3	10,3	10,1	4,4
	SD	7,1	6,4	7,3	3,6	12,7	4,9	0,7	5,5	4,7	7,2	12,5	13,6	3,0
Saury	Mean	23,0	12,1	5,9	0,5	0,1	0,5	0,4	0,2	0,3	2,7	6,7	16,8	5,8
	SD	20,0	19,5	12,3	1,2	0,4	1,5	0,9	0,5	0,6	4,3	7,6	18,6	7,7
Hake	Mean	<0,1	0,2	0,3	0	0	0,3	1,8	1,3	2,5	0,7	0,4	0,6	0,7
	SD	0,1	0,2	0,9	0	0	0,7	3,8	2,3	3,7	1,3	0,8	1,4	0,8
Snoek	Mean	2,0	1,1	5,3	0,4	0,1	0,3	0,1	0,2	2,3	2,5	4,0	3,4	1,8
	SD	2,4	2,2	8,1	1,0	0,1	0,5	0,3	0,4	4,7	3,7	5,8	6,7	1,7
Onderbaadjie	Mean	0,5	0	0	0	0	1,8	0	<0,1	0	0	0	0,4	0,2
	SD	1,4	0	0	0	0	5,2	0	0,1	0	0	0	1,1	0,5
Southern Mullet	Mean	<0,1	0,1	1,0	0	0	0	0	2,1	0,1	0,1	0,2	0,2	0,3
	SD	0,2	0,3	2,8	0	0	0	0	4,2	0,1	0,2	0,3	0,4	0,6
Maasbanker	Mean	4,4	0,6	0,6	<0,1	0,3	0,5	0,9	0,1	0,5	2,1	9,0	6,5	2,1
	SD	4,9	0,5	1,5	0,1	0,4	1,0	2,0	0,2	1,1	4,6	10,3	5,4	2,9
Mackerel	Mean	1,4	0,1	0,9	<0,1	<0,1	0,2	0	0	0,5	0,3	0,3	0,1	0,3
	SD	3,1	0,2	1,5	0,1	<0,1	0,5	0	0	1,2	0,8	0,8	0,2	0,4
Lightfish	Mean	0	0	4,1	0	0	0	0	0	0,2	0	0	0	0,4
	SD	0	0	11,7	0	0	0	0	0	0,5	0	0	0	1,2
Redeye Roundherring	Mean	2,1	1,8	0,4	0,2	0,8	1,8	1,1	1,5	7,9	1,8	2,1	1,9	2,0
	SD	5,7	3,0	0,4	1,5	2,0	2,9	2,7	2,3	19,1	3,0	2,5	4,5	2,0
Squid	Mean	0,1	0	<0,1	0	0	0	0	0,8	1,9	1,1	1,0	0,5	0,5
	SD	0,3	0	0,1	0	0	0	0	1,2	3,9	1,9	1,2	0,6	0,6
Offal	Mean	0,1	0	4,1	0	0	0	0	0	<0,1	0	0,1	0,3	0,4
	SD	0,2	0	11,7	0	0	0	0	0	0,4	0	0,4	0,6	1,2
Unidentified	Mean	1,0	0	0,1	0	0	0,1	0	0	0	<0,1	<0,1	0,5	0,1
	SD	2,5	0	0,3	0	0	0,2	0	0	0	<0,1	0,1	1,5	0,3
Other	Mean	0	0	<0,1	<0,1	0,1	0,5	0	0,2	0	0,1	<0,1	<0,1	0,1
	SD	0	0	0,1	0,1	0,2	1,6	0	0,5	0	0,1	0,1	0,1	0,1
	N	9	9	8	7	8	9	6	9	8	8	8	8	9

TABLE 12.

THE MEAN MONTHLY SPECIES COMPOSITION (% MASS OR VOLUME - SEE METHODS) OF THE DIET OF THE CAPE GANNET AT LAMBERT'S BAY, DECEMBER 1977-AUGUST 1986

Species		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
Cape Anchovy	Mean	50,2	65,8	50,0	86,9	86,8	73,6	71,1	61,9	55,1	62,4	44,6	47,7	63,0
	SD	36,4	28,4	30,9	15,7	19,5	27,2	33,0	25,0	39,4	31,7	31,3	39,0	14,4
South African Pilchard	Mean	6,9	6,3	8,0	6,5	9,0	5,2	3,6	6,4	3,6	9,3	24,7	16,6	8,8
	SD	9,3	8,9	15,6	12,9	17,3	7,3	7,3	15,0	6,4	11,4	29,3	17,2	6,0
Saury	Mean	25,6	18,0	8,1	3,2	0,9	0,3	0,2	0,1	0,2	4,8	7,0	18,7	7,3
	SD	24,1	21,0	13,7	7,9	2,4	1,0	0,5	0,2	0,3	9,5	7,9	17,2	8,8
Hake	Mean	0,5	1,7	0,2	0	0	5,6	15,9	12,2	16,3	6,0	1,9	2,3	5,2
	SD	1,0	3,2	0,3	0	0	12,9	31,0	15,3	21,8	12,2	3,3	5,8	6,2
Snoek	Mean	4,4	4,3	17,6	2,4	0,5	4,8	2,0	3,0	9,0	4,7	6,3	4,6	5,3
	SD	4,2	9,0	28,0	6,4	0,9	7,5	4,9	7,1	20,1	7,8	8,9	7,3	4,4
Onderbaadjie	Mean	0,2	0	0	0	0	0,5	0	<0,1	0	0	0	0,1	0,1
	SD	0,5	0	0	0	0	1,5	0	0,1	0	0	0	0,3	0,1
Southern Mullet	Mean	0,4	0,3	2,0	0	0	0	0	8,6	0,8	0,5	0,8	1,3	1,2
	SD	1,3	1,0	5,7	0	0	0	0	15,5	2,0	0,9	1,5	2,8	2,4
Maasbanker	Mean	4,1	0,9	0,7	<0,1	0,2	0,4	0,8	0,1	0,2	1,0	4,6	4,3	1,4
	SD	5,5	1,3	1,3	0,1	0,3	0,9	1,9	0,2	0,4	2,2	5,8	4,4	1,8
Mackerel	Mean	5,0	0,7	4,3	0,7	0,4	4,5	0	0	0,7	2,5	1,6	1,6	1,8
	SD	9,7	1,5	6,9	1,2	1,2	13,4	0	0	1,7	6,9	4,6	3,9	1,8
Lightfish	Mean	0	0	4,1	0	0	0	0	0	0,2	0	0	0	0,4
	SD	0	0	11,6	0	0	0	0	0	0,5	0	0	0	1,2
Redeye Roundherring	Mean	1,7	1,9	0,2	0,2	1,8	3,0	6,3	6,5	12,7	7,1	6,6	1,7	4,1
	SD	4,7	3,0	0,4	0,4	3,5	5,2	15,4	8,8	27,0	9,4	10,6	3,0	3,7
Squid	Mean	0,2	0	<0,1	0	0	0	0	1,0	1,3	1,6	1,4	0,5	0,5
	SD	0,4	0	0,1	0	0	0	0	1,3	2,4	3,3	1,4	1,2	0,6
Offal	Mean	0,2	0	4,1	0	0	0	0	0	<0,1	0	0,3	0,3	0,4
	SD	0,7	0	11,6	0	0	0	0	0	0,1	0	0,7	0,5	1,2
Unidentified	Mean	0,7	0	0,2	0	0	0,3	0	0	0	<0,1	0,1	0,2	0,1
	SD	1,3	0	0,5	0	0	0,9	0	0	0	<0,1	0,4	0,6	0,2
Other	Mean	0	0	0,5	0,1	0,4	1,8	0	0,3	0	0,1	0,1	<0,1	0,3
	SD	0	0	1,4	0,3	1,1	5,4	0	0,7	0	0,2	0,3	<0,1	0,5
	N	9	9	8	7	8	9	6	9	8	8	8	8	9

TABLE 13.

THE MEAN MONTHLY SPECIES COMPOSITION (% FREQUENCY OF OCCURRENCE-SEE METHODS) OF THE DIET OF THE CAPE GANNET AT LAMBERT'S BAY, DECEMBER 1977-AUGUST 1986

Species		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
Cape Anchovy	Mean	63,9	79,9	72,3	95,8	98,1	87,1	84,1	78,0	65,7	74,1	61,0	61,6	76,8
	SD	27,4	23,5	30,9	5,9	2,9	15,2	14,9	22,8	32,6	22,7	28,9	38,0	12,7
South African Pilchard	Mean	12,2	12,1	18,2	14,3	15,5	8,1	6,4	7,0	7,1	12,0	24,6	24,5	13,5
	SD	14,3	14,2	21,0	16,3	22,2	12,2	8,9	13,5	11,0	13,0	24,6	19,4	6,3
Saury	Mean	35,2	20,3	10,9	1,5	0,7	0,7	2,5	7,3	1,4	6,9	10,0	23,9	10,1
	SD	29,5	24,7	15,8	2,6	2,7	2,2	4,8	9,3	2,7	11,5	10,0	21,9	11,0
Hake	Mean	0,5	1,7	1,0	0	0	3,0	13,7	8,0	14,8	5,6	2,2	2,7	4,4
	SD	1,0	2,4	2,1	0	0	5,6	20,6	11,3	18,4	10,2	3,6	5,8	5,1
Snoek	Mean	6,2	4,2	14,7	1,1	0,5	3,3	1,1	3,0	7,5	7,7	9,3	5,3	5,3
	SD	5,3	7,0	19,7	3,0	0,9	5,5	2,7	6,5	12,2	10,7	9,7	9,2	4,1
Onderbaadjie	Mean	0,6	0	0	0	0	0,5	0	0,6	0	0	0	0,3	0,2
	SD	1,7	0	0	0	0	1,5	0	1,9	0	0	0	0,8	0,3
Southern Mullet	Mean	0,4	1,0	2,3	0	0	0	0	4,5	1,2	0,9	0,7	1,1	1,0
	SD	1,1	2,0	6,7	0	0	0	0	6,2	2,4	1,5	1,1	2,2	1,3
Maasbanker	Mean	11,3	3,8	1,5	1,0	0,3	2,0	1,9	0,9	2,0	4,3	14,7	13,9	5,0
	SD	11,0	3,9	2,0	1,9	0,3	3,6	3,3	2,6	3,2	0,4	14,3	15,6	5,1
Mackerel	Mean	4,0	0,4	3,3	0,6	0,3	1,1	0	0	2,8	3,8	1,4	3,7	1,8
	SD	6,9	0,8	5,2	1,0	0,7	3,3	0	0	6,1	10,6	3,3	8,2	1,6
Lightfish	Mean	0	0	12,3	0	0	0	0	0	0,5	0	0	0	1,1
	SD	0	0	34,6	0	0	0	0	0	1,5	0	0	0	3,5
Redeye Roundherring	Mean	6,2	10,8	3,0	3,3	8,3	8,9	5,0	7,3	15,2	8,9	8,9	2,7	7,4
	SD	5,3	15,5	2,7	7,5	20,2	12,3	12,2	9,3	27,6	14,6	9,9	4,1	3,6
Squid	Mean	0,8	0	0,5	0	0	0	0	4,0	6,7	6,3	5,3	3,5	2,3
	SD	1,6	0	0,9	0	0	0	0	4,7	10,1	8,1	5,6	4,1	2,7
Offal	Mean	0,2	0	12,3	0	0	0	0	0	0,4	0	0,2	1,9	1,3
	SD	0,7	0	34,6	0	0	0	0	0	1,0	0	0,5	3,7	3,5
Unidentified	Mean	2,8	0	0,4	0	0	0,7	0	0	0	0,4	0,6	0,9	0,5
	SD	3,5	0	1,0	0	0	2,0	0	0	0	0,8	1,7	2,8	0,8
Other	Mean	0	0	0,8	0,6	0,8	1,2	0	0,9	0	1,0	0,2	0,3	0,5
	SD	0	0	2,3	1,5	2,1	3,7	0	1,9	0	1,5	0,6	0,8	0,4
	N	9	9	8	7	8	9	6	9	8	8	8	8	9

TABLE 14.

THE MEAN MONTHLY SPECIES COMPOSITION (% NUMERICAL ABUNDANCE - SEE METHODS OF THE DIET OF THE CAPE GANNET AT MALGAS ISLAND, DECEMBER 1977-AUGUST 1986.

Species		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
Cape Anchovy	Mean	40,9	43,2	40,2	73,1	76,1	71,2	70,5	62,5	57,3	82,7	79,0	62,6	63,3
	SD	28,0	30,6	25,1	26,7	26,5	28,6	12,4	31,6	29,1	12,7	19,3	23,9	15,0
South African Pilchard	Mean	2,4	7,3	2,1	4,1	3,8	1,8	2,1	2,7	2,7	4,6	1,5	4,3	3,3
	SD	2,2	7,7	2,1	6,9	6,1	2,4	2,8	2,1	2,4	9,0	2,0	6,7	1,6
Saury	Mean	48,4	45,3	48,9	13,2	8,7	1,5	1,4	0,2	4,9	5,7	6,7	22,1	17,3
	SD	22,0	24,5	26,7	21,4	11,4	2,3	2,0	0,3	7,8	6,5	6,2	15,7	19,2
Hake	Mean	0,9	2,4	4,2	5,8	8,4	23,9	19,3	15,8	14,3	2,6	2,0	2,1	8,5
	SD	1,0	2,2	3,4	7,9	11,6	26,3	12,7	16,1	12,2	2,3	2,7	2,6	7,9
Snoek	Mean	0,4	0,3	0,4	0,4	0,1	0	0,1	0,3	0,1	0,7	0,8	0,2	0,3
	SD	0,5	0,6	0,7	0,8	0,3	0	0,2	0,6	0,1	1,3	1,1	0,4	0,2
Onderbaadjie	Mean	5,4	0	0	0	0	0	3,4	1,3	4,7	1,2	7,1	5,9	2,4
	SD	15,2	0	0	0	0	0	9,6	3,7	7,0	2,6	17,5	13,4	2,7
Southern Mullet	Mean	0,1	<0,1	0,7	0,1	0,1	0	0	<0,1	0,1	0,1	0,1	<0,1	0,1
	SD	0,3	0,1	1,9	0,2	0,2	0	0	0,1	0,1	0,2	0,1	0,1	0,2
Maasbanker	Mean	1,1	0,2	1,4	1,3	0,2	0	0,7	0,4	0,1	1,0	0,3	1,6	0,7
	SD	2,3	0,4	2,7	3,1	0,6	0	1,4	0,7	0,3	1,4	0,4	3,2	0,6
Mackerel	Mean	0,1	0,1	0,2	0,2	0,1	0	0	0	0	0,1	0,1	0,1	0,1
	SD	0,1	0,2	0,3	0,3	0,4	0	0	0	0	0,2	0,1	0,1	0,2
Lightfish	Mean	0	0	0	0	0	0,1	0	11,8	13,3	0,4	0	0	2,1
	SD	0	0	0	0	0	0,2	0	21,6	31,9	1,1	0	0	4,9
Redeye Roundherring	Mean	0,4	0,6	1,4	1,7	0,4	0,7	0,6	0,4	1,6	0,3	0,2	0,5	0,7
	SD	0,6	1,5	1,6	2,6	1,1	0,8	0,7	1,0	2,1	0,4	0,3	1,3	0,5
Squid	Mean	<0,1	0	0	0	0	0	0,5	0,4	0,4	0,5	0,3	0,6	0,2
	SD	0,1	0	0	0	0	0	1,2	0,9	0,8	0,6	0,3	1,1	0,2
Offal	Mean	0	0,6	0,3	0	1,6	0,8	1,4	0,7	0,2	0	0,1	<0,1	0,5
	SD	0	1,6	0,3	0	3,1	1,2	2,6	1,4	0,4	0	0,2	0,1	0,6
Unidentified	Mean	0	<0,1	<0,1	0,1	<0,1	0	0	0,2	<0,1	<0,1	2,2	0,1	0,2
	SD	0	0,2	0,1	0,1	0,1	0	0	0,4	0,1	0,1	5,9	0,1	0,6
Other	Mean	<0,1	0	0	0	0,5	0	0	3,3	0,3	<0,1	0	0	0,3
	SD	0,1	0	0	0	1,5	0	0	9,4	0,6	0,1	0	0	0,9
	N	8	8	8	7	8	6	8	8	8	8	8	8	8

TABLE 15.

THE MEAN MONTHLY SPECIES COMPOSITION (% MASS OR VOLUME - SEE METHODS) OF THE DIET OF THE CAPE GANNET AT MALGAS ISLAND, DECEMBER 1977-AUGUST 1986

Species		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
Cape Anchovy	Mean	23,4	23,2	13,1	38,8	34,6	16,9	19,4	23,7	27,2	57,7	63,3	41,9	31,9
	SD	20,7	21,8	8,7	37,1	22,4	11,6	18,5	27,0	22,7	22,9	19,4	18,7	15,9
South African Pilchard	Mean	5,9	10,3	4,3	8,2	7,7	4,3	3,5	6,2	4,2	14,0	6,1	11,8	7,2
	SD	5,4	10,8	5,6	11,4	11,8	5,5	3,0	6,2	3,5	20,4	8,4	16,3	3,3
Saury	Mean	61,6	53,5	60,4	19,6	18,1	1,0	3,1	0,2	1,6	5,2	11,1	30,5	22,2
	SD	14,1	16,8	19,4	26,7	19,2	1,4	3,7	0,5	2,7	5,5	9,4	13,1	23,8
Hake	Mean	4,9	10,4	15,2	27,5	30,8	76,6	62,2	57,3	50,7	18,2	12,3	11,4	31,5
	SD	4,8	9,8	10,3	33,4	17,6	14,7	24,7	26,0	29,4	15,9	15,2	12,6	24,1
Snoek	Mean	0,5	0,6	1,7	2,5	1,1	0	1,2	1,2	0,4	1,0	1,0	0,2	1,0
	SD	0,6	1,0	2,9	5,4	3,2	0	2,3	2,7	1,1	2,1	1,4	0,5	0,7
Onderbaadjie	Mean	0,9	0	0	0	0	0	1,7	0,1	0,8	0,2	2,4	1,3	0,6
	SD	2,5	0	0	0	0	0	4,8	0,2	1,4	0,3	6,4	2,9	0,8
Southern Mullet	Mean	0,9	0,3	1,8	0,4	0,5	0	0	0,2	1,2	1,2	0,6	0,1	0,6
	SD	2,1	0,7	4,6	1,0	1,5	0	0	0,7	2,1	2,6	1,1	0,2	0,6
Maasbanker	Mean	1,1	0,1	0,2	0,9	0,2	0	0,2	0,1	0,2	0,7	0,1	0,4	0,4
	SD	2,3	0,3	0,2	2,0	0,5	0	0,5	0,2	0,6	1,4	0,1	0,9	1,9
Mackerel	Mean	0,1	0,6	1,8	0,6	1,3	0	0	0	0	<0,1	0,9	0,5	0,5
	SD	0,1	1,0	2,0	1,3	3,7	0	0	0	0	0,1	1,1	0,6	0,6
Lightfish	Mean	0	0	0	0	0	0,1	0	1,6	6,0	0,1	0	0	0,7
	SD	0	0	0	0	0	0,2	0	3,0	16,7	0,2	0	0	1,7
Redeye Roundherring	Mean	0,8	0,4	0,9	1,5	0,9	0,5	1,2	2,7	5,6	1,2	0,2	0,8	1,4
	SD	1,0	0,9	1,2	2,7	2,6	0,8	2,1	7,6	7,0	1,9	0,5	1,5	1,5
Squid	Mean	<0,1	0	0	0	0	0	1,6	0,9	0,6	0,4	0,6	0,5	0,4
	SD	0,1	0	0	0	0	0	4,3	1,8	1,1	0,5	1,2	0,9	0,5
Offal	Mean	0	0,6	0,6	0	2,1	0,7	5,7	1,5	0,4	0	0,6	<0,1	1,0
	SD	0	1,8	0,8	0	3,9	1,2	9,3	2,0	0,7	0	1,6	0,1	1,6
Unidentified	Mean	0	<0,1	0,1	<0,1	0,1	0	0	0,6	<0,1	<0,1	0,8	0,6	0,2
	SD	0	<0,1	0,3	<0,1	0,1	0	0	1,1	<0,1	0,1	1,5	1,1	0,3
Other	Mean	<0,1	0	0	0	2,5	0	0	3,7	1,0	<0,1	0	0	0,6
	SD	0,1	0	0	0	7,0	0	0	10,4	2,1	0,1	0	0	1,2
	N	8	8	8	7	8	6	8	8	8	8	8	8	8

TABLE 16.

THE MEAN MONTHLY SPECIES COMPOSITION (% FREQUENCY OF OCCURRENCE-SEE METHODS) OF THE DIET OF THE CAPE GANNET AT MALGAS ISLAND, DECEMBER 1977 AUGUST 1986

Species		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
Cape Anchovy	Mean	32,1	33,7	24,0	50,8	51,3	31,7	31,5	32,1	39,5	70,0	74,6	51,4	43,6
	SD	23,6	24,3	14,7	33,8	24,2	18,3	18,9	25,3	21,9	19,3	16,1	19,7	16,2
South African Pilchard	Mean	6,8	13,6	5,6	7,7	10,9	4,9	3,8	5,9	5,6	13,0	8,2	11,0	8,1
	SD	4,7	12,9	6,4	12,0	14,0	4,1	3,5	5,1	4,0	18,3	10,2	15,2	3,3
Saury	Mean	63,7	58,9	62,3	19,4	17,7	2,7	2,2	0,6	2,9	9,6	13,6	36,2	24,2
	SD	15,7	19,4	17,2	22,9	16,5	3,3	2,0	1,0	3,6	8,1	10,8	11,5	24,7
Hake	Mean	5,2	11,9	15,5	23,7	29,4	70,8	61,9	53,5	43,6	13,5	9,6	10,5	29,1
	SD	4,3	11,6	11,4	29,1	16,8	21,1	25,1	24,5	23,7	10,5	11,9	11,5	22,7
Snoek	Mean	1,2	1,3	1,2	1,8	1,1	0	0,7	1,3	0,3	2,0	1,3	2,6	1,2
	SD	1,3	2,1	1,8	3,6	3,2	0	1,3	2,6	0,7	4,2	1,4	6,3	0,7
Onderbaadjie	Mean	1,0	0	0	0	0	0	1,7	0,8	3,2	0,5	2,6	2,6	1,0
	SD	2,8	0	0	0	0	0	4,7	1,6	4,1	0,9	5,7	6,3	1,2
Southern Mullet	Mean	1,0	0,4	1,7	0,4	0,6	0	0	0,3	1,3	1,0	0,6	0,3	0,6
	SD	2,0	0,8	4,1	1,2	1,8	0	0	0,8	1,9	2,2	1,1	0,7	0,5
Maasbanker	Mean	1,1	0,9	1,3	1,9	1,3	0	0,8	1,2	1,1	3,8	1,0	3,2	1,5
	SD	1,6	1,5	1,9	3,7	3,5	0	1,5	1,8	1,7	5,6	1,7	5,5	1,1
Mackerel	Mean	0,6	0,8	1,5	1,3	0,8	0	0	0	0	0,5	1,1	0,8	0,6
	SD	1,0	1,7	1,6	2,2	2,3	0	0	0	0	1,4	1,5	1,0	0,5
Lightfish	Mean	0	0	0	0	0	0,6	0	4,6	6,9	0,6	0	0	1,1
	SD	0	0	0	0	0	1,3	0	7,6	18,8	1,2	0	0	2,3
Redeye Roundherring	Mean	1,4	2,3	3,2	3,5	0,8	2,5	2,6	2,0	4,7	1,5	1,1	1,4	2,3
	SD	1,9	5,8	3,2	5,3	2,3	2,5	3,5	5,6	5,4	1,8	2,1	2,3	1,1
Squid	Mean	0,3	0	0	0	0	0	1,7	3,1	1,0	4,7	3,6	2,8	1,4
	SD	0,7	0	0	0	0	0	3,6	6,5	1,6	4,7	4,6	4,8	1,7
Offal	Mean	0	1,0	1,7	0	3,0	3,1	6,7	2,5	1,0	0	0,8	0,3	1,3
	SD	0	2,8	1,9	0	3,3	5,4	12,3	3,1	1,8	0	2,0	0,7	1,8
Unidentified	Mean	0	0,1	0,3	0,5	0,6	0	0	0,9	0,2	0,1	2,1	0,8	0,5
	SD	0	0,2	0,8	1,3	1,6	0	0	1,6	0,6	0,4	4,3	1,3	0,6
Other	Mean	0,2	0	0	0	2,5	0	0	4,5	1,8	0,5	0	0	0,8
	SD	0,4	0	0	0	7,1	0	0	12,7	2,7	1,4	0	0	1,4
	N	8	8	8	7	8	6	8	8	8	8	8	8	8

At Lambert's Bay, Cape Anchovy dominated throughout the year, but was most abundant in the diet in April and May, and least abundant from November to January. South African Pilchard occurred throughout the year, with marked peaks in contribution by mass in November and December in some years as a result of large adults being consumed. Hake occurred mainly from June to September. Redeye Roundherring occurred primarily from June to November. A number of species occurred mostly in spring and summer: Saury between November and February, Southern Mullet from August to March, Maasbanker from November to January, Mackerel from October to March (although the June figure is also high), Snoek from September to March and Squid from September to November. Rare species or groups which did not show a clear seasonal pattern of occurrence were Onderbaadjie, Lightfish, Offal, Other and Unidentified.

At Malgas Island, the percentage Cape Anchovy was highest from October to December with a smaller peak in April and May. Saury was highly seasonal, and occurred from November to May with a distinct peak in January and February. Hake and Offal was most important in winter from June to September. Three species which were rare dietary items occurred in the late winter and spring period; Onderbaadjie (July to December), Lightfish (August to September) and Squid (July to September). South African Pilchard occurred at low levels throughout the year, although large adult fishes resulted in an increase in its contribution by mass between October and December. Four minor contributors occurred throughout the year; Snoek (except June and July), Maasbanker (except June and July) and Redeye Roundherring, while Mackerel were not recorded between June and September. Southern Mullet were rare dietary items, but were most frequent between August and March. Fishes grouped in the Unidentified and Other categories were rare and showed no distinct pattern of occurrence.

There are similar trends in the composition of the diet at Lambert's Bay and at Malgas Island from 1978 to 1986. At Lambert's Bay between 1978 to 1982, Cape Anchovy dominated and became increasingly important (Tables 17-19). South African Pilchard, Mackerel and Redeye Roundherring decreased in importance in this period. From 1983 to 1985, gannet diet at Lambert's Bay has become more diverse, Cape Anchovy decreasing in relative importance and Saury, hake and South African Pilchard increasing. In 1986, Cape Anchovy once again increased, and the increase in South African Pilchard also continued, whereas hake and Saury decreased again. Snoek remained variable throughout, contributing most strongly in 1980 and 1982.

At Malgas Island, the proportion of Cape Anchovy in the diet of gannets was relatively stable between 1978 and 1982 (Tables 20-22), while the contributions of South African Pilchard and Redeye Roundherring decreased. The contribution of Saury was variable, but the combined contributions of Saury and Cape

TABLE 17.

ANNUAL COMPOSITION (% NUMERICAL ABUNDANCE - SEE METHODS) OF PRE SPECIES IN CAPE GANNET DIET AT LAMBERT'S BAY, 1978 -1986

Fish species		1978	1979	1980	1981	1982	1983	1984	1985	1986
Cape Anchovy	Mean	76,8	73,5	89,0	90,8	93,5	83,1	78,4	61,0	85,4
	SD	23,5	29,2	16,4	11,7	9,9	12,8	35,5	30,1	17,1
S. African Pilchard	Mean	2,7	3,3	2,4	0,5	0,9	5,4	5,7	10,4	8,2
	SD	6,8	5,1	3,9	1,1	1,9	10,3	13,0	10,9	8,6
Saury	Mean	6,3	2,9	3,7	3,3	0,8	5,0	4,7	19,7	5,3
	SD	9,1	4,6	10,4	7,9	1,6	8,9	10,9	25,3	9,6
Hake	Mean	0,5	0,1	<0,1	1,3	0,1	1,3	0,9	1,8	0,1
	SD	1,3	0,2	0,1	3,4	0,1	2,7	1,6	2,2	0,1
Snoek	Mean	3,1	3,7	1,5	2,0	0,7	<0,1	4,2	0,8	0,4
	SD	6,7	5,9	2,2	4,2	2,0	0,1	6,7	1,1	1,2
Onder-baadjie	Mean	0	0	0	0	<0,1	0	0,3	1,7	0
	SD	0	0	0	0	0,1	0	0,9	4,6	0
Southern Mullet	Mean	0,9	0,3	0,1	1,4	0,3	<0,1	0,1	0,1	0
	SD	2,7	0,8	0,3	4,3	0,7	0,1	0,3	0,2	0
Maasbanker	Mean	2,5	0,6	1,1	0,4	3,1	3,5	4,2	1,6	0,4
	SD	4,1	0,7	2,0	0,5	5,4	6,8	8,3	1,8	1,0
Mackerel	Mean	1,6	0,5	0,5	<0,1	0	0,2	0	0,2	<0,1
	SD	3,1	1,1	0,9	0,1	0	0,6	0	0,7	0,1
Lightfish	Mean	0	3,0	0	0	0	0	0,1	0	0
	SD	0	10,0	0	0	0	0	0,4	0	0
Redeye Roundherring	Mean	4,4	7,7	1,5	0,2	0,2	1,1	0,6	1,0	0,1
	SD	5,7	10,0	2,8	0,5	0,3	2,3	0,9	1,0	0,3
Squid	Mean	0,2	1,2	0,2	0	0,3	0,3	0,7	0,9	0
	SD	0,4	3,2	0,3	0	0,6	0,6	1,6	1,4	0
Offal	Mean	0	3,3	0	0	0	0	0	0,3	0,1
	SD	0	10,5	0	0	0	0	0	0,6	0,2
Unident-ified	Mean	0,9	0,1	<0,1	0	0,1	0	<0,1	0,1	0
	SD	2,6	0,2	0,1	0	0,1	0	0,1	0,2	0
Other	Mean	<0,1	0,1	0	0	0,1	<0,1	<0,1	0,5	0
	SD	0,1	0,2	0	0	0,1	0,1	<0,1	1,4	0
	N	9	11	12	9	12	12	12	12	8

TABLE 18.

ANNUAL COMPOSITION (% MASS OR VOLUME - SEE METHODS) OF PRE

SPECIES IN CAPE GANNET DIET AT LAMBERT'S BAY, 1978-1986

Fish species		1978	1979	1980	1981	1982	1983	1984	1985	1986
Cape Anchovy	Mean	49,9	58,9	69,0	75,4	84,5	60,8	64,6	36,8	68,5
	SD	33,0	31,7	24,2	30,0	19,7	23,8	41,0	34,1	24,7
S. African Pilchard	Mean	10,3	5,3	3,2	1,5	2,0	9,6	8,2	21,4	21,4
	SD	24,6	10,1	4,6	4,1	3,5	14,5	15,3	18,7	15,0
Saury	Mean	10,2	4,5	4,2	4,0	2,5	9,5	4,6	19,0	6,7
	SD	14,1	8,5	9,9	8,0	4,2	13,1	10,4	28,0	11,3
Hake	Mean	4,3	0,2	0,3	6,4	0,2	13,2	7,8	10,8	0,4
	SD	11,2	0,6	1,1	12,8	0,6	24,5	16,9	12,2	0,7
Snoek	Mean	8,3	5,6	6,4	10,9	2,0	0,1	10,7	3,8	1,4
	SD	14,2	6,7	7,4	19,1	5,8	0,2	22,7	6,1	3,2
Onder-baadjie	Mean	0	0	0	0	<0,1	0	0,1	0,5	0
	SD	0	0	0	0	0,1	0	0,2	1,3	0
Southern Mullet	Mean	2,2	2,3	1,5	0,5	3,8	0,1	0,5	0,5	0
	SD	5,3	6,7	3,0	1,1	13,0	0,1	1,2	1,6	0
Maasbanker	Mean	1,1	0,3	0,6	0,3	3,5	2,9	1,6	1,2	0,4
	SD	2,3	0,4	1,5	0,3	5,5	5,1	3,0	1,6	1,2
Mackerel	Mean	5,1	2,2	6,8	0,1	0	1,1	0	0,4	0,6
	SD	8,0	5,9	12,8	0,3	0	3,7	0	1,5	1,2
Lightfish	Mean	0	3,0	0	0	0	0	0,1	0	0
	SD	0	9,9	0	0	0	0	0,4	0	0
Redeye Roundherring	Mean	7,9	13,8	7,8	0,8	0,9	1,8	0,7	2,6	0,2
	SD	6,4	23,2	13,8	1,7	1,5	3,4	1,2	3,4	0,6
Squid	Mean	0,1	0,4	0,4	0	0,3	0,5	1,1	1,2	0
	SD	0,1	1,0	0,7	0	0,6	1,2	2,8	2,1	0
Offal	Mean	0	3,3	0	0	0	0	0	0,3	0,3
	SD	0	10,4	0	0	0	0	0	0,7	0,7
Unident-ified	Mean	0,4	0,2	<0,1	0	0,3	0	0,1	0,1	0
	SD	1,3	0,8	<0,1	0	0,7	0	0,1	0,4	0
Other	Mean	0,1	0,1	0	0	0,2	0,4	<0,1	1,6	0
	SD	0,2	0,2	0	0	0,4	1,1	<0,1	4,7	0
	N	9	11	12	9	12	12	12	12	8

TABLE 19.

ANNUAL COMPOSITION (% FREQUENCY OF OCCURRENCE - SEE METHODS) OF PREY SPECIES IN CAPE GANNET DIET AT LAMBERT'S BAY, 1978-1986

Fish species		1978	1979	1980	1981	1982	1983	1984	1985	1986
Cape Anchovy	Mean	64,2	78,4	83,1	85,3	90,6	83,4	73,0	50,0	84,2
	SD	6,3	26,7	15,0	23,0	14,9	14,9	35,8	30,9	17,5
S. African Pilchard	Mean	8,1	14,0	7,2	3,9	4,9	20,7	10,6	26,7	26,2
	SD	17,1	14,3	11,4	8,0	10,5	18,2	18,8	16,8	18,7
Saury	Mean	11,1	6,8	6,4	5,7	2,3	12,1	6,1	25,5	9,4
	SD	14,9	9,7	16,8	12,4	4,1	19,5	14,3	30,8	12,9
Hake	Mean	4,5	0,7	0,3	4,5	0,9	8,0	6,4	10,6	1,0
	SD	12,1	1,8	1,0	10,4	2,6	15,8	12,0	11,1	1,4
Snoek	Mean	7,5	10,7	5,4	9,2	1,9	0,5	8,8	4,0	1,5
	SD	12,7	10,3	5,2	10,9	5,4	1,7	15,9	5,7	3,4
Onderbaadjie	Mean	0	0	0	0	0,5	0	0,2	0,8	0
	SD	0	0	0	0	0,2	0	0,7	1,9	0
Southern Mullet	Mean	2,5	1,3	1,0	1,4	1,9	0,6	0,3	0,5	0
	SD	6,3	3,2	2,0	3,3	5,0	1,9	0,9	1,1	0
Maasbanker	Mean	4,5	4,8	3,1	2,7	9,2	8,6	6,2	3,6	0,8
	SD	7,5	5,4	4,2	3,9	15,1	13,4	9,8	3,4	1,5
Mackerel	Mean	4,2	4,6	2,9	0,4	0	1,3	0	0,5	0,5
	SD	6,6	9,8	5,0	1,3	0	3,1	0	1,6	0,9
Lightfish	Mean	0	8,4	0	0	0	0	0,3	0	0
	SD	0	29,5	0	0	0	0	1,2	0	0
Redeye Roundherring	Mean	13,0	23,0	6,8	1,8	3,3	4,4	8,1	4,9	0,6
	SD	10,4	27,3	11,7	2,9	4,7	8,0	15,1	3,5	1,0
Squid	Mean	1,6	3,9	1,2	0	2,0	2,0	3,1	4,7	0
	SD	3,5	7,6	2,0	0	3,6	4,3	6,7	6,8	0
Offal	Mean	0	9,8	0	0	0	0	0	1,6	0,2
	SD	0	31,0	0	0	0	0	0	3,1	0,7
Unidentified	Mean	1,1	0,9	0,2	0	0,7	0	0,6	0,2	0
	SD	3,3	1,8	0,6	0	1,7	0	1,9	0,8	0
Other	Mean	0,5	0,5	0	0	0,8	0,7	0,3	1,3	0
	SD	1,4	1,8	0	0	1,9	1,9	0,8	3,2	0
	N	9	11	12	9	12	12	12	12	12

TABLE 20.

ANNUAL COMPOSITION (% NUMERICAL ABUNDANCE - SEE METHODS) OF PREY SPECIES IN CAPE GANNET DIET AT MALGAS ISLAND, 1978-1986

Fish species		1978	1979	1980	1981	1982	1983	1984	1985	1986
Cape Anchovy	Mean	66,4	60,7	60,9	58,6	78,9	67,3	66,6	50,3	56,5
	SD	25,6	30,6	36,5	33,6	17,3	23,3	19,6	29,3	30,0
S. African Pilchard	Mean	1,8	3,5	3,7	2,8	1,0	0,7	2,7	6,1	8,0
	SD	0,1	4,2	6,5	3,8	1,3	1,3	2,7	7,9	6,9
Saury	Mean	10,3	17,8	28,8	21,4	9,9	16,5	10,6	16,9	25,8
	SD	9,3	24,3	30,8	28,3	15,3	24,7	13,9	22,5	31,5
Hake	Mean	7,0	3,7	4,3	4,5	8,4	10,3	10,3	16,2	6,8
	SD	13,9	6,9	10,7	6,8	11,5	8,4	13,3	22,4	5,2
Snoek	Mean	0	0,7	0,2	0,3	0,1	0,2	0,7	0,4	<0,1
	SD	0	1,0	0,2	0,6	0,2	0,4	1,1	0,7	0,1
Onder-baadjie	Mean	13,3	3,2	0	1,0	0,2	1,5	4,2	5,0	0
	SD	24,8	11,0	0	2,7	0,8	5,3	8,5	12,2	0
Southern Mullet	Mean	0	<0,1	<0,1	<0,1	0,6	0,1	0,1	<0,1	<0,1
	SD	0	0,1	0,1	<0,1	1,5	0,2	0,3	0,1	0,1
Maasbanker	Mean	0	1,0	0,5	1,2	0	0,8	0,8	1,0	0,5
	SD	0	2,4	0,9	2,3	0	2,6	2,1	1,2	0,9
Mackerel	Mean	0,1	0,2	0,1	<0,1	<0,1	0,1	0,1	0,1	0
	SD	0,1	0,3	0,2	<0,1	0,1	0,2	0,1	0,2	0
Lightfish	Mean	0	5,1	0	9,1	0,3	0,8	1,3	2,0	0
	SD	0	17,6	0	28,8	0,9	2,6	4,3	6,9	0
Redeye Roundherring	Mean	1,0	1,3	1,0	0,3	0,2	0,1	0,5	1,4	0,7
	SD	1,8	1,6	1,7	0,5	0,4	0,3	1,3	1,9	1,4
Squid	Mean	0,1	0,3	0,1	0,1	0,1	0,7	0,3	0,2	0
	SD	0,1	0,9	0,2	0,3	0,2	1,2	0,7	0,3	0
Offal	Mean	0	<0,1	0,3	0,2	0,3	0,9	0,5	0,3	1,8
	SD	0	0,1	0,8	0,3	0,7	2,2	1,1	0,6	3,3
Unident-ified	Mean	<0,1	0	0,1	0,1	0,1	0	1,5	0,1	0
	SD	0,1	0	0,2	0,2	0,3	0	4,8	0,1	0
Other	Mean	0	2,4	0	0,5	0	0,1	<0,1	0	0
	SD	0	7,7	0	1,3	0	0,2	0,1	0	0
	N	4	12	11	10	12	12	12	12	8

TABLE 21.

ANNUAL COMPOSITION (% MASS OR VOLUME - SEE METHODS) OF PREY SPECIES IN CAPE GANNET DIET AT MALGAS ISLAND, 1978-1986

Fish species		1978	1979	1980	1981	1982	1983	1984	1985	1986
Cape Anchovy	Mean	47,1	37,8	39,4	33,1	42,5	27,4	34,5	16,7	16,7
	SD	28,2	28,4	31,1	31,9	28,5	18,0	23,3	16,8	11,2
South African Pilchard	Mean	9,4	6,5	5,8	7,1	1,8	2,0	7,2	14,6	14,7
	SD	3,9	9,0	8,9	6,0	2,1	4,1	7,9	19,7	10,3
Saury	Mean	15,7	24,3	33,4	27,2	15,8	21,8	15,7	19,8	29,5
	SD	13,3	27,0	30,4	34,2	24,2	26,5	19,4	23,3	33,7
Hake	Mean	20,0	18,1	14,5	21,5	34,3	41,8	36,3	44,7	35,5
	SD	38,8	25,5	13,1	27,0	28,1	28,7	31,9	34,0	25,9
Snoek	Mean	0	1,9	1,1	1,2	0,2	0,2	2,1	1,0	0,1
	SD	0	4,3	1,4	2,5	0,6	0,5	3,2	2,1	0,3
Onder-baadjie	Mean	4,7	0,7	0	0,3	<0,1	0,3	1,2	0,7	0
	SD	9,0	2,4	0	0,6	0,1	1,1	3,9	2,0	0
Southern Mullet	Mean	0	0,6	0,2	0,5	2,3	0,5	0,5	0,1	0,2
	SD	0	1,7	0,4	0,9	4,1	0,9	1,7	0,4	0,7
Maasbanker	Mean	0	0,6	0,7	0,3	0	0,2	0,4	0,3	0,1
	SD	0	1,5	1,3	0,3	0	0,8	1,0	0,3	0,2
Mackerel	Mean	0,7	1,3	0,7	0,3	0,3	0,8	0,4	0,3	0
	SD	0,9	3,0	1,3	0,7	0,9	1,6	1,0	0,7	0
Lightfish	Mean	0	0,7	0	4,7	<0,1	0,3	0,1	0,1	0
	SD	0	2,5	0	15,0	0,1	1,0	0,3	0,3	0
Redeye Roundherring	Mean	1,5	4,7	2,4	0,6	1,2	<0,1	0,4	1,1	0,7
	SD	1,7	7,3	3,6	1,5	3,6	0,1	0,9	1,4	0,9
Squid	Mean	0,1	0,2	0,3	0,4	0,1	1,5	0,3	0,2	0
	SD	0,1	0,7	0,8	1,1	0,2	3,7	0,7	0,5	0
Offal	Mean	0	<0,1	1,3	0,5	1,1	2,7	0,6	0,3	2,6
	SD	0	<0,1	2,3	1,1	3,4	7,6	1,0	0,5	3,9
Unident-ified	Mean	0,8	0	0,3	0,2	0,3	0	0,4	0,1	0
	SD	1,6	0	0,8	0,5	0,9	0	1,0	0,2	0
Other	Mean	0	2,5	0	2,2	0	0,5	<0,1	0	0
	SD	0	8,4	0	6,2	0	1,8	<0,1	0	0
	N	4	12	11	10	12	12	12	12	8

TABLE 22.

ANNUAL COMPOSITION (% FREQUENCY OF OCCURRENCE - SEE METHODS) OF PREY SPECIES IN CAPE GANNET DIET AT MALGAS ISLAND, 1978-1986

Fish species		1978	1979	1980	1981	1982	1983	1984	1985	1986
Cape Anchovy	Mean	56,9	47,7	47,5	43,2	54,1	40,6	45,6	29,2	34,8
	SD	25,8	29,3	33,8	30,9	25,2	22,3	23,7	22,6	11,7
S. African Pilchard	Mean	8,8	7,1	6,3	7,1	2,5	2,7	8,6	16,0	18,9
	SD	2,8	8,3	9,3	6,0	2,3	3,7	9,9	17,3	11,6
Saury	Mean	17,4	25,5	30,5	28,7	16,7	23,4	17,9	25,4	36,7
	SD	15,2	26,2	30,6	34,3	24,2	24,2	20,1	28,4	35,6
Hake	Mean	17,5	17,3	12,2	22,8	30,5	38,7	33,3	41,6	32,4
	SD	32,3	23,7	17,8	27,6	25,6	28,8	29,2	33,5	21,8
Snoek	Mean	0	1,9	1,1	1,1	0,3	0,5	2,4	1,1	0,2
	SD	0	3,0	1,2	2,2	1,0	1,2	4,0	2,0	0,5
Onder-baadjie	Mean	4,7	1,8	0	1,3	0,3	0,3	2,1	2,1	0
	SD	8,1	5,2	0	3,2	0,9	1,0	4,4	2,4	0
Southern Mullet	Mean	0	0,6	0,3	0,6	2,4	0,5	0,5	0,2	0,3
	SD	0	1,5	0,7	1,1	3,7	1,0	1,6	0,6	0,8
Maasbanker	Mean	0	2,5	0,9	3,3	0	1,7	1,6	1,5	1,1
	SD	0	3,6	1,5	3,1	0	4,7	4,3	1,3	1,7
Mackerel	Mean	1,1	1,6	0,7	0,2	0,4	0,5	0,5	0,7	0
	SD	1,3	2,2	1,6	0,5	0,9	1,1	1,1	1,6	0
Lightfish	Mean	0	1,8	0	5,3	0,3	1,0	0,5	0,4	0
	SD	0	5,7	0	16,9	0,9	3,6	1,1	1,3	0
Redeye Roundherring	Mean	1,0	4,6	2,5	1,0	1,6	0,6	2,0	3,4	2,3
	SD	1,8	4,7	3,6	1,8	4,1	1,9	4,8	4,2	3,0
Squid	Mean	1,6	1,7	1,2	1,6	0,9	3,6	1,4	1,0	0
	SD	2,0	4,1	1,3	4,5	1,7	6,4	3,5	1,5	0
Offal	Mean	0	0,2	1,5	1,0	1,2	4,5	1,7	1,2	2,7
	SD	0	0,6	2,8	1,8	2,3	10,8	2,6	1,7	3,7
Unident-ified	Mean	0,5	0	0,6	0,4	0,4	0	1,6	0,6	0
	SD	1,0	0	1,7	1,1	1,0	0	3,5	1,2	0
Other	Mean	0	3,7	0	2,7	0	0,3	0,1	0	0
	SD	0	10,3	0	6,4	0	1,0	0,3	0	0
	N	4	12	11	10	12	12	12	12	12

Anchovy were more or less constant; decreases in Cape Anchovy associated with increases in Saury and *vice versa*. Gannet diet at Malgas Island between 1983 and 1986 was more variable. Cape Anchovy decreased while both hake and South African Pilchard became increasingly important. The contribution of Saury was generally smaller during this period, but was high in 1986.

Cape Anchovy, South African Pilchard and Saury dominated gannet diet at Lambert's Bay; Cape Anchovy, hake and Saury dominated the diet at Malgas Island and Cape Anchovy, South African Pilchard and Saury at Algoa Bay (Table 23). The lumping of frequencies of occurrence of "Other" species at Algoa Bay did not result in a notable overestimate of their importance in terms of frequency of occurrence as they were ranked fifth in frequency of occurrence and mass, and fourth in numerical abundance.

Fish Length

Seasonal changes in the caudal lengths of Cape Anchovy ingested were apparent (Fig. 6). At Lambert's Bay, fishes less than 70 mm Lc began to appear in numbers in January, with modal sizes decreasing to a minimum between May and September and increasing until December. At Malgas Island, recruits less than 70 mm Lc appeared in February. Modal lengths decreased until August. Modal lengths increased from 80 mm Lc in October to 95

TABLE 23.

PREY SPECIES OF CAPE GANNET AT LAMBERT'S BAY AND MALGAS ISLAND 1977-1986, AND ALGOA BAY 1978-1981 (BATCHELOR 1981). SPECIES WERE RANKED SEPARATELY IN TERMS OF NUMERICAL ABUNDANCE, VOLUME OR MASS AND FREQUENCY OF OCCURRENCE. THESE THREE SUBRANKINGS WERE SUMMED AND RANKED FROM HIGHEST TO LOWEST TO ACHIEVE THE RANK GIVEN FOR EACH SPECIES

	Lambert's Bay	Malgas Island	Algoa Bay
Cape Anchovy	1	1	2
South African Pilchard	2	4	1
Saury	3	3	3
Hake	7	2	7,5
Snoek	4,5	10	-
Redeye Roundherring	4,5	5	6
Southern Mullet	12	13	-
Maasbanker	6	6	9
Mackerel	9	14	4
Onderbaadjie	14,5	9	-
Squid[1]	8	11,5	7,5
Other	13	11,5	5
Lightfish	10	8	-
Offal	11	7	-
Unidentified	14,5	15	-

1. *Loligo vulgaris* and *Lolliguncula* at Lambert's Bay and Malgas Island, *L. vulgaris* and *Ommastrephes bartrami* at Algoa Bay.

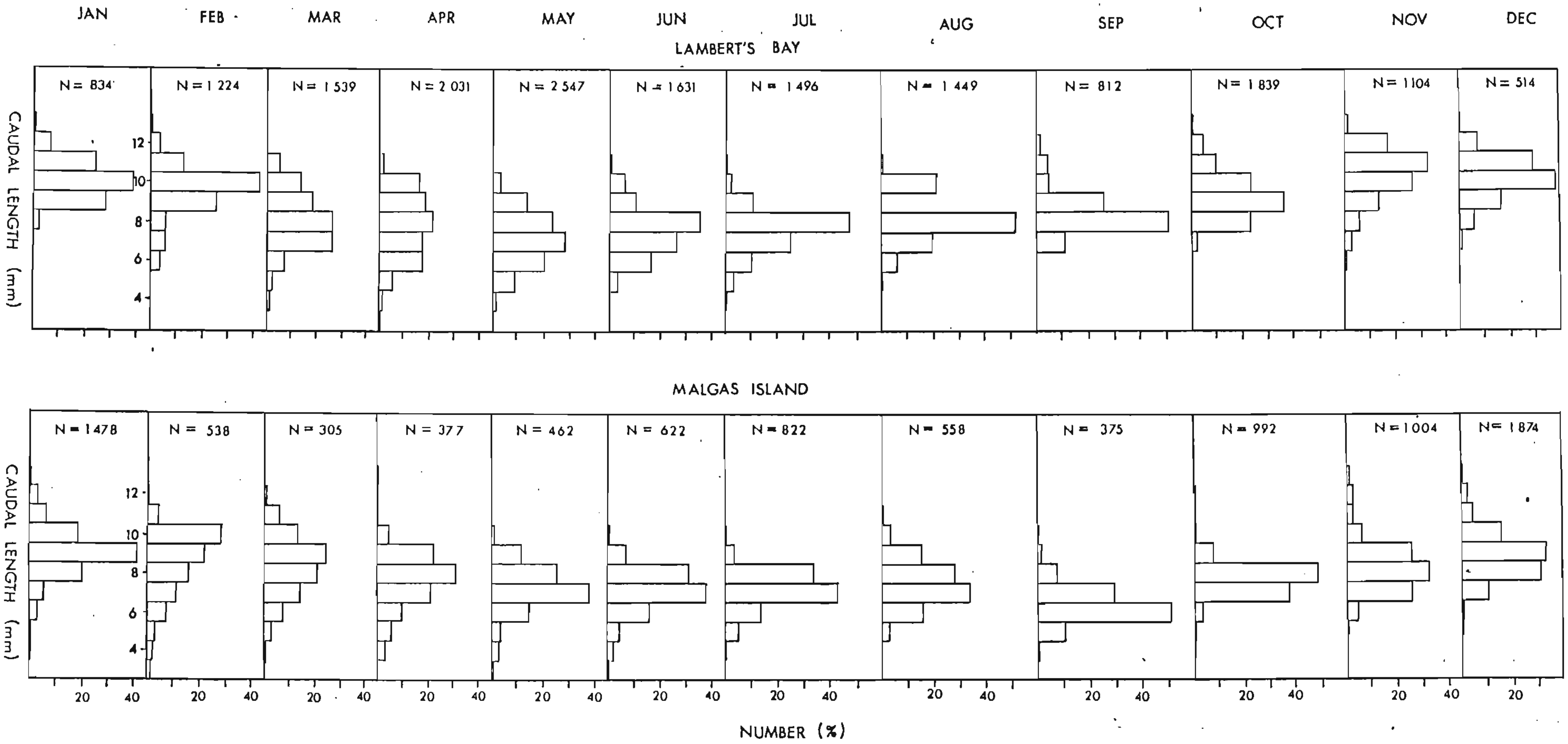


FIGURE 6

Monthly caudal length frequencies for whole Cape Anchovy from Cape Gannets at Lambert's Bay, December 1977 to August 1986, and Malgas Island, September 1978 to August 1986.

mm in October and 105 mm in November and December. Trends were less apparent for the South African Pilchard (Fig. 7) except that large fishes (>160 mm Lc) were most numerous from November to February. Small pilchard (<130 mm Lc) occurred mainly between January and June at Lambert's Bay. Very few pilchard less than 130 mm Lc were eaten by gannets at Malgas Island, but were recorded mainly in the spring and summer months. There was no seasonal trend in the modal size of Saury, although small fish were not represented in April and May (Fig. 8). At both Malgas Island and Lambert's Bay, but particularly at the former, the modal length of all prey species combined was smallest in May, then increased slowly until January, when it remained constant until March (Fig. 9). Fishes from gannets at Malgas Island were significantly larger than fishes from gannets at Lambert's Bay in all months (Kolmogorov-Smirnov test; P <0,05) (Fig. 9).

The lengths of all fish prey from Lambert's Bay and Malgas Island varied between 29 and 429 mm Lc. Fish prey from gannets were significantly larger at Malgas Island than at Lambert's Bay (Kolmogorov-Smirnov test; P <0,01)(Fig. 10). The trend to larger prey at Malgas Island was statistically significant for several prey species; Cape Anchovy, South African Pilchard, Saury, Maasbanker and Redeye Roundherring were significantly larger (Kolmogorov-Smirnov test; P <0.01) while Snoek, Onderbaadjie, Southern Mullet and Mackerel did not show significant differences (Fig. 11).

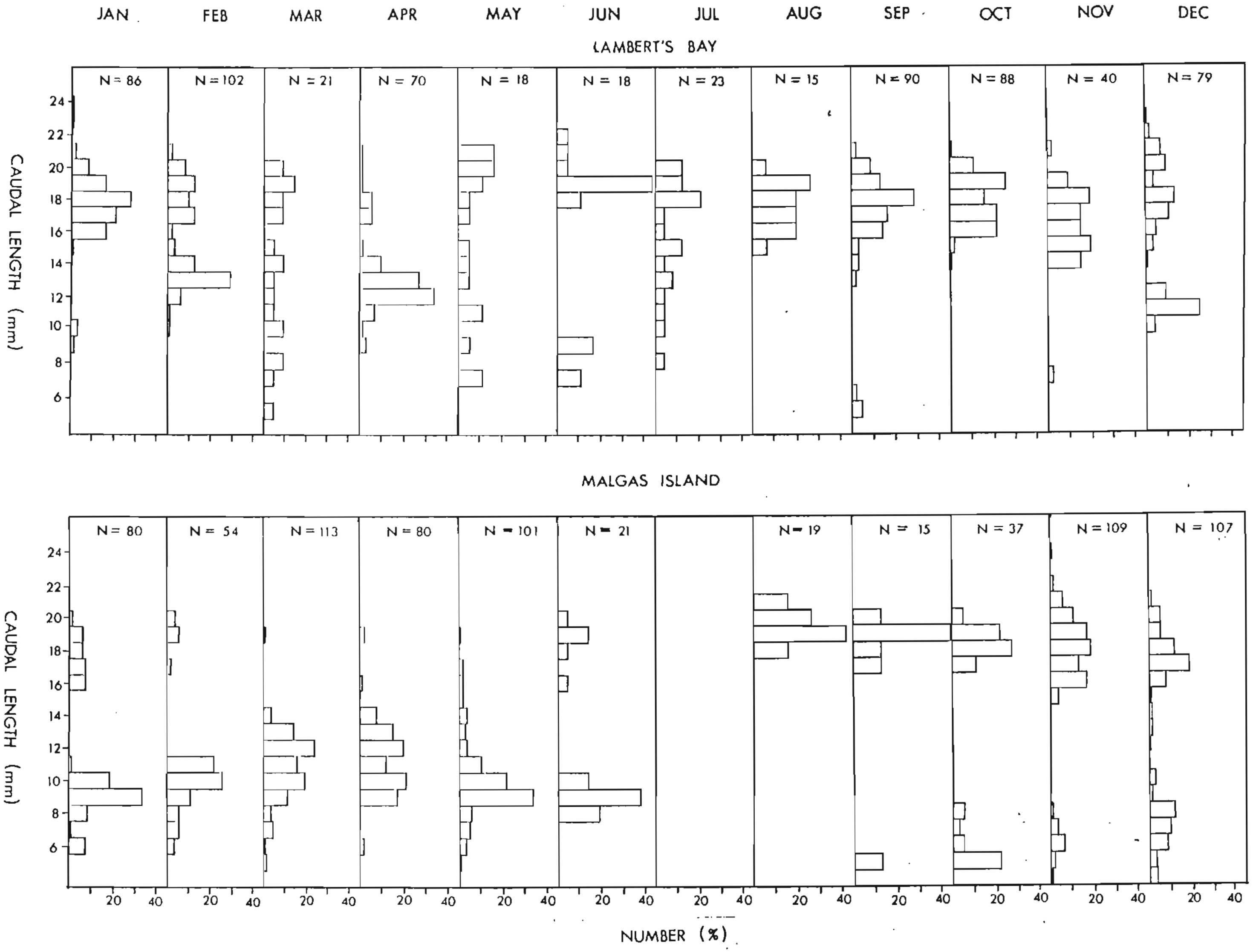


FIGURE 7

Monthly caudal length frequencies for whole South African Pilchard from Cape Gannets at Lambert's Bay, December 1977 to August 1986, and Malgas Island, September 1978 to August 1986.

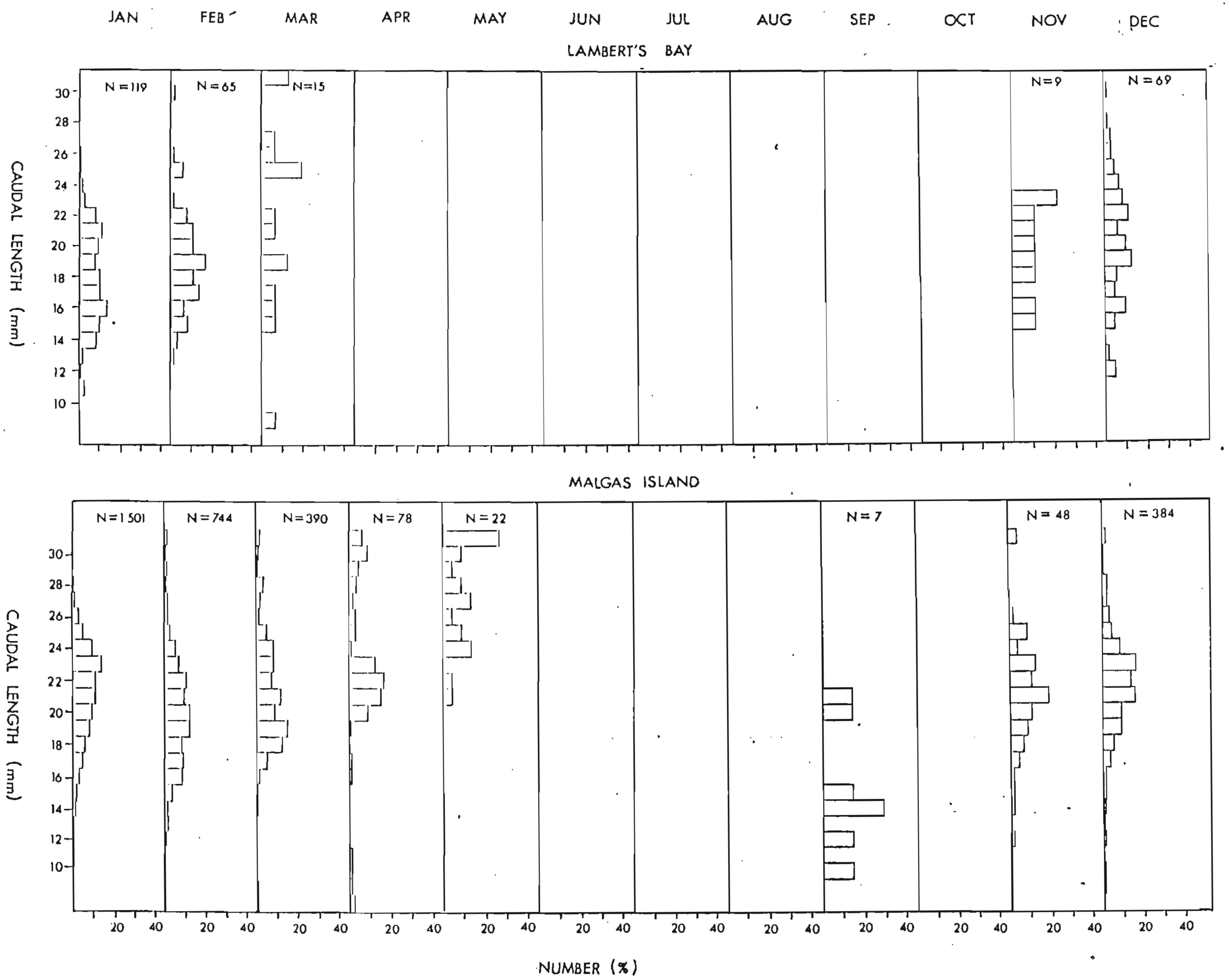


FIGURE 8
Monthly caudal length frequencies of whole Saury from Cape Gannets at Lambert's Bay, December 1977 to August 1986, and Malgas Island, September 1978 to August 1986.

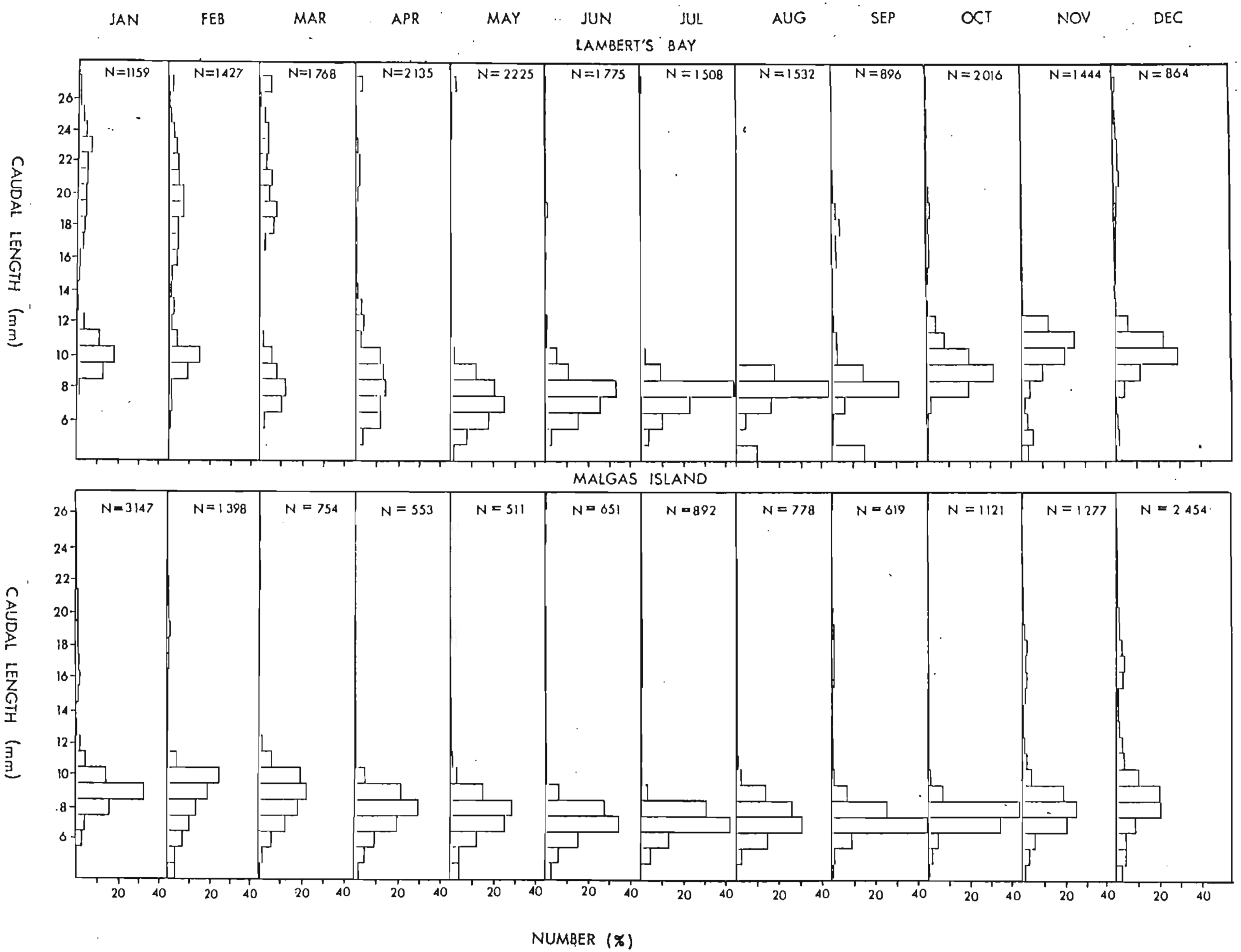


FIGURE 9

Monthly caudal length frequencies for all fish prey from Cape Gannets at Lambert's Bay, December 1977 to August 1986, and Malgas Island, September 1978 to August 1986.

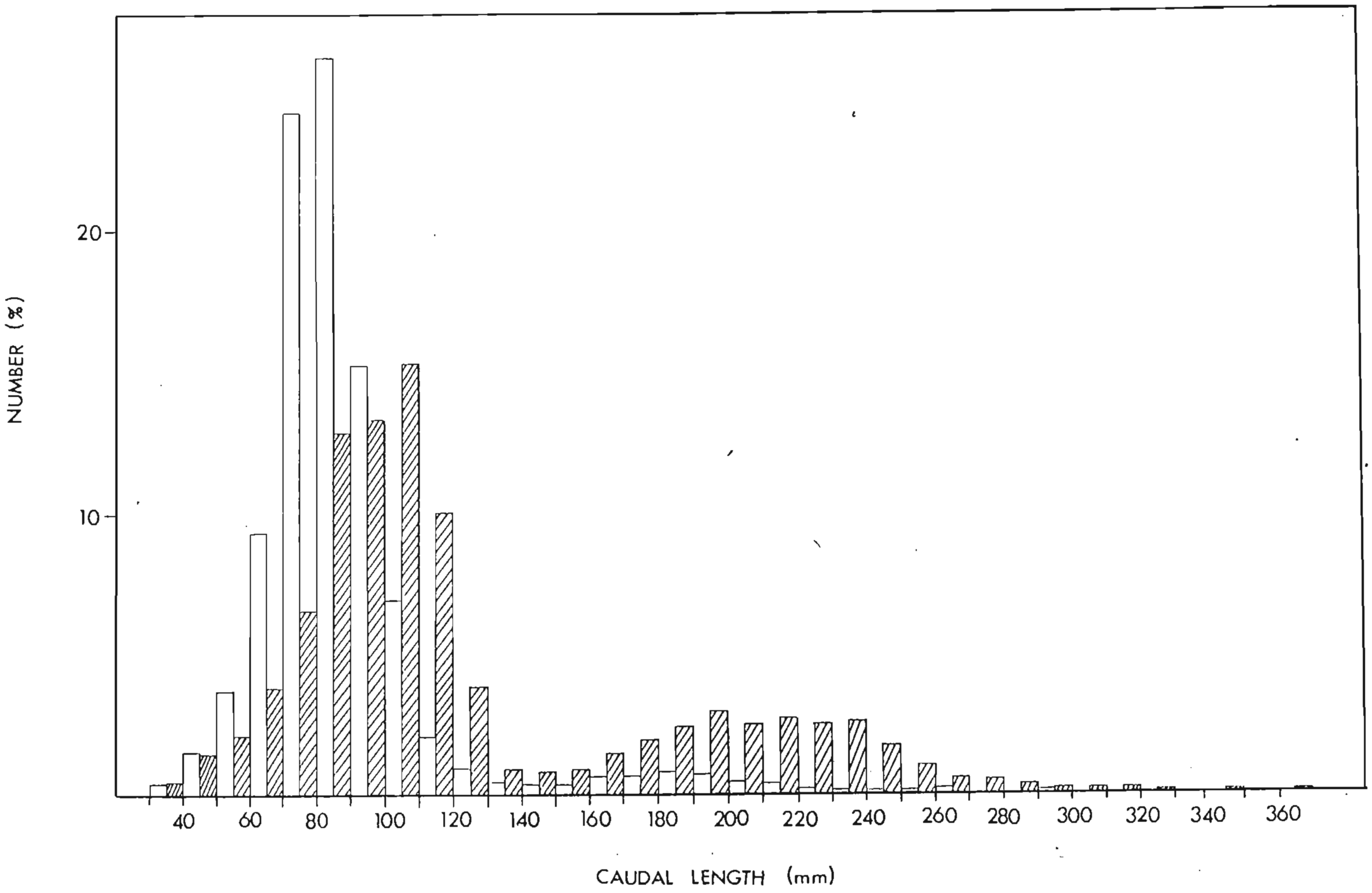


FIGURE 10

Total caudal length frequencies of fishes (all species) eaten by Cape Gannets at Lambert's Bay (open blocks; n=18 724), December 1977 to August 1986, and at Malgas Island (diagonal lines; n=14 152), September 1978 to August 1986.

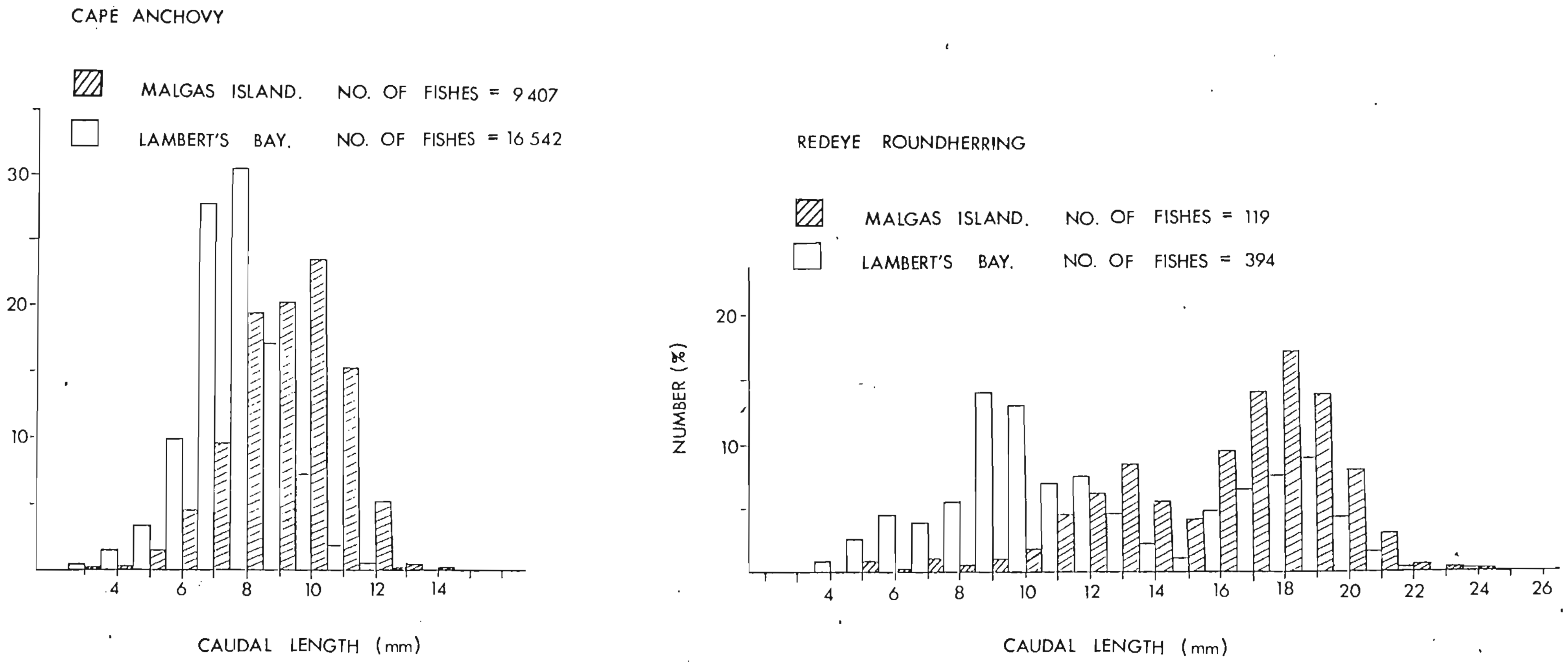


FIGURE 11

Total caudal length frequencies for selected prey species of Cape Gannets at Lambert's Bay, December 1977 to August 1986, and Malgas Island, September 1978 to August 1986.

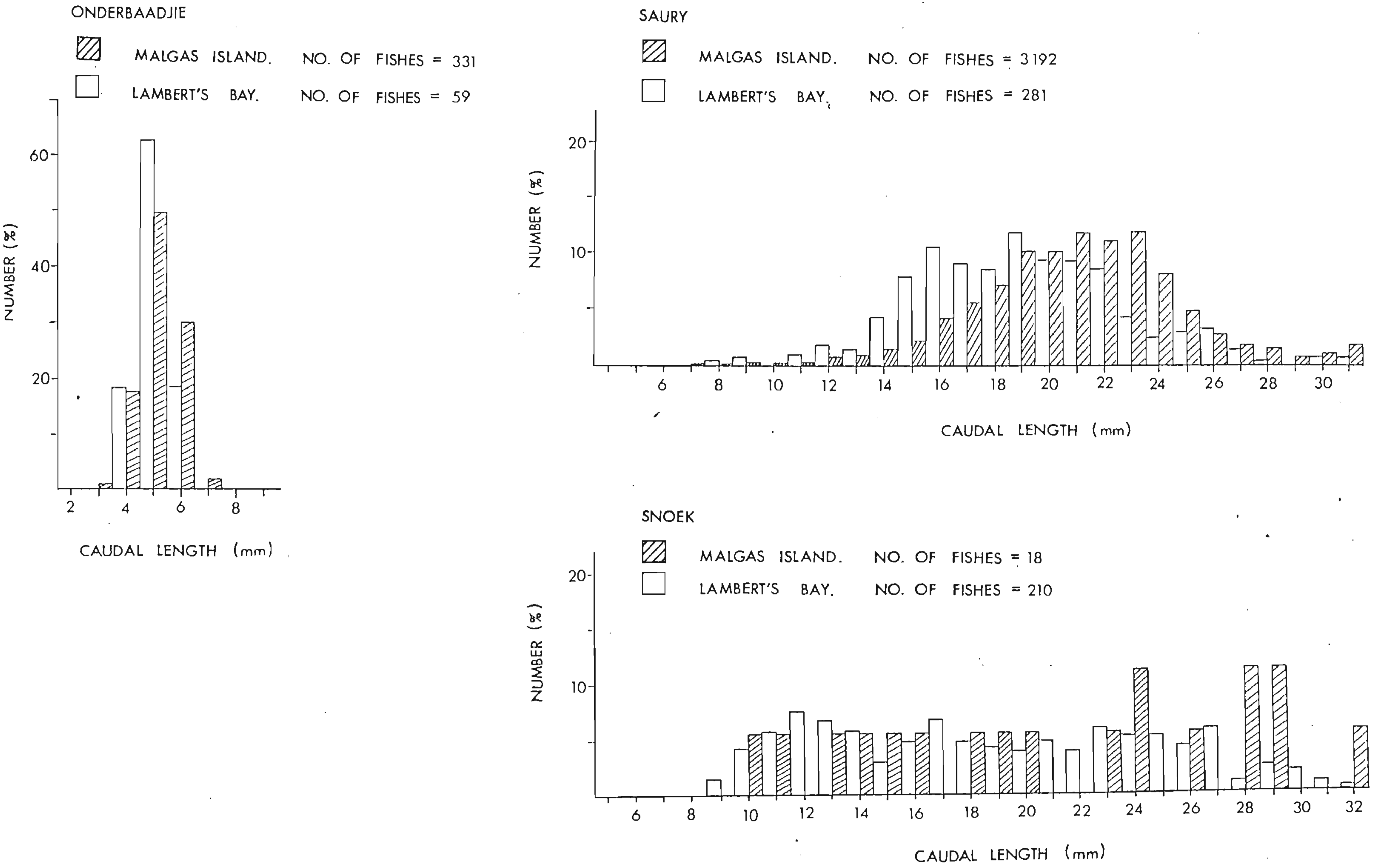


FIGURE 11 (CONTINUED)

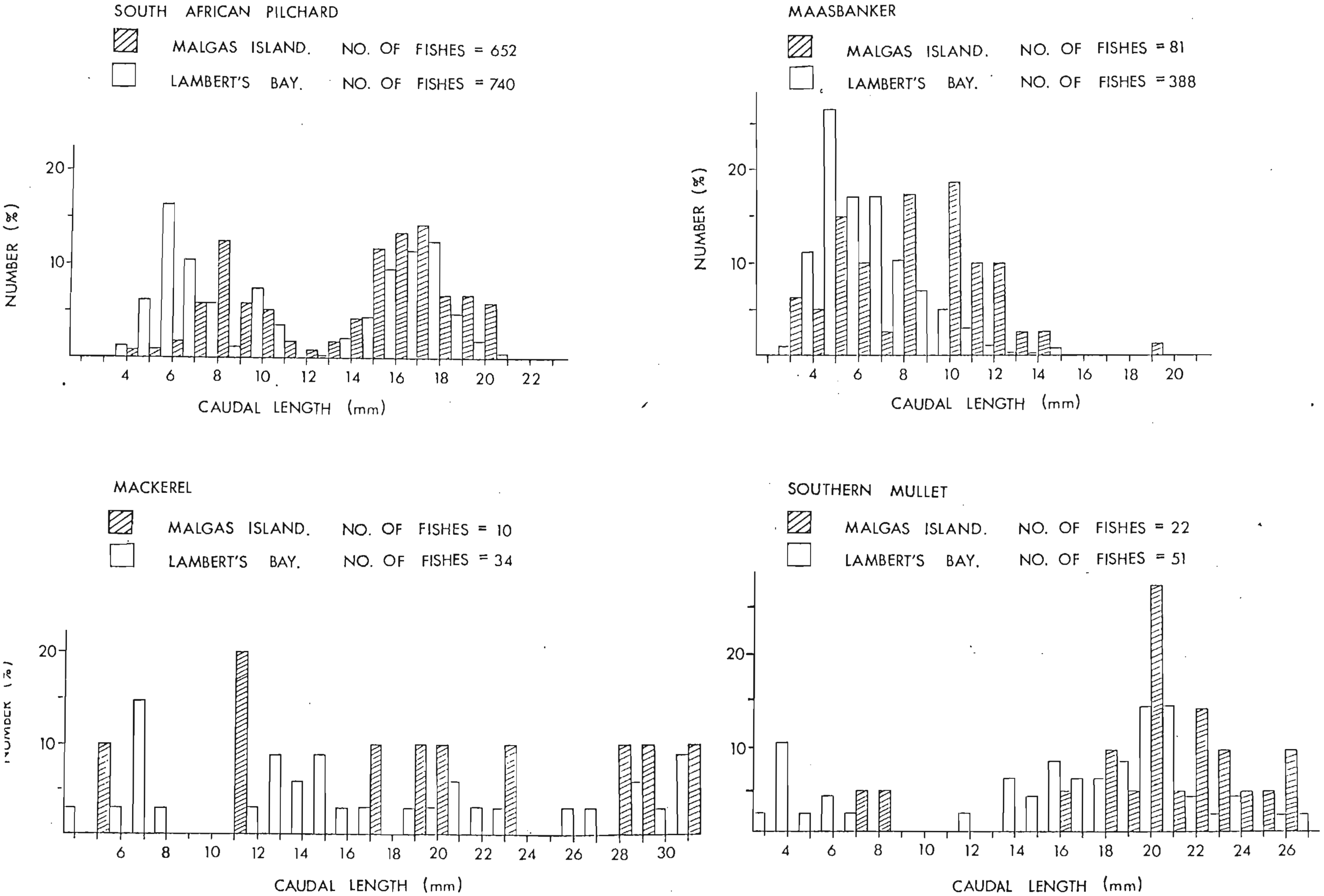


FIGURE 11 (CONTINUED)

Proportion with food and regurgitation mass

The mean monthly proportion of birds handled which regurgitated food (including hake and Offal) was lowest in August and September at Lambert's Bay, and from September to November at Malgas Island (Fig. 12). Proportions of birds handled which regurgitated were significantly higher at Lambert's Bay than at Malgas Island for December only (Mann-Whitney test; $P < 0,05$). The annual proportions of birds handled which regurgitated food (including hake and Offal) varied little at both localities between 1978 and 1986 (Fig. 13). Differences between the annual proportions measured at the two colonies were significantly different in 1979 and 1980 (Mann-Whitney test; $P < 0,05$). Proportions in other years were not significantly different.

At Lambert's Bay, the mean monthly proportion of birds handled whose regurgitations contained epipelagic fish only was highest between March and May (Fig. 14). The proportion declined until September and then increased until March. At Malgas Island, the trend was similar. The mean proportion was highest from December until March, declined to its lowest between June and September and then increased until January (Fig. 14). The monthly proportions measured at Lambert's Bay were significantly higher (Mann-Whitney test; $P < 0,05$) than the proportions measured at Malgas Island in March, from May to August and in November.

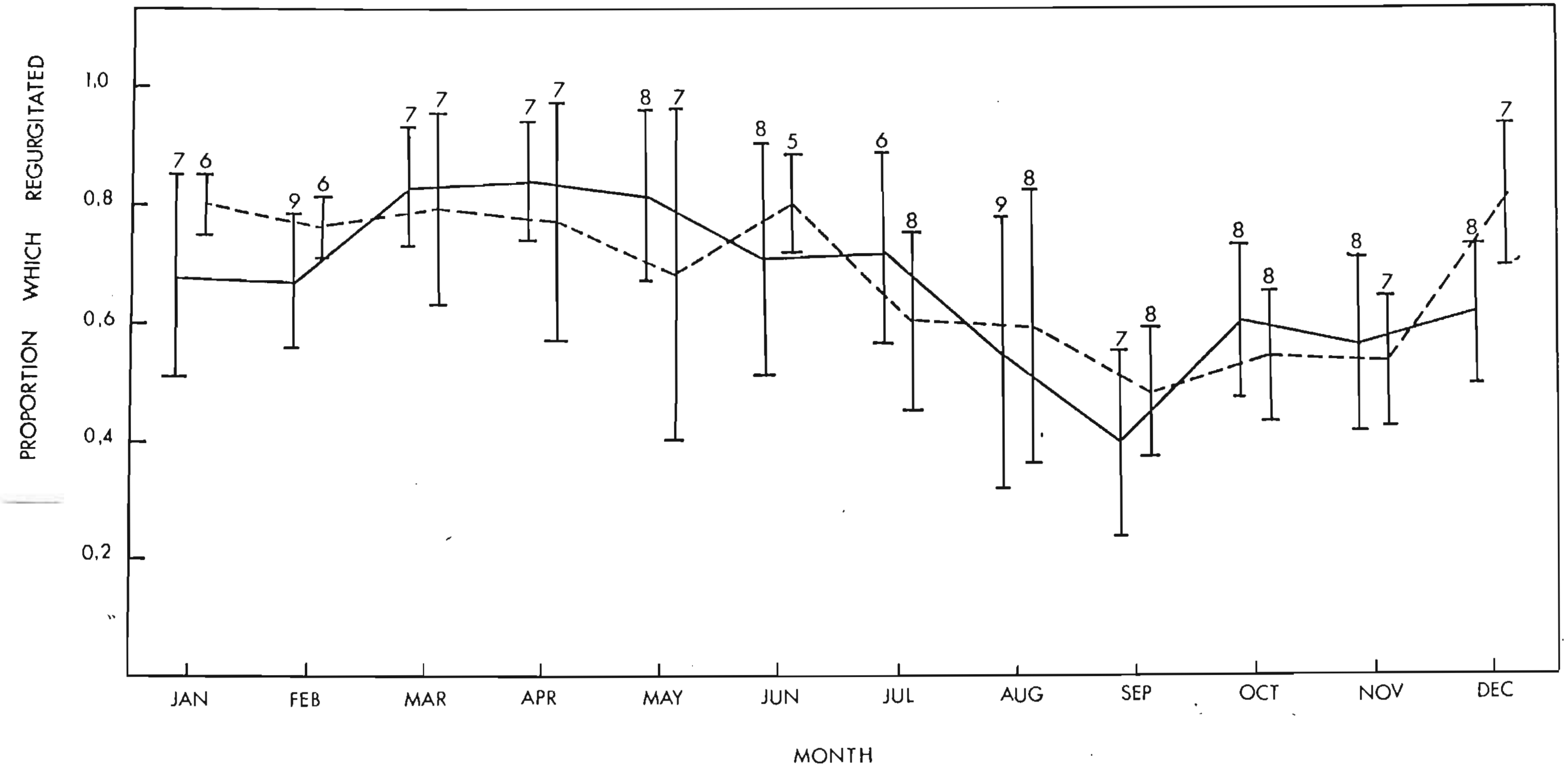


FIGURE 12

Mean (±one standard deviation) monthly proportions of Cape Gannets handled that regurgitated food (including Hake and Offal) at Lambert's Bay (solid line), December 1977 to August 1986, and at Malgas Island (dashed line), September 1978 to August 1986. Sample sizes are given above the range.

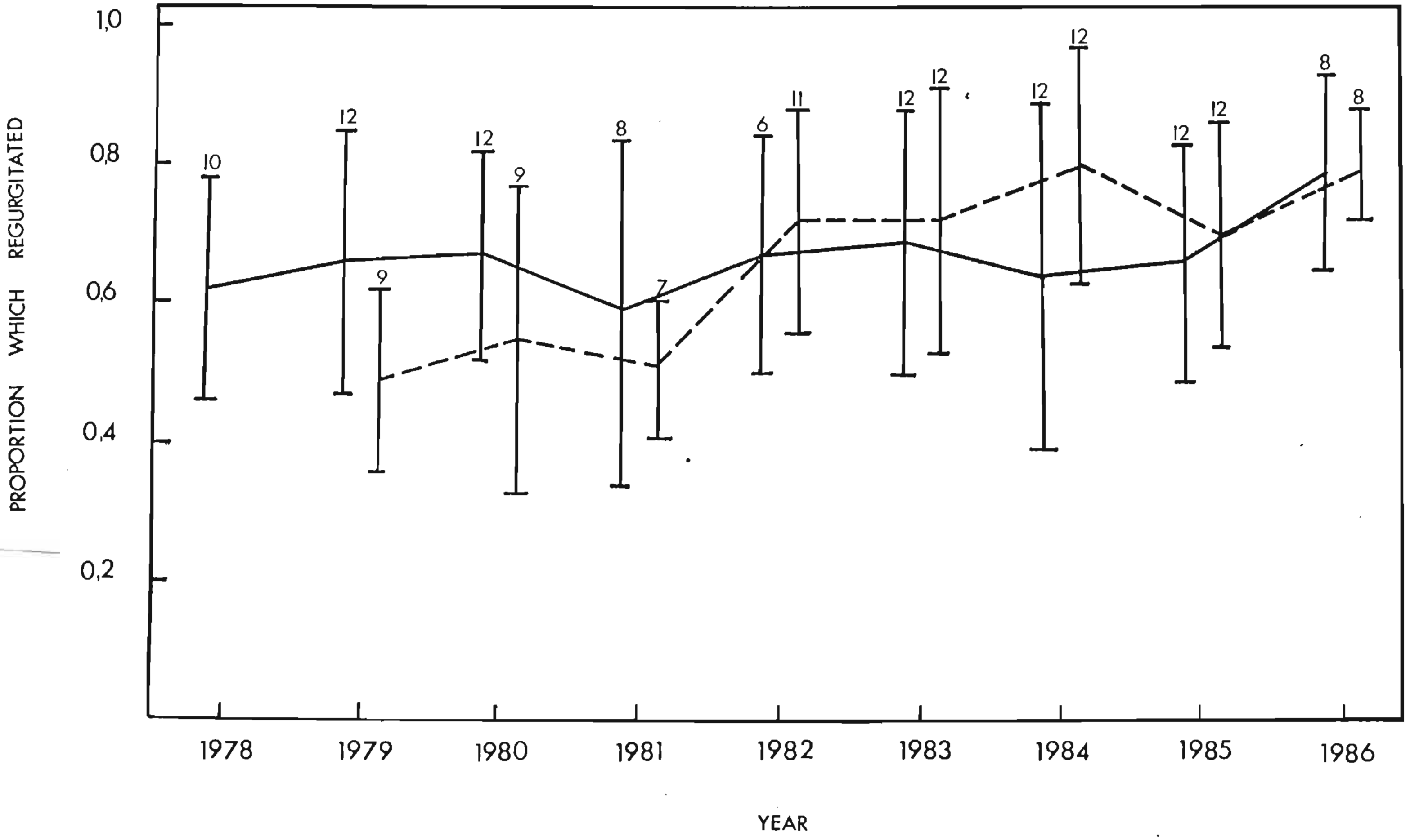


FIGURE 13

Mean annual proportions (± one standard deviation) of Cape Gannets handled that regurgitated food (including Hake and Offal) at Lambert's Bay (solid line), December 1977 to August 1986, and at Malgas Island (dashed line), September 1978 to August 1986. Sample sizes are given above each range.

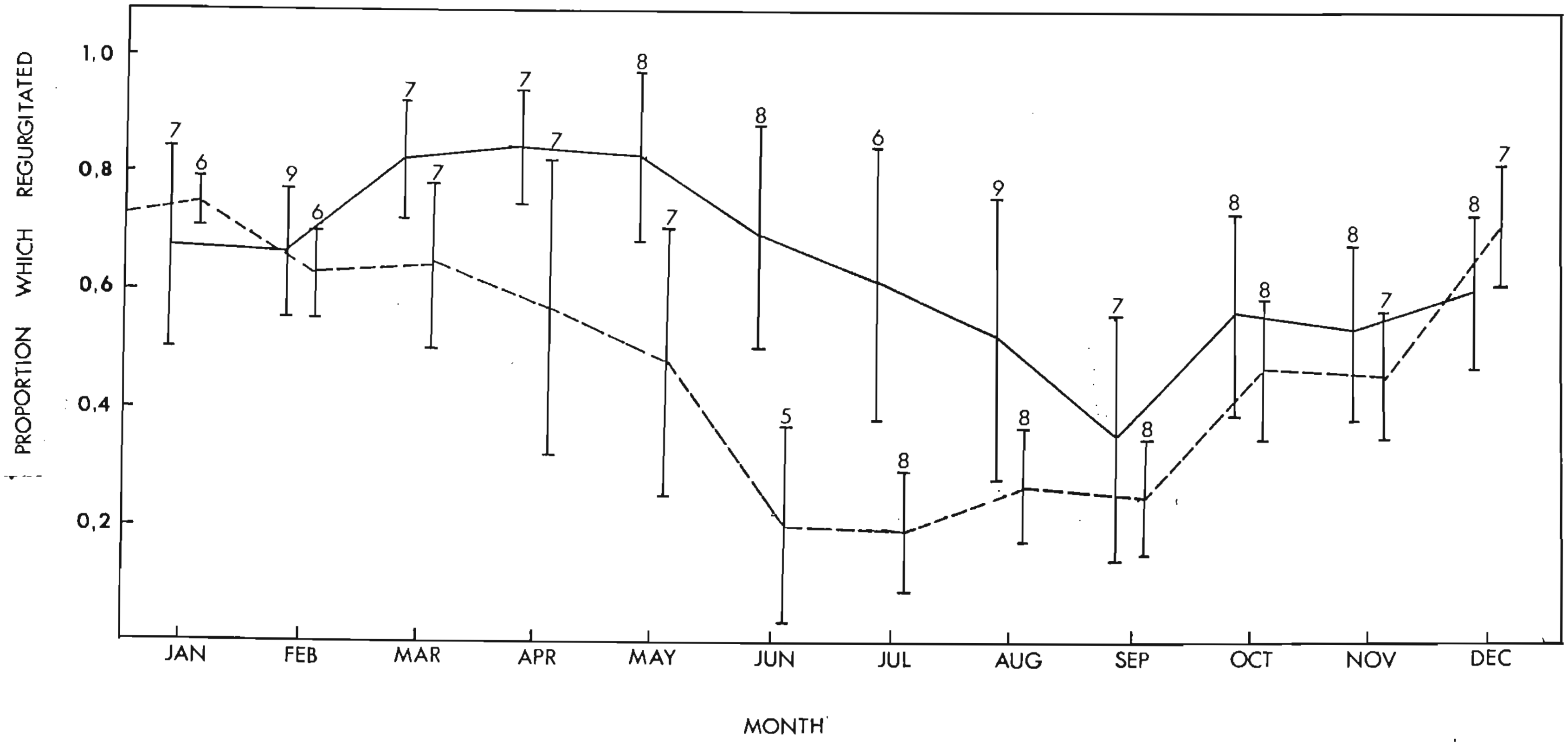


FIGURE 14

Mean monthly proportions (± one standard deviation) of Cape Gannets handled that regurgitated food (excluding samples containing Hake or Offal) at Lambert's Bay (solid line), December 1977 to August 1986, and at Malgas Island (dashed line), September 1978 to August 1986. Sample sizes are given above each range.

Proportions in other months were not significantly different. There were no clear long-term trends in the mean annual proportions of birds handled which regurgitating only epipelagic fish, but the proportions at the two colonies changed annually in the same direction except in 1984 (Fig. 15). The annual proportions measured at Lambert's Bay were significantly higher (Mann-Whitney test: P <0,05) than proportions measured at Malgas Island from 1979 to 1981, and in 1983 and 1986. Proportions in other years were not significantly different.

The mean monthly regurgitation mass (all regurgitations included) was larger at Malgas Island than at Lambert's Bay (Fig. 16). Monthly means at the two localities were significantly different (Students t-test) at the P <0,01 level for all months except May and October, which were significantly different at the P <0,05 level. At both colonies, mean regurgitation mass was highest in the nestling period (February and March).

At Lambert's Bay, the mean monthly regurgitation masses of samples which contained only epipelagic fish were similar to the means of all regurgitations because hake and Offal were infrequent dietary items (Fig. 17). However, at Malgas Island, mean monthly regurgitation masses of samples which contained only epipelagic fishes were far lower between April and September than the means for all regurgitations. Monthly means of regurgitations which contained only epipelagic fished at the two colonies were sig-

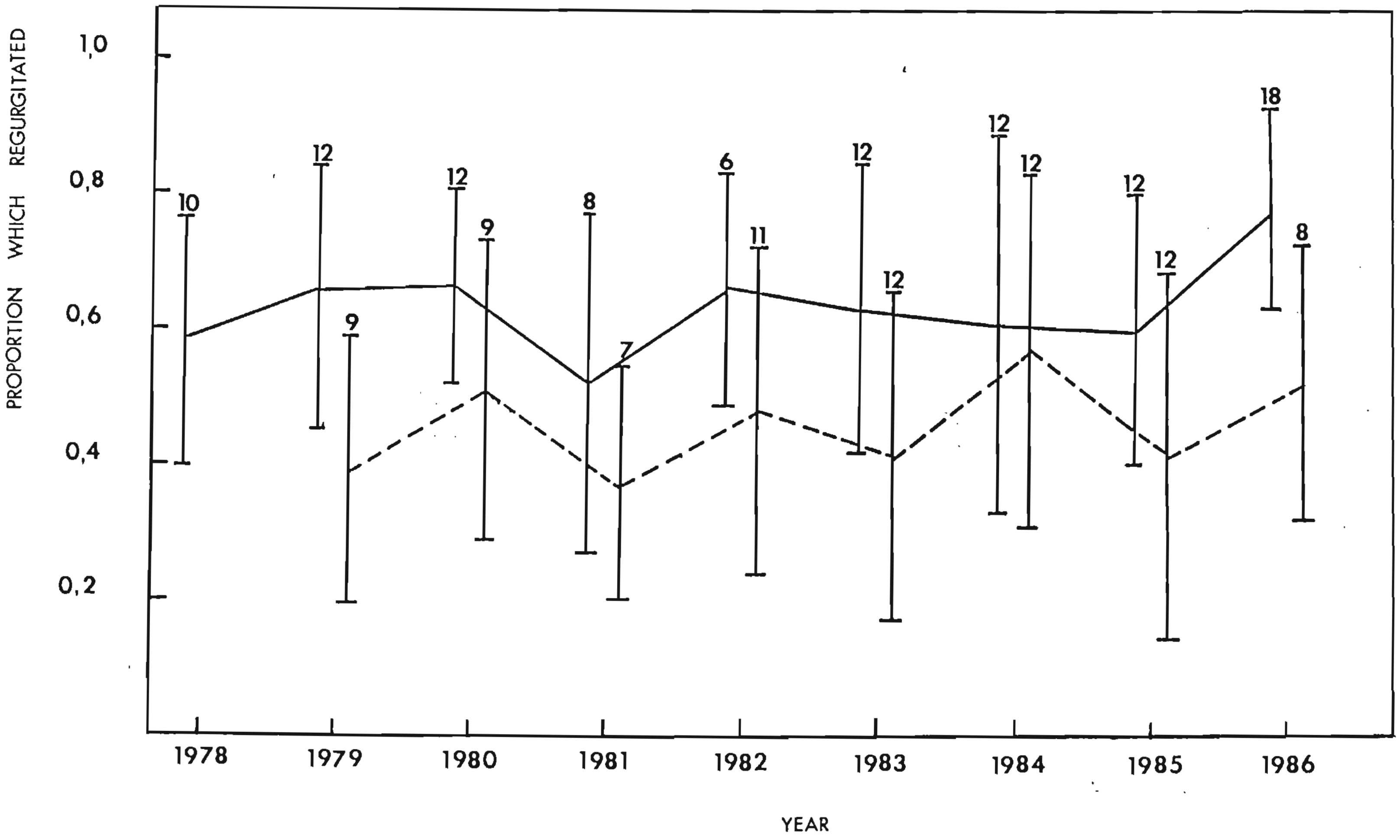


FIGURE 15

Mean annual proportions (± one standard deviation) of Cape Gannets handled that regurgitated food (excluding samples containing Hake or Offal) at Lambert's Bay (solid line), December 1977 to August 1986, and at Malgas Island (dashed line), September 1978 to August 1986. Sample sizes are given above each range.

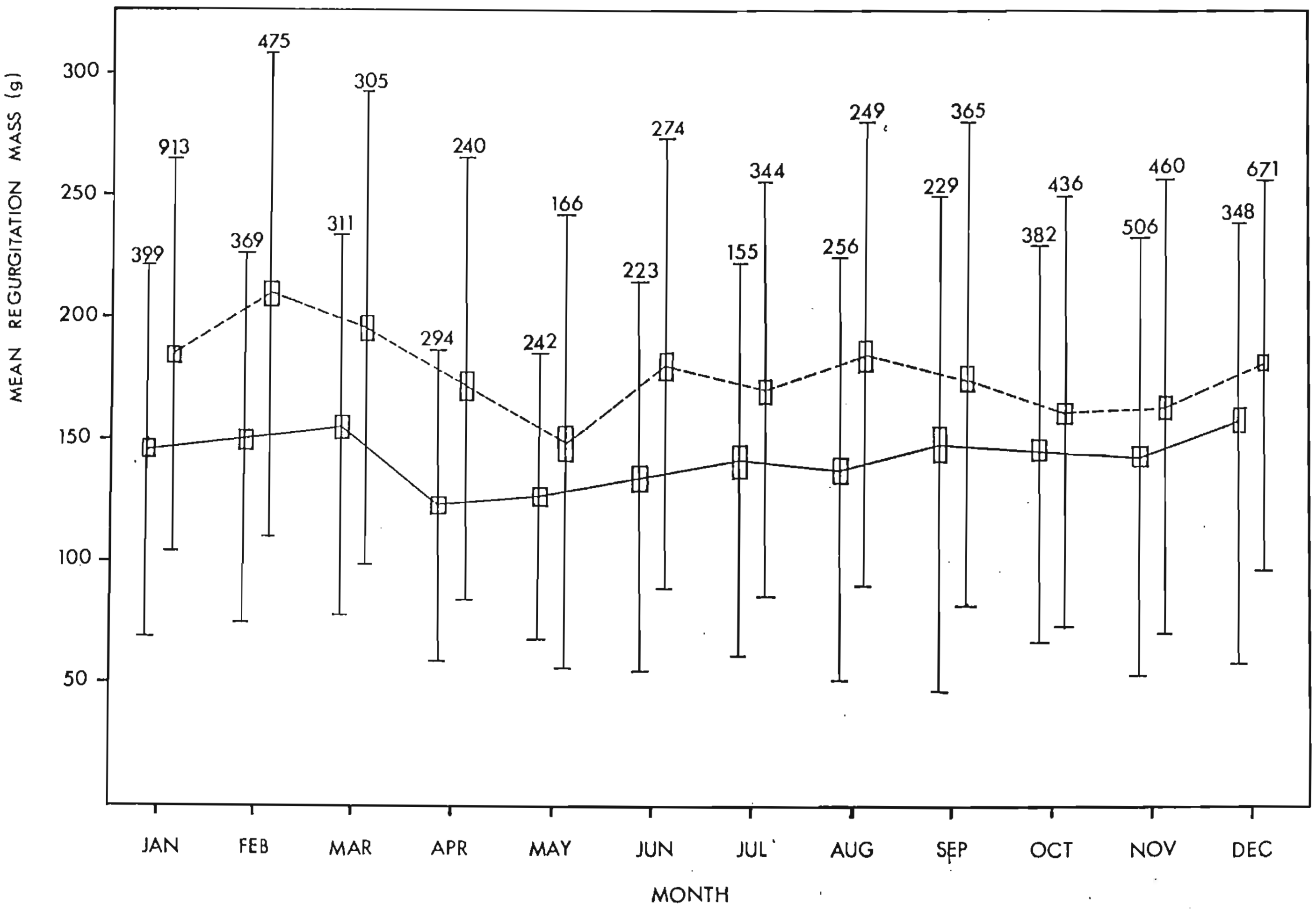


FIGURE 16

Mean monthly regurgitation mass (± one standard deviation, box encloses ± one standard error) (all regurgitations) of Cape Gannets at Lambert's Bay (solid line), December 1977 to August 1986, and at Malgas Island (dashed line), September 1978 to August 1986. Sample sizes are given above each range.

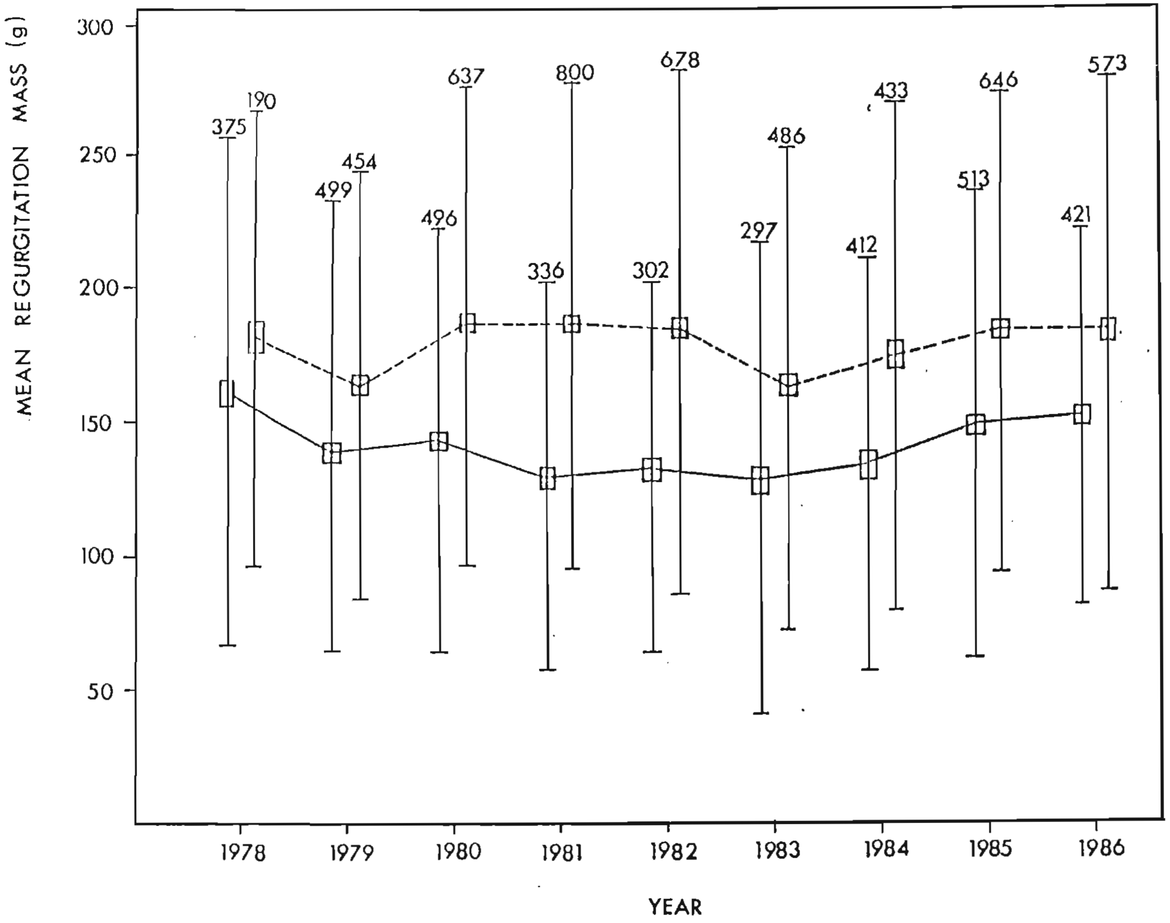


FIGURE 17

Mean annual regurgitation mass (± one standard deviation, box encloses ± one standard error) (all regurgitations) of Cape Gannets at Lambert's Bay (solid line), December 1977 to August 1986, and at Malgas Island (dashed line), September 1978 to August 1986. Sample sizes given above each range.

nificantly different (Students t-test; P <0,01) between December and April but not in other months.

At Lambert's Bay, the mean annual masses for all regurgitations together and for those which contained only epipelagic fishes were similar from 1978 to 1986 because hake and Offal are infrequent dietary items. Both means showed a slight decline from 1978 to 1982 followed by a slight increase until 1986 (Figs 17 & 19). At Malgas Island, the mean annual masses for all regurgitations and for those which contained only epipelagic fishes were high (Figs 17 & 19), because of the large number of regurgitations obtained during the breeding season when regurgitation masses were high. The mean annual regurgitation masses (all regurgitations) were significantly larger (Students t-test; P <0,05) in all years at Malgas Island than at Lambert's Bay. For regurgitations which contained only epipelagic fishes, the mean annual masses were significantly heavier at Malgas Island (Students t-test; P <0,05) for all years except 1978.

Purse-seine fishery

Mean monthly catches of various species by the South African purse-seine fishery during the period 1978 to 1984 are presented in Table 24. Fishing effort was mainly concentrated in the first six months of the year as many fleets filled their quotas by July (Table 24). Comparative data for the second half of the year are

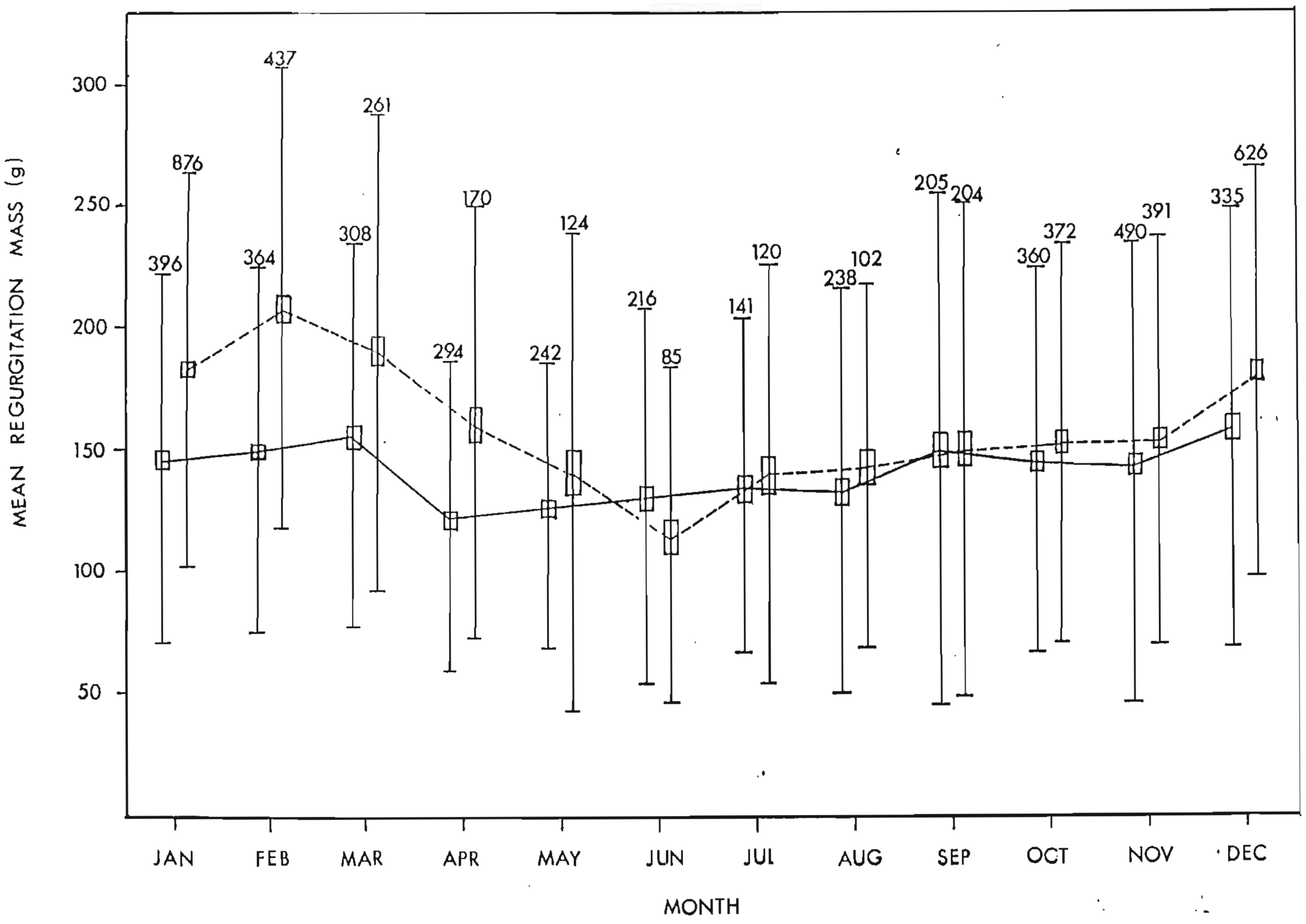


FIGURE 18

Mean monthly regurgitation mass (± one standard deviation, box encloses ± one standard error) (excluding regurgitations containing Hake or Offal) of Cape Gannets at Lambert's Bay (solid line), December 1977 to August 1986, and at Malgas Island (dashed line), September 1978 to August 1986. Sample sizes are given above each range.

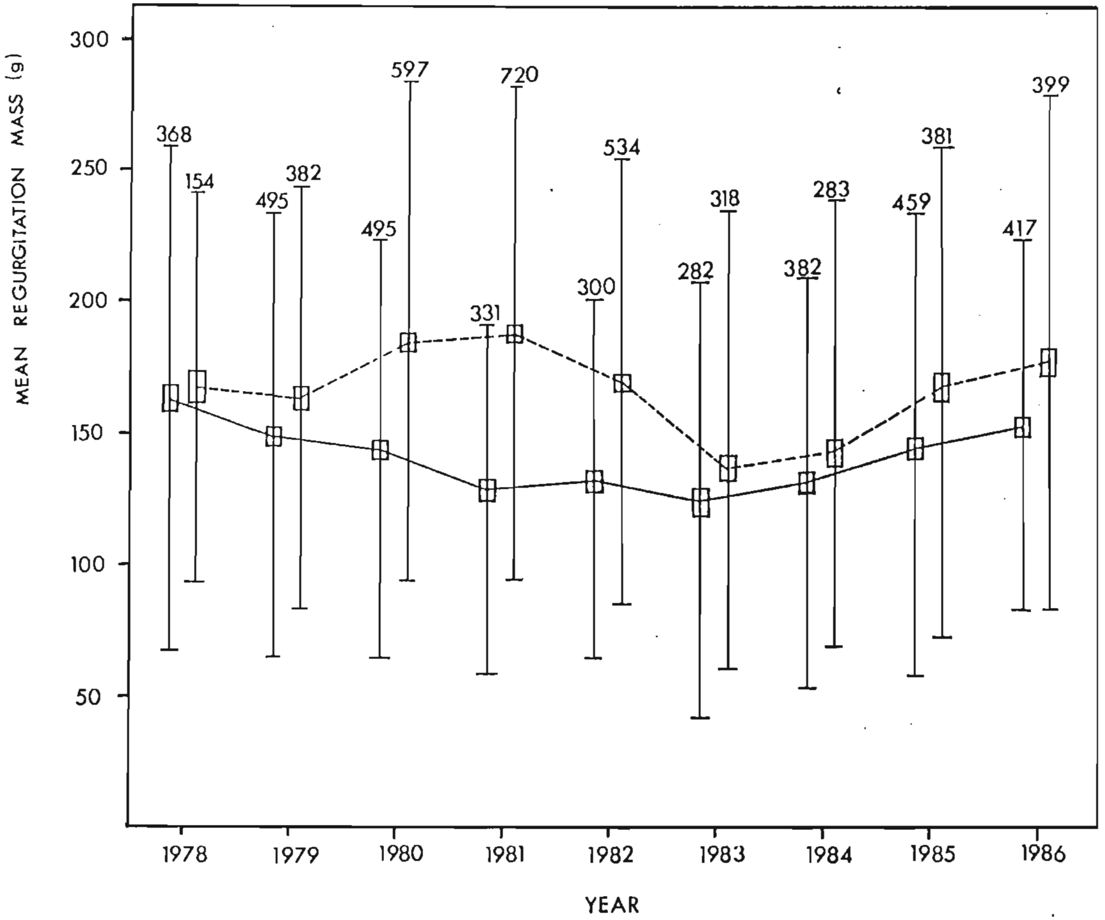


FIGURE 19

Mean annual regurgitation mass (± one standard deviation, box encloses ± one standard error) (excluding regurgitations containing Hake or Offal) of Cape Gannets at Lambert's Bay (solid line), December 1977 to August 1986, and at Malgas Island (dashed line), September 1978 to August 1986. Sample sizes are given above each range.

TABLE 24.

MEAN MONTHLY CATCHES IN THOUSANDS OF TONNES OF THE PELAGIC FISHERY IN SOUTH AFRICA, 1978-1984

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Cape Anchovy	24,6	26,2	37,5	52,6	68,9	40,0	16,6	3,0	-	37,6	22,7	2,3
South African Pilchard	6,6	15,2	10,6	7,5	5,2	2,2	1,0	<0,1	-	0,3	0,1	0,1
Maasbanker	1,1	0,4	0,5	0,2	0,3	<0,1	<0,1	<0,1	-	0,1	0,2	0,4
Mackerel	0,1	0,2	0,5	0,2	0,1	<0,1	-	-	-	-	<0,1	<0,1
Redeye Roundherring	5,4	10,8	11,2	5,9	2,2	0,5	0,1	<0,1	-	1,4	0,1	<0,1
Onderbaadjie	1,2	4,7	0,7	1,6	0,1	<0,1	-	-	-	-	<0,1	<0,1
	39,0	57,5	61,0	68,0	76,8	42,7	17,7	3,0	-	39,4	23,1	2,8
N	8	8	8	8	8	8	4	2	-	2	2	1

few. Between 1978 and 1985, fishery catches were dominated by the Cape Anchovy, which comprised 73,4% of the landings and was mostly offloaded between March and June with a peak in April and May. South African Pilchard was the next most important catch, comprising 13,2% of the overall total with a peak in landings in February and March. Redeye Roundherring was third most important, comprising 9,8% of the catch and being caught mainly in February and March. Mackerel and Maasbanker provided tiny bycatches, Maasbanker occurring between January and March and Mackerel in March. Onderbaadjie were caught mainly in February. The mean annual catches of various species and their contribution to the overall catch are presented for the areas north and south of Cape Columbine (Columbine North and Columbine South) in Table 25.

Between 1978 and 1985, total catches were controlled by quota and have varied little in recent years (Table 1). Annual catches of South African Pilchard decreased until 1984, when the pilchard catch was specifically restricted by quota.

Demersal fishery

Catches by the South African demersal fishery is dominated by the hakes M. paradoxus and M. capensis, which make up about 70% of the catch (Botha 1980). The mean monthly catch of hake in between 1978 and 1984 was 11 207 tonnes (SD ±1 884) (Table 26). The mean annual catch of hakes between 1977 and 1983 was 139 724

TABLE 25.

CONTRIBUTIONS (MEAN ANNUAL TOTAL CATCH IN TONNES) AND % OF TOTAL CATCH) OF MAJOR SPECIES TO THE PELAGIC FISHERY LANDINGS, FROM COLUMBINE NORTH AND SOUTH FISHING GROUNDS, 1978-1985

	Columbine North		Columbine South	
Species	Catch	%	Catch	%
Cape Anchovy	176 251	47,0	112 870	30,1
South African Pilchard	17 302	4,6	10 638	2,8
Maasbanker	2 163	0,6	734	0,2
Mackerel	1 112	0,3	721	0,2
Redeye Roundherring	20 352	5,4	23 538	6,3
Onderbaadjie	9 146	2,4	385	0,1
	226 326		148 886	

TABLE 26.

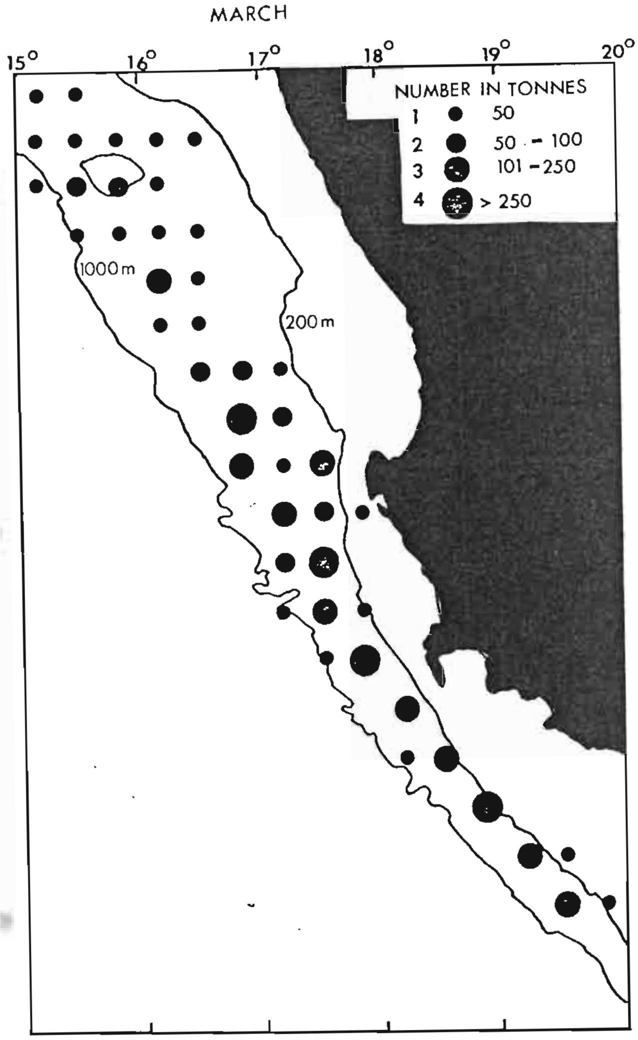
MONTHLY CATCHES IN TONNES OF HAKE BY THE DEMERSAL FISHERY
IN SOUTH AFRICA, 1981-1985

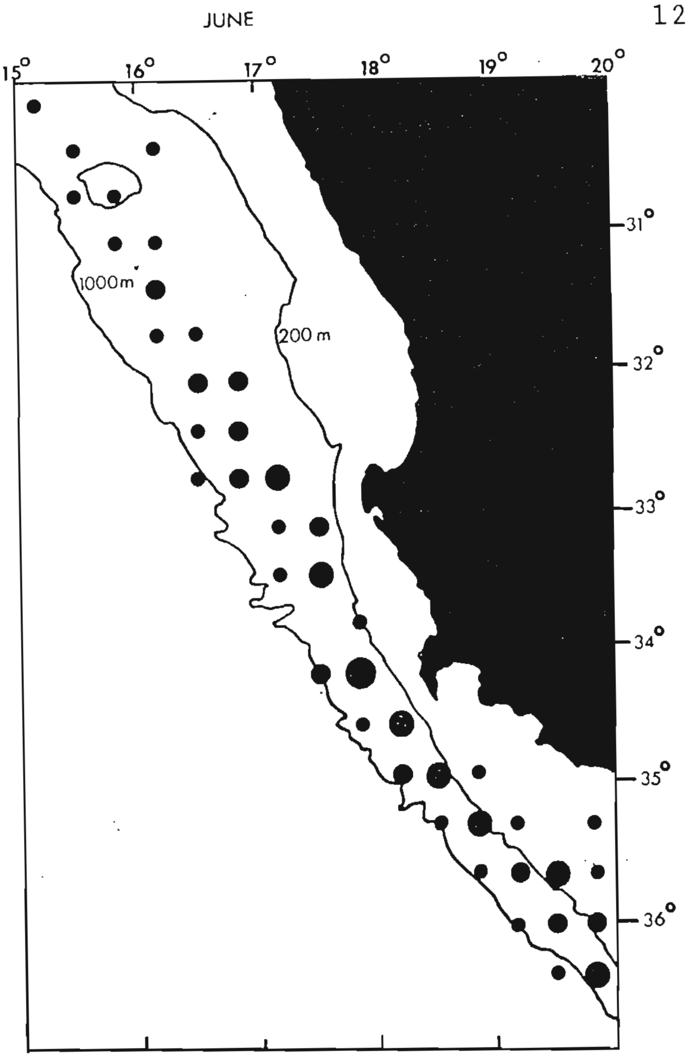
	Year						
Month	1981	1982	1983	1984	1985	Mean	S.D.
January	8 853	9 702	11 388	9 433	9 717	9 819	945
February	11 567	13 233	10 081	8 825	11 802	11 101	1 694
March	12 571	13 861	10 196	9 667	11 693	11 597	1 716
April	14 753	11 725	8 784	9 538	11 645	11 289	2 327
May	14 337	14 517	9 746	14 409	12 149	13 031	2 085
June	13 864	14 743	11 117	13 651	10 699	13 014	2 093
July	11 708	12 634	10 093	11 077	13 807	11 864	1 427
August	8 927	9 430	10 053	11 743	13 294	10 689	1 802
September	8 785	9 396	8 597	10 563	10 832	9 635	1 019
October	9 978	9 941	9 906	13 257	9 617	10 540	1 526
November	10 111	11 208	12 003	10 353	9 380	10 611	1 016
December	10 139	12 387	12 752	11 646	13 800	12 145	1 364
Total	135 593	142 777	125 216	134 162	138 437		

tonnes (SD ±8 038). The tonnage of hake caught in 30' by 30' blocks off the western Cape in March, June, September and December 1985 is given in Fig. 20. Although there are seasonal trends in the location of catches of hake (B. Rose, SFRI, pers. comm.), large catches are made close to Malgas Island throughout the year.

DISCUSSION

Methods for studying seabird diet were reviewed recently by Duffy & Jackson (1986), who discussed four basic measurements of diet: frequency of occurrence, mass and volume, numerical abundance and state of digestion. Frequency of occurrence may be the most appropriate method when only a few similarly-sized prey items are taken, or the prey is well digested. Frequency of occurrence of a particular prey is regarded as a measure of variability of prey availability. Mass and volume are preferred measurements when prey vary greatly in size, to avoid small abundant prey appearing disproportionately abundant. Mass and volume are regarded as measures of approximate nutritional contribution of prey to the diet. Numerical abundance is most suitable when prey are more or less the same size but is useless when prey do not exist in discrete units e.g. offal such as hake liver. Duffy & Jackson (1986) regard numerical abundance as a measure of frequency of prey encounter, but if prey are shoaling species and many fishes may be caught from one shoal, then frequency of occurrence may be a more accurate measure of frequency


MARCH
15°
16°
17°
18°
19°
20°
NUMBER IN TONNES
1 ● 50
2 ● 50 - 100
3 ● 101 - 250
4 ● > 250
1000m
200m


JUNE
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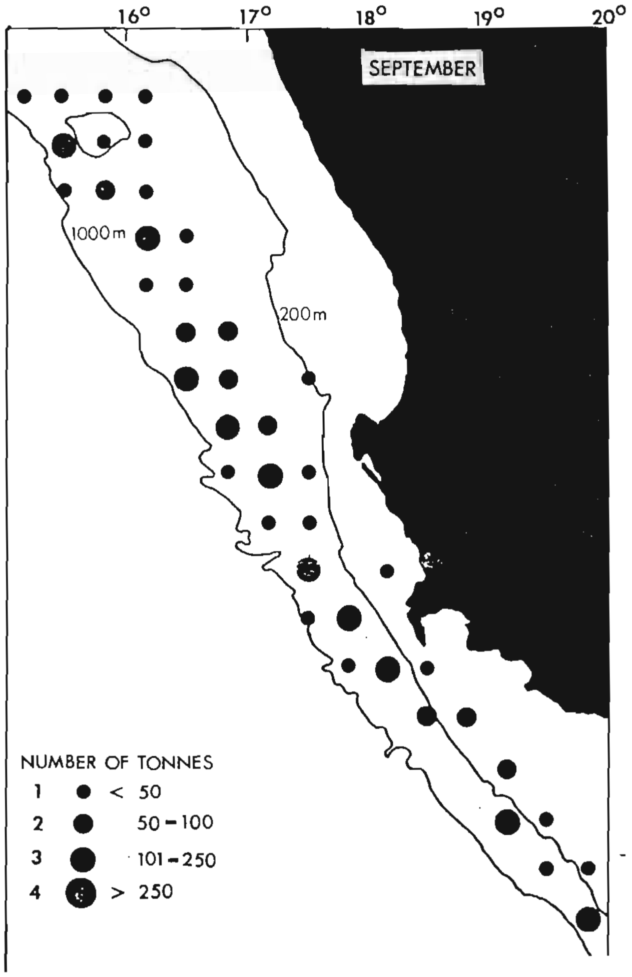
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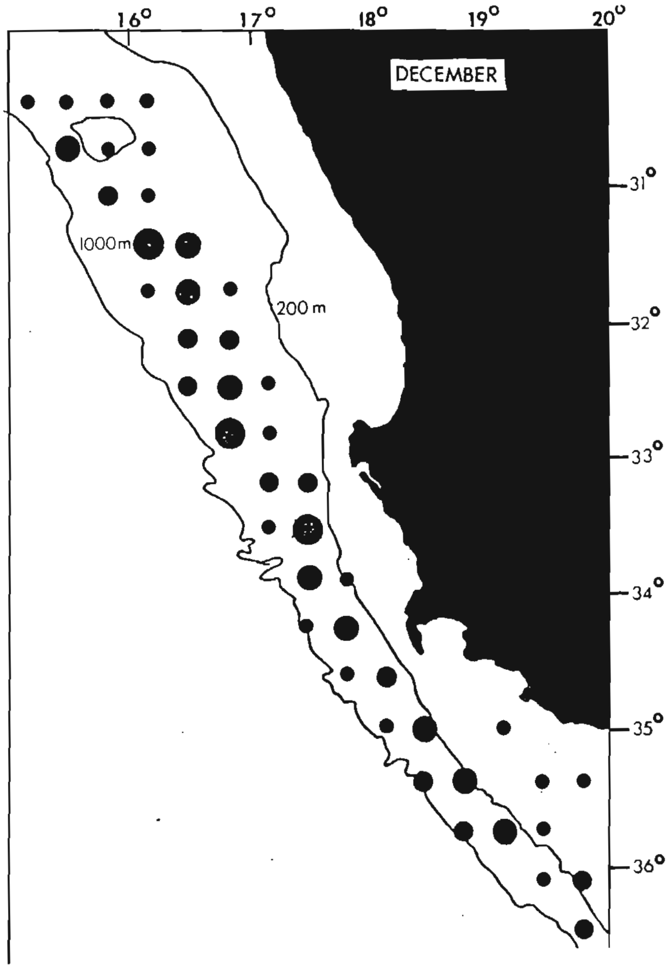
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of prey encounter. Duffy & Jackson (1986) suggest that the state of digestion provides information on the foraging behaviour of seabirds, but is difficult to use because little is known of rates of digestion.

While numerical abundance would appear to be less useful in this study than mass, volume and frequency of occurrence because of the presence of offal and the occasional occurrence of large numbers of very small fish, all three measures are presented. Duffy & Jackson (1986) concluded that diet data are best summarised by ranking prey for each of these three methods of analysis and then summing the ranks. This procedure has been followed.

Batchelor (1982), Batchelor & Ross (1984) and J. Colclough (Port Elizabeth Museum, in litt.) have used information from otoliths to reconstruct original prey masses and hence meal sizes. This technique is most appropriate when the rate of digestion varies between species (Duffy & Jackson 1986). This technique is not used here because otoliths were not collected until 1982. Also the vast majority of prey were fish, reducing the likelihood of differential digestion.

Although data have not been presented, no intra-colonial differences in diet were observed, unlike the situation for the Thickbilled Murre _Uria lomvia_ in the Canadian Arctic (Gaston & Nettleship 1981). If the "information- centre" hypothesis (Ward &

Zahavi 1973) holds for gannets, gannets in the colony may use the direction of departing and arriving birds as cues for foraging. Any gannet in the colony can see arrivals and departures over the entire tightly-packed colony. Thus intra-colonial differences in diet based on this mechanism are unlikely in the Cape Gannet.

A problem with the determination of regurgitation mass is that gannets may regurgitate two boluses, particularly if small or highly digested prey are involved (Batchelor & Ross 1984). This would tend to reduce the regurgitation mass of Cape Anchovy in particular. Handling time and methods of different observers may have influenced results, particulary for the estimation of annual regurgitation masses.

The proportion of birds handled which regurgitate food is affected by two factors unrelated to food availability. Firstly, some persons sampling gannets learnt to recognise visually flying gannets with distended stomachs which contained large meals, and deliberately selected such birds at times. Secondly, in windy conditions, gannets are able to take off far more easily; birds engaged in pair-bonding and nest-site establishment are far more active in windy conditions, and usually do not regurgitate food, but form a relatively larger percentage of birds landing in the colony.

Species composition of gannet diet

The Cape Gannet in the western Cape feeds mainly on epipelagic shoaling fish, as recorded in all previous diet studies. Recently, the use of discarded fish and offal from demersal trawlers has increased, particularly at Malgas Island (Crawford & Shelton 1981; Cooper 1984). Except for hake in gannet diet at Malgas Island, the same three species (Cape Anchovy, Saury, South African Pilchard) dominated gannet diet at colonies off South Africa. In the 1950s and presently in Algoa Bay, South African Pilchard dominated the diet of gannets, and the Cape Anchovy became the dominant prey item off western southern Africa after the collapse of the pilchard stocks (Crawford & Shelton 1981; Crawford et al. 1985). Although many species have now been recorded as prey of gannets, only five (South African Pilchard, Cape Anchovy, Maasbanker, hake and Saury) have constituted more than 15% by mass in any dietary study. Of these, Maasbanker was a major prey in the western Cape only in the 1950s and this stock subsequently collapsed in the mid 1960s.

Comparison between seasonal and geographic trends in the species contributing to the diet of the Cape Gannet and to purse-seine catches

There were similar trends in the seasonal patterns of the species composition of gannet diet at both western Cape colonies. These patterns can only be compared with purse-seine fishery catches for the first half of the year because there were few fisheries data for the second half. Cape Anchovy showed a peak in abundance in gannet diet at both islands in April and May, consisting of juveniles (<90 mm Lc), while a second peak at Malgas Island in October and November consisted of larger fishes of 100 mm to 130 mm Lc. Many of these large anchovy were virtually undigested, indicating they were caught close to the colony. Purse-seine fishery catches consisted almost entirely of anchovy from April to August between 1978 and 1984, with largest catches in April and May when the main period of southward migration occurs (Crawford 1981a). Large anchovy (>120 mm Lc) were rarely caught by the purse-seine fishery west of Cape Point (SFRI unpubl.), although purse-seine fishermen reported their appearance in deeper waters in summer (Anon. 1983). South African Pilchard occurred in the diet of gannets throughout the year, juvenile fishes (<130 mm Lc) dominating in winter and larger fish (160 mm to 220 m Lc) from September to February at both colonies. Armstrong et al. (in press) combined information on length-frequencies of South African Pilchard from commercial and research catches and gannet diet in different areas to describe the distribution of an isolated and relatively strong year class between 1983 and 1985. Occurrence of pilchard between October and December off the west coast during this period was only noted in gannet diet, as there was no commercial fishing. Because gannets from Malgas Island may range east of Cape Point to feed, it could be argued that the large pilchard eaten by gannets were caught east of Cape

Point. However, some pilchard in regurgitations from gannets were very fresh showing they had been caught close to the colonies, and large pilchard were found in gannets shot west of Lambert's and Saldanha Bays and west of the Cape Peninsula in February 1984. Historically, adult South African Pilchard occurred inshore on the west coast throughout the fishing season, and a recovery of pilchard stocks to a state where adult fishes are abundant could see this pattern re-established. Saury occurs in gannet diet in summer months (November to April). A review of available data (Chapter 10) shows that the Saury is a highly seasonal summer visitor to waters off the western Cape.

Hake occurs in gannet diet in winter and spring (May to October), but is readily available all year round off the west coast, although demersal catches are relatively larger north of the Cape Peninsula in winter when trawlers tend to move north to avoid adverse weather conditions to the south (B. Rose, SFRI, pers. comm.). Hake is an important food of the gannet colonies off Namibia (Crawford _et al_. 1985), which are declining in number (Crawford _et al_. 1983) and was recorded in gannet diet at Algoa Bay at a time of small meal sizes and nest desertions suggesting food shortage (J. Colclough, Port Elizabeth Museum, pers. comm.). Hake has a lower energy content than the epipelagic species (Batchelor & Ross 1984), and may be used as a predictable secondary food source by gannets when high-energy epipelagic fish are unavailable. Gannets should select epipelagic prey when they are available because of their higher energy content (Batchelor & Ross 1984) and because epipelagic fishes (particularly juveniles) occur inshore (Crawford 1980), closer to the colony than hake. Hake is not eaten by nonbreeders in the breeding season suggesting that selection for energy-rich foods by parents for feeding chicks is not the reason for the absence of hake in summer diet. Discarded whitefish is taken by Great Skuas <u>Catharacta skua</u> in the North Sea as a secondary food source when the energetically richer Sandeels <u>Ammodytes marinus</u> are absent (Furness & Hislop 1981). The occurrence of hake in gannet diet is investigated further in Chapter 8.

Of the prey species contributing small amounts to gannet diet, several showed distinct seasonal patterns. Gannets ate small Maasbanker (<120 mm Lc) in small quantities throughout the year, with a peak from November to January at Lambert's Bay. Crawford (1981d) recorded peaks in availability of younger age classes of Maasbanker in January, March and April, while purse-seine catches between 1978 and 1984 showed a peak in March. Gannets ate Mackerel from 50 mm to 370 mm in length, mainly between October and March. Crawford (1981f) found that availability of juvenile Mackerel decreased sharply in winter, while recent purse-seine fishery catches, although small, showed a peak in March. Redeye Roundherring (mainly juveniles) occurred in gannet diet from July to November. Crawford (1981c) found that catches of juvenile Redeye Roundherring were high in September and from February to

May, but decreased in winter. Recent catches (1978-1984) of Redeye Roundherring showed a peak in February and March, but data for the latter part of the year are few. Onderbaadjie was found (although rarely) in gannet diet between July and December, but yielded peak catches in February both in 1978-1984 and in earlier years (Crawford 1981e). Both adult Redeye Roundherring and Onderbaadjie usually occur at greater depths during the day than other species (Hulley & Prosch in press). Southern Mullet showed peaks in the gannet diet between August and March. De Villiers (in press) found that Southern Mullet measuring 210-300 mm Lc were most abundant off the west coast in summer.

Generally, the seasonal patterns of abundance of juveniles of Cape Anchovy, South African Pilchard, Maasbanker, Mackerel and Redeye Roundherring in gannet diet correspond to purse-seine fishery catches of the same species. Juvenile fishes occur inshore, migrating southwards past the gannet colonies (Crawford 1980). Comparison with the known distribution patterns of adults of these species is more difficult, because their movements are less well known. If adult fish select shelf-edge or frontal zones (Armstrong _et_ _al_. in press; Chapter 10), it is less likely that they will be caught by commercial or research fishing, particularly if they occur in small shoals. The way in which data from sources as different as commercial and research catches and gannet diet were combined to produce a coherent picture of the distribution of the South African Pilchard (Armstrong _et_ _al_. in press) suggests that it will be possible to find relationships between adequate series of fishery catches or research data once movements of adults are understood. This is investigated further in Chapter 9. There is also poor correspondence between fishery catches of mesopelagic fishes (adult Redeye Roundherring and Onderbaadjie) and gannet diet, and between demersal fishery catches of hake and gannet diet. Gannets may rely on other predators, such as dolphins and tunas, to force mesopelagic species to the surface, so that the occurrence of mesopelagic fishes in gannet diet may be closely linked to seasonal movements of such predators. In Algoa Bay, Batchelor & Ross (1984) found that seasonal changes in gannet diet were less marked than inter-annual differences.

The higher proportions of Cape Anchovy, Maasbanker and Mackerel in purse-seine fishery catches between 1978 and 1984 in the Columbine North fishing grounds compared to the Columbine South grounds corresponded to their relatively greater abundance in the gannet diet at Lambert's Bay compared to Malgas Island. Hake is a far larger component of the gannet diet at Malgas Island than at Lambert's Bay. The trawling grounds lie as close as 40 km to Malgas Island, but 150 km from Lambert's Bay. Saury are associated with the inshore occurrence of frontal systems, which also lie far closer inshore off Malgas Island than Lambert's Bay. However, Redeye Roundherring was more abundant in purse-seine fishery catches in the Columbine South grounds despite its relatively greater contribution to gannet diet at Lambert's Bay.

This is explained by the fact that purse-seine catches consisted mainly of adults, whereas most roundherring in gannet diet are juveniles which occur inshore in mixed shoals with other species (Crawford 1980).

Prey length

Gannets ate fishes within the size range 29 mm to 429 mm Lc. The average size of prey items at Malgas Island was larger than shown in Fig. 10 because the heads and tails of hake were not measured, but were considerably larger than most prey items. During the 1950s, large pilchard were common dietary items and the size distribution of gannet prey was bimodal (Davies 1955, 1956, 1958; Rand 1959a). The collapse of the South African Pilchard stock almost eliminated the upper mode of larger fish between 1978 and 1985, particularly at Lambert's Bay. The bimodal length distribution of pilchard reflects the eastward emigration of fishes approaching one year in age, to beyond the foraging range of gannets returning to islands on the west coast (Armstrong _et al_. in press).

There is a distinct seasonal trend in fish lengths, smallest fishes being present from April to June, and thereafter fish length gradually increasing until the chicks leave the nest in March. This process results from the growth of the numerically dominant Cape Anchovy which recruit early in the year, and the occurrence of larger species (Saury and Mackerel) or older age classes (South African Pilchard, Cape Anchovy and Redeye Round-herring) in summer.

Regurgitation mass and proportion of gannets handled which regurgitate food

The mean regurgitation mass and proportion of birds handled which regurgitated food should be related to food availability, in this case the availability of epipelagic fishes. However, at Malgas Island, gannets consumed much hake which was available all year round irrespective of the availability of epipelagic fish. Therefore, the regurgitation masses and proportions of birds handled which regurgitate food should only be considered if the sample contained solely epipelagic fish. At Lambert's Bay, measures of all regurgitations and of regurgitations containing only epipelagic fish were similar because hake was an infrequent dietary item there. If gannets usually obtain all their food from one shoal of pelagic fish, then regurgitation mass should vary less in relation to prey abundance, although search time should vary greatly. However, feeding groups of gannets form and disperse rapidly, and usually comprise less than ten birds, particularly north of Cape Columbine (Chapter 7). This suggests that there is insufficient time for gannets to catch a full meal from one school of fish, although prolonged feeding bouts in association with cetaceans were seen south of Cape Point. Batchelor & Ross

(1984) showed that meals containing large fishes weighed more than meals containing small fishes, suggesting that the more dives required to catch prey, the smaller the regurgitation mass.

The proportion of birds which regurgitated epipelagic fishes only, but not regurgitation mass, varied seasonally at Lambert's Bay, and showed a decline in winter and spring. At Malgas Island, both these parameters varied seasonally, declining in winter and spring. The annual means of these parameters do not suggest any clear changes in the availability of epipelagic fishes between 1978 and 1986.

Seasonal availability of food

A seasonal pattern in the availability of epipelagic prey to gannets off the western Cape is suggested by the seasonal trends in regurgitation mass, the proportion of birds handled which regurgitate food, the size of prey and the species composition of the diet. In April and May, prey is predictable and consists mainly of juvenile Cape Anchovy. In late winter and spring, the distribution of epipelagic fish inshore apparently becomes more patchy and unreliable. The mean regurgitation mass decreases and the proportion of birds which regurgitate food drops. At Malgas Island, the proportion of hake, a secondary food source eaten when epipelagic prey are not available, increases. The food supply remains highly variable until October or November, when the arrival of larger fishes, particularly south of Cape Columbine, provides a more predictable food supply with greater energetic return. That epipelagic fishes are less abundant and patchily distributed in late winter and spring is suggested by the desertions of breeding Cape Cormorants at this time (Crawford _et al_. 1980, 1986; pers. obs.) and the high starvation rate of Jackass Penguin chicks at Marcus Island, Saldanha Bay, between October and January (Wilson 1985a). At Lambert's Bay, Cape Anchovy is available all year round. The same trends in availability as recorded at Malgas Island occurred but were less pronounced. Cape Cormorants at Lambert's Bay usually continue breeding for one to four months longer than at Malgas Island (pers. obs.), suggesting prey is predictably available for a longer period in the year.

Annual changes in the species composition of gannet diet and prey availability, 1978 to 1986

The species composition of gannet diet at Lambert's Bay showed clear interannual trends between 1978 and 1986; gannets fed increasingly on Cape Anchovy until 1982 but between 1983 and 1985, Saury, South African Pilchard and hake increased at the expense of Cape Anchovy. South African Pilchard decreased in abundance in gannet diet from 1978 to 1982, then increased steadily from 1983 to 1986. Similar changes occurred in gannet diet at Malgas Island but were not as clearly defined. It appears that a change occurred in 1983, with poorer relative recruitment of Cape Anchovy until 1986 when Cape Anchovy again contributed a greater proportion of the gannet diet at Lambert's Bay. These changes may have been linked to changes in environmental conditions in 1983. The frequency of upwelling-favourable winds decreased in late 1983 leading to the 'warm event' of that year (Duffy et al. 1983). Contributions of Saury to the diet have varied greatly at both localities, presumably in accordance with the proximity of frontal zones to the colonies. Hake increased in gannet diet at both localitites between 1983 and 1985. If gannets travel to deeper waters to eat hake only when epipelagic fish are not available inshore, then the quantity of hake in gannet diet suggests a decline in the inshore availability of epipelagic fish stocks (primarily Cape Anchovy) at this time. This trend was reversed in 1986 when epipelagic fish (dominated by Cape Anchovy but with a larger component of South African Pilchard) became more abundant.

Conclusions

The Cape Gannet eats epipelagic shoaling fish, mainly measuring 50-240 mm Lc, and offal and trash fish discarded from demersal trawlers. Where adequate comparative data (for juvenile fishes less than 140 mm Lc) exist, seasonal changes in the species composition and length of prey in gannet diet generally parallels seasonal changes in the species composition and size of fishes caught by the purse-seine fishery. This is evidence that the gannet, as suggested for other seabirds, consumes prey in proportion to their availability. However, there is no general correlation between the availability of hake and of mesopelagic fishes as shown by fisheries data and their occurrence in gannet diet. Hake is used as a secondary food when energy-rich epipelagic prey is not available inshore, while mesopelagic fishes are seldom available during the day at the surface. Changes in mean regurgitation masses and in the proportion of birds handled which regurgitate food suggest a strong seasonal pattern in the availability of food. Epipelagic prey are least available and least predictable in late winter and spring, which is the time when hake is most abundant in gannet diet.

CHAPTER 6

THE EFFECT OF BREEDING STATUS ON THE DIET OF THE CAPE GANNET

INTRODUCTION

Breeding increases the energetic requirements of parent gannets and reduces their potential foraging time, and may therefore greatly affect their foraging strategy and diet. Simultaneous studies of the diet of breeding and nonbreeding seabirds in the same area (Furness & Hislop 1981; Kirkham et al. 1985), so eliminating geographical and temporal variation, are rare. Breeding and nonbreeding birds are not usually readily identifiable and present in sufficient numbers to sample their diet. However, gannets are an exception, so providing an opportunity to test the effect of breeding on diet (Kirkham et al. 1985).

The distinct seasonal trends in the species composition and length of prey eaten by gannets in the western Cape (Chapter 5) could be related to the breeding and nonbreeding seasons of the gannet. Regurgitations were obtained mainly from breeding birds during the breeding season, although some regurgitations were obtained from nonbreeding birds as well. If breeding birds select prey differently from nonbreeders, the diet will reflect changes in gannet foraging behaviour rather than changes in food availability during the breeding season (September to March). This chapter reports on the effect of breeding status on the diet of Cape Gannets.

METHODS

Diet sampling is described in Chapter 5. Breeding birds usually land on the nest site, whereas nonbreeding birds land at the perimeter of the colony, usually joining a club of nonbreeding birds (Jarvis 1971a). Occasionally, a breeding bird may land on the periphery of the colony before moving through the colony to its nest. These attempts are infrequent, and are vigorously resisted by the occupants of surrounding densely-packed nests. However, a very small percentage of birds classed as nonbreeders could have been breeding birds (Kirkham _et_ _al_. 1985).

During November 1983, 50 regurgitations each were obtained from breeding and nonbreeding gannets at Lambert's Bay. Five samples each were taken from breeding and nonbreeding birds on ten sampling days in the month. All breeding birds were incubating eggs. Between 1 November 1983 and 31 January 1983, totals of 60 and 59 regurgitations were obtained from breeding and nonbreeding birds at Malgas Island. Five samples each were obtained from breeding and nonbreeding birds on 12 sampling days, except on one occasion when only four samples were obtained from nonbreeding birds. All breeding birds were feeding chicks.

Differences in mean caudal lengths of fishes, regurgitation masses and number of fishes per sample between breeding and non-breeding birds at the same locality were tested using the Student's t-test. Differences between the frequency of occurrence of species in the diet of breeding and nonbreeding birds at the same locality were tested ofr significance using *chi*-square evaluation. For this test, the less abundant species in regurgitations at the same locality were lumped together so that their expected frequency of occurrence was greater than five.

RESULTS

The frequency of occurrence of prey species in gannet diet at Lambert's Bay and Malgas Island respectively is given in Tables 27-28. The same three prey species at Malgas Island and the same five prey species at Lambert's Bay were the most important species (measured by numerical abundance, mass and frequency of occurrence) in the diet of breeding and nonbreeding birds, although not always in the same order of abundance (Tables 27-28). The frequency of occurrence of prey species was not significantly different between birds of different breeding status at the same locality (P >0,1; *chi*-square test). Nonbreeding birds at both localities took more Saury and South African

TABLE 27.

THE FREQUENCY OF OCCURRENCE OF PREY SPECIES IN THE DIET OF 50 BREEDING AND 50 NONBREEDING CAPE GANNETS AT LAMBERT'S BAY IN NOVEMBER 1983

Fish Species	Breeders		Nonbreeders	
	Observed	Expected	Observed	Expected
Cape Anchovy	41	30,5	30	30,5
Maasbanker	21	22,0	23	22,0
Mackerel	5	6,0	7	6,0
S. African Pilchard	2	5,5	9	5,5
Other	5	6,5	8	6,5
Redeye Roundherring	2		3	
Hake	1		1	
Saury	0		1	
Monkfish	2		0	
Squid	0		3	

TABLE 28

THE FREQUENCY OF OCCURRENCE OF PREY SPECIES IN THE DIET OF 70 BREEDING AND 69 NONBREEDING CAPE GANNETS AT MALGAS ISLAND, DECEMBER 1982 TO JANUARY 1983

	Breeders		Nonbreeders	
Fish Species	Observed	Expected	Observed	Expected
Cape Anchovy	48	40,3	32	39,7
Saury	26	31,2	36	30,8
Other	5	7,1	9	6,9
Hake	2		4	
Squid	1		0	
Southern Mullet	1		1	
S. African Pilchard	1		3	
Snoek	0		1	

Pilchard than breeding birds. Nonbreeding gannets at Lambert's Bay took more Redeye Roundherring than breeding birds. Mackerel, Maasbanker and Redeye Roundherring occurred only in gannet diet at Lambert's Bay but Cape Anchovy and Saury were more important at Malgas Island.

The significance of differences between mean regurgitation mass, the mean number of fishes per regurgitation and the mean caudal length of fish prey of birds of different breeding status at the same locality produced two significant (P <0,05) results in six tests (Tables 29-30). Breeders at both localities produced heavier regurgitations containing more fishes with a greater mass per item. Only the number of fishes per regurgitation of breeding birds at Lambert's Bay was statistically greater (P <0,05). The caudal-length frequencies of all fish are given in Fig. 21. Although nonbreeders took significantly larger fishes (P <0,05) than breeders (Table 30), the mean mass per item eaten by breeders at Malgas Island was heavier (Table 29). This is attributed to generally more advanced state of digestion of nonbreeders (small mass per item) despite the larger initial body size.

DISCUSSION

To meet the increased energetic requirements of chick-rearing and to overcome the reduction in potential foraging time through incubation and chick attendance, parent gannets can maximize their

TABLE 29

PARAMETERS OF DIET OF BREEDING AND NONBREEDING CAPE GANNETS AT LAMBERT'S BAY AND MALGAS ISLAND

	Lambert's Bay		Malgas Island	
	Breeding	nonbreeding	Breeding	nonbreeding
Mean regurgitation mass(g)	144,4	110,5	195,8	169,6
Mean no. fishes/meal	13,8	12,5	13,5	10,3
Mean fish length (mm)	9,2	9,1	11,0	11,7
Mass per item (g)	10,4	8,8	16,8	16,4

TABLE 30

LEVELS OF SIGNIFICANCE (STUDENT'S T TEST) IN MEAN REGURGITATION SIZE, NUMBER OF FISHES PER REGURGITATION, AND MEAN FISH LENGTH (Lc) FROM BREEDING AND NONBREEDING CAPE GANNETS AT LAMBERT'S BAY AND MALGAS ISLAND

Colony/ Breeding status	Colony/ Breeding status	Probability	Significance
Regurgitation size			
Malgas: Breeder	Malgas: Nonbreeder	> 0,05	NS
Lambert's: Breeder	Lambert's: Nonbreeder	> 0,05	NS
No. of fish			
Malgas: Breeder	Malgas: Nonbreeder	> 0,05	NS
Lambert's: Breeder	Lambert's: Nonbreeder	< 0,05	Significant
Fish length			
Malgas: Breeder	Malgas: Nonbreeder	< 0,01	Significant
Lambert's: Breeder	Lambert's: Nonbreeder	> 0,50	NS

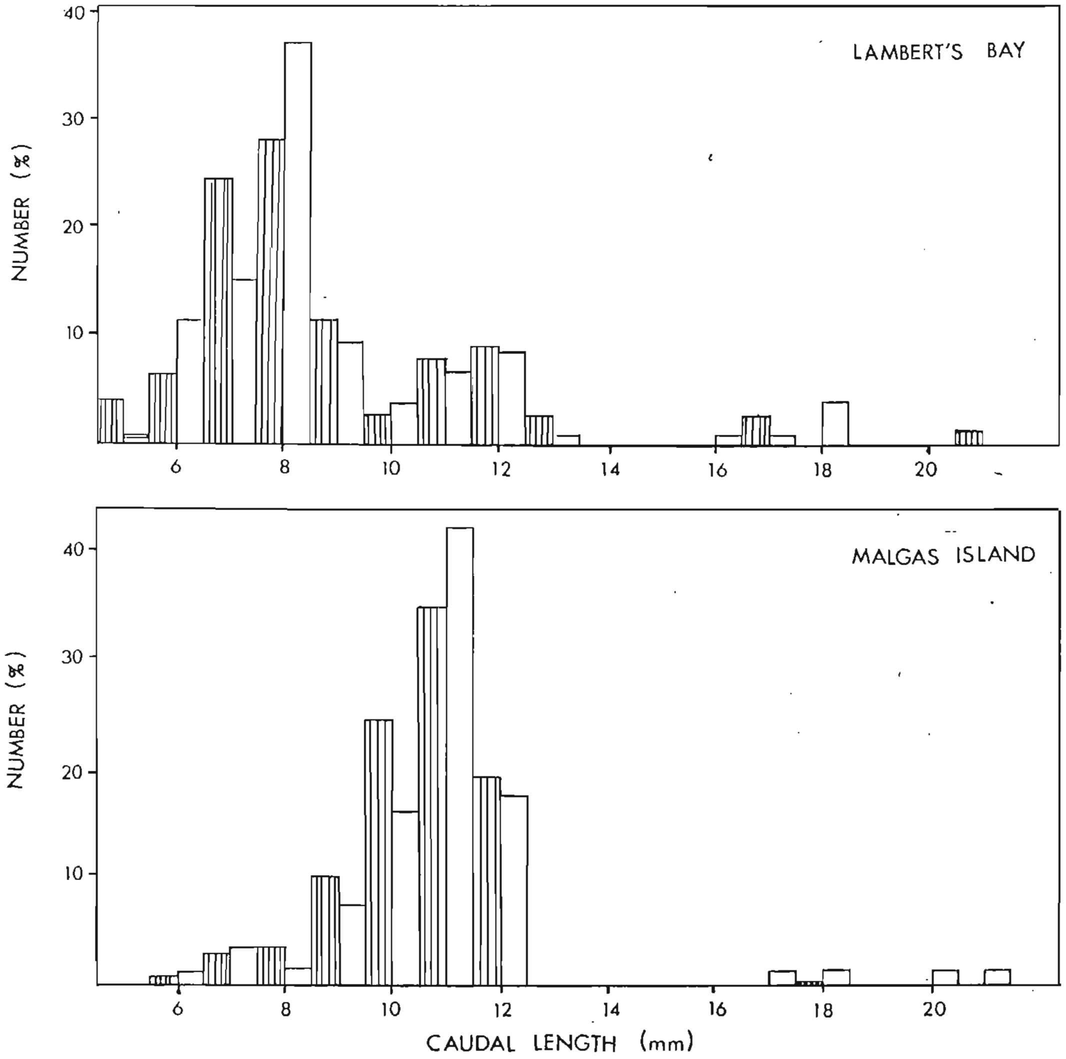


FIGURE 21

The caudal length frequencies for all whole fish found in the diet of breeding (vertical lines; n=78) and nonbreeding (open blocks; n=106) Cape Gannets at Lambert's Bay and in the diet of breeding (vertical lines; n=141) and nonbreeding (open blocks; n=69) Cape Gannets at Malgas Island.

energy intake per unit time when foraging in three ways: by catching more prey, by catching larger prey or by selecting energy-rich prey. Alternatively breeding gannets may forage in the same way as nonbreeders, but may take more time to increase total energy intake. If food is superabundant and hence foraging time short, gannets may not have to increase foraging effeciency or foraging time by much. However, the relative stability in gannet population sizes (Crawford et al. 1983a) and purse-seine fishery catches (Armstrong et al. 1985) in recent years do not suggest superabundance of prey. In fact, recent mortalities and the decline in numbers of Cape Cormorants and numbers of Jackass Penguin (Duffy et al. 1984; Crawford et al. 1986) which depend on epipelagic shoaling fish suggest shortages in food supply.

Breeding gannets at both colonies regurgitated heavier samples containing more fishes with a greater mass per regurgitated item, although only one of these differences was statistically significant. These trends are consistent with the increased energetic demands of chick-rearing and provisioning for long incubation spells. Breeding birds at Malgas Island, which were feeding chicks, took significantly smaller fishes than nonbreeders, although actually delivering a heavier mass per regurgitated item. This may be because the chicks cannot swallow larger items. This constraint is of short duration because larger chicks can swallow any food items regurgitated by the parents with the exception of occasional very large Saury (Batchelor & Ross

1984) or large hake heads (pers. obs.). Breeding Northern Gannets regurgitated heavier meals and took larger Mackerel *Scomber scombrus*, the dominant prey, in one of two years, and the same size in the other year compared to nonbreeders (Kirkham *et al*. 1985).

There was no significant difference in the prey-species composition by frequency of occurrence between breeders and nonbreeders, but there was a tendency for nonbreeders to catch species richer in energy such as South African Pilchard and Saury (Batchelor & Ross 1984). Adult South African Pilchard provide the best energetic return per capture and are considered to be the preferred prey species of gannets (Davies 1956; Batchelor & Ross 1984; Chapter 8). Historically, South African Pilchard were the dominant prey of gannets (Davies 1956; Rand 1959). However, Saury, adult Redeye Roundherring and adult South African Pilchard are primarily species of the shelf-edge or thermal fronts, available to gannets primarily in warmer and deeper waters further offshore (Crawford 1981; Dudley *et al*. 1985; Armstrong *et al*. in press; Chapter 10). Comparisons of prey profitability are complicated by the fact that these are shoaling fishes, and should take into account the rate of energy gain per shoal encounter and the rate of shoal encounters per species, rather than energy gain per individual fish. Inshore shoals of small Cape Anchovy (the most abundant pelagic fish) may be the most profitable food resource to breeders tied to colonies, because the larger fish prey with a higher energetic density occur offshore. The availability of larger fishes to gannets off the western Cape may be low. South African Pilchard are still relatively rare (Armstrong 1986), adult Redeye Roundherring are available on the surface mainly at night (Crawford 1981c) and Saury do not shoal as readily as other epipelagic species (Chapter 10). The differences in frequency of occurrence of prey species may be linked to spatial variation in foraging; nonbreeders feeding further offshore, where larger, energy-rich prey occurs. Breeding gannets regurgitate larger samples but it is not clear whether foraging time or efficiency is increased.

It is possible that the need to return to the colony, whether the bird is breeding or not, influences the selection of prey. Even nonbreeding birds may usually require one or more large energy-rich meals or have adequate energy reserves before being able to spend time at the colony.

Temporal and spatial variations in the composition of gannet diet are considerable (Davies 1958; Matthews 1961; Rand 1959; Batchelor & Ross 1984; Chapter 5). Recent seabird studies have shown major dietary differences in populations of the same species separated by tens to hundreds of kilometers (Furness & Hislop 1981; Schneider & Hunt 1984; Vermeer & Westrheim 1984; Hislop & Harris 1985). The effect of breeding on diet composition in the Cape Gannet is small compared to spatial and temporal variations.

CHAPTER 7

THE FEEDING ECOLOGY OF THE CAPE GANNET

INTRODUCTION

Not all epipelagic shoaling fishes in southern African waters are available to Cape Gannets; the biological characteristics of both fish and gannets and abiotic characteristics of the environment determine the portion of fish populations available to gannets (Wiens 1984). The way in which gannets use the available part of the resource is determined by their behavioural preferences, feeding patterns, morphological constraints and metabolic requirements (Wiens 1984). In the western Cape, Rand (1959) investigated the pelagic distribution of Cape Gannets and their diet and feeding behaviour within 20 km of the shore. Little further work has been undertaken since then on the pelagic feeding ecology of the Cape Gannet. The feeding behaviour of the Cape Gannet is summarized in Chapter 2.

The feeding ecology of Cape Gannets, particularly their foraging area must be understood before comparisons can be made with commercial or research catches, or before the diet can be used to interpret changes in prey abundance or availability. In this chapter, the foraging area of gannets from each of the two western Cape colonies is defined. Foraging strategies of gannets are suggested in relation to prey quality and distribution and the presence of oceanic thermal fronts and marine predators other than gannets. The effect of long-term changes in prey abundance on the foraging strategies of gannets is discussed.

METHODS

The pelagic distribution and feeding of the Cape Gannet were investigated during the nonbreeding season (April to July) and breeding season (August to March).

Ship surveys were made in February 1984, November 1985 and June and July 1986. The numbers of gannets visible to the naked eye and seen by one or more observers on both sides of the ship, the 32 m R.V. Sardinops, were recorded. I made the vast majority of observations on all three trips. Observers were seated about 8 m above sea level on top of the superstructure, providing unobstructed all-round vision, protected by a chest-high barrier from wind and spray. The numbers of gannets counted during 1-m intervals were recorded on standard forms. Their activity was recorded as flying, sitting on water or feeding. Flight direction was recorded. The cruise track covered most of the foraging area of gannets from island colonies in the western Cape and also virtually the entire fishing area. However, the daily cruise track was influenced by weather, position of oceanic thermal fronts and diversions to trawlers and feeding groups of gannets. The distribution of birds was plotted as birds per km over distances of at least 15 km, and the direction of flight was indicated with arrows if the sample size exceeded 10 within the count period and if 40% or more of birds seen were flying in that direction. Feeding was classed as "scattered" (one or more birds diving over a large area) or "group" (more than one bird feeding within a few meters of each other within a minute). At feeding groups, the group size and the presence of other predators were recorded. When possible, one or two birds from each feeding group were shot with a shotgun in order to collect stomach samples. If gannets were seen resting on the sea surface and had difficulty in taking off when approached indicating full stomachs, one or two birds were shot. Totals of 17, 28 and 15 gannets were shot in February 1984, November 1985 and June-July 1986 respectively. A further four gannets were shot at sea in November 1983 between Cape Point and Saldanha Bay. Birds were retrieved with a long-handled scoop net. The stomach contents were immediately removed, then frozen or preserved in 96% ethanol until they could be processed ashore according to the methods described in Chapter 5. Not all birds contained fresh prey remains. The composition (percent of species by frequency of occurrence and caudal length frequencies) of fresh prey remains (fish with backbone and most of the skin intact) in the stomachs of birds shot at sea was divided into birds shot within and beyond 20 km of the shore. The Kolmogorov-Smirnov test (Tate & Clelland 1957) was used to test differences between length-frequency distributions for statistical significance. The minimum sample size was 30.

Between 21 and 27 February 1984, 70 hours observations were made on a ship survey within the 200-m depth contour between Mossel Bay (30° 43'S 17° 24'E) on the west coast, and near Cape Agulhas (34° 50'S 20° 00'E) on the south coast. This cruise was designed primarily to investigate cetacean distribution and only one leg of the cruise track ran further than 30 km offshore. A total of 124 hours of observations were collected between 5 and 18 November 1985 when the ship surveyed between Lambert's Bay and Cape Agulhas, and offshore as far as the 1000-m depth contour in places. Between 23 June and 4 July 1986, 109 hours of observation were made on a ship survey between Island Point (31° 35'S 18° 08'E) and Danger Point (34° 40'S 19° 20'E).

Gannets attending net hauls of the R.S. Africana were counted by B. Rose and R. Leslie (SFRI) during two extensive bottom trawling surveys between 8 January 1986 and 4 February 1986, and 2 and 24 July 1986 in the area between Orange River and the Agulhas Banks, in waters 80 m to 500 m deep. The numbers of birds seen were placed in one of the following abundance categories: 1-10, 11-50, 51-100, 101-500 and >500.

On 12 and 13 November 1985, during the ship survey, the number of gannets flying north and south past the Cape Columbine lighthouse was counted hourly. The observation point was about 10 m above sea level and about 200 m from the sea. All gannets seen with the naked eye were recorded.

The distribution and activity of gannets were recorded during three aerial surveys in late 1983 during incubation and early nestling stages. I recorded the numbers and activity (flying, sitting on water, or feeding) of gannets and associations with other predators from a fixed upperwing Partenavia P68B aircraft, at an airspeed of 200 km/hr and a height of 150 m to 300 m depending on the altitude of the base of cloud cover. All gannets visible on one side of the aircraft within a distance of about 2 km (estimated by eye) were counted. Dives by gannets were clearly visible. Numbers counted in each minute were recorded on standard forms. A watch attached to the clipboard holding the forms allowed me to keep track of 1-m time intervals with ease. I estimated the numbers in very large groups, notably at trawlers and near Malgas Island because there were too many birds to count individually. Flight direction of gannets was recorded. The aerial surveys covered a set grid within the 200-m depth contour on 24 Niovember 1983 and 6 December 1983. Coastal fog considerably disrupted further planned flights and on 30 November 1983, the area beyond the 200-m depth contour was searched for demersal trawlers because the inshore area was covered by fog. At trawlers and large feeding groups, the aircraft circled to allow a better estimate of the number of gannets present. Flights began at about 08h30 and were completed by about 15h00, starting at Doring Bay

(31° 40'S, 18° 14'E) and finishing at Cape Hangklip (33° 24'S 18° 49'E). The density of birds was recorded as number of birds per m over 2-m periods.

Before the cruise in November 1985, 850 incubating gannets were dyed with Picric acid solution at Lambert's Bay and another 1 100 with Rhodamine B solution at Malgas Island. Before the cruise in June-July 1986, 1 170 nonbreeding gannets were marked with Rhodamine B solution between 29 June and 2 July at Lambert's Bay, and another 1 033 with Picric acid solution between 25 and 26 June at Malgas Island. Each bird was sprayed on the back with about 40 ml of solution from a commercial dose dispenser.
With the aid of binoculars where necessary, the number of colour-marked gannets seen at sea from the R.V. Sardinops, net hauls of the R.S. Africana and opportunistically from other vessels and the shore were recorded. Totals of 50 and 204 dyed gannets were seen at sea in November 1985 and June and July 1986 respectively. In November 1985, 12 sightings were made by shore-based observers on the Cape Peninsula, six from a commercial trawler; 31 from the R.V. Sardinops and one from the R.S. Africana. In June and July 1986, four sightings were made by skiboat fishermen off Hout Bay, 145 from the R.V. Sardinops and 55 from the R.S. Africana.

An accidental oil spill provided an unusual opportunity to determine whether gannets returning to each colony occurred in the area covered by the oil slick. Between 6 and 8 August 1983, 160 000-190 000 tons of crude oil was spilt by the breakup of the supertanker Castillo del Bellver off Cape Columbine (Schumann 1984). The resultant slick covered a huge area. Large numbers of gannets were oiled, revealing the relative numbers of gannets from each of the two colonies which were feeding in the area. Totals of 194 and 1297 oiled gannets were captured at the Lambert's Bay and Malgas Island colonies for cleaning and rehabilitation. Nearly all oiled gannets were collected at Lambert's Bay, but the total number of oiled gannets at Malgas Island was estimated at 5 000 birds. The diets of oiled and unoiled gannets were compared in order to determine the principal prey in the vicinity of the oil slick. Diet samples were collected and analyzed as described in Chapter 5. Prey species were classed as hake, epipelagic fish or squid, but values for hake and epipelagic fish only were tested for significance using *chi*-square evaluation as their expected values exceeded 5.

The length of 59 incubation shifts in November 1983 and November 1985 at Lambert's Bay and of 19 shifts in October 1982 and November 1985 at Malgas Island were determined. One member of the pair was marked with Picric Acid solution. The nest was visited every four hours between 07h00 and 19h00 for five days in 1983 and 1985, and every two hours between 06h00 and 20h00 for three days in 1982. Gannet arrivals and departures after 19h00 and before 07h00 were few.

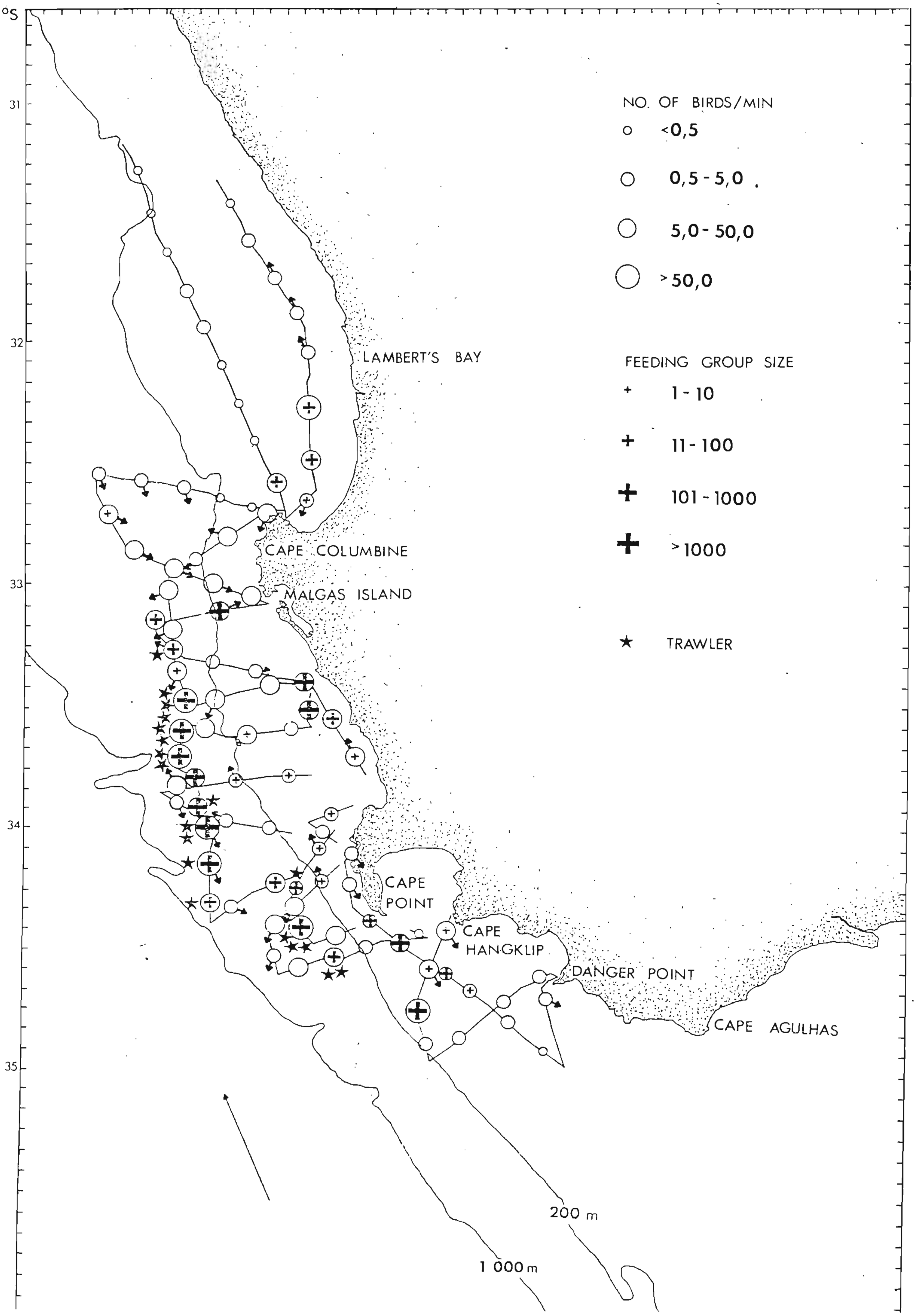
RESULTS

The results of aerial and ship surveys are shown in Figs. 22-27. Gannets showed similar distributions and flight directions during the breeding season (Figs 22, 23, 26 & 27). Gannets flew along a north-south flight path from Malgas Island, west of Dassen Island along the Cape Peninsula, then dispersed in an easterly to southerly direction into False Bay and the Agulhas Bank. Gannets returning to the colony apparently stayed closer inshore than those moving south to feed. Gannets also dispersed from Malgas Island in a northwesterly to southwesterly direction to the trawling grounds. This movement was not as discrete as the north-south flyway because of the wide dispersion of trawlers over the trawling grounds. Gannets occurred in large numbers on the trawling grounds over a distance of 300 km (Fig. 25). Beyond this area to the north, gannets were widely but thinly scattered.

In the nonbreeding season, relatively few gannets from Malgas Island flew along the Cape Peninsula flyway, but movements to and from the trawling grounds were more evident (Fig. 24). Numbers of birds feeding at trawlers were higher in winter than in summer (Fig. 25). During winter, there was a clearer distinction between inshore scattered feeding and feeding at the trawlers. Few gannets caught epipelagic fish in deeper waters.

FIGURE 22

The numbers (birds per km), flight direction (see text) an feeding areas of Cape Gannets in the western Cape as determin by ship survey between 21 and 27 February 1984.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NO. OF BIRDS/MIN
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FEEDING GROUP SIZE
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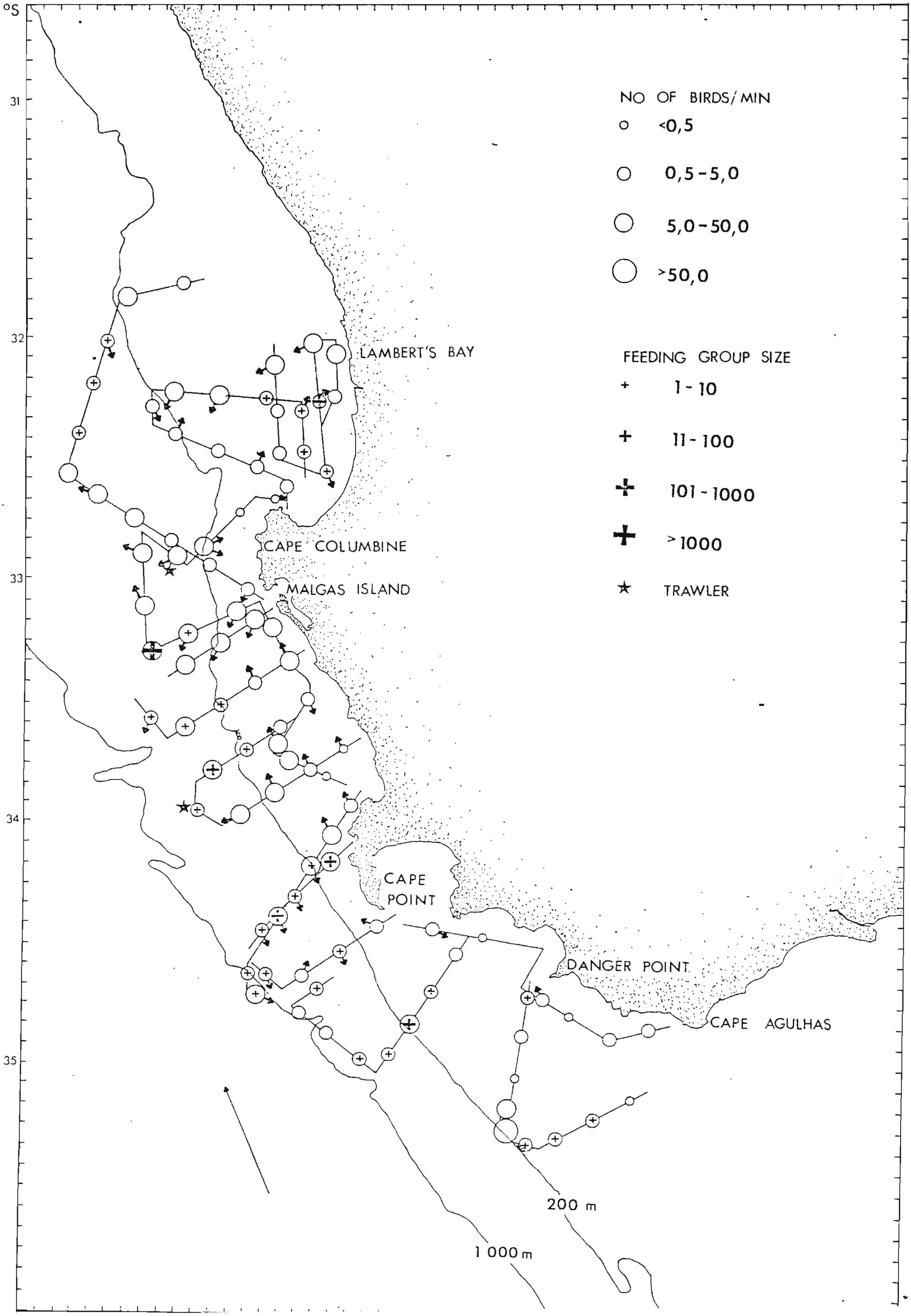
11 - 100
101 - 1000
>1000
★ TRAWLER
LAMBERT'S BAY
CAPE COLUMBINE
MALGAS ISLAND
CAPE POINT
CAPE HANGKLIP
DANGER POINT
CAPE AGULHAS
200 m
1 000 m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FEEDING GROUP SIZE
1-10
11-100
101-1000
>1000
TRAWLER
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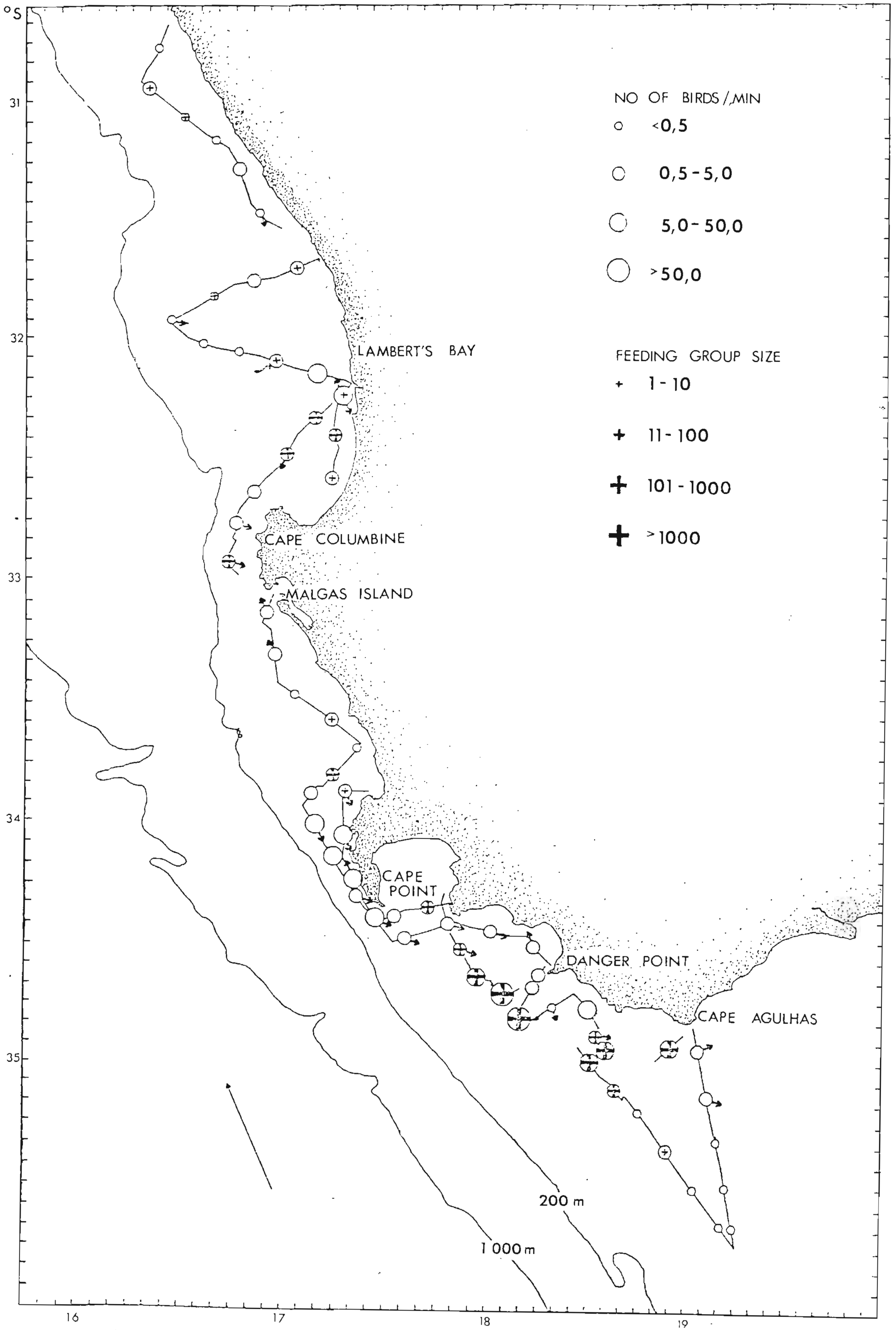
CAPE POINT
DANGER POINT
CAPE AGULHAS
200 m
1 000 m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FEEDING GROUP SIZE
1-10
11-100
101-1000
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MALGAS ISLAND
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CAPE AGULHAS
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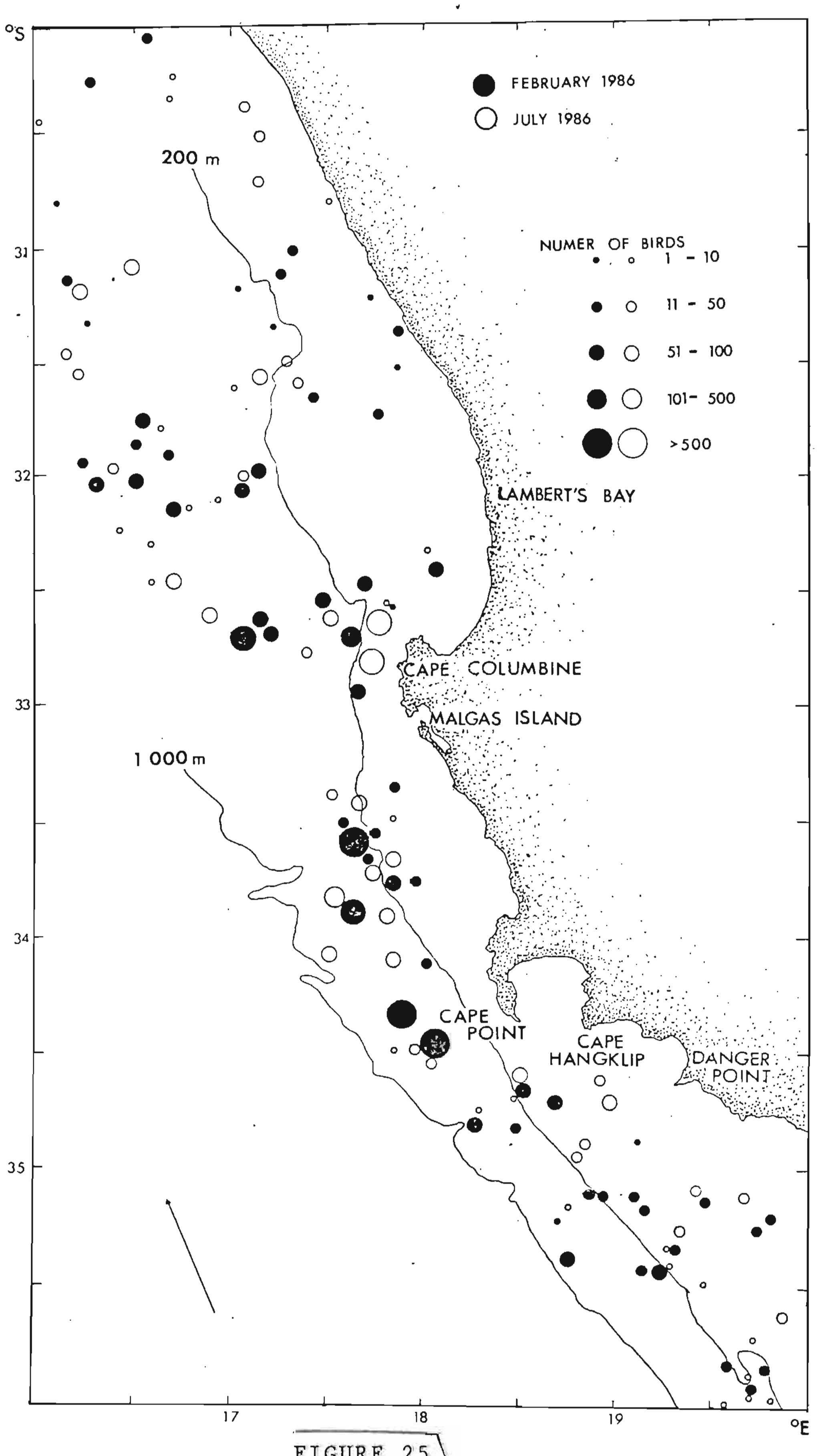


FIGURE 25

Numbers of Cape Gannets at net haul

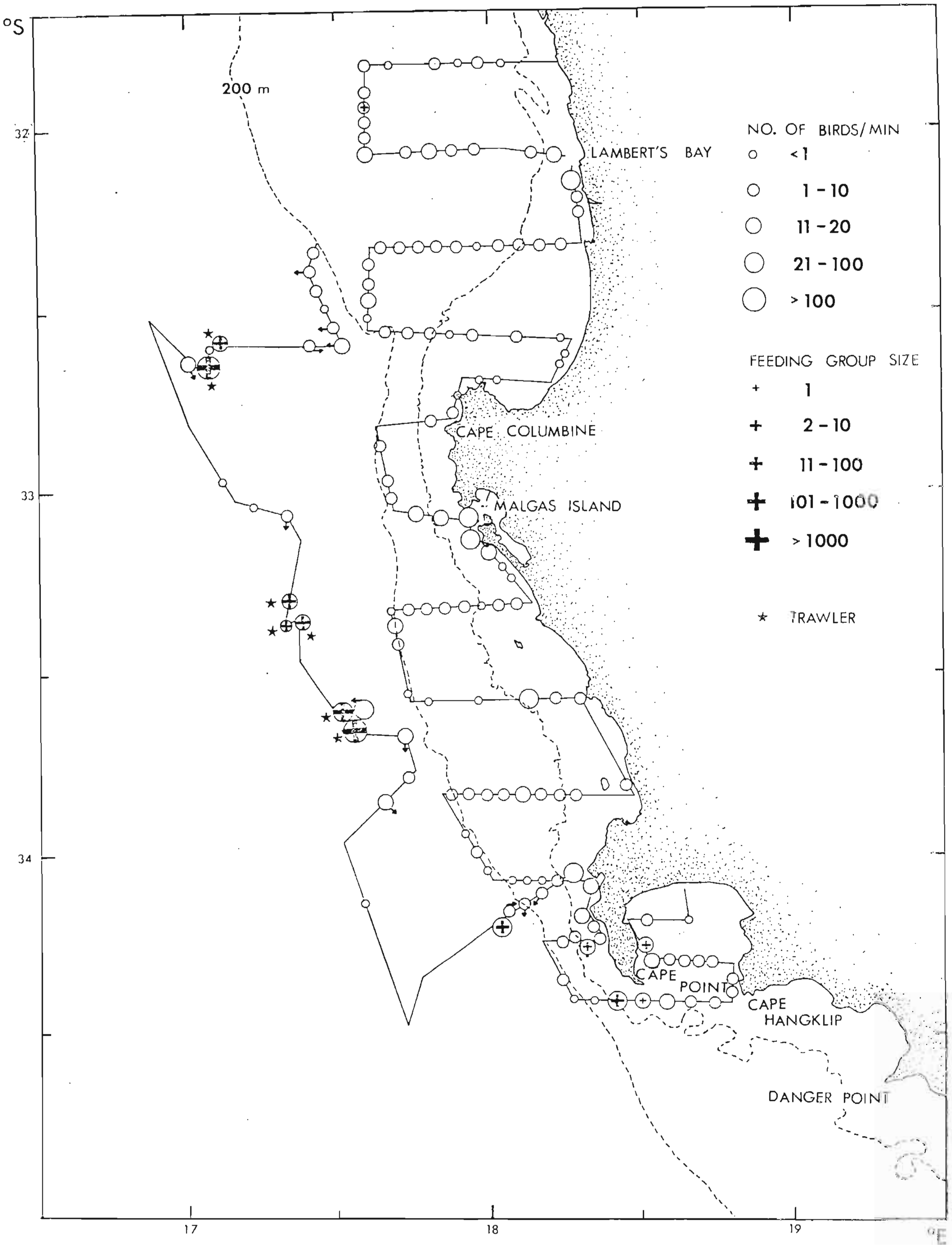


FIGURE 26

The numbers (birds per km) and feeding areas of Cape Gannets determined by aerial survey on 24 November 1983 and 30 November

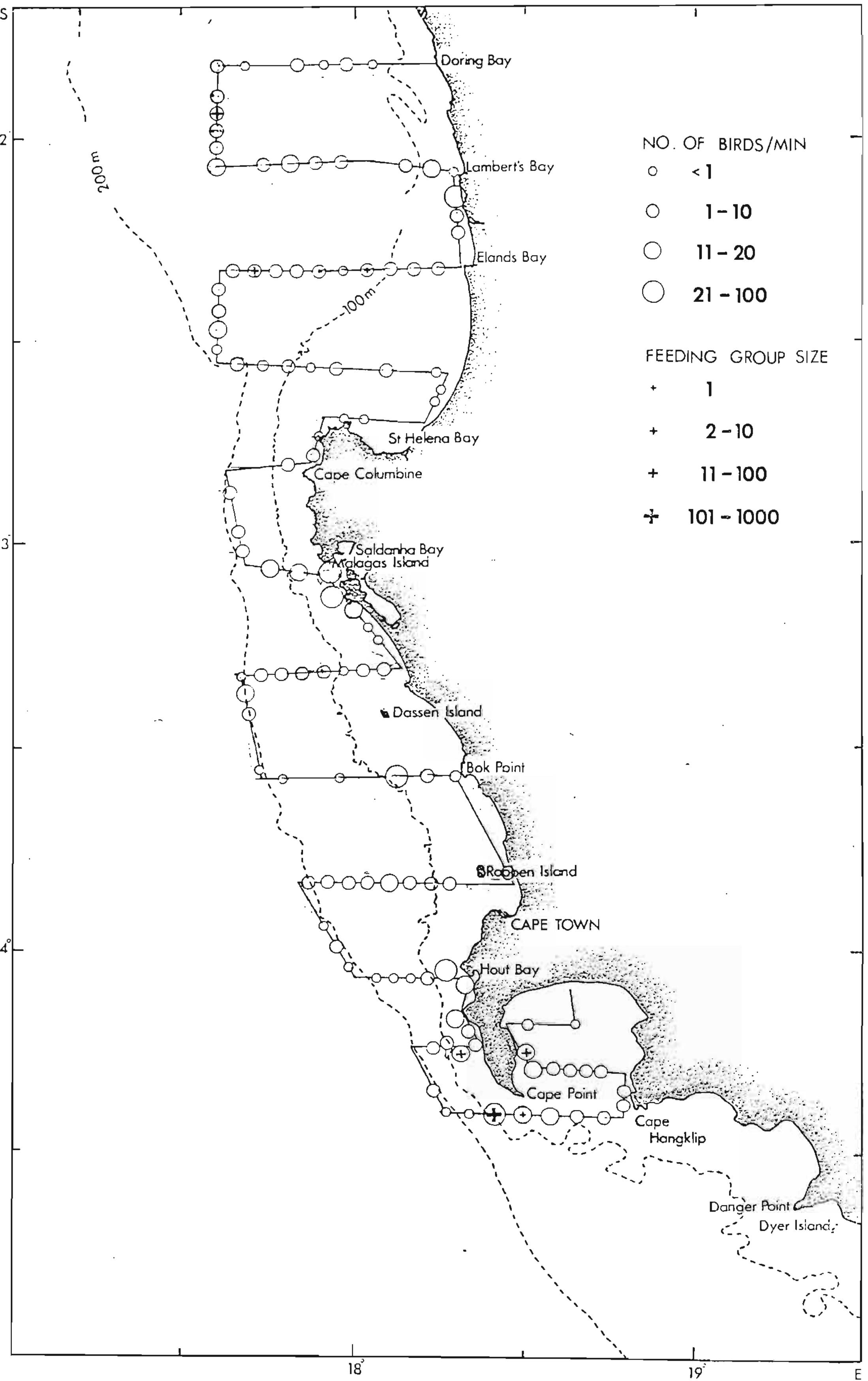


FIGURE 27

The numbers (birds per km) and feeding areas of Cape Gannets determined by aerial survey on 6 December 1983 off the western

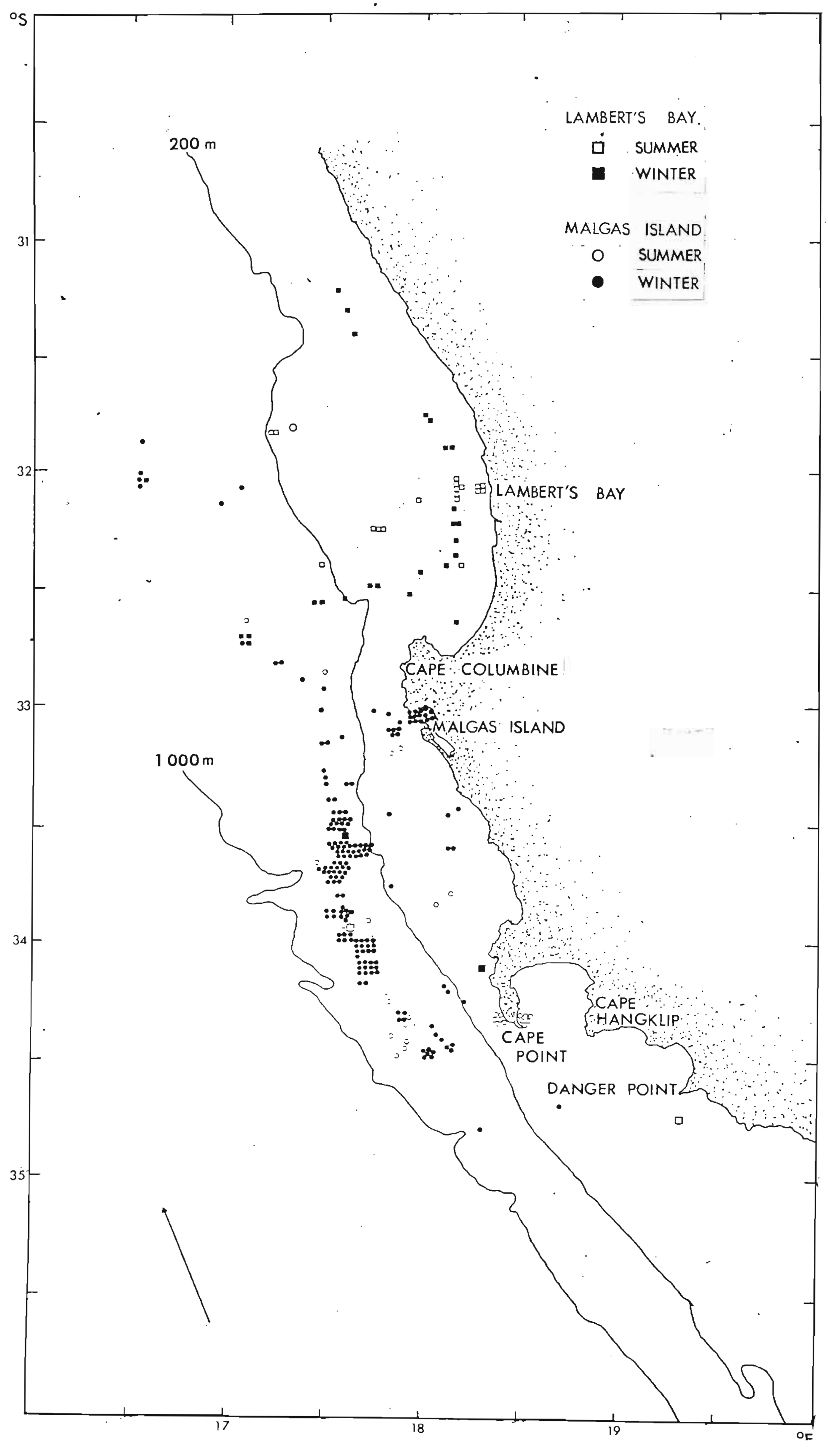
In both seasons, large groups of feeding gannets were found at the demersal trawlers, in False Bay and the area south of Cape Peninsula to Danger Point, off the the Cape Peninsula in shallow and deep waters and in deeper water west of Saldanha Bay. Scattered feeding was recorded throughout the inshore zone, on the Agulhas Bank east of Cape Point and in deeper water off the Cape Peninsula (Figs. 22 & 23, 26 & 27).

During the breeding season, in the area north of Cape Columbine, predominant flight directions appeared to radiate out from, and in the direction of, the Lambert's Bay colony. Ship, aerial and ground surveys (Figs. 22-27) showed that relatively few gannets pass around Cape Columbine, despite its close proximity to Malgas Island. Totals of 878 and 2 489 gannets flew past Cape Columbine on 12 and 13 November, representing about 2% and 5% respectively of the total number of breeding pairs (36 000) in the western Cape in 1985.

In the area north of Cape Columbine during the nonbreeding season, the dominant flight directions were to and from the colony at Lambert's Bay. Hardly any gannets were seen offshore, or flying to shore from deeper waters. In this area throughout the year, most feeding was scattered, and occurred in St Helena Bay. The size of feeding groups of gannets was small.

Sightings of colour-marked gannets from the two colonies in both breeding and nonbreeding season were separated (Fig. 28). A zone of overlap between 210° and 245° from Cape Columbine was observed further than 70 km from the shore, but the two populations were clearly separated by a line running 210° from Cape Columbine within 70 km of the shore (Fig. 28). Of 47 gannets from Lambert's Bay, only four were seen south of the zone of overlap. Of 212 gannets from Malgas Island, only one was seen north of the zone of overlap. In addition, a further three birds from Lambert's Bay were seen at Malgas Island itself in 1985 and two Malgas Island birds were seen at Lambert's Bay. On 24 November 1985, a single bird from Malgas Island was seen at Ichaboe Island (26° 17'S 14° 56'E) which lies 722 km to the north. In 1986, one bird from Lambert's Bay was seen at the Malgas Island colony. Comparatively fewer birds were seen in 1985 because the Rhodamine B dye used on birds from Malgas Island faded within 1-2 weeks, observer effort was smaller and birds were more scattered.

Most of the oil slick in August 1983 lay south of the zone of overlap and covered waters beyond the 200-m depth contour, including part of the demersal trawling grounds (Fig. 29). The slick subsequently moved westwards over the next few days. The numbers of pairs of breeding gannets based on aerial photography in November 1982 at Malgas Island and Lambert's Bay was estimated as 19 500 and 4 300 (SFRI unpubl.; Table 2). The number of oiled gannets at Malgas Island was significantly higher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LAMBERT'S BAY
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MALGAS ISLAND
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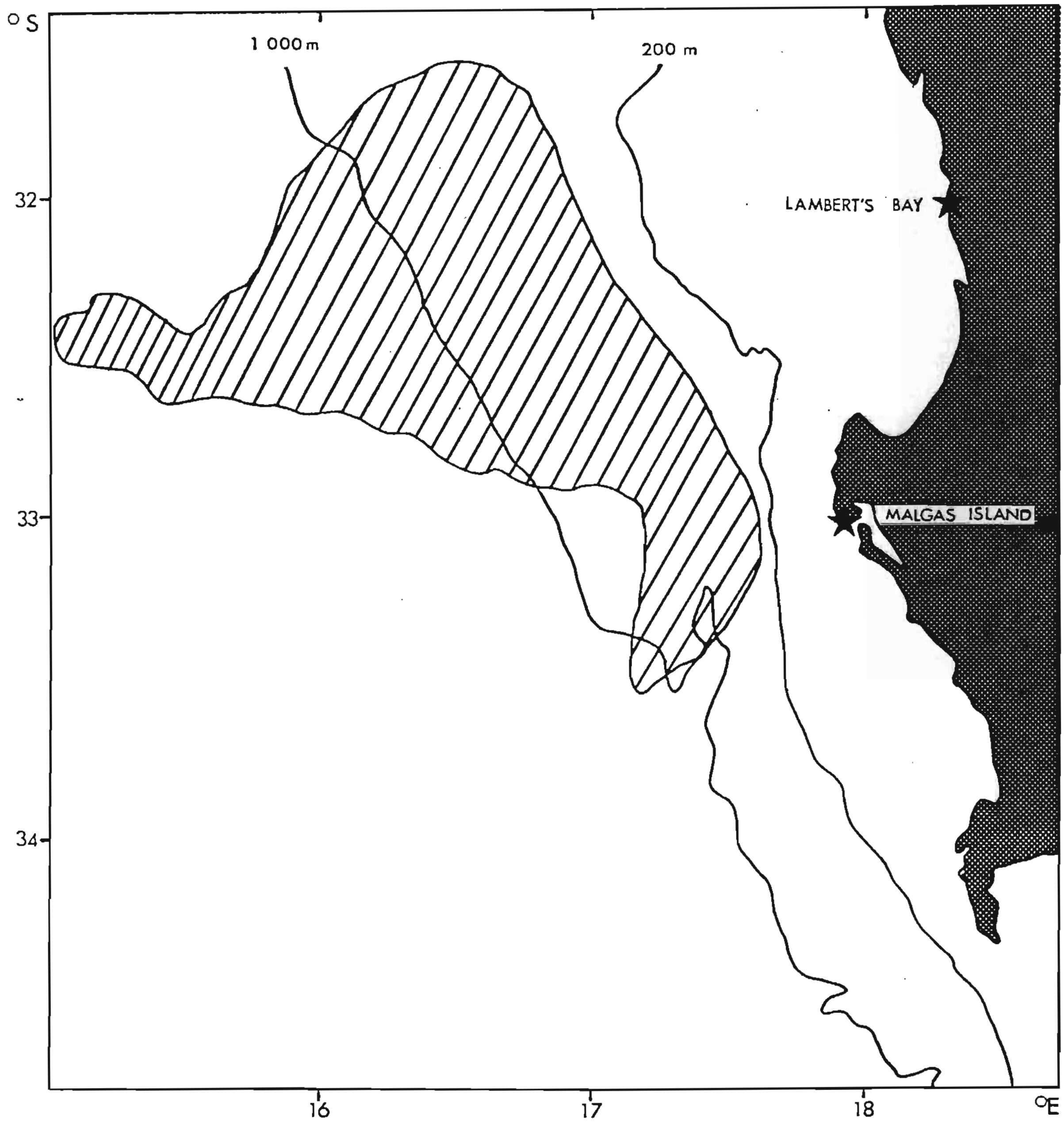


FIGURE 29

Location of the oilspill (diagonal lines) from the <u>Castillo del Bellver</u>, 15 August 1983.

(P <0,001; *chi*-square =13,54; df=1) than expected if the area of the oil slick was exploited by each colony in proportion to numbers. The diet of oiled birds contained significantly more hake (P <0,05; *chi*-square=8,52; df=3) and less epipelagic fish than unoiled gannets, showing that oiled gannets were eating trawler offal (Table 31).

The foraging zone of the Cape Gannet is divided into three areas: Area 1 (north of Cape Columbine), Area 2 (Cape Columbine to Cape Point) and Area 3 (east of Cape Point). Size of feeding groups of gannets increased from north to south (Table 32). The frequency of feeding associations between gannets and marine predators, the Common Dolphin Delphinus delphis, Dusky Dolphin Lagenorhyncus obscurus, Brydes Whale Balaenoptera edeni and Yellowfin Tuna also increased from north to southeast (Table 33). Large mixed associations of seabirds, cetaceans and seals, which were feeding on South African Pilchard, were seen close to a strong thermal front running offshore between Cape Agulhas and Cape Hangklip in February 1984. A possible association between Snoek and gannets occurred south of Lambert's Bay on 30 June 1986. Snoek were caught close to areas where gannets were feeding and sitting on the water.

The mean duration of 59 incubation shifts at Lambert's Bay was 41,9 h (S.D. ± 14,0 h; range 20-68 h). The mean duration of 19 incubation shifts at Malgas Island was 52,5 h (S.D. ± 14,2 h; range 32-96 h). The difference between the means is significantly

TABLE 31.

THE FREQUENCY OF OCCURRENCE OF PREY SPECIES IN THE DIET OF 21 OILED AND 18 UNOILED CAPE GANNETS AT MALGAS ISLAND IN AUGUST 1983

	Oiled		Unoiled	
	Observed	Expected	Observed	Expected
Hake	13	10,0	4	7,0
Pelagic fish	4	8,8	11	6,2
Cape Anchovy	2		8	
S. African Pilchard	0		1	
Redeye Roundherring	2		0	
Lightfish	0		2	
Squid	4	4,1	3	2,9

TABLE 32

SIZE OF FEEDING GROUPS OF CAPE GANNETS (% OF OBSERVATIONS IN EACH ABUNDANCE CLASS) IN AREAS 1 (NORTH OF CAPE COLUMBINE), 2 (BETWEEN CAPE COLUMBINE AND CAPE PENINSULA) AND 3 (EAST OF CAPE POINT)

	Group size of gannets				
Area	1-10	11-100	101-1000	>1000	n
1	78,1	19,5	2,4	0	41
2	59,6	29,0	11,3	0	62
3	56,7	13,3	23,3	6,7	30

TABLE 33

PERCENTAGE OF NUMBER OF OBSERVATIONS OF CAPE GANNETS IN VARIOUS GROUP SIZES IN FEEDING ASSOCIATIONS IN AREAS 1-3 (SEE TABLE 32)

	Abundance category					
Area	1-10	11-100	101-1000	>1000	n	% of feeding obs.
1	54,6	36,4	9,1	0	11	26,8
2	10,5	63,2	26,3	0	19	30,7
3	5,2	47,4	36,8	10,5	19	63,3

different (P <0,01; t=2,866; df=76).

Gannets feeding within 20 km of the shore ate smaller fishes than gannets feeding further offshore (Fig. 30). Sample sizes were only large enough in area 2 to allow the differences in length-frequency distributions of prey caught by gannets inshore and offshore to be tested for statistical significance. The prey caught inshore were significantly smaller (Kolmogorov-Smirnov test; P <0.01) than prey caught offshore. Size of prey increased southwards (Fig. 30). The proportion of South African Pilchard increased towards the north, while Saury occurred almost exclusively offshore in the central region off the Cape Peninsula (Table 34). The proportion of Cape Anchovy was greatest in the south. Adult South African Pilchard and Cape Anchovy were caught offshore only west of Cape Point or more rarely in deeper waters further north.

DISCUSSION

Aerial and ship surveys of gannet distribution at sea are not directly comparable, as gannets were counted in different ways, and were analyzed over differing distance and time scales (Briggs et al. 1985a, b). Only with caution may these surveys be used to estimate absolute densities of gannets at sea, because of problems of differential visibility, speed of movement and ship attraction

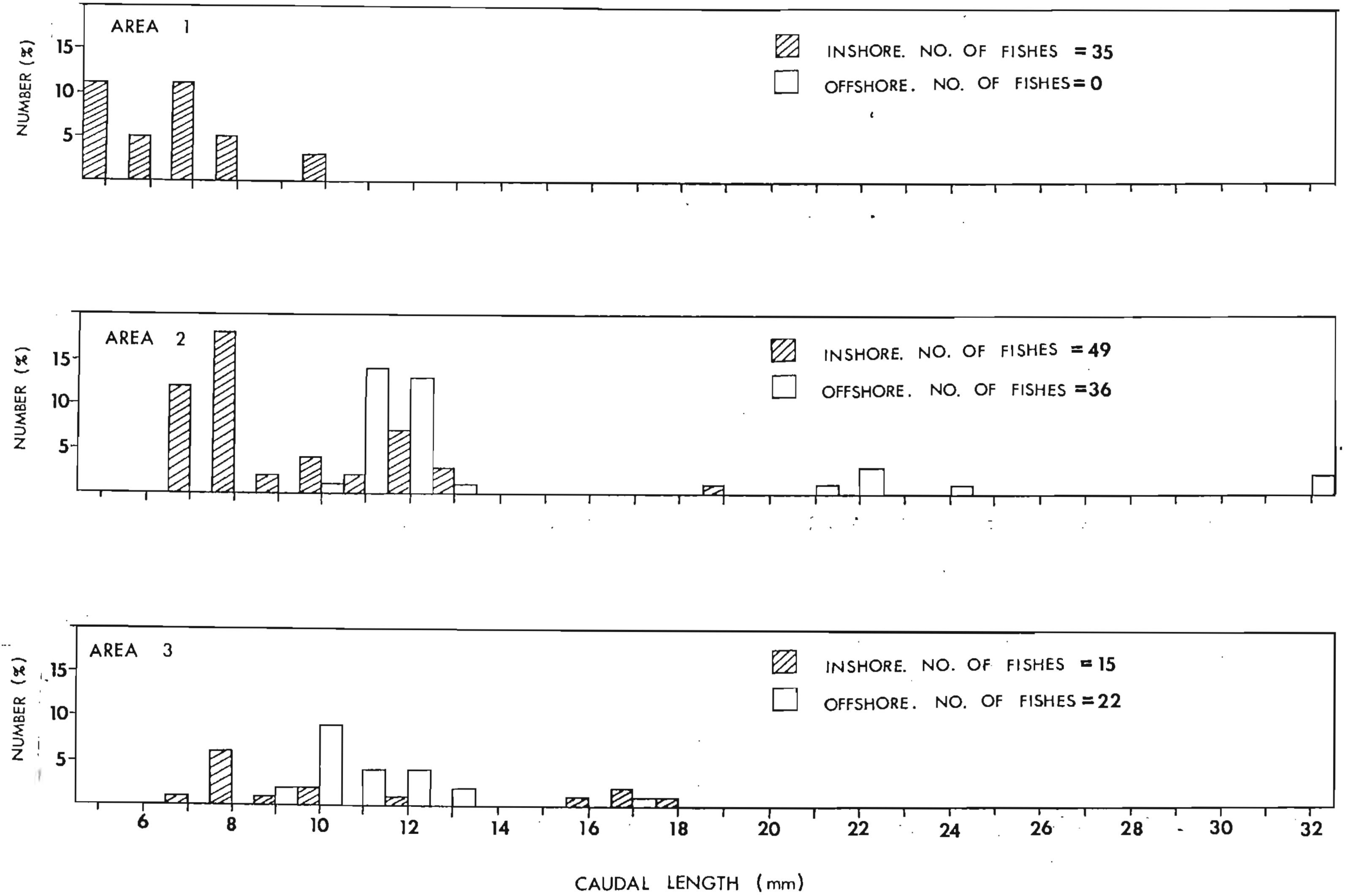


FIGURE 30

Caudal length frequencies of fresh fish prey of Cape Gannets shot within and beyond 20km of the shore in three sectors: north of Cape Columbine (Area 1), Cape Columbine to Cape Point (Area 2) and east of Cape Point (Area 3).

TABLE 34

PERCENTAGE OCCURRENCE OF FRESH PREY REMAINS IN CAPE GANNETS SHOT AT SEA WITHIN AND BEYOND 20 KM OF THE SHORE IN AREAS 1-3 (SEE TABLE 32), AND IN EACH AREA SEPARATELY

	Area				
	1-3		1	2	3
	<20km	>20km			
Cape Anchovy	65,6	60,0	66,7	52,4	84,6
South African Pilchard	24,1	20,0	26,7	19,2	15,4
Saury	3,5	15,0	0	19,1	0
Squid	3,5	0	0	4,8	0
Hake	0	5,0	6,7	0	0
Red Mullet	3,5	0	0	4,8	0
n	29	20	15	21	13

(Briggs *et al*. 1985a, b). Nevertheless, the distributional surveys are valid for assessment of the relative density of gannets at sea within their foraging range.

Spatial separation in the foraging areas of gannets from the two colonies was suggested by consistent intra- and interannual differences in their diet (Chapter 5). Gannets from Lambert's Bay and Malgas Island feed north and south respectively of a line running 210° from Cape Columbine and within 70 km of the shore. Further offshore, there is a zone of overlap between 210° and 245° from Cape Columbine. The separation of foraging zones of the two populations was demonstrated by the sightings of dyed birds, the occurrence of oiled birds in the colonies and the small scale of movement around Cape Columbine.

Further evidence of spatial separation is provided by the analysis of diet of oiled gannets and gannets shot at sea and the distributional ecology of their prey. Oiled gannets ate more hake and less epipelagic fish than unoiled gannets. This was expected because the oil slick covered part of the trawling grounds. Hake is far more important in the diet of gannets at Malgas Island than at Lambert's Bay (Chapter 5). This suggests that the area covered by the oil slick, which lies mainly south of the zone of overlap, is consistently exploited by gannets from Malgas Island but not by birds from Lambert's Bay. Greatest concentrations of gannets at trawlers were found between Saldanha

Bay and the Cape Peninsula in winter, when hake offal dominates gannet diet at Malgas Island. All Saury and most adult South African Pilchard and adult Cape Anchovy occurred in birds shot south of Cape Columbine and are characteristic of gannet diet at Malgas Island (Chapter 5). Saury occur in warmer waters and near frontal zones which lie far closer to Malgas Island than Lambert's Bay (Chapter 10). Adult South African Pilchard occur mainly east of Cape Point (Crawford 1980a) but may be associated with the edge of the continental shelf off the west coast (Armstrong et al. in press). Juveniles of Cape Anchovy and South African Pilchard dominated the diet of gannets shot north of Cape Columbine, and are characteristic of diet at Lambert's Bay (Chapter 5). Juvenile Cape Anchovy and South African Pilchard recruit north of Cape Columbine where they occur inshore, then migrate south around Cape Point (Crawford 1980a).

At Lambert's Bay, the longshore foraging range was about 100 km in summer, shrinking to 75 km in winter. The northern limit of foraging is not known, and may well include the northern part of the upwelling plume off Hondeklip Bay north of Lambert's Bay. The offshore boundary of gannet foraging in this area is the inshore edge of the trawling grounds, because hake offal comprised only 5% by mass of gannet diet at Lambert's Bay. This is a distance of about 75 km. The oiled gannets in August 1983 ranged at least 100 km from Lambert's Bay, but comprised a relatively small percentage of the population. In April and May 1986, several hundred gannets were seen eating Cape Fathead _Cubiceps capensis_, a small pelagic fish, at dawn and dusk 150 km west of Lambert's Bay (M. Johnson pers. comm.). This species has never been recorded in 3 647 regurgitations at Lambert's Bay between December 1977 and August 1986. At Malgas Island, the longshore foraging range was about 200 km in summer. The southeastern limit of foraging is unknown, but may lie as far east as Danger Point. The foraging range reduces to 150 km in winter with most birds probably feeding within 120 km of the colony and remaining north of Cape Point. In July 1986, a gannet shot off Hout Bay, 142 km south of Malgas Island, contained a Southern Rover (Red or Deep-sea Harder) _Emelichthys nitidus_. This species has never been identified in 4 513 regurgitations from Malgas Island. The offshore boundary is the outer edge of the demersal trawling grounds within the 1 000-m depth contour, a distance of 90 km offshore.

Rand (1959) suggested that the longshore foraging range was 270 km to 360 km during the breeding season, based on sightings and the recovery of ringed adults during the breeding season. However, Rand (1959) could not determine to which colony the birds belonged or whether ringed adult birds were actually breeding. Jarvis (1971a) showed on the basis of parental nest attendance and estimated flight speed that the potential foraging range was 470 km. Nelson (1978b) estimated the foraging range of the North Atlantic Gannet as 320-480km, based on parental nest attendance and estimated flight speed; although previously

(Nelson 1966b) he suggested a foraging range of 160 km. On a similar basis, Montevecchi & Porter (1980) suggested a foraging range of 120 km for the North Atlantic Gannets breeding in Newfoundland. Moisan & Scherrer (1973) found that 14 of 15 ringed adult North Atlantic Gannets were recovered within 160 km of the colony at Bonaventure Island, Canada, during the breeding season. Tasker _et al_. (1985), based on ship surveys, suggested a maximum foraging range of 150 km for the North Atlantic Gannet in the North Sea, with most birds feeding within 50 km of the colony. Kirkham _et al_. (1985) used aerial surveys to show that North Atlantic Gannets from Funk Island, Newfoundland, usually fed within 60 km of the colony. All the estimates are for the breeding season, as the North Atlantic Gannet deserts colonies in winter and migrates south.

The diet of Cape Gannet caught at the breeding colonies represents the diet of birds returning to the colony only and not that of the population as a whole. That the diets of birds at the colony and further away may differ is shown by observations at sea of gannets eating two species (Cape Fathead and Southern Rover) which have not been recorded at the islands. Nonbreeding gannets may wander widely, particularly in winter (Rand 1959a; Broekhuysen _et al_. 1961; Crawford _et al_. 1983a).

Gannets catch prey more frequently in association with other animals to the south and east, principally in association with the Common Dolphin and Brydes Whales, and to a lesser extent with Yellowfin Tuna. Common Dolphins do not usually occur in the foraging area of gannets from Lambert's Bay (Best *et al*. in press). The importance of fish predators in making prey available to gannets may be underestimated; Snoek on the west coast and Yellowfin Tuna west of the Cape Peninsula may be important to gannets. These feeding associations have been recorded further east, and gannets frequently occur in feeding associations with cetaceans in Algoa Bay (Randall 1983; Batchelor & Ross 1984). Smale (1983) described how gannets fed on a shoal of South African Pilchard trapped in a tight ball at the surface, while Skipjack *Katsuwonus pelamis*, Jackass Penguins and sharks *Carcharinus brachyurus* attacked the school from below. Randall (1983) noted that gannets were involved in feeding associations with other seabirds in Algoa Bay when larger fish such as South African Pilchard were involved, as were predatory fishes such as sharks. Gannets were absent from feeding groups involving terns and penguins attacking small fishes. The North Atlantic Gannet frequently associates with cetaceans during feeding (Evans 1982). Au & Pitman (1986) regarded the Yellowfin Tuna and dolphins as being important in providing food for surface-feeding seabirds in the eastern tropical Pacific Ocean by chasing prey to the surface.

There are apparently three foraging strategies available to gannets. In cool waters of less than 16°C, inshore of 200-m depth contour, gannets feed singly or in scattered groups, seldom in association with other predators except perhaps for Snoek. Their prey is epipelagic fish: juvenile Cape Anchovy, South African Pilchard and Redeye Roundherring less than 100-mm Lc. This strategy is followed by gannets feeding north of Cape Columbine and their diet seldom contains trawler offal or large epipelagic fishes. Juvenile fishes are generally distributed throughout this area. Strong oceanic fronts where warm water (>20^{o} C) meet colder inshore waters do not occur frequently within the foraging range of gannets in this area. Gannets feeding in deeper and warmer waters have two options. They may obtain offal, primarily hake, from trawlers. This food is reliable but energy-poor. Gannets may also catch larger epipelagic fishes such as adult Cape Anchovy and South African Pilchard and Saury, which are more characteristic of the frontal zone (Armstrong et al. in press). Gannets feeding in deeper and warmer waters are frequently associated with cetacean predators and tuna, particularly in the south. Gannets from Malgas Island use all three strategies, and individuals may switch when conditions are favourable as both hake and epipelagic fish occasionally occur in the same regurgitation. In summer, most gannets catch large pelagic fishes associated with the occurrence of marked offshore fronts and the presence of tunas. These large energy-rich prey are taken when food demands are greatest. Offal is available all year round, but forms a major part of the diet only of birds returning to the island in winter.

The central-place foraging theory predicts that large energy-rich prey is selected on long foraging trips, and that multiple loads of small items are selected during short foraging trips (Orians & Pearson 1979). The shorter foraging range at Lambert's Bay is associated with smaller regurgitations comprised of many small fish, whereas the longer foraging range at Malgas Island is associated with larger regurgitations comprised of fewer but larger fish (Chapter 5).

In the early 1950s, Rand (1959) found that most gannets were distributed within 32 km of the shore, and that the diet of gannets in this region consisted mainly of South African Pilchard (51% by mass), Cape Anchovy (12% by mass) and Maasbanker (20% by mass). Prey were larger than those recorded in the present study. Historically, the foraging strategy of gannets was the capture of large energy-rich prey, apparently close to shore (Rand 1959). In recent times, adult South African Pilchard and adult Maasbanker have greatly diminished in importance to gannets, whereas Cape Anchovy, hake and Saury have all increased in importance (Chapter 5). Gannets now occur up to 80 km offshore in large numbers, catching Saury and taking hake from the trawlers. Clearly, the drastic reduction in South African Pilchard in the late 1960s and Maasbanker in the late 1950s off the western Cape removed the predictable occurrence of large energy-rich prey close to the shore. Trawler offal became increasingly available at this time, hake catches increasing from 64 000-76 000 tonnes in

1951-53, to 96 000-119 000 tonnes in 1966-70, to a peak of 151 000 tonnes in 1979 (Chalmers 1976; Botha 1980). Catches of hake have stabilised at 125 000-143 000 tonnes in recent years (Table 26). With a decrease in the size of prey available inshore and hence a decrease in the energetic profitability of inshore foraging, the option of foraging offshore for hake and large epipelagic fishes became viable. Gannets avoid energy-poor trawler offal in summer. It is suggested that the oceanic thermal fronts, which occur close to shore in summer, serve to concentrate prey and bring larger prey such as Saury close inshore. Although breeding birds show a slight degree of selection for larger prey, this is insufficient to explain the large change from a diet dominated by hake in winter to one dominated by epipelagic fishes in summer.

The collection of gannets within 20 km of the shore in the 1950s (Davies 1955, 1956, 1958; Rand 1959) may have masked the fact that Saury were regularly caught by gannets at that time. Saury comprised 3,5% (by mass) of fresh prey of gannets shot within 20 km of the shore in this study, but 15,0% of prey of gannets shot further offshore. Similarly, hake may have already been important in gannet diet in the 1950s. Because trawler offal was available 50 km or more offshore, the inshore collection of feeding or roosting gannets would tend to underestimate its importance in their diet. Nevertheless, gannets would feed on inshore shoals of large energy-rich fishes before foraging offshore and the drastic reduction in pilchard stocks in the mid-1960s suggests strongly that a real shift in the prey eaten by gannets has occurred.

CHAPTER 8

PREY SELECTION OF THE CAPE GANNET

INTRODUCTION

It is necessary to assess whether gannets preferentially select prey before diet parameters can be used to indicate changes in prey abundance. Otherwise the appearance of a different species or a new cohort of the same species in gannet diet may result purely from a decline in the preferred prey. Gannets may then prey on less favoured prey which had always been present. Many authors e.g. Ainley (1980) and Harrison *et al*. (1983) have concluded that seabirds feed opportunistically on any available prey of the appropriate size given certain constraints of seabird morphology, fishing techniques, prey size and behaviour. This statement embodies a considerable degree of selection based on the size and behaviour of the prey which places it within reach of the seabird and also does not preclude choice of feeding area by the seabird. Cape Gannets eat epipelagic shoaling fish, mainly measuring 50-240 mm (Lc), or offal from demersal trawlers taken during the day in the uppermost six metres of the continental shelf marine waters during the day (Chapter 5). Whether gannets show preferential selection between species of epipelagic fish and hake requires investigation.

Prey selection by gannets may be based on relative abundance of prey (Holling 1059; Pearson 1968), prey size (Swennen & Duiven 1977), energy content (Harris & Hislop 1978; Furness & Hislop 1981), shoaling characteristics (Batchelor & Ross 1984) or on a combination of these factors so as to maximise energy intake (Hislop & Harris 1978; Furness & Harris 1981). Direct comparisons of the abundance of various size classes of all the dominant epipelagic fish potentially available to gannets in the southern Benguela System cannot be made. Hydroacoustics and directed trawling on acoustic targets offers the only system which can make quantitative assessments of the abundance of epipelagic fish in the foraging area of gannets. However, estimates were available only for Cape Anchovy until mid-1986. Furthermore, Saury, which is an active surface-dwelling fish important in gannet diet, is seldom caught by commercial fishing and biomass estimates of this species are unavailable (Chapter 10). The mass of hake and offal available can be estimated directly from demersal catches.

The abundance of juvenile epipelagic fish prey in the diet of Cape Gannets in the western Cape was broadly related to their abundance as measured by fishery catches in the first half of the year, but hake and other species scavenged offshore from demersal trawlers were apparently a secondary source of low-energy food used only when epipelagic fish were scarce (Chapter 5). Of the epipelagic fish species, adult South African Pilchard was considered to be the preferred prey by Batchelor & Ross (1984) and Davies (1956). Selection on the basis of the species taxon can be investigated further by comparing the rank of importance of particular prey species in gannet diet and purse-seine fishery catches (Duffy & Jackson 1986). It is possible to test the relationship between the proportion of hake in gannet diet and the absolute abundance of hake. Whether gannets preferentially select larger fishes than those of the same species caught by purse-seiners or the research vessel R.V. Africana may be tested by comparing catches made in the same area at the same time.

METHODS

The abundance of fish species in purse-seine fishery catches and gannet diet were compared with a ranking system (Waldron & King 1963; Iverson & Pinkas 1971; Harrison et al. 1983). This ranking of prey importance is a simple measure but as the sampling of epipelagic fishes by gannets and purse-seiners is not directly comparable, more sophisticated techniques are not appropriate and might impart an air of spurious accuracy (Duffy & Jackson 1986).

The caudal lengths of fish of the same species caught by gannets and purse-seine or research fishing in the same area at the same time were compared. The caudal length frequencies of Cape Anchovy, South African Pilchard and Maasbanker caught by gannets, purse-seiners or the R.V Africana were compared for selected months. The sampling of gannet diet is described in Chapter 5. Data on the diet of gannets from Lambert's Bay and Malgas Island were used for months during which gannets were sampled on at least four days, producing at least 40 regurgitations and a length-frequency distribution of at least 30 measurements for a given species (Table 35). The monitoring of the purse-seine fishery catches is described in Chapter 5. Length-frequency distributions of each species obtained in samples of purse-seine catches were weighted by the total catch to obtain estimates of the total numbers of fishes in each 10-mm Lc size class caught by the purse-seine fishery during the month. Purse-seine fishery data were used for areas north (pool areas 1-7) and south (pool areas 8-12) of Cape Columbine to Cape Point (Fig. 31) for months during which all fleets with quotas were still fishing (Table 35). In practice, very few purse-seine catches are made east of Danger Point. Length frequency data from surveys of the R.V. Africana were provided by Dr M.J. Armstrong (SFRI). The sample areas were north of Cape Columbine and between Cape Columbine and Danger Point (Fig. 31). This included the area between Cape Point and Danger Point which was not included in purse-seine fishery catches. The larger area was used to increase the number of net hauls by the R.V. Africana in the sample area. Fishes between the sea bottom and six metres of the surface were detected acoustically with a calibrated Simrad EKS 38 kHz scientific echo-sounder. Major acoustic targets were sampled with a commercial-sized midwater trawl (Engels 308) to establish species

TABLE 35.

MONTHS IN WHICH THE LENGTH AND ABUNDANCE OF FISH IN CAPE GANNET DIET SAMPLES (NUMBER OF SAMPLES, NUMBER OF DAYS SAMPLED), PELAGIC FISHERY CATCHES AND SURVEYS OF THE R.V. <u>AFRICANA</u> WERE COMPARED

Locality	Date	Gannet sampling		Pelagic fishery sample	R.V. Africana sample
		No. days	No. samples		
Lambert's Bay	Nov. 1983	14	130	Yes	Yes
	Oct. 1984	8	92	Yes	No
	Nov. 1984	8	75	Yes	Insufficient
	May 1985	4	40	Yes	Yes
	Jun. 1985	4	45	Yes	No
	Nov. 1985	8	75	No	No
	Jan. 1986	6	106	Yes	No
	Feb. 1986	5	53	Yes	No
	Apr. 1986	4	46	Yes	No
	May 1986	5	51	Yes	Yes
Malgas Island	Jan. 1981	30	301	Yes	No
	Feb. 1981	18	180	Yes	No
	Jan. 1982	25	251	Yes	No
	Jan. 1983	8	79	Yes	No
	Nov. 1983	11	125	Yes	Yes
	Jan. 1984	8	80	Yes	No
	Nov. 1985	8	95	No	Yes
	Jun. 1986	5	75	Yes	Yes
	Jul. 1986	6	90	Yes	No

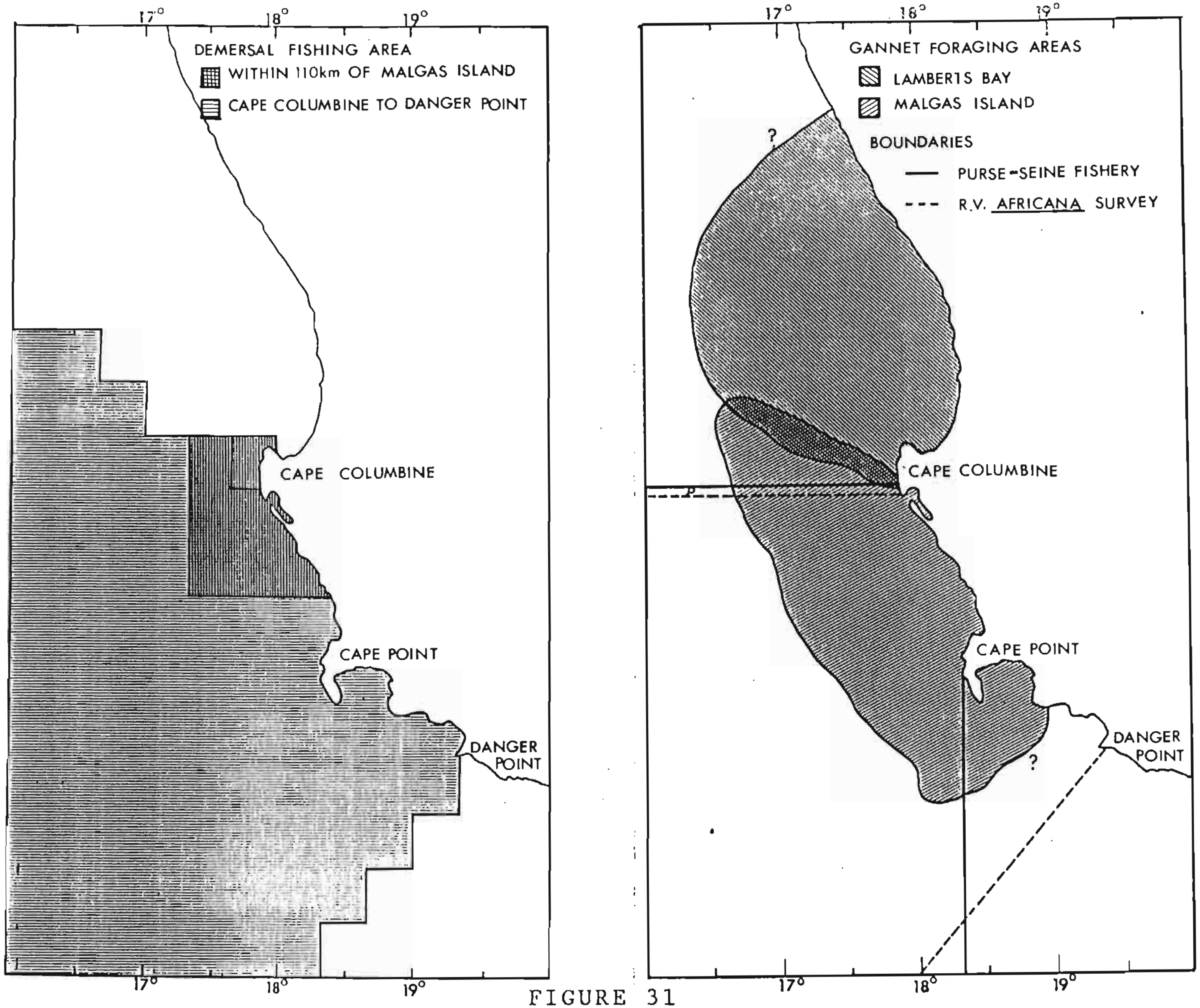


FIGURE 31

Designated areas for comparison of catches of Cape Gannets, demersal fishery, purse-seine fishery and R.V. <u>Africana</u> off the western Cape.

and length composition. The length frequencies used comprised all fishes of one species in each 10-mm size class caught in the sample area and were not weighted according to the abundance of different size classes as determined by acoustics. The designated areas of the purse-seine fishery and research fishing areas correspond roughly to the foraging areas of the gannets from Lambert's Bay and Malgas Island (Fig. 31). Differences between these length-frequency distributions were tested for significance with the Kolmogorov-Smirnov test.

The contribution of hake to the diet of gannets was compared with its absolute abundance. Significant correlations are expected if hake is a preferred species. The mass of hake offal discarded is proportional to catches (Chapter 5). Hake catches can be accurately determined in each 30' by 30' block. The mass of hake caught in each of three areas of increasing size (Fig. 31) and at monthly and annual time scales were linearly regressed against the percentage by mass of hake in gannet diet. The three spatial scales were: the entire hake catch in South African waters; the area between lines zigzagging in a northwesterly direction from Cape Columbine and in a southwesterly direction from Danger Point and all 30' by 30' blocks which lay mainly within 110 km of Malgas Island (Fig. 31). Hake is a rare dietary item in gannet diet at Lambert's Bay, so that data on gannet diet from this locality was not used.

RESULTS

Cape Anchovy was the important species in the diet of the gannets at the two colonies and in fishery catches north and south of Cape Columbine (Table 36). However, Redeye Roundherring was second in importance to the fishery, but was far less important to the gannets. Saury was far more important to the gannets. Onderbaadjie and Mackerel were relatively more important to the fishery while Maasbanker and South African Pilchard were more or less equally important to the purse-seine fishery and gannets.

Of the 21 tests for differences in Cape Anchovy length-frequency distributions between the diet of the Cape Gannet at both islands and the purse-seine fishery catches (Figs 32-33), 19 were significant (Kolmogorov-Smirnov test; P <0,05). Significant differences between gannet diet at Lambert's Bay and purse-seine catches north of Cape Columbine were found in March, May to July 1985 and January to July 1986 (Fig. 32); between gannet diet at Malgas Island and purse-seine catches south of Cape Columbine were found in January, March, May and July 1985 and January, March, April and July 1986 (Fig. 33). The differences were not significant in April 1985 at Lambert's Bay and July 1985 at Malgas Island. The anchovy eaten by gannets were smaller than those taken by the fishery in 15 (83%) of these 19 tests. However the modes were seldom more than 20 mm apart. All of the three tests of the differences in pilchard length-frequency distribution

TABLE 36.

RANKING OF IMPORTANCE OF FISH SPECIES TO THE PURSE-SEINE FISHERY NORTH AND SOUTH OF CAPE COLUMBINE AND TO CAPE GANNET AT LAMBERT'S BAY AND MALGAS ISLAND, 1977-1986. NOT ALL PREY SPECIES OF CAPE GANNETS ARE INCLUDED. SPECIES WERE RANKED SEPARATELY IN TERMS OF NUMERICAL ABUNDANCE, VOLUME OR MASS AND FREQUENCY OF OCCURRENCE. THESE THREE SUBRANKINGS WERE SUMMED AND RANKED FROM HIGHEST TO LOWEST TO ACHIEVE THE RANK GIVEN FOR EACH SPECIES

	North of Cape Columbine		South of Cape Columbine	
Species	Cape Gannet (Lambert's Bay)	Purse-seine catches	Cape Gannet (Malgas Island)	Purse-seine catches
Anchovy	1	1	1	1
South African Pilchard	2	3	4	3
Redeye Roundherring	4,5	2	5	2
Maasbanker	6	5	6	4
Onderbaadjie	14,5	4	9	6
Mackerel	9	6	14	5
Saury	3	7	3	7
Hake	7	-	2	-

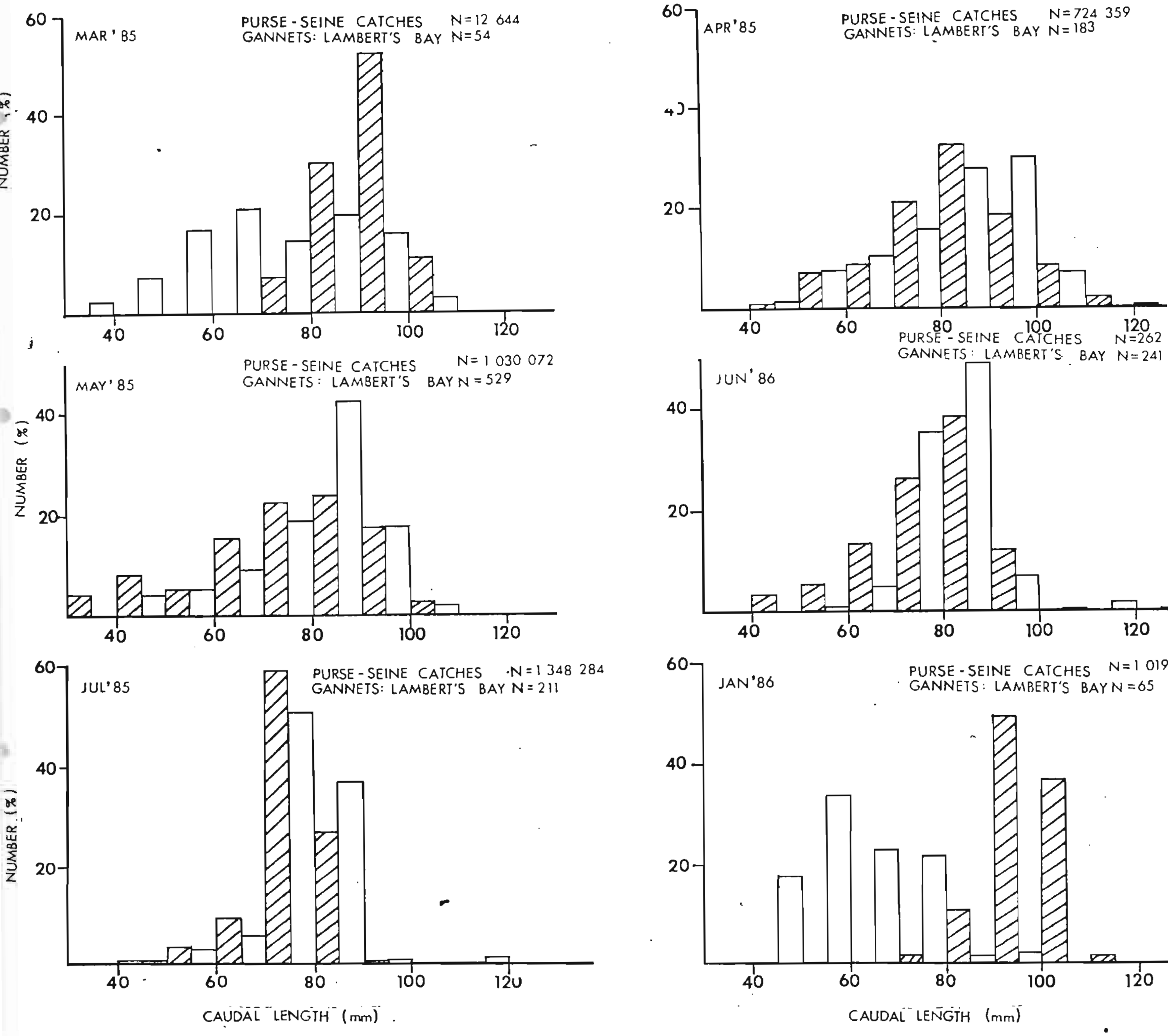


FIGURE 32

Monthly caudal length frequencies of Cape Anchovy caught by purse-seiners (open blocks; sample size given in thousands of fishes) north of Cape Columbine (pool areas 1-7) and by Cape Gannets (diagonal lines) from Lambert's Bay, March to July 1985

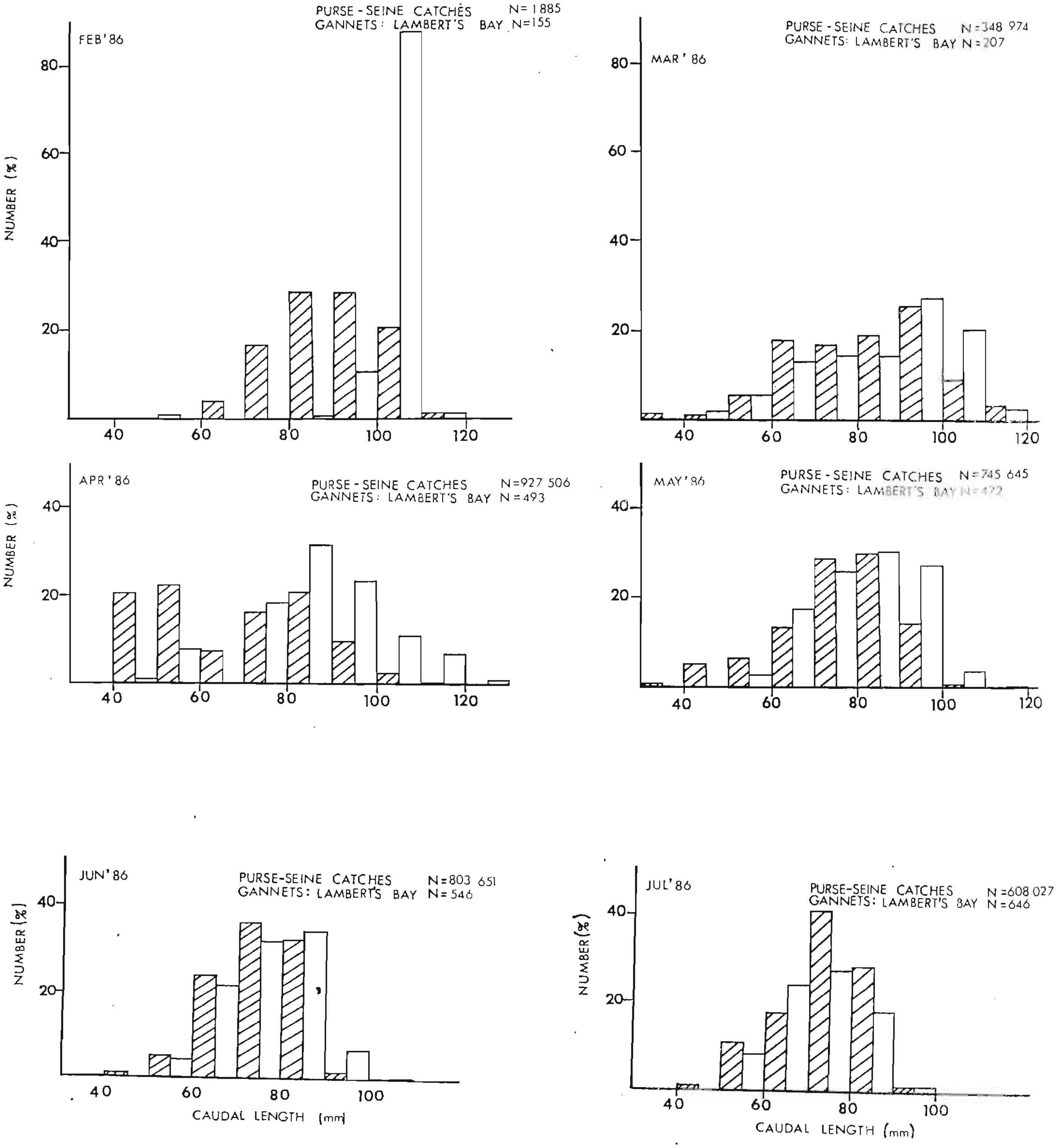
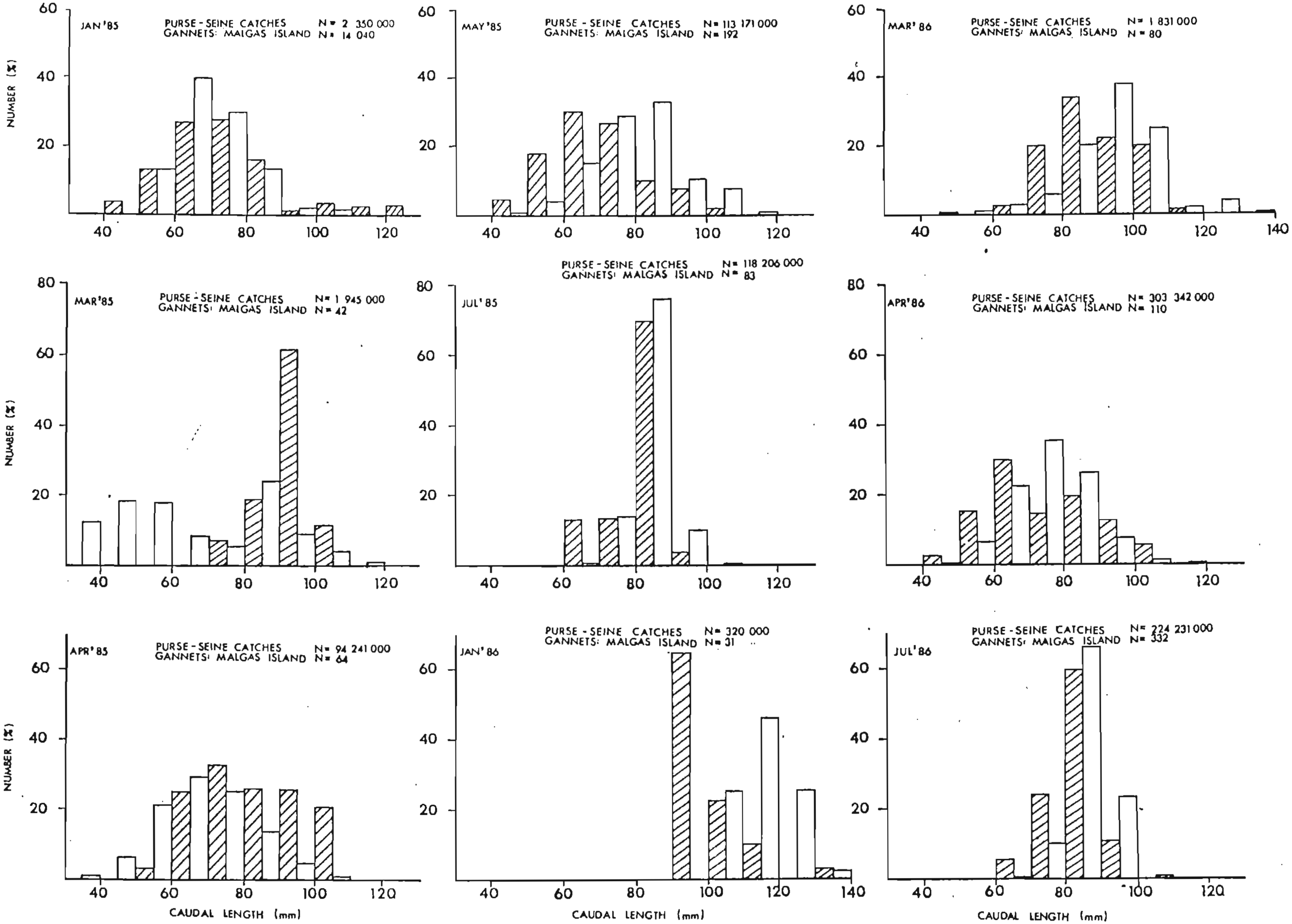


FIGURE 32 (CONTINUED)


JAN'85
PURSE-SEINE CATCHES N = 2 350 000
GANNETS: MALGAS ISLAND N = 14 040
MAY'85
PURSE-SEINE CATCHES N = 113 171 000
GANNETS: MALGAS ISLAND N = 192
MAR'86
PURSE-SEINE CATCHES N = 1 831 000
GANNETS: MALGAS ISLAND N = 80
MAR'85
PURSE-SEINE CATCHES N = 1 945 000
GANNETS: MALGAS ISLAND N = 42
JUL'85
PURSE-SEINE CATCHES N = 118 206 000
GANNETS: MALGAS ISLAND N = 83
APR'86
PURSE-SEINE CATCHES N = 303 342 000
GANNETS: MALGAS ISLAND N = 110
APR'85
PURSE-SEINE CATCHES N = 94 241 000
GANNETS: MALGAS ISLAND N = 64
JAN'86
PURSE-SEINE CATCHES N = 320 000
GANNETS: MALGAS ISLAND N = 31
JUL'86
PURSE-SEINE CATCHES N = 224 231 000
GANNETS: MALGAS ISLAND N = 332
NUMBER (%)
0
20
40
60
80
CAUDAL LENGTH (mm)
40
60
80
100
120
140

in gannet diet and the purse-seine fishery produced significantly different results (Kolmogorov-Smirnov test; P <0,05) between February and April 1986 (Fig. 34). Gannets did not catch large pilchard in these months. All of the five tests of Cape Anchovy length-frequency distribution between the diet of gannets (November 1983, May 1985 and May 1986 at Lambert's Bay and November 1983 and November 1985 at Malgas Island) and catches of the the R.V. Africana were significantly different (Kolmogorov-Smirnov test; P <0,05) (Figs 35-38). Gannets caught smaller prey in three of the five instances. The only comparison between the length-frequency distribution of Maasbanker (caught by gannets at Lambert's Bay in November 1983) and R.V. Africana was not significantly different (Fig. 35).

None of the three linear regressions between the monthly demersal hake catches and the percentage by mass of hake in gannet diet between January 1983 and October 1986 were significantly correlated: within 110 km of Malgas Island (y=0,0097x + 23,81; r=0,25; df=44; P >0,05) (Fig. 39), between Cape Columbine and Danger Point (y=0,0046x + 14,95; r=0,25; df=44; P >0,05)(Fig. 40) and in South African waters as a whole (y=0,0024x + 14,48; r=0,122; df=44; P >0,05) (Fig. 41). There were sufficient data to undertake only one test at the annual scale; between the annual percentage of hake by mass in gannet diet and the entire South African catch of hake for the same period between 1978 and 1985. This correlation was not significant (y=-0,00095x + 161,48;

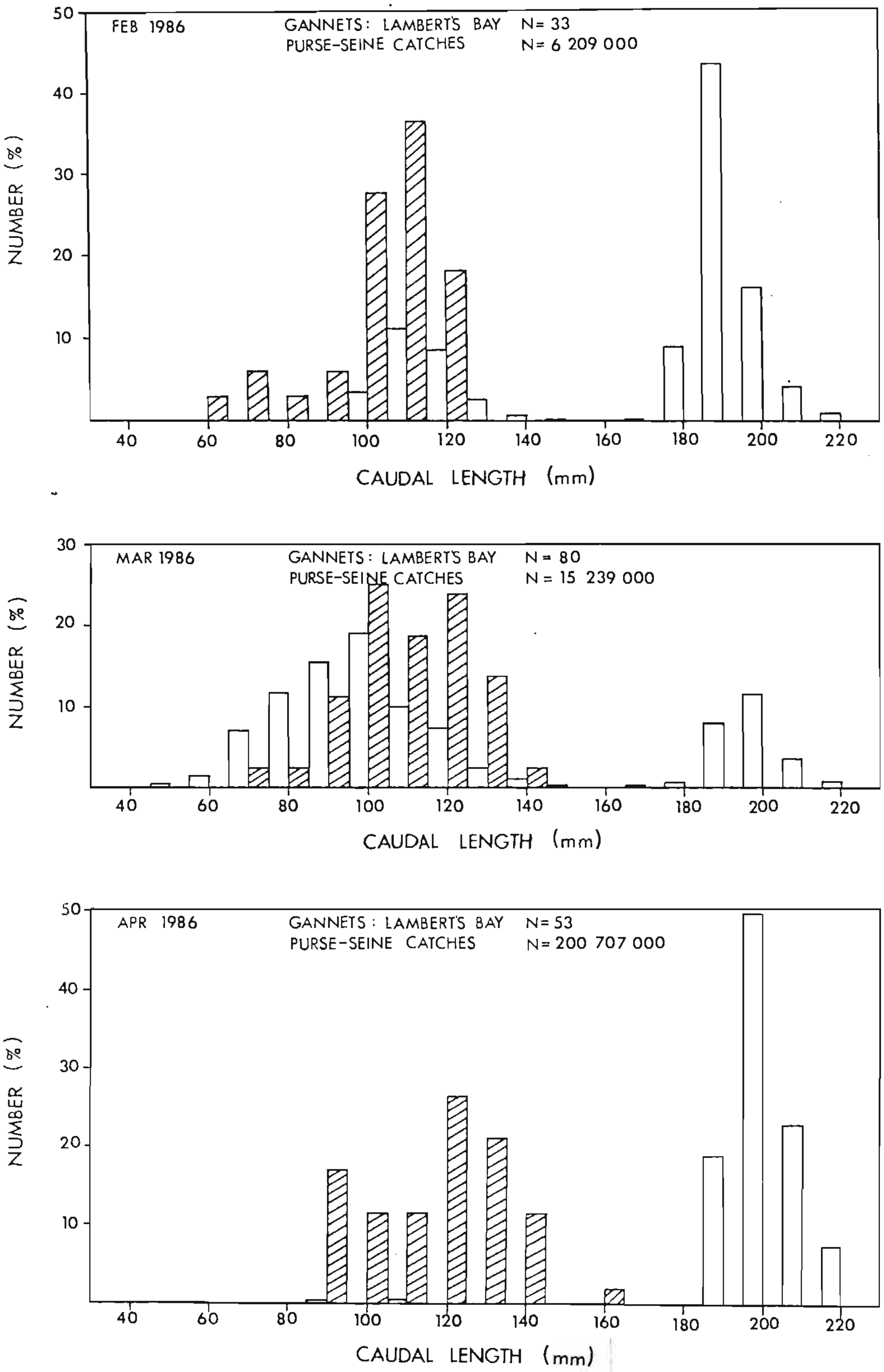


FIGURE 34

Monthly caudal length frequencies of South African Pilchard caught by purse-seiners (open blocks) north of Cape Columbine

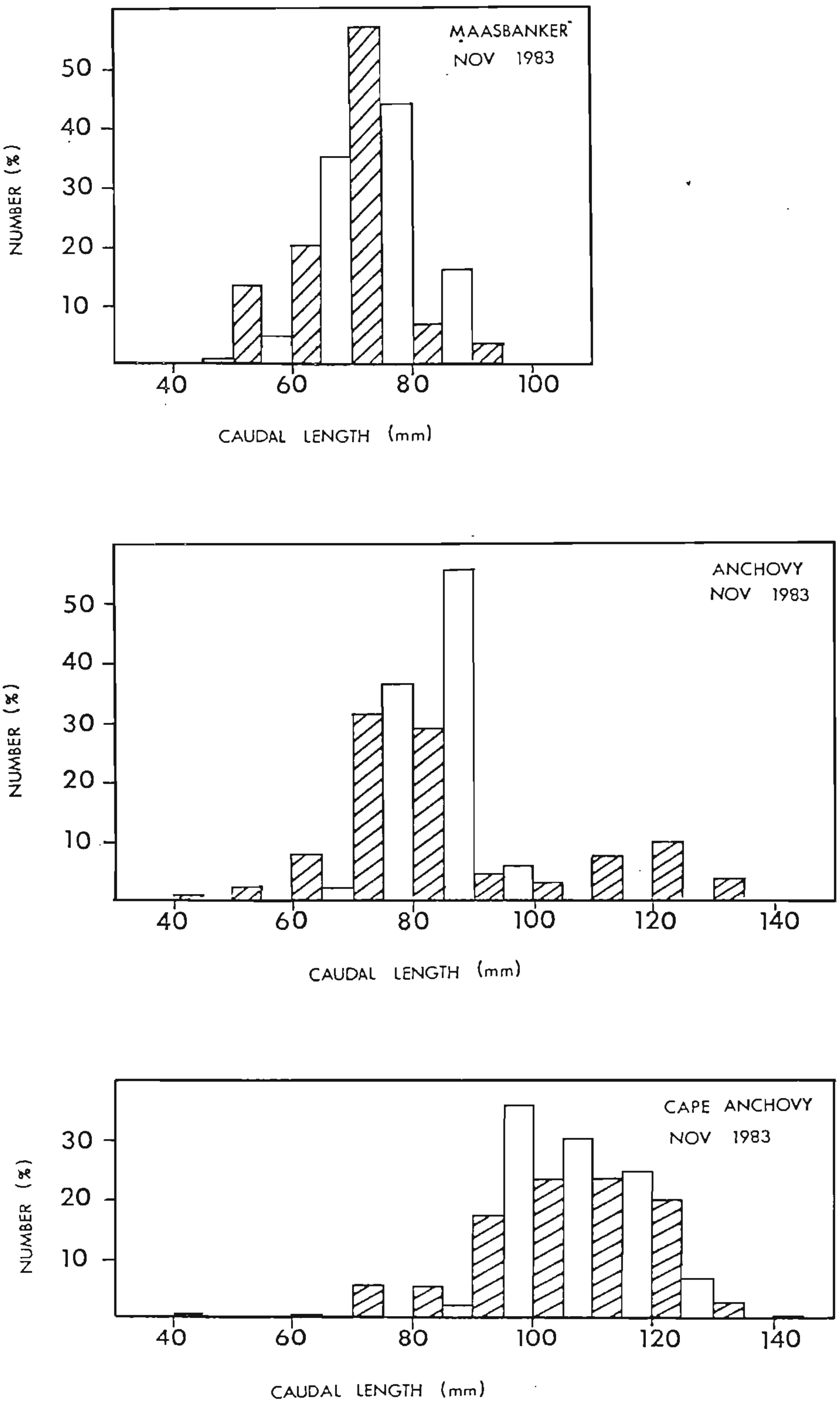


FIGURE 35

Caudal length frequencies of (a) Maasbanker (n=146 and 30 respectively) and (b) Cape Anchovy (n=5484 and 600 respectively) caught by the R.V. Africana (open blocks) north of Cape Columbine and by Cape Gannets from Lambert's Bay (diagonal lines) and (c) Cape Anchovy caught by the R. V. Africana (open blocks; n=737) south of Cape Columbine to Danger Point and by Cape Gannets (diagonal lines; n=496)

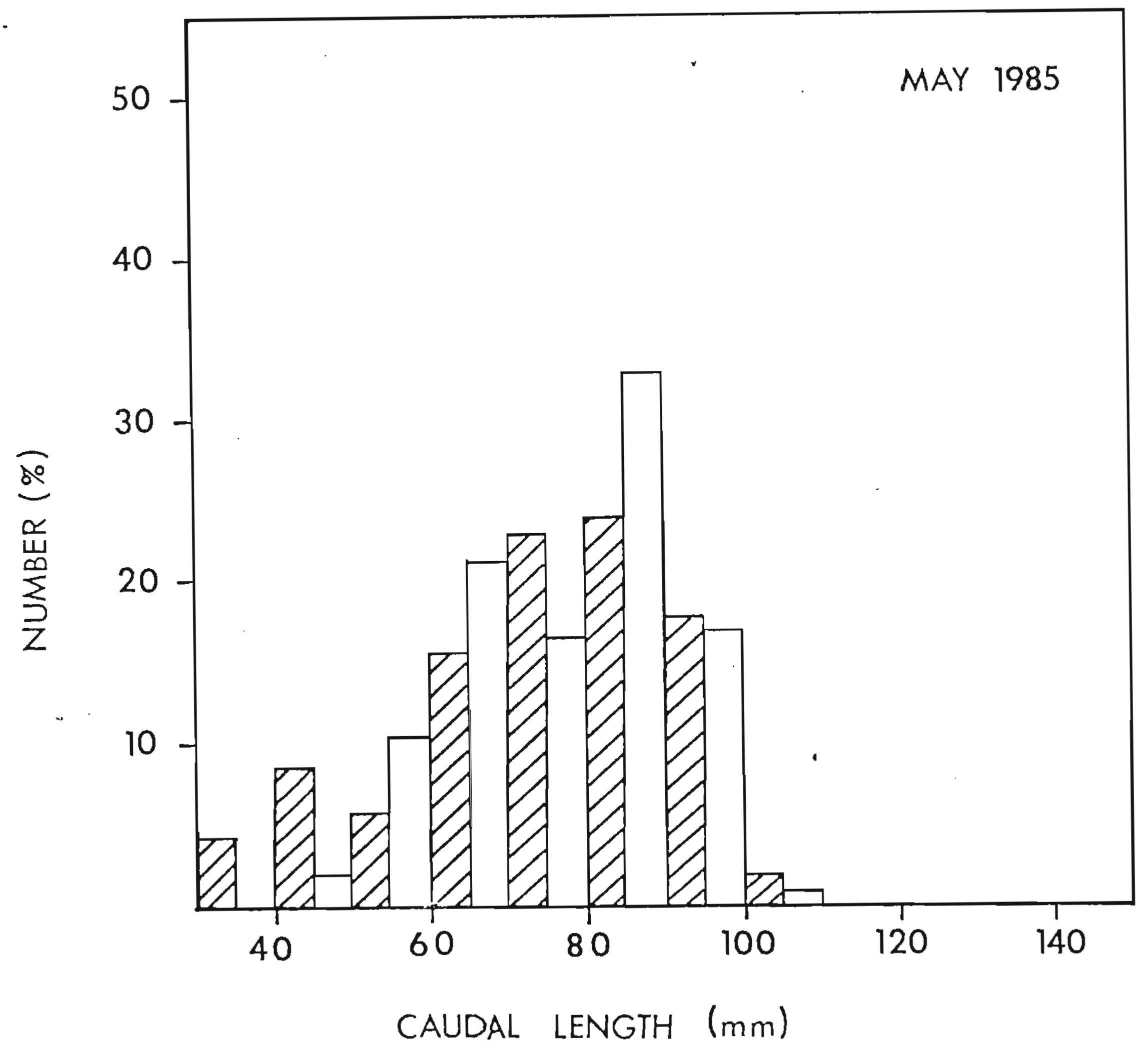


FIGURE 36

Caudal length frequencies of Cape Anchovy caught by the R.V. Africana (diagonal lines; n=1353) north of Cape Columbine and by Cape Gannets (open blocks; n=529) from Lambert's Bay, May 1985.

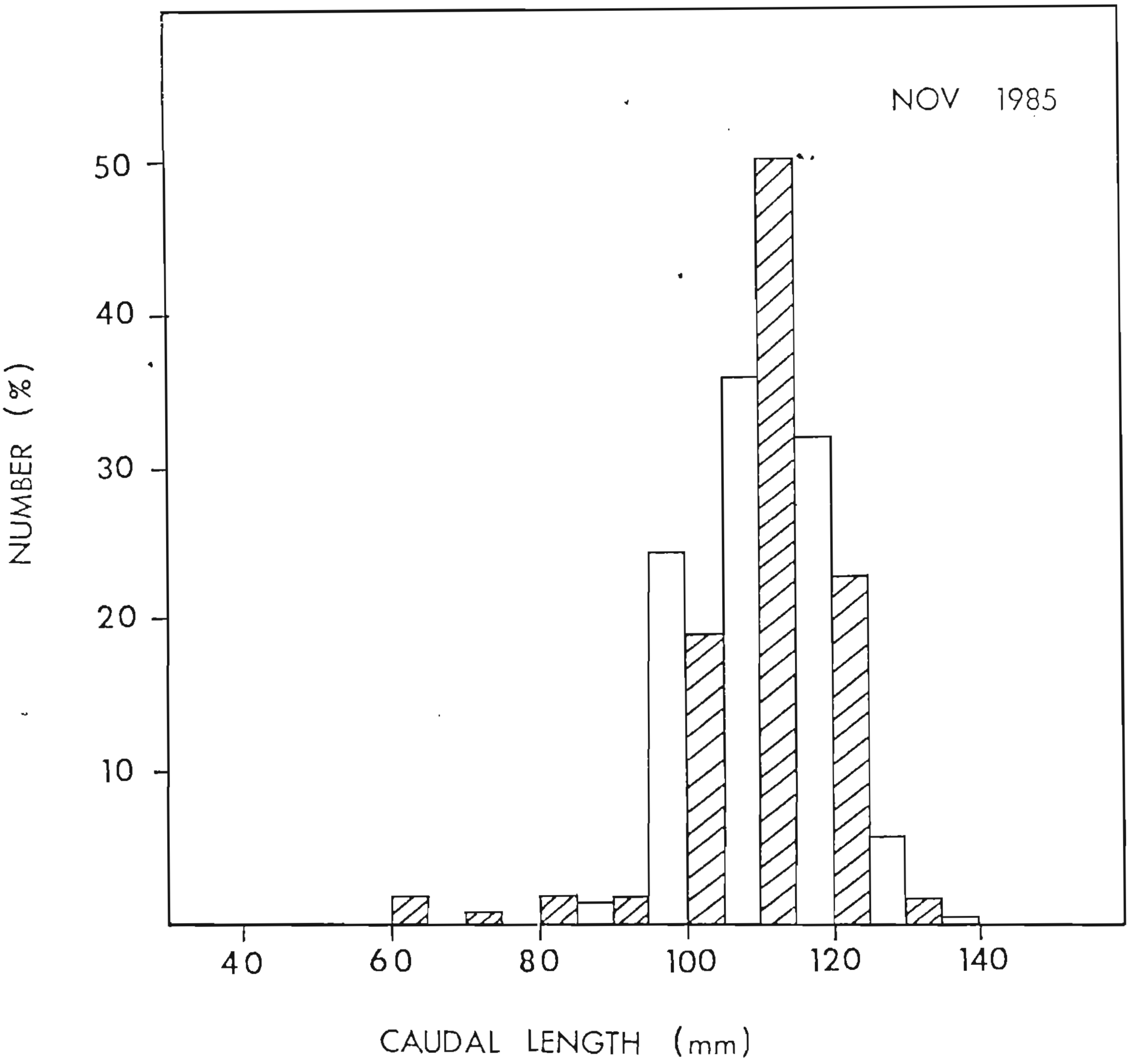


FIGURE 37

Caudal length frequencies of Cape Anchovy caught by the R.V. Africana (diagonal lines; n=1232) south of Cape Columbine to Danger Point and by Cape Gannets (open blocks; n=110) from Malgas Island, November 1985.

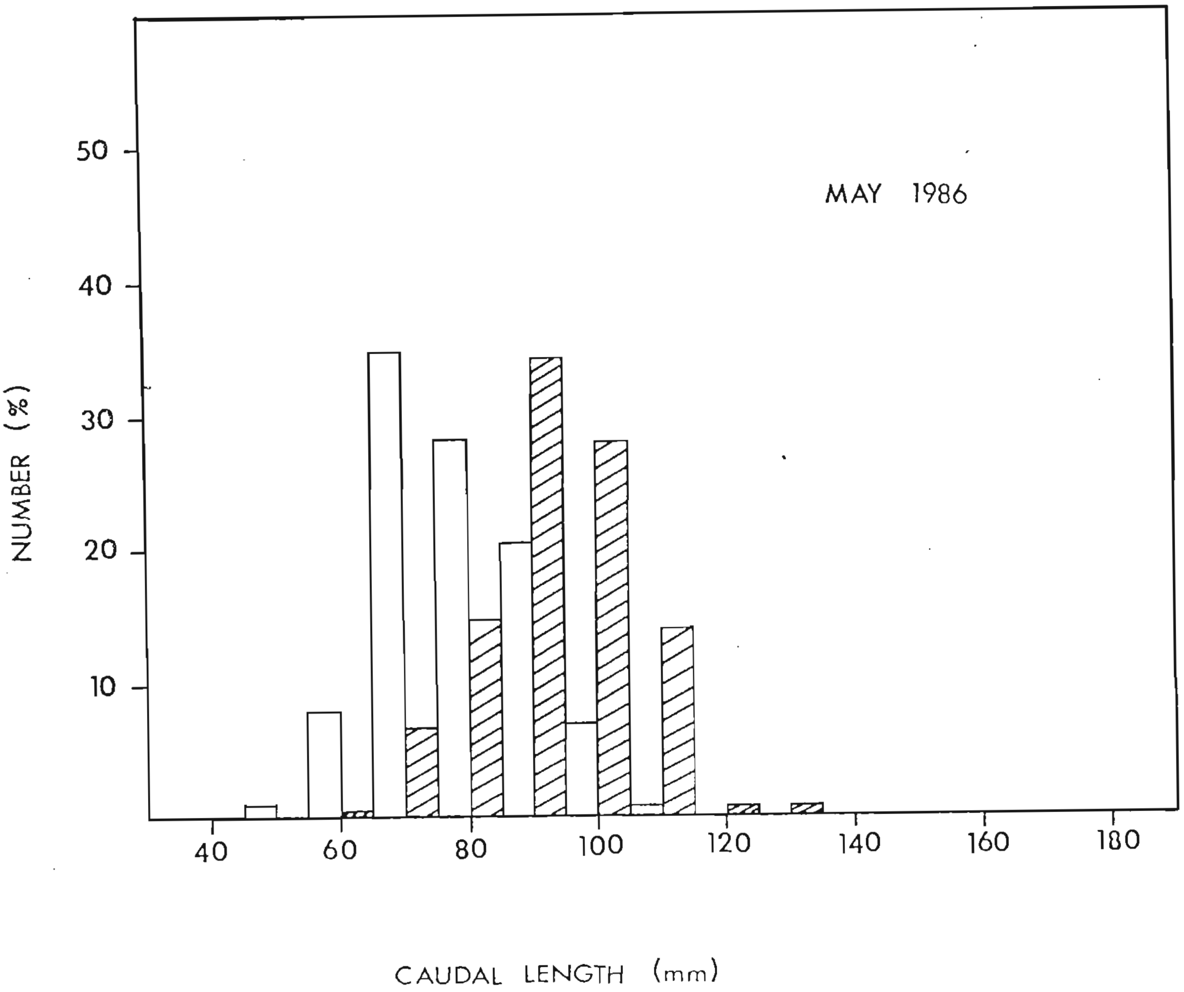


FIGURE 38

Caudal length frequencies of Cape Anchovy caught by the R.V. *Africana* (diagonal lines; n=1587) north of Cape Columbine and by Cape Gannets (open blocks; n=472) from Lambert's Bay, May 1986.

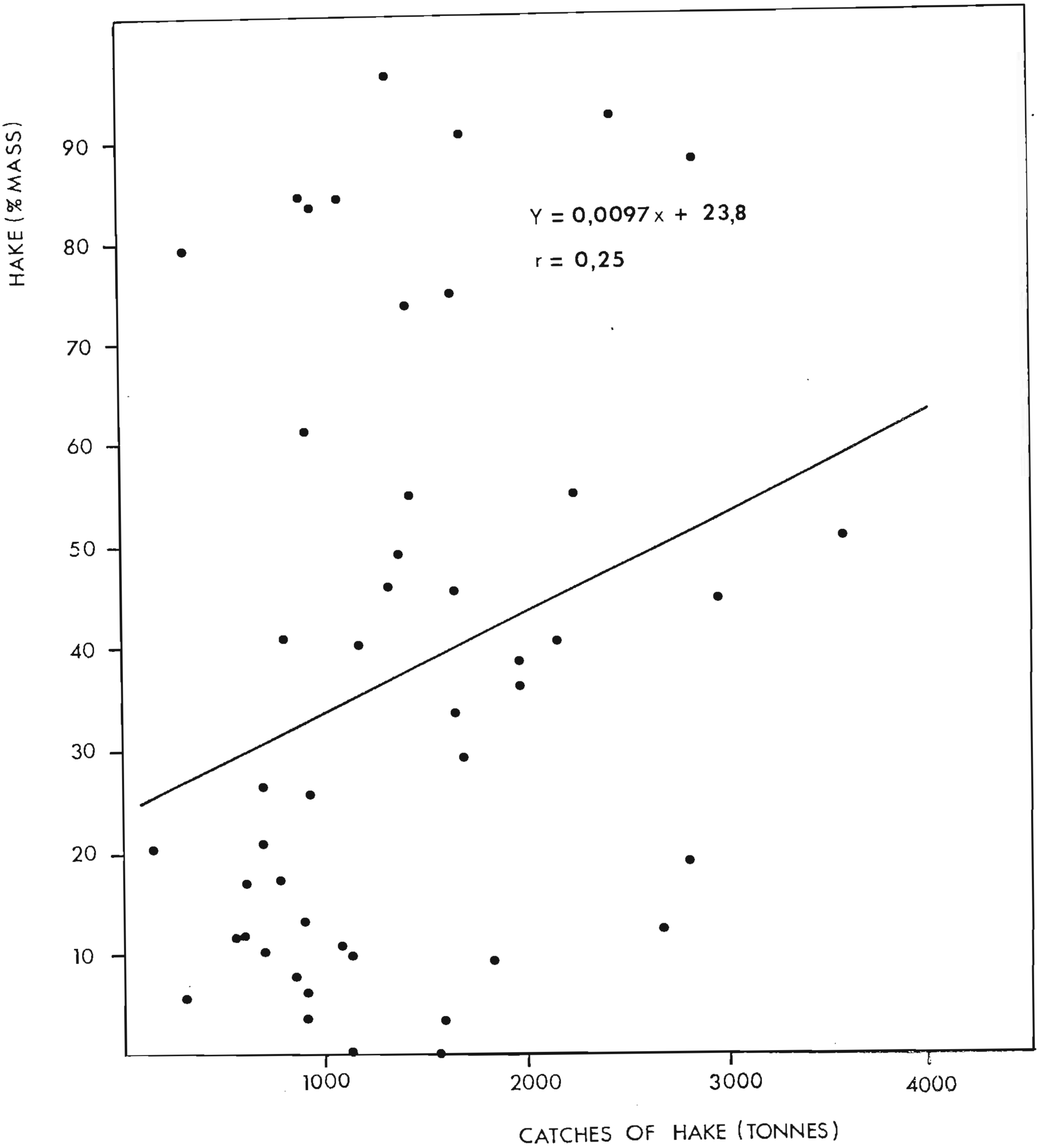


FIGURE 39

Monthly catches of Hake by the demersal fishery within 110 km of Malgas Island against the monthly percentage of hake by mass in the diet of Cape Gannets from Malgas Island, January 1983 to October 1986.

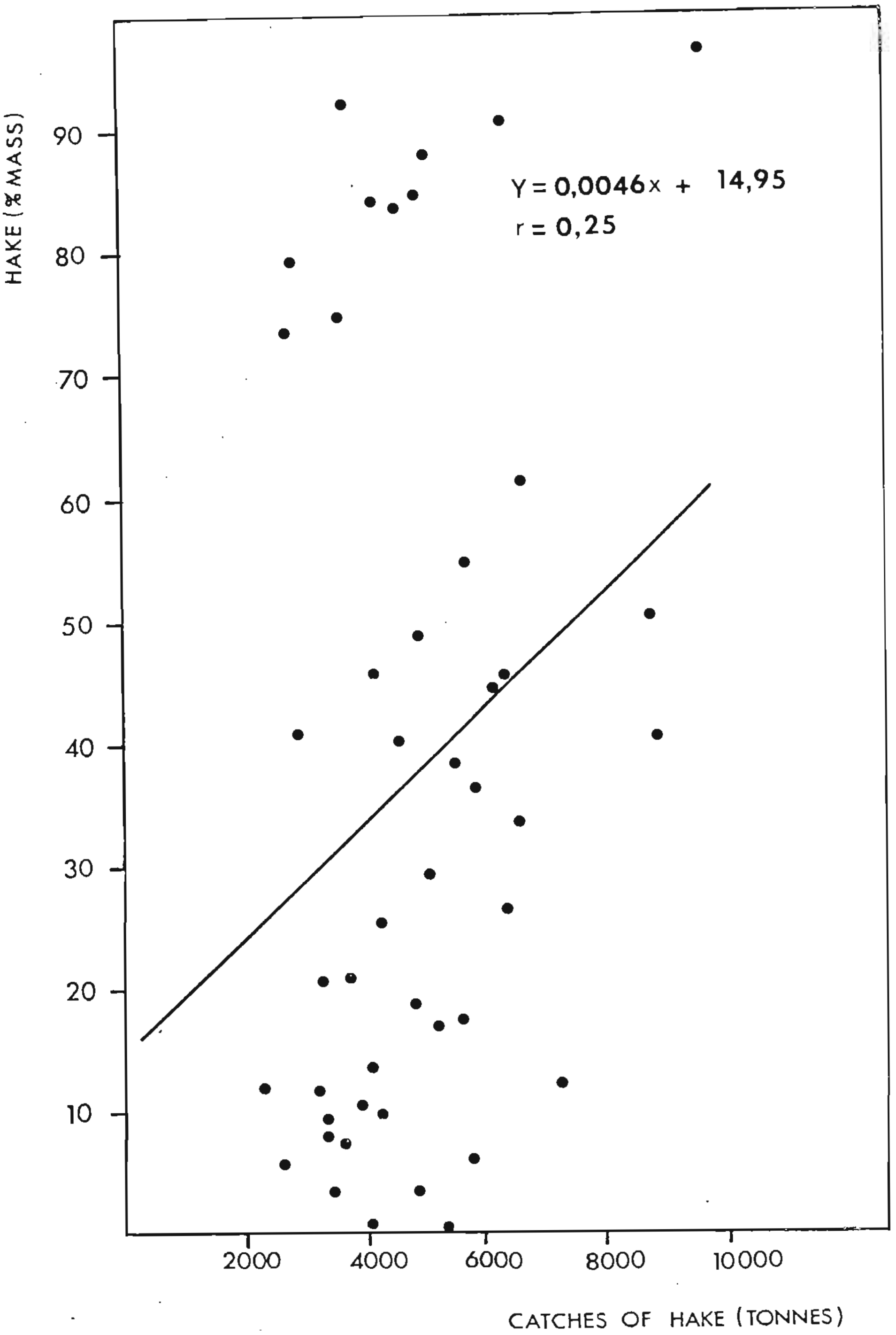


FIGURE 40

Monthly catches of Hake by the demersal fishery between Cape Columbine and Danger Point against the monthly percentage of hake by mass in the diet of Cape Gannets from Malgas Island, January 1983 to October 1986.

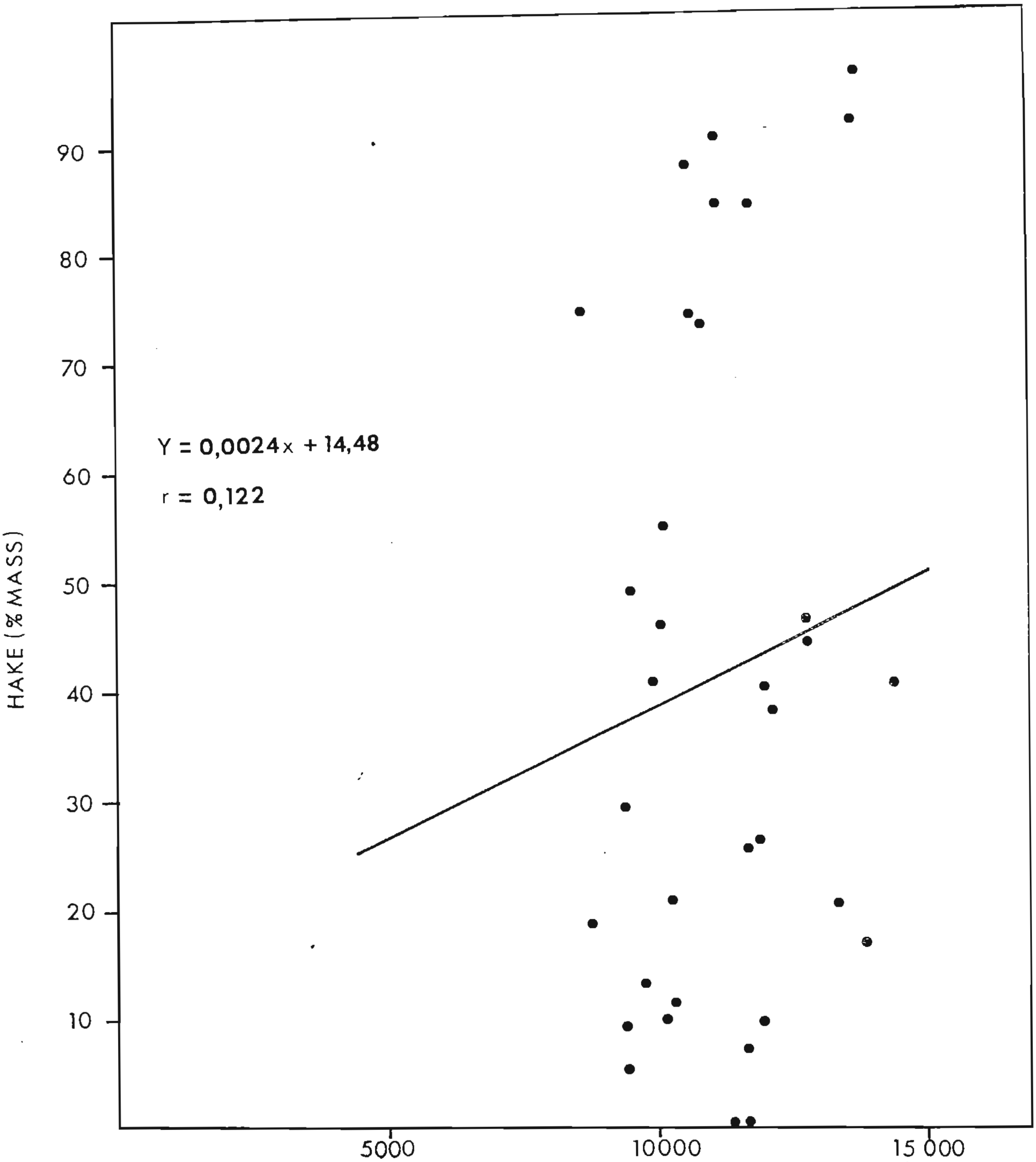


FIGURE 41

Monthly catches of Hake by the demersal fishery in South African waters against the monthly percentage of hake by mass in the diet of Cape Gannets from Malgas Island, January 1983 to October 1986.

$r=0,62$; $df=6$; $P > 0,05$)(Fig. 42). It is concluded that the hypothesis that gannets select hake prey preferentially can be rejected because the percentage of hake (by mass or volume) in gannet diet bore no relation to the mass of hake available at the monthly level over three scales of distance and at the annual scale for the entire annual catch of hake in South African waters.

Comparison of sampling techniques

The differences in fishing techniques of the three sampling methods are given in Table 37. Gannets are able to catch prey which occur in small shoals and throughout the year. The gannet population as a whole searches a far wider area in a shorter time than purse-seiners or the R.V. Africana. However, gannets catch only surface-dwelling fish during the day. Apart from its limitations in being unable to detect prey in shallow waters or which occur in small shoals, the R.V. Africana is less restricted by limitations in the time of day and depth at which fishes may be caught. However, it is only able to survey for short periods of the year and time limitations preclude making large numbers of trawls. Purse-seiners catch most fish inshore and concentrate on large concentrations of fishes within the uppermost 40 m. The purse-seine fishery has provided the largest and longest available time-series on epipelagic fish abundance. Any tendency for part of the population to occur in small groups will tend to result in their underrepresentation in purse-seine and R.V. Africana catches.

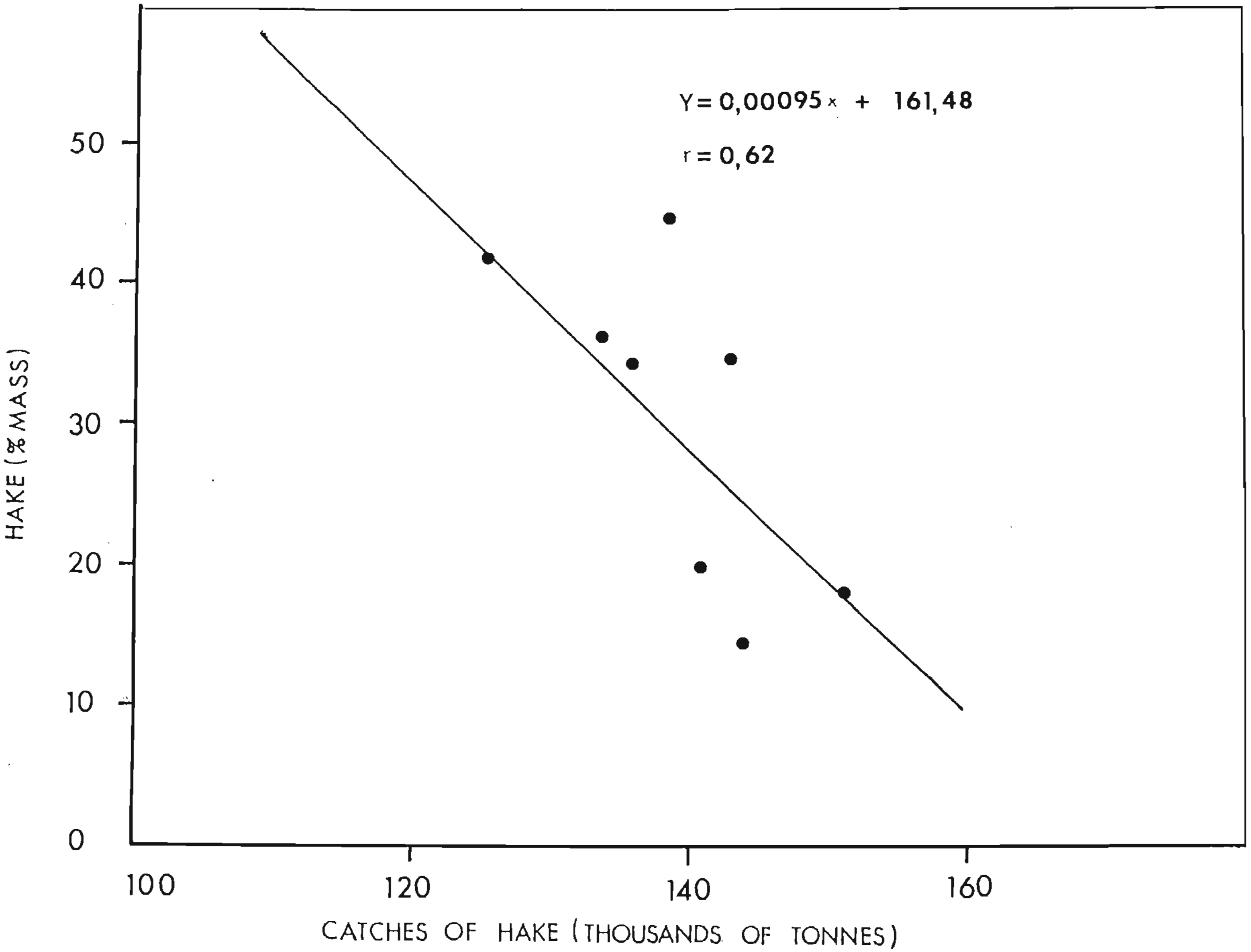


FIGURE 42

Annual catches of Hake by the demersal fishery in South African waters against the annual percentage of hake by mass in the diet of Cape Gannets from Malgas Island, 1978 to 1986.

TABLE 37.

CHARACTERISTICS OF THE MANNER IN WHICH CAPE GANNETS, THE PURSE-SEINE FISHERY AND THE R.V. AFRICANA SAMPLE PELAGIC FISH POPULATIONS

Characteristic	Cape Gannet	Purse-seine boat	R.V. *Africana*
Water depth	<6 m	<35m	>6m
Distance			
Offshore	c.100 km	c.50 km	up to 150 km
Inshore	no limit	breaker line	3 km
Longshore	c.28°S-Danger Point	c.28°S-Danger Point	variable, but usully large
Time			
Annual	1978-1986	1974-1986	1983-1986
Seasonal	throughout	usually Jan.-Jul./Aug.	usually May & Nov.
Daily	daylight	dusk-morning	throughout
Detection system	visual	acoustics/visual	acoustics
Prey shoal size	tiny-large	large	large
Catching system	plunge-dive	purse-seine net	mid-water trawl
Search pattern	dispersed, rapid aggregation	clumped	stratified random grid
Weather restriction	very bad weather?	poor weather	very bad weather
Moon influence	nil	severe	nil
Closed area	nil	yes	nil
Technological changes	nil	nil	nil

DISCUSSION

Mesopelagic species (adult Redeye Roundherring and Onderbaadjie) are relatively more important to the purse-seiners than to the gannets. Two myctophid species, Onderbaadjie and Lightfish, are abundant in waters off the western Cape (Shelton & Davies 1979; Hulley 1986). Lightfish are not caught by purse-seiners. While these species occur at greater depths during the day (Hulley & Prosch in press), S. Jackson (Percy FitzPatrick Institute in prep.) found that Onderbaadjie were sometimes taken in large numbers by Sooty Shearwaters feeding in association with large numbers of other predators in west-coast waters during the day and suggested that predators may chase mesopelagic fishes to the surface. It is possible that Onderbaadjie occurs regularly at the surface during the day, but that gannets do not select these fishes because of their small size (usually less than 70 mm Lc - Prosch 1986a). On the basis of commercial and research fishing, Onderbaadjie is most abundant in the uppermost 50 m of the sea during summer but occurs in gannet diet mainly in late winter and spring when their energy content is low. Similarly, peak catches of adult Redeye Roundherring occurred in summer, but they occurred in gannet diet mainly in late winter and spring. It was suggested that hake was eaten at this time of year because epipelagic fishes were unavailable. The inclusion of Onderbaadjie and the occurrence of adult Redeye Roundherring in gannet diet in late winter and spring supports this suggestion because they are most available to purse-seiners in summer. The apparently infrequent occurrence of Onderbaadjie and adult Redeye Roundherring at the surface during the day, the small size of Onderbaadjie and their occurrence offshore suggests that these species do not usually provide a profitable energetic return for effort expended by the foraging gannet.

The lack of correlation between the mass of hake available to gannets and its contribution to their diet supports the hypothesis that hake is a secondary food resource used only when epipelagic prey richer in energy content is not available closer to the colony. This hypothesis was founded on a number of lines of evidence: gannets do not select hake when breeding; gannets eat hake mainly in late winter and spring when the fronts with which Saury are associated have moved further offshore (Shelton _et al_. 1985) and the main southward migration of Cape Anchovy is complete (Crawfod 1981b). Furthermore, hake appeared in gannet diet in Algoa Bay under conditions which suggested food shortage (desertion of nests and small meal sizes) (J. Colclough, Port Elizabeth Museum, pers. comm.). Captive gannet chicks fed hake _ad lib_ grew more slowly and attained lighter peak masses than chicks fed on pilchard (Batchelor & Ross 1984).

Although the differences in the sizes of fishes of the same species caught by gannets, purse-seiners or the R.V. Africana were usually statistically significant, the differences in modes were seldom more than 20 mm. Gannets usually caught more smaller fishes and a wider range of lengths than purse-seiners or the R.V. Africana. The R.V. Africana makes comparatively few catches and is therefore less likely to sample a range of sizes because the length of fishes in the same shoals tends to be uniform (Crawford 1981a, b & e). The purse-seiners may avoid small fish (less than 60 mm). Any tendency for fishes to occur close inshore, nearer the surface or in small shoals will make them more available to gannets than to commercial and research fishing.

The seasonal occurrence and abundance of Cape Anchovy in Cape Gannet diet corresponds to its seasonal occurrence and abundance in purse-seine catches (Chapter 5). The seasonal occurrence of pilchard in gannet diet corresponds to the known patterns of distribution and movement of this species (Armstrong et al. in press). The occurrence of Saury, an oceanic species, in the diet of the Cape Gannet in summer is related to the inshore occurrence of warm water at that time (Chapter 10). It is suggested that Cape Gannets select epipelagic shoaling fishes (mainly Cape Anchovy, South African Pilchard and Saury) which occur inshore and eat mesopelagic fishes and hake offal only when epipelagic prey is unavailable inshore. Batchelor & Ross (1984) proposed that South African Pilchard was the preferred prey, a conclusion reached by Davies (1956) with less supporting evidence. Davies

(1956) suggested that Cape Anchovy, then Maasbanker, were the next species in order of preference.

Batchelor & Ross (1984) suggested that the optimal prey size of the Cape Gannet was about 200 mm and that adult pilchard was the preferred prey on the grounds of length, mass and energy content. Preferential selection for pilchard ahead of anchovy should be based on the larger size and greater energetic return of pilchard. Meals of gannets which contain pilchard were heavier than those of Cape Anchovy at Algoa Bay (Batchelor & Ross 1984). Whilst gannets are able to catch the largest Saury (about 450 mm Lc - Hubbs & Wisner 1980), fish measuring less than 100 mm are rare in their diet but occurred frequently in surface icthyoneuston samples within their foraging range on the west coast (Dudley _et al_. 1985). Gannets do not select juvenile Saury. If gannets do select primarily on length, the choice is likely to be between fishes of different species rather than fishes of different lengths within the same species. The selection is likely to be based on the energetic profitability of prey if a choice of species is available (Hislop & Harris 1978; Furness & Hislop 1978). The choice of prey will therefore be based on a complex of factors such as the shoaling behaviour (Batchelor & Ross 1984), relative abundance, proximity to the colony, energy content and prey length. Little data exist on the behaviour and energy content of epipelagic fishes in the southern Benguela System. If the occurrence and behaviour of Saury and Pilchard on the west coast are compared, it is apparent that South African Pilchard form larger shoals and are present throughout the year and occur closer inshore than Saury (Du Plessis 1959; Anon. 1983; Chapter 10). There is no evidence to refute the hypothesis that adult pilchard are the preferred prey of Cape Gannets. Historically, pilchard was the dominant prey of gannets (Davies 1958; Rand 1959) and any increase in the abundance of adult fish should be reflected immediately by its increased representation in gannet diet, if it is the preferred prey. Increases in the relative abundance of other epipelagic species may reduce the degree of preferential selection by gannets for pilchard (Holling 1959). Large Mackerel *Scomber scombrus* was the preferred prey of the Northern Gannet in Canada because of its size and energy content (Kirkham *et al*. 1985).

North of Cape Columbine, juveniles of Redeye Roundherring, Cape Anchovy and South African Pilchard occur in mixed schools of fish of similar size (Armstrong 1986). Larger fishes such as Saury and adult pilchard were comparatively rare in this area (Chapter 5). Because differences in length, shoaling characteristics and distribution between species were apparently small in this area, it is suggested that the relative abundance of juvenile fishes in this area may have determined their contribution to gannet diet.

CHAPTER 9

A COMPARISON OF THE ABUNDANCE OF SOUTH AFRICAN PILCHARD IN CAPE GANNET DIET AND COMMERCIAL CATCHES

INTRODUCTION

Formerly the South African Pilchard was the major contributor to South African puse-seine catches, but the stock collapsed in the mid-1960s and showed a trend of decreasing catches in the late 1970s and early 1980s, until the imposition of quotas in 1984 (Armstrong et al. 1985 - Table 1). The South African Pilchard is commercially more valuable because it may be canned for human consumption, whereas Cape Anchovy is reduced to fishmeal and oil (Armstrong 1986). However, the assessment of South African Pilchard stock size is difficult, particularly at low population biomasses (Chapter 3). If South African Pilchard is a preferred prey of Cape Gannets, its occurrence in the diet of the gannet should reflect pilchard abundance and indicate the trend in the size of pilchard stocks.

This chapter considers the hypothesis that the abundance of South African Pilchard in gannet diet, total catches and catch per unit effort (CPUE) are proportional to South African Pilchard abundance. This hypothesis cannot be tested directly, because no suitable time series of accurate determinations of stock size exists. One prediction of this hypothesis that can be tested is that fishery catches and the abundance of South African Pilchard in gannet diet should be correlated if both are proportional to stock size. This relationship and its implications for fisheries management are examined in this chapter.

METHODS

The sampling of gannet diet at the two western Cape colonies is described in Chapter 5. Percentage numerical abundance was not used because large South African Pilchard are much larger than average prey size on the west coast (Chapter 5) and their contribution to the diet would be underestimated in terms of energy content.

Monitoring of puse-seine fishery catches is described in Chapter 5. The localities of all catches were recorded, and allocated to areas north or south of Cape Columbine (termed Columbine North and Columbine South grounds). These two areas correspond roughly to the boundaries of the foraging areas of gannets breeding at Lambert's Bay (Columbine North) and Malgas Island (Columbine South) respectively (Chapter 7).

The percentage contribution of South African Pilchard (mass or volume) to the monthly diet of the gannets at the three gannet colonies (individually or in all combinations) was linearly regressed against monthly pilchard catches (total catches and CPUE) in the Columbine North and Columbine South grounds, and also against catches in the entire fishing area for all months in which total fishing effort exceeded 1 000 boat-days. The annual percentage of South African Pilchard (mass or volume) at the three colonies (individually or in all combinations) was linearly regressed against annual commercial pilchard catches in the total catch, and against catches in the Columbine North and Columbine South grounds, for the period 1978 to 1983. Pelagic fish quotas were usually filled by July between 1978 and 1982, but in 1983 the season reopened between October and December. Because this was the only year in which fishing took place late in the year and because purse-seiners were not allowed to catch pilchard east of Cape Point where much pilchard is caught, the data for October to December were not included in the calculation of pilchard CPUE in 1983 for the annual CPUE-versus-gannet regression. Similarly, the pilchard CPUE (total pilchard catch divided by total effort) was regressed against the percentage (by mass) of pilchard in gannet diet on a monthly and annual time scale. Total effort was estimated in standard boat-days (Crawford 1981a). Insufficient data exist to calculate directed effort (Butterworth 1983).

RESULTS

There was a significant correlation (P <0,05) between the annual mean percentage of South African Pilchard in gannet diet at Malgas Island and Lambert's Bay combined and the annual catches of Pilchard for the period 1978 to 1983 (Fig. 43). No other correlations were statistically significant (Table 38). Catches in the Columbine North ground showed very poor correlation with gannet diet, except at Lambert's Bay. The gannet diet at Malgas Island and Algoa Bay, or combinations including Lambert's Bay, showed moderate but non-significant correlations with catches in the Columbine South ground and over the entire area. Correlations for monthly data were poor, and none achieved a level of statistical significance (P <0,05).

There was a significant correlation (P <0, 01) between the annual mean percentage of pilchard in gannet diet at Malgas Island and Lambert's Bay and the pilchard CPUE for the entire area (Fig. 44). Trends in the other correlations were similar to those obtained between gannet diet and total catch (Table 39). Correlations for monthly data were poor, and none achieved a level of statistical significance (P <0,05).

The annual mean percentage (by mass) of South African Pilchard in gannet diet at each of the three colonies, and total annual pilchard catch were plotted for the period 1978 to 1983 (Fig. 45). The percentage pilchard in gannet diet at all three

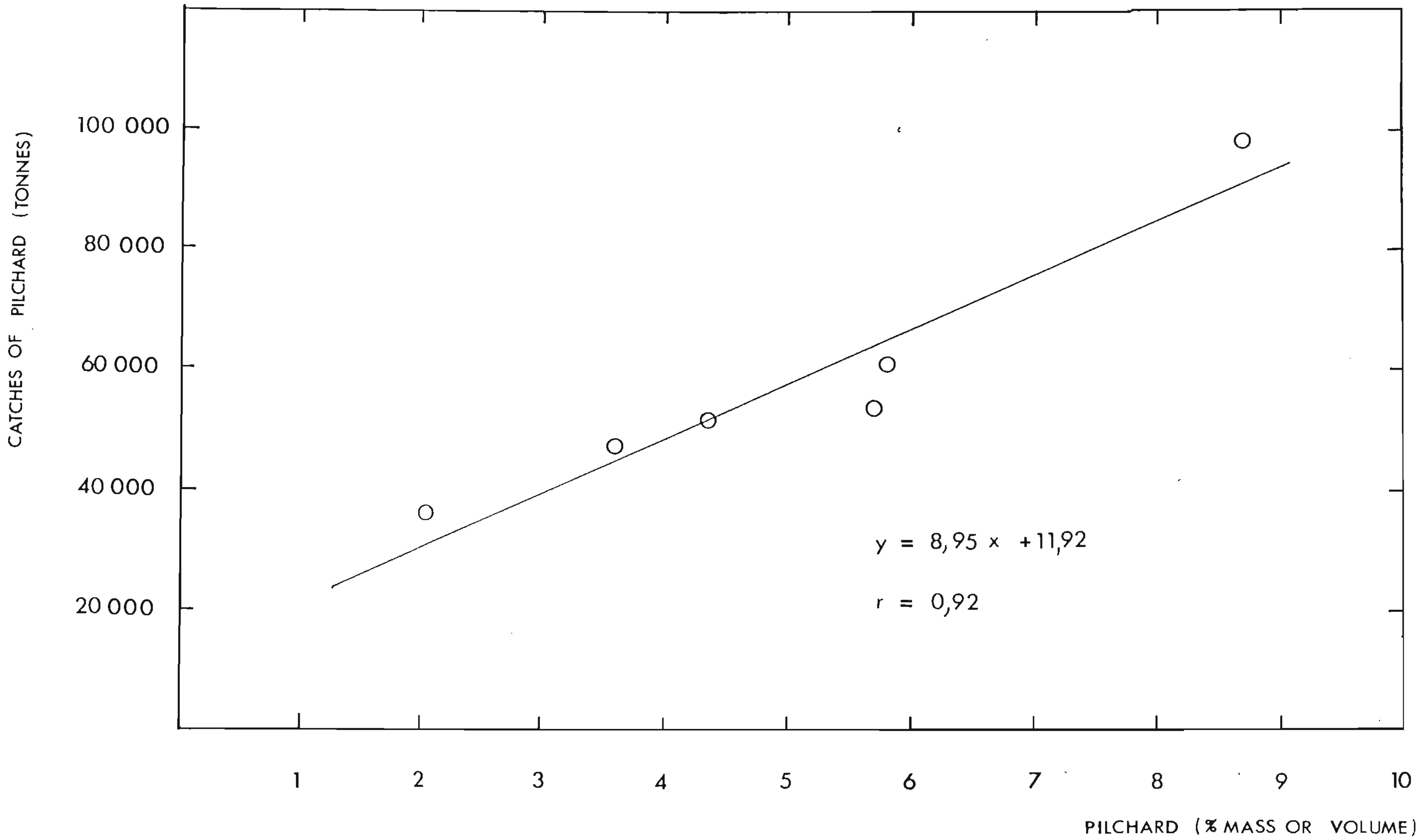


FIGURE 43

Linear regression of annual percentage South African Pilchard (mass or volume) in Cape Gannet diet at Malgas Island and Lambert's Bay against total annual South African Pilchard catch, 1978 to 1983.

colonies and total catches decreased between 1978 and 1982 (with a slight increase at Malgas Island in 1981) and increased between 1983 and 1985, except for a decrease at Lambert's Bay in 1984 .

Total catches and CPUE are significantly correlated ($P<0,05$) and do not constitute fundamentally different measures of the abundance of pilchard. Total effort varied little during this period.

DISCUSSION

That South African Pilchard is preferred by both gannets and purse-seine fishery is an underlying assumption of the test that the abundance of pilchard in gannet diet and fishery catches are correlated. If this were not the case, the abundance of South African Pilchard in gannet diet and fishery catches would be dependent on the availability of other preferred species. The case for large pilchard as preferred prey and lack of selection between juvenile pilchard, Cape Anchovy, Redeye Roundherring and Maasbanker are discussed in Chapter 8. Given equal availability of South African Pilchard and other species and lack of restrictions, the fishery should select large pilchard because of its high commercial value (Armstrong 1986). The purse-seine fishery catches of juvenile pilchard in mixed schools with similarly-sized Cape Anchovy are reduced to fishmeal and oil (Armstrong 1986).

TABLE 38.

CORRELATION COEFFECIENTS FOR LINEAR REGRESSIONS OF ANNUAL MEAN PERCENTAGE SOUTH AFRICAN PILCHARD (MASS OR VOLUME) IN CAPE GANNET DIET FROM DIFFERENT COLONIES AND COMBINATIONS OF COLONIES AGAINST ANNUAL TOTAL SOUTH AFRICAN PILCHARD CATCHES FROM DIFFERENT FISHING GROUNDS, 1978-1983. LB = LAMBERT'S BAY, M = MALGAS ISLAND AND AB = ALGOA BAY.

	Single colonies			Two colonies			All colonies
Fishing grounds	LB	M	AB	LB+M	LB+AB	M+AB	LB+M+AB
Columbine North	0.57	0.04	0.15	0.19	0.19	0.12	0.16
Columbine South	0.22	0.67	0.50	0.73	0.49	0.55	0.54
Entire Area	0.51	0.46	0.64	0.92*	0.67	0.66	0.69

*Significant at P<0,05

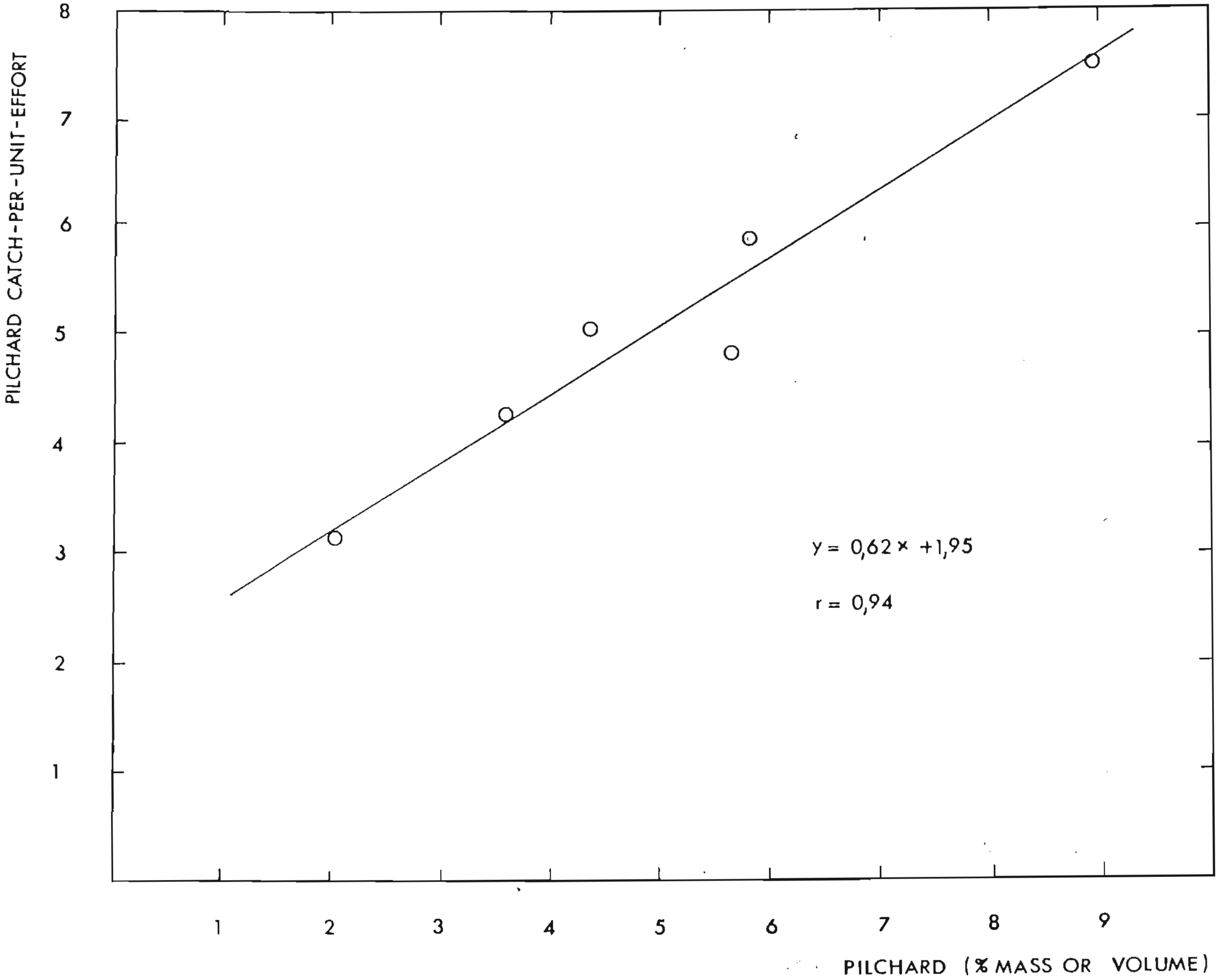


FIGURE 44

Linear regression of annual percentage South African Pilchard (mass or volume) in Cape Gannet diet at Malgas Island and Lambert's Bay against South African Pilchard CPUE, 1978 to 1983.

TABLE 39.

CORRELATION COEFFICIENTS FOR LINEAR REGRESSIONS OF ANNUAL MEAN PERCENTAGE SOUTH AFRICAN PILCHARD (MASS OR VOLUME) IN CAPE GANNET DIET FROM DIFFERENT COLONIES AND COMBINATIONS OF COLONIES AGAINST ANNUAL SOUTH AFRICAN PILCHARD CPUE IN DIFFERENT FISHING GROUNDS, 1978-1983. LB = LAMBERT'S BAY, M = MALGAS ISLAND AND AB = ALGOA BAY.

	Single colonies			Two colonies			All colonies
Fishing grounds	LB	M	AB	LB+M	LB+AB	M+AB	LB+M+AB
Columbine North	0,53	0,13	0,05	0,11	0,08	0,03	0,05
Columbine South	0,07	0,69	0,62	0,51	0,57	0,67	0,62
Entire Area	0,67	0,34	0,64	0,94*	0,68	0,64	0,69

*Significant at P<0.01

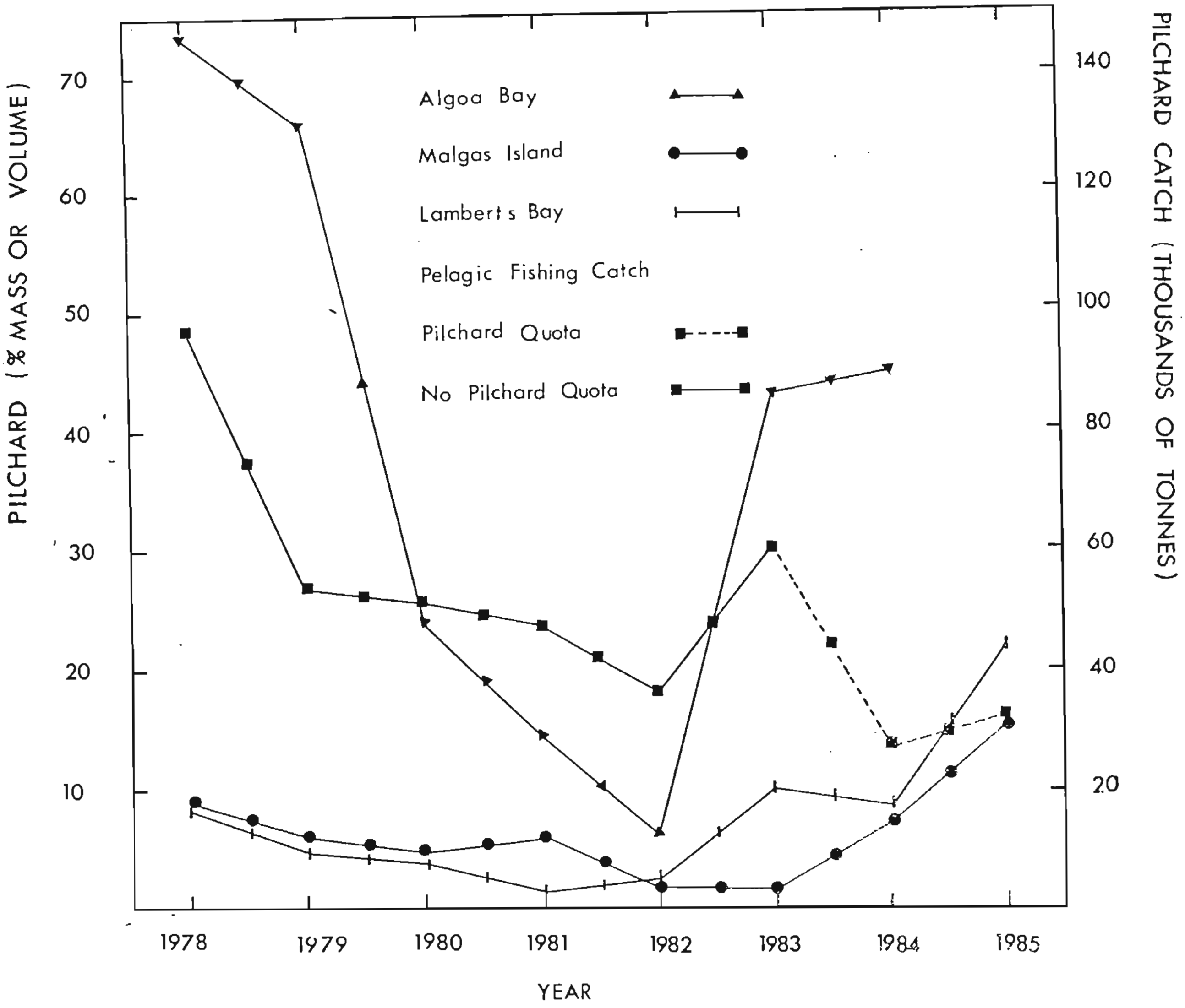


FIGURE 45

Percentage South African Pilchard (mass or volume) in Cape Gannet diet at Lambert's Bay, Malgas Island and Algoa Bay, and annual total South African Pilchard catch, 1978 to 1985.

Therefore, both the fishery and gannets should select large pilchard when available, but should not distinguish between juvenile pilchard and other species (in the absence of legislative restrictions) if only small fish were available.

The lack of demonstrated correlation between gannet and fishery catches at monthly time scales has at least two possible explanations. Firstly, fishery catches and gannet diet were not monitored over the same period each month. Gannet diet was usually sampled only once per month, whereas purse-seiners fish on many days each month. Secondly, the fishing strategies of gannets and purse-seiners are very different, and short-term availability of pilchard to each may differ greatly (Chapter 8). Gannets feed diurnally, catching prey within five meters of the surface up to 100 km offshore. Feeding flocks may exceed 1 000 birds, but gannets search for prey individually or in small groups, catching much prey in association with cetaceans (Chapter 7). Local availability of prey, concentrated by oceanographic features such as convergences, is important to seabirds (Brown 1980, Briggs et al. 1984). Purse-seiners catch fish during the day and night within 35 m of the surface and are subject to restricted areas and seasons, and are far more dependent on weather and moonlight than gannets (Newman et al. 1979). Communication between ships ensures that fishing is concentrated in certain areas at any one time. With these differing fishing strategies, short-term correlations are less likely. Tests of short-term correlations between gannet diet and commercial catches require more stringent sampling and control of variables.

Improved correlations between data from fisheries and gannet diet at an annual time scale may be attributed to more adequate sampling of gannet diet at this scale, and a smoothing of variation in short-term availability of prey to birds and purse-seiners. The level of correlation increases when gannet diet and commercial catches originate from the same fishing area. The best correlation was obtained when the the gannet foraging area (Malgas Island and Lambert's Bay combined) included all age classes of South African Pilchard (Armstrong et al. in press), and covered the entire fishing area. The addition of the Algoa Bay colony reduced the level of correlation, presumably because of the bias to the predominantly one-year-old pilchard that are not commercially fished in that area, but which make up a far greater percentage of gannet diet than on the west coast. Anderson et al. (1982) found the breeding success of Brown Pelicans, which feed on Northern Anchovy in the southern Californian Bight, was significantly related to the abundance of anchovy determined by hydroacoustic survey over distances of hundreds of kilometres from the breeding colony, but not at smaller (tens of kilometres) or greater (thousands of kilometres) distances.

An alternative explanation of these results is that fishery catches and the abundance of pilchard in gannet diet are measures of availability and not of abundance. However, between 1978 and 1985, the simultaneous decreases in the proportion of pilchard in gannet diet at three widely spaced colonies, and in total catches between 1978 and 1982, and subsequent increase from 1983 to 1985, are good support for regional increases in biomass. Armstrong et al. (in press) traced the migration and distribution patterns of the relatively strong and isolated 1983 year class until 1986, demonstrating the mechanism by which a strong year class would become available in different geographical areas at different times. If fishery catches and the percentage by mass of pilchard in gannet diet are proportional to pilchard biomass, the 1983 year class should have been relatively strong. Support for this prediction came in 1985 from the occurrence reported by fishermen of two-year-old pilchard off the west coast (Anon. 1985) and their appearance in the greatest numbers since 1978 in the gannet diet.

Historical data on gannet diet show that it is unlikely that the relationship between pilchard abundance in gannet diet and fishery catches is linear (Davies 1958; Rand 1959). South African Pilchard comprised 54% (by mass) of the diet of gannets shot mainly on the Columbine North ground between 1952 and 1954 (Davies 1958), and 51% (by mass) of the diet of birds shot mainly in the Columbine South ground between 1954 and 1956 (Rand 1959). In the early 1950s, fishery catches of South African Pilchard were restricted mainly to the area north of Cape Columbine (Du Plessis 1959). The relationship between gannet diet and total catches predicts a catch of 481 000 tonnes at the combined level of 52,5% for gannet diet in both areas in the mid-1950s, yet the maximum catch of 410 000 tonnes in 1962 was achieved only after a series of years of good recruitment (Crawford 1981b). A sigmoid functional response of a predator to food abundance can be expected (Holling 1959; Anderson & Gress 1984; Beddington 1984, 1986; Chapter 3). However, at the low levels of South African Pilchard biomass in the southern Benguela System between 1978 and 1985, the responses are likely to be linear. Even if other species become relatively more abundant, the response is likely to remain linear although the rate of change may decrease. Until South African Pilchard biomass increases by an order of magnitude, the rate of change in the percentage by mass of pilchard in gannet diet in response to changes in pilchard biomass is unlikely to level off.

The relationship between gannet diet and total catches has limited application because it is a *post hoc* measurement available at the end of the year. It has limited predictive value in that strong recruitment should lead to strong year classes. It could be used, conceivably, to estimate total potential fishery catch in a given year when catches are restricted by quota. There are difficulties with this application. Firstly, as previously discussed, the shape of the relationship between gannet diet and pilchard catches, although apparently linear between 1978 and 1983, is unlikely to be so at higher pilchard biomasses. Secondly, during this period, commercial fishing caused a heavy mortality in the pilchard. Removal or reduction of this mortality could greatly increase the amount of pilchard available to gannets with subsequently increased occurrence in the diet that year. Therefore, during a year of quota restriction, the percentage of pilchard in gannet diet could be higher than during a year of unrestricted fishing despite the same initial biomass.

It is suggested that, at low South African Pilchard biomasses, the percentage by mass of pilchard in gannet diet is a reliable monitor of the trend in pilchard stock size.

CHAPTER 10

PREDATION ON AND DISTRIBUTION OF THE SAURY IN THE CONTINENTAL SHELF WATERS OF SOUTH AFRICA

INTRODUCTION

Saury is the only major prey species of the Cape Gannet which is not commercially important. It has therefore not been well studied, and its trophic relationships (Bergh _et_ _al_. 1985) and distribution are poorly known. There are two geographical populations of the Saury _Scomberesox_ _saurus_: _S_. _s_. _saurus_ in the north Atlantic and Mediterranean and _S_. _s_. _scombroides_ in the cool and temperate waters of the southern hemisphere (Parin 1968; Hubbs & Wisner 1980). While the biology of the northern population has been well studied (Sauskan & Semenov 1968; Zilanov & Bogdanov 1968; Hartmann 1970; Nesterov & Shiganova 1976; Dudnik _et_ _al_. 1981), the southern population has received less attention (Dudnik 1975; Brownell 1983; Dudley _et_ _al_. 1985). The Saury is an abundant epipelagic fish off both east and west coasts of southern Africa, extending as far north as 18^{o}S on the west coast (Smith & Heemstra 1986; Hubbs & Wisner 1980; Smale 1983; Dudley _et_ _al_. 1985). Although it sometimes occurs in large shoals (Barnard 1950; B. Rose, SFRI, pers. comm.) and is a major prey of the Cape

Gannet and the Yellowfin Tuna Thunnus albacares (Smale 1983; Talbot & Penrith 1963), it yields only tiny bycatches to the South African purse-seine fishing industry.

This chapter reviews the occurrence of and predation on Saury in the continental shelf waters of South Africa in relation to seasonal oceanographic changes, information necessary in understanding prey selection by the gannet (Chapter 8).

METHODS

Monitoring of purse-seine fishery catches is described in Chapter 5. In 1983 and 1984, the mass of Saury in subsamples of catches and in total catches was estimated. In 1985 its occurrence was not usually quantified and the total catch could not estimated. The distribution of purse-seine catches was plotted for 1983-1985. The caudal lengths of Saury in some purse-seine catches were measured in 1985. The caudal lengths of the dominant species in purse-seine catches in which Saury occurred were measured and compared against the length frequencies for the entire annual purse-seine catch of those species. Saury occurred frequently in association with Redeye Roundherring. The relationship between Saury in gannet diet and Redeye Roundherring in purse-seine catches was investigated by linearly regressing monthly purse-seine catches of Redeye Roundherring against monthly percentage (mass or volume) of Saury in gannet diet at

Malgas Island.

The sampling of gannet diet is described in Chapter 5, detailing collection of monthly length-frequency distributions and the contribution of Saury to gannet diet.

Information on the temporal distribution and abundance of Saury was obtained from dietary studies of predators in the western Cape (Talbot & Penrith 1963; Nepgen 1970, 1982; Walter _et_ _al_ in press) and in the eastern Cape (Smale 1983; Batchelor & Ross 1984).

Dudnik (1975) defined Saury larvae as being up to 25 mm Lc long and Dudley _et_ _al_. (1985) defined early juveniles as measuring 25-100 mm Lc. These definitions are followed here. Late juveniles are defined as fishes between 100 mm and 250 mm Lc. Sexual maturity occurs at lengths greater than 250 mm Lc or more off the coast of Africa (Dudnik 1975) and fishes larger than 250 mm Lc are regarded as adults.

RESULTS

Although purse-seine catch data are available for the years 1983-1985 only, Saury has always been a rare bycatch. Total catches were estimated as 87 tonnes in 1983 and 71 tonnes in 1984. In 1983, Saury were caught in greatest numbers between the

Cape Peninsula and Cape Columbine and northwest of Cape Columbine, largest catches being in the inshore waters of Table Bay and the Cape Peninsula (Fig. 46). In 1984, nearly all catches were made between Cape Peninsula and Cape Columbine, the largest catches being west of Dassen Island (Fig. 46). In 1985, nearly all catches were recorded north of Lambert's Bay. Saury were almost never caught by purse-seine east of Cape Point. The largest single catch in 1983 was 12,3 tonnes in Table Bay and 16,4 tonnes west of Dassen Island in 1984, confirming that Saury may occur in large schools at times. Saury were almost invariably caught in association with Redeye Roundherring and less frequently with South African Pilchard, Mantis Shrimp Squilla armata and Mackerel (Table 40). Most of the purse-seine catches were made from February to March (Table 41). In 1985, 446 fishes from eight catches measured 140-270 mm Lc, with 91% measuring 190-240 mm Lc (Fig. 47). These fishes were larger on average than those caught by gannets from Lambert's Bay between 1978 and 1985. Saury caught by gannets from Malgas Island are significantly larger (Kolmogorov-Smirnov test; P <0,01) than those from Lambert's Bay with median caudal lengths of 210 and 190 mm respectively (Fig. 11). A linear regression of monthly purse-seine catches of Redeye Roundherring against monthly percentage (mass or volume) of Saury in gannet diet at Malgas Island was statistically significant (P<0,05) (Fig. 48). The length-frequency distributions of Redeye Roundherring and South African Pilchard for all measured purse-seine catches in each year from 1983 to 1985 were compared with fishes

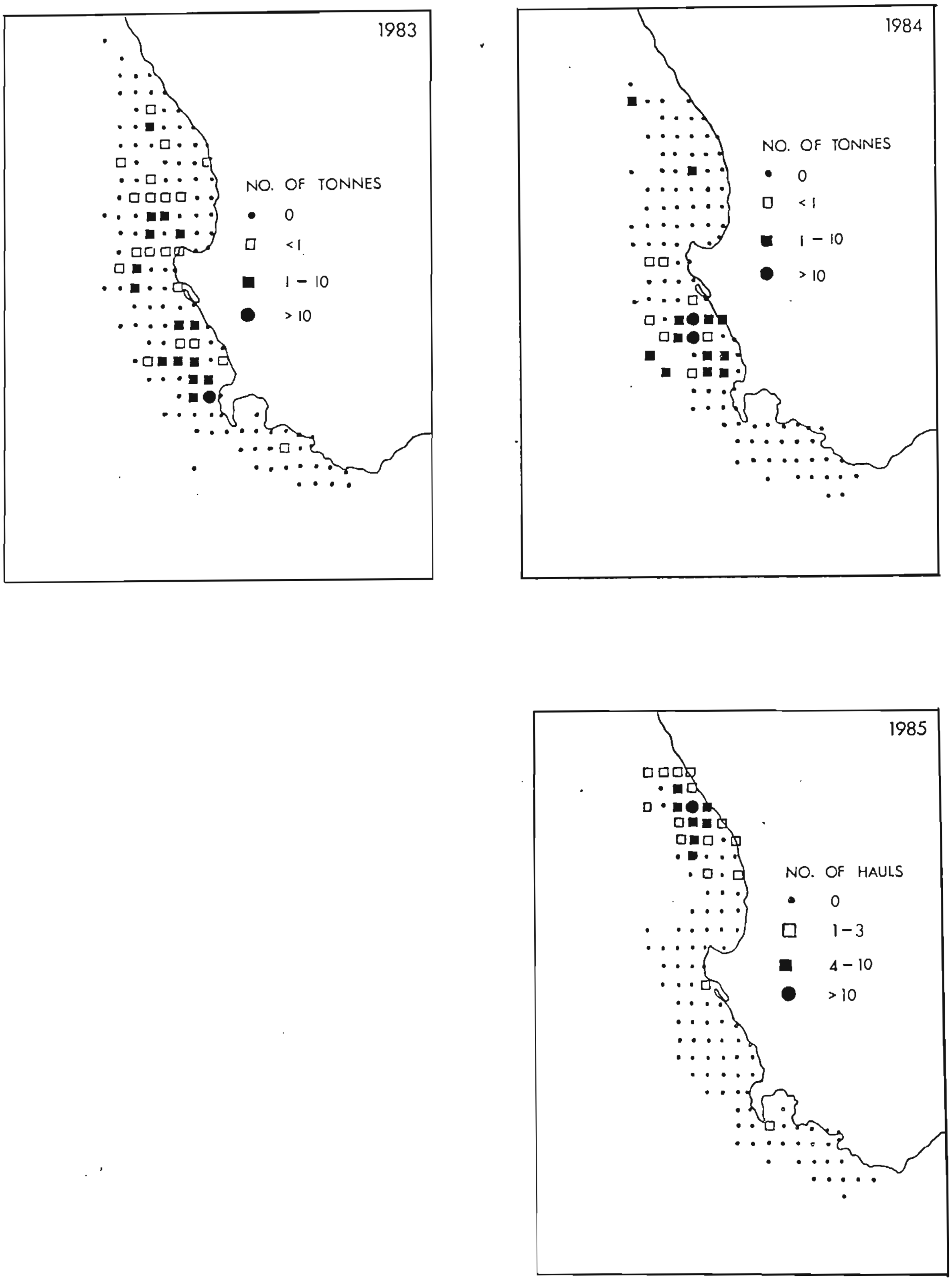


FIGURE 46

Distribution of Saury catches (by mass in 1983 and 1984, number of hauls in 1985) by the purse-seine fishery in the western Cape.

TABLE 40.

CONCURRENCE (%) OF OTHER SPECIES WITH SAURY IN PELAGIC FISHERY CATCHES IN 1983-1985

	Year		
Fish species	1983	1984	1985
Redeye Roundherring	92,6	100,0	98,0
Mackerel	77,9	4,5	52,0
South African Pilchard	41,2	4,5	73,5
Mantis Shrimp	32,4	11,4	0
Jellyfish	0	0	29,6
Snoek	0	0	8,2
Pelagic Goby	7,4	0	0
Cape Anchovy	1,5	0	3,1
Onderbaadjie	1,5	0	3,1
Ribbonfish	0	0	4,1
Hake sp.	0	0	2,0
Shark sp.	0	0	5,1
Tuna sp.	0	0	2,0
Squid sp.	0	0	2,0
Maasbanker	0	0	2,0

TABLE 41.

MONTHLY CATCH (TONNES) (1983 AND 1984) OR PERCENTAGE OF NUMBER OF HAULS (1985) OF THE TOTAL REPORTED SAURY CATCH BY THE PELAGIC FISHERY

	Year		
Month	1983	1984	1985
January	0,5	59,5	46,9
February	34,9	11,9	52,0
March	51,8	0	1,0
April	0,4	0	0
N	68	44	98

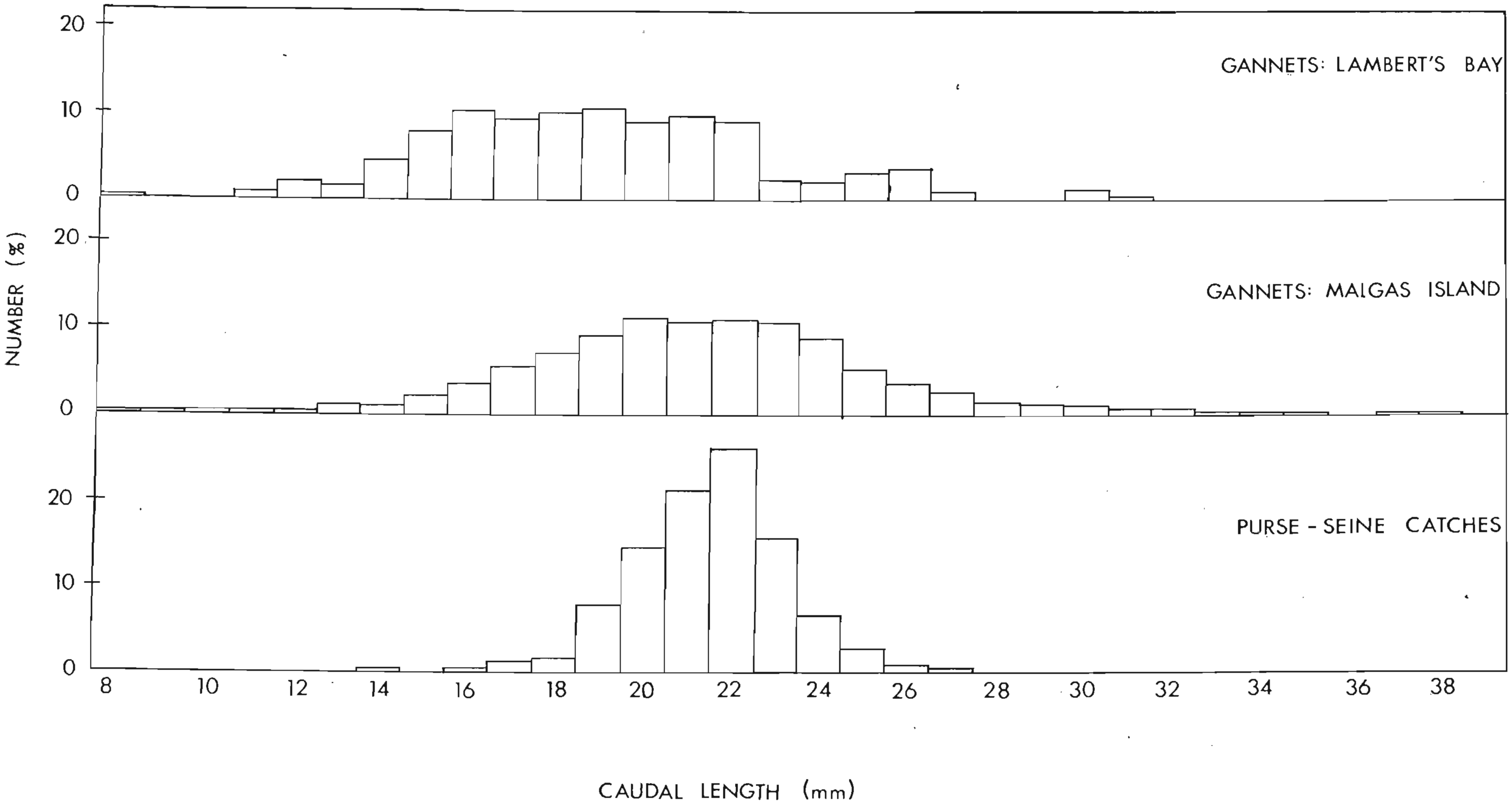


FIGURE 47

Caudal length frequencies for Saury in eight purse-seine catches in 1985 (n=446) and in Cape Gannet diet at Malgas Island (n=2807) and Lambert's Bay (n=254), 1978 to 1985.

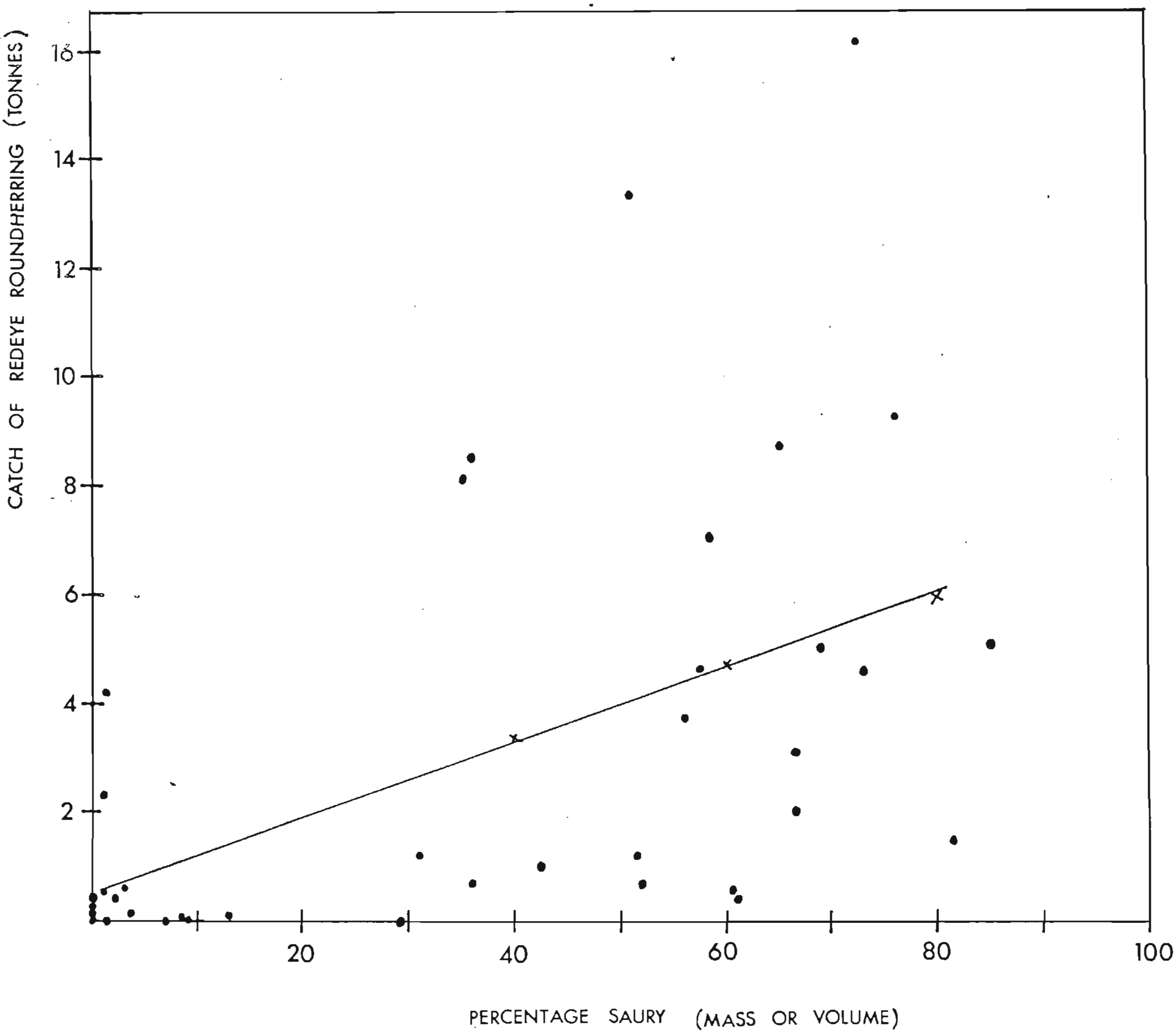


FIGURE 48

Linear regression of monthly commercial catches of Redeye Roundherring against monthly percentage (by mass or volume) of Saury in monthly Cape Gannet diet at Malgas Island, 1978 to 1985.

caught in association with Saury (Fig. 49).

Saury were consistently more abundant in the diet of gannets at Malgas Island than at Lambert's Bay (Tables 11-16). Saury were highly seasonal in gannet diet at Lambert's Bay, occurring between November and March, with peak occurrence from December to February. At Malgas Island, Saury occurred between November and May, with peak occurrence from December to March. Although smaller Saury disappeared from the diet in late summer, there was no increase in modal or median length (Fig. 18).

DISCUSSION

Predators

The major predators of early juvenile Saury are unknown. Swift Terns breeding at the Saldanha Bay islands and feeding within 10 km of the shore, occasionally ate Saury in autumn (Walter *et al*. in press). Although the sizes of these fishes were undetermined, other fishes in the diet measured 17-138 mm Lc. Saury were not taken by inshore-feeding Roseate Terns *Sterna dougalli* breeding on St Croix Island in Algoa Bay (Randall & Randall 1978).

Late-juvenile and adult Saury constituted 9-15% (by mass or

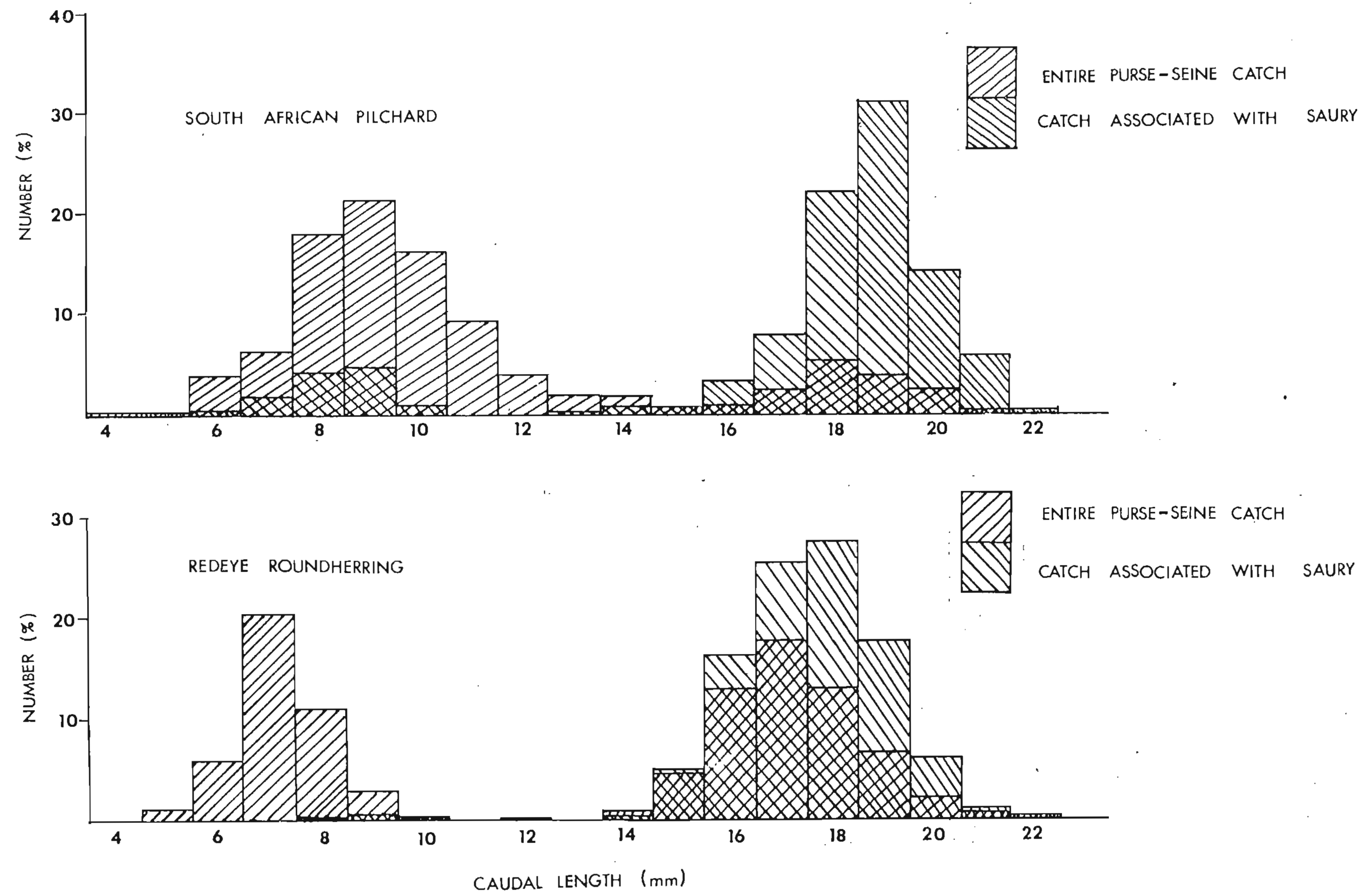


FIGURE 49

Caudal length frequencies for Redeye Roundherring and South African Pilchard in the purse-seine catch as a whole and caught in association with Saury annually between 1983 and 1985.

volume) of gannet diet annually at Lambert's Bay and 10-44% (by mass or volume) at Malgas Island between 1978 and 1986. In Algoa Bay, Saury annually constituted 11-47% (by mass) between 1978 and 1982 (Batchelor & Ross 1984). An abundant visitor to South African waters in summer, Cory's Shearwater Calonectris diomedea consumes Saury regularly (B. Rose, SFRI, pers. comm.), and two of four diet samples obtained off the western Cape contained Saury (S. Jackson, FitzPatrick Institute, pers. comm.). Kelp Gulls Larus dominicanus have been observed catching Saury in the lights of ships at night (B. Rose, SFRI, pers. comm.).

Yellowfin Tuna is apparently the most important fish predator of late-juvenile and adult Saury in South African waters (Talbot & Penrith 1963; Smale 1983; Shannon 1986). Saury were abundant in the diet of large Yellowfin Tuna (fork length 800-1400 mm) in offshore waters off Port Elizabeth and East London, but fewer were eaten by smaller Yellowfin Tuna (fork length < 800 mm) (Smale 1983). Saury are also eaten by Bigeye Tuna Thunnus obesus and Longfin Tuna Thunnus alalunga (Nepgen 1970). In the eastern Cape, small numbers of Saury were taken by Elf Pomatomus saltatrix, Yellowtail Seriola lalandi and Skipjack Katsuwonnus pelamis. Several species of pelagic, reef and inshore-bottom fish predators in the eastern Cape and False Bay did not eat Saury (Hecht 1976; Nepgen 1982; Smale 1983). Saury was a rare prey of the hakes,t he dominant demersal fish predators (Hecht 1976; Chlapowski 1977; Botha 1980; Payne et al. in press), and of Snoek, the dominant inshore fish predator west of Cape Agulhas (Nepgen 1982; S. Dudley, University of Cape Town, pers. comm.). Snoek were seen catching Saury in the lights of a ship in January 1986, and three containing Saury were caught (B. Rose, SFRI, pers. comm.). Saury has not been recorded as prey of Squid _Loligo_ _reynaudi_ (J. Augustyn, SFRI, pers. comm.) and was a rare prey of Cape Fur Seals _Arctocephalus_ _pusillus_ (David in press). Saury was a very rare dietary item of the piscivorous Brydes Whale _Balaenoptera_ _edeni_ and the Sei Whale _B_. _borealis_ which eats mainly crustaceans (Best 1967; Kawamura 1974).

Late-juvenile and adult Saury occur mainly in surface waters (Hartmann 1970) where they are eaten only by fast-moving predators. Nocturnal predation on Saury in the lights of ships by species not otherwise known to eat Saury suggests that this feeding is opportunistic.

Geographical and depth distribution

In the western and southern Cape, Dudley _et_ _al_. (1985) showed that Saury eggs were concentrated in offshore waters between Cape Columbine and Cape Point, with a further concentration east of 21°E and south of 35°S which may have extended further east. Larvae and early juveniles were found in the same areas, except in autumn when high densities were located offshore further east between Cape Point and Still Bay. The extent of the spawning range east of Still Bay is unknown, although Batchelor (1982) recorded well developed ova in female Saury eaten by gannets in Algoa Bay throughout the year. Dudnik (1975) showed that the spawning range extended far beyond South African waters to the northwest, and across the southern Atlantic. Peak densities of larvae and juveniles were located offshore of strong thermal fronts.

It appears that Saury were more available to gannets from Malgas Island and in Algoa Bay where deeper and warmer waters, and thermal fronts, lie close inshore (Shannon _et_ _al_. 1985; Shelton _et_ _al_. 1985). However, late-juvenile and adult Saury were usually caught by purse-seine boats within 10 km of the shore, downstream of the major upwelling plumes off the Cape Peninsula and Cape Columbine, and off the band of upwelling north of Lambert's Bay. Very few Saury were caught between Cape Point and Danger Point. The inshore catches of Saury on the west coast contrasted with the evidence for offshore occurrence from neuston net samples (eggs, larvae and early juveniles). However, nearly all purse-seine catches are made within 50 km of the shore, and comparative catch data for deeper warmer waters are lacking.

Size distribution

On the west coast, Saury caught by gannets from Lambert's Bay were significantly smaller on average than those caught by gannets from Malgas Island (Chapter 5). The modal sizes of Saury caught by gannets from Malgas Island and by the purse-seine fishery were similar but the gannets caught Saury larger and smaller than those caught by purse-seine. On the east coast most Saury eaten by gannets in Algoa Bay were much larger, exceeding 300 mm fork length (approximately 280 mm Lc) and measuring 150-420 mm fork length (Batchelor 1982). Large Saury (exceeding 270 mm Lc) were apparently rare in the gannet foraging area in western Cape waters, which includes the entire South African purse-seine fishery area. Dudnik (1975) found that Saury in the southeastern Atlantic measured 250-350 mm in size. Saury in the continental waters of South Africa increased in size from northwest to east. Size-specific distribution of Saury eaten by pelagic predatory fishes was shown in the eastern Cape waters (Smale 1983). Inshore fishes measured 116-315 mm total length, whereas offshore fishes measured 208-460 mm total length.

Saury grow at an estimated 0,5 mm per day during the first year of life (Brownell 1983), yet there was no observable growth trend in the size of Saury taken by gannets during summer on the west coast or winter on the east coast. The size range eaten by gannets (100-380 mm Lc) was large enough to show the growth of a particular dominant cohort if it were present. Extended recruitment and size-dependent migration and distribution would explain the lack of growth trend.

Distribution in relation to temperature

Dudley _et al_. (1985) found Saury eggs, larvae and early juveniles occurred between 12,7°C and 22,7°C but showed a preferred temperature of 18-22°C. Dudnik (1975) found Saury between 10,4°C and 19,4°C in the south Atlantic in winter but showed size-specific temperature preference. Larvae and juveniles up to 50 mm in length occurred in waters of 16-19,2°C. Larger juveniles occurred in water of 10-16°C, with a preferred range of 13,2-15,8°C, whilst adults occurred at 14,2-19,4°C. Dudnik (1975) suggested that reproduction took place between 16°C and 19,4°C. Elsewhere, Parin (1968) found Saury between 14°C and 23°C but usually 16-19°C, in the southwestern Pacific and southern Indian oceans. Andriashev & Permitin (1961 in Parin 1968) found Saury between 9,7°C and 19,5°C, but usually between 12°C and 18°C in the southeastern Pacific. Zilanov & Bogdanov (1968) regarded 17-19°C as the temperature range in the northeastern Atlantic.

Larger Saury occur seasonally in cooler water than larvae and early juveniles, entering cooler highly productive upwelled waters for foraging only, while reproduction occurs in warmer water (Parin 1968; Dudnik 1975). Thus the greater abundance of smaller size classes off the southern Cape coast compared to the west coast (Dudley _et_ _al_. 1985) may be explained by the presence of larger Saury off areas of highly productive upwelling plumes.

On the east coast increased occurrence of adult Saury is associated with lower winter temperatures. Saury apparently prefers water temperatures less than 20°C (Dudnik 1975; Dudley _et_ _al_. 1985), suggesting that summer water temperatures of the oceanic waters of the east are too high. Christensen (1980) showed that mean surface temperatures less than 20°C do not occur east of Cape Agulhas in March. In winter on the west coast a movement of Saury further offshore and perhaps to the east takes place. On the east coast the Saury may move further south and west rather than offshore, returning in the winter months.

Seasonal occurrence and reproduction

In the western and southern Cape eggs, larvae and early juveniles were found throughout the year, with strong peaks in February and April (Dudley _et_ _al._ 1985). Spawning takes place at the surface (Dudley _et_ _al._ 1985). Dudley _et_ _al_. (1985) suggested a link between peak Saury reproduction and the period of intensive upwelling in summer.

In this area, adults are highly seasonal, occurring in both gannet diet between December and March and the purse-seine fishery between January and March. The purse-seine fishing season usually lasts from January to June but included October and November in 1983 and 1984. Saury of undetermined size were occasionally eaten by Swift Terns in April.

The major part of the Saury stock occurs in oceanic waters offshore of the thermal front (Dudnik 19759; Dudley _et al_. 1985). During summer months on the west coast, Saury was caught inshore at night by purse-seiners and occasionally during the day in autumn by Swift Terns close to shore. Gannets occasionally caught Saury within 15 km of the shore during the day (Rand 1959; Chapter 7). Offshore of the oceanic front, Saury was caught during the day in spring and summer by Yellowfin Tuna and gannets.

In the eastern Cape, Saury was a major prey of gannets between March and November (Batchelor 1982). Yellowfin Tuna occur in this area between November and June (Smale 1983) and Saury were recorded in their diet between March and June. In the eastern Cape, adult Saury occur primarily in autumn and winter months (Batchelor 1982, Smale 1983).

Concurrence

Saury was caught off the western Cape at night by purse-seiners as a bycatch with adult Redeye Roundherring (>140 mm Lc), and, to a lesser extent, with Mackerel and adult South African

Pilchard (>150 mm Lc). They did not necessarily occur in mixed shoals but certainly occurred in the same area. This concurrence was not seen in gannet diet because regurgitations usually comprised only one species (Batchelor & Ross 1984) and Redeye Roundherring were not available to gannets(Chapter 8). However, there is a statistically significant correlation between the monthly purse-seine catches of Redeye Roundherring and the percentage by mass of Saury in monthly diet samples of gannets at Malgas Island. Most Redeye Roundherring were caught by the purse-seine fishery in January to April following the opening of the season in January. An association between Mackerel and Redeye Roundherring in purse-seine catches was previously noted by Crawford (1981c) who noted 15% of Redeye Roundherring landed between 1964 and 1976 came from such mixed shoals. Since 1978 the Mackerel stocks have declined, producing annual catches less than 4 000 tonnes (Armstrong _et al_. 1985).

Although most catches of Redeye Roundherring are made close to the coast, Crawford (1981c) reported that nighttime aerial fish-spotting surveys found most Redeye Roundherring shoals further than 15 km and as far as 100 km offshore. Most catches of Redeye Roundherring occured downstream of the major upwelling plumes off Cape Columbine and Cape Peninsula and off the upwelling band north of Lambert's Bay, suggesting that this species is consuming zooplankton which may occur at high densities in matured upwelling plumes. Armstrong _et al_. (in press) suggested that adult South African Pilchard (>160mm Lc) and adult Redeye Roundherring inhabit shelf-edge and frontal zone regions. It is suggested that the movements of Saury and adults of South African Pilchard, Redeye Roundherring and Cape Anchovy are related to concentrations of zooplankton in these areas, and to the movements of frontal zones. It is suggested that adults of these species enter matured upwelled waters to consume zooplankton.

Commercial Potential

The bycatch of Saury is reduced to fishmeal. Although this catch is very small, it is underexploited because Saury is the most expensive fresh fish bait available to marine fishermen in the western Cape. It can be eaten by man (Smith & Heemstra 1986).

Conclusions

The principal predators of late-juvenile and adult Saury are the Yellowfin Tuna, Cape Gannet and Cory's Shearwater and, to a lesser extent, Bigeye and Longfin Tuna. Predators of early juveniles are unknown. All are fast-moving surface-feeding predators. The seasonal occurrence of Saury inshore on the west coast appears to be linked to the formation of strong thermal fronts close to upwelled waters in summer. Larger Saury feed on zooplankton in cool waters downstream of matured upwelling plumes but are close to warm waters required for spawning. Peak reproduction in this region occurs in summer and autumn. The concurrence of large Redeye Roundherring and Mackerel and to a lesser extent, large South African Pilchard and possibly large Cape Anchovy as well, suggests that adults of several species of epipelagic fish may follow a similar strategy, entering highly productive cool waters to feed. In winter Saury occur further offshore and some reproductive activity occurs, but these Saury are not available to gannets or the fishery.

On the south and east coasts concentrations of Saury may similarly be linked to more localized areas of upwelling. However, temperatures in summer may exceed the temperatures preferred by adult Saury for reproduction. Saury are less available to predators at this time, possibly migrating elsewhere to breed.

CHAPTER 11

SYNTHESIS

The interactions between seabirds and fisheries have been studied primarily from two approaches: the estimation of consumption by seabirds of commercially valuable fishes (Schaefer 1970; Furness 1982; Furness & Monaghan 1986) and the actual or potential impact of fisheries on seabirds (Anderson & Gress 1984; Harrison et al. 1983). This thesis is an investigation of another aspect of the seabird-fishery interaction; the use of seabirds, specifically the Cape Gannet, to provide advice useful for the management of the purse-seine fishery of the western Cape of South Africa. The subject is broad and the investigation aimed primarily at establishing the biological basis on which the use of seabirds in this context could be based. Attempts were made to provide information useful in the management of the purse-seine fishery.

The use of seabirds as indicators of the status of fish stocks has usually been proposed by ornithologists in general terms, whereas fisheries managers require highly specific information. The concept of using seabirds as biological indicators, which was previously loosely defined, was examined critically. The discussion was based on the premise that an aspect of seabird biology is related to an aspect of fisheries biology about which information is required. The successful use of seabirds in fisheries management must depend on a systematic approach incorporating an understanding of the requirements of fisheries managers rather than a study of the seabird with possibly fortuitous fishery-related results. A fisheries-orientated programme will usually require several years of data.

Seabirds would appear to be most useful as indicators of surface-shoaling species which are short-lived. The responses of seabirds to changes in fish biology may be grouped into categories: population dynamics, reproductive biology, feeding ecology and adult condition and chick growth. The responses to be monitored should be determined by the requirements of existing management objectives and whether information from the seabirds can contribute towards them. Ultimately fisheries management is usually concerned with the determination of the quantity of a species that can be harvested without unacceptable changes in prey stocks or ecosystem integrity. The responses of seabirds have different integration times (the duration of time over which the response is determined) and may only give information at set times of the year. Most responses reflect changes in the availability of prey, but only analysis of the diet provides direct data on the size and age composition of the prey.

The Cape Gannet was chosen as the indicator species for this study since it eats epipelagic fish exploited by the fishery, the diet can be easily sampled throughout the year, diet samples are relatively undigested, baseline diet data were available, it has a high tolerance of human disturbance and its biology is well-known. The diet was chosen as the response to be monitored because a time series of diet data existed, diet can be determined throughout the year allowing year-round monitoring, diet provides information on a wide range of fish parameters and dietary parameters are linked without time lag to availability of prey.

The use of seabirds as indicator species depends on an understanding of the relationships between the monitored response and the aspect of the fishery being investigated. In particular, knowledge of the abundance of fishery stocks is a very important aspect of fishery management. However, abundance of prey is seldom the same as the availability of prey to the predator (Wiens 1984). Only part of the population is available to the gannets at any time. The determination of the relationships between the availability and absolute abundance of prey requires comparative data on the absolute abundance of various prey species. In practice, it is impossible to test this directly (Newton 1980). Indeed, if it were, there would be no need to use birds as indicators of epipelagic fish stocks in the first place. It was vital to attempt to assess whether the availability of prey was related to the abundance of prey. This was attempted by comparing the gannet diet with purse-seine fishery catches and to a lesser degree with research catches. Furthermore, a good understanding of the feeding ecology of gannets and of the distributional ecology of their prey should indicate a major mismatch between prey abundance, its availability and occurrence in gannet diet. The classic work of Holling (1959) suggests that the functional responses of seabirds to changes in prey abundance are likely to be sigmoid in shape, a suggestion followed by Anderson & Gress (1984) and Beddington (1984, 1986). All four types of functional response proposed by Holling (1959) showed a period of linearity or near-linearity in the response of the predator to changes in prey abundance before levelling off. The presence of alternate food sources slowed the rate of response and resulted in a lower asymptote but the period of linearity or near-linearity was still present.

Trends in the species composition and length of prey in monthly collections of regurgitations totalling 8 465 samples for the two western Cape colonies were described at monthly and annual time scales and compared to purse-seine fishery catches. Cape Anchovy, South African Pilchard and Saury dominated the diet of gannets at Lambert's Bay and the same three species with hake at Malgas Island. The major prey at Lambert's Bay was juvenile epipelagic fishes, measuring 50-110 mm, whereas larger epipelagic fishes measuring up to 330 mm and large pieces of hake offal were more important to gannet diet at Malgas Island. Larger fish occurred mainly in the summer months. The seasonal occurrence and abundance of juvenile fishes in the diet of gannets corresponded well with fishery catches, but the seasonal occurrence and abundance of mesopelagic fishes (adult Redeye Roundherring and

Onderbaadjie) in gannet diet was not related to their occurrence in purse-seine fishery catches. The occurrence of hake in gannet diet was highly seasonal despite its availability all year round. Saury is the least well known of the major prey species of the Cape Gannet. Available information on its distributional ecology were reviewed in this investigation. The occurrence of Saury, an oceanic species, in coastal waters was associated with the inshore occurrence of warm water and intense thermal fronts in summer.

Differences between the diets of breeding and nonbreeding birds were small, suggesting that the increased energetic demand of breeding did not greatly affect prey choice. A similar result was obtained for the North Atlantic Gannet (Kirkham _et_ _al_. 1985).

Gannets from Malgas Island fed south of Cape Columbine and apparently used three foraging strategies; inshore feeding on juvenile epipelagic fishes in cool waters, offshore feeding on larger epipelagic fishes in warmer waters and offshore scavenging at demersal trawlers. Feeding groups of these gannets varied in number from a single bird to thousands. The larger groups usually fed in association with Brydes Whales and Common Dolphins. In summer, gannets fed east of Cape Point in False Bay and possibly as far east as Danger Point. The foraging range was at least 200 km. Availability of epipelagic fishes to gannets at this time was apparently high, as suggested by the mean mass of regurgitations containing epipelagic fishes and proportion of birds handled with regurgitations comprising epipelagic fishes. Gannets breed in summer when the availability of food is apparently high. This would be expected if seabirds breed at the time of maximum food availability (Lack 1968). In winter, gannets roosting at Malgas Island did not apparently fly east of Cape Point and the foraging range shrank to about 120 km. The availability of epipelagic prey close inshore was low; regurgitation masses and proportion of birds handled which regurgitated epipelagic fishes were low. In winter gannets eat large quantities of hake which was available further offshore than epipelagic fishes.

Gannets from Lambert's Bay fed north of Cape Columbine. The size of feeding groups of these gannets was small and the frequency of associations with other predators were fewer. The foraging strategy of gannets from Lambert's Bay was apparently one of feeding on juvenile fishes in cool inshore waters throughout the year, although larger fishes occurred more frequently in summer. The foraging range of these gannets in summer was about 100 km, and shrank to about 75 km in winter. The recovery of stocks of South African Pilchard may change the feeding ecology of gannets in this area if large pilchard become increasingly available. gannets may then feed further offshore where adult pilchard tend to occur (Armstrong et al. in press). The pattern of seasonal availability of epipelagic prey was the same as at Malgas Island except that small epipelagic fishes (mainly Cape Anchovy) were more regularly available throughout the year.

Changes in the annual availability of epipelagic fishes between 1978 and 1986 are suggested by changes in the species composition of the diet, the annual mean mass of regurgitations comprising epipelagic fishes and the annual proportions of birds handled which regurgitated epipelagic fish. The Cape Anchovy became increasingly important in gannet diet from 1978 to 1982. After 1983, other species became more abundant in the diet. Availability of epipelagic prey as a whole was apparently lower from 1983 to 1985 than in the period 1978 to 1982 and in 1986. This is suggested by the steady increase of hake in gannet diet from 1981 to 1985 at Malgas Island, the higher contributions of hake to gannet diet at Lambert's Bay from 1983 to 1985 and lower masses of regurgitations containing only epipelagic fishes. A notable feature in the gannet diet at both localities has been the steady increase in the contribution of South African Pilchard from 1983.

Circumstantial evidence suggests that the availability of epipelagic shoaling fishes (Cape Anchovy, South African Pilchard, Saury) to gannets was directly related to their relative abundance as the seasonal occurrence and abundance of these species in gannet diet corresponded to their occurrence and abundance in fishery catches. There was no correlation between the absolute abundance of hake offal available to gannets and its contribution to gannet diet. It is suggested that its contribution to gannet diet was inversely proportional to the availability of epipelagic fishes inshore. It is a low-energy substitute available at some distance from the gannet colonies. The occurrence and abundance of mesopelagic fishes (adult Redeye Roundherring and Onderbaadjie) in gannet diet were not related to their availability to purse-seiners, but apparently inversely to the availability of epipelagic fishes inshore. Although the length-frequency distributions of fish species caught by gannets and purse-seine or research fishing at the same time in the same area were usually significantly different, modes seldom differed by more than 20 mm, suggesting that man and gannets were usually catching the same cohort.

The hypothesis that gannets prefer adult South African Pilchard to other sources of food, because of its high energy content, large size and occurrence in gannet diet in relation to abundance of prey as shown by purse-seine catches (Batchelor & Ross 1984; Davies 1956), is supported in this study. The shoaling characterisitics of South African Pilchard suggest that it is more vulnerable to gannets than Saury (the other important large prey) or Cape Anchovy (Anon. 1983). However, there is generally little information on the shoaling behaviour of fishes in the southern Benguela System. There was a significant correlation between the annual quantities of pilchard in the combined overall diet of gannet from Malgas Island and Lambert's Bay and in purse-seine catches made over the the range of operation of of the purse-seine fleet. Correlations over shorter time and distance scales were not significant. This was attributed to short-term variability and different sampling strategies by gannets and purse-seiners which are smoothed out over longer time and distance scales. A relatively strong year class may have arisen in 1983. Increases in the proportion of two-year-old pilchards in gannet diet in 1985 compared to previous years also suggested the 1983 year class was strong. If the abundance of pilchard in gannet diet is related to their absolute abundance, the increases in the percentage of pilchard in gannet diet at Algoa Bay, Malgas Island and Lambert's Bay suggest that the stock of South African Pilchard may have been gradually increasing. Even if the availability of other prey is high, the abundance of pilchard in gannet diet is likely to increase rapidly as the pilchard biomass increases. It is argued that the percentage of pilchard in the diet of gannets is a reliable indicator of the trend in pilchard abundance at low biomass levels when direct surveys are most vulnerable to bias.

Information from gannet diet may be used by fisheries managers to test assumptions about prey ecology on which the design of sampling systems and the interpretation of results might be based. For example, refinement of the understanding of the distribution and movements of South African Pilchard (Armstrong _et al_. in press) in South African waters depended in large part on information from gannet diet. The understanding of the distribution of a species is vital to the design of direct surveys of their abundance. Similarly, Duffy et al. (1985) used information on the diet of Jackass Penguins at Dyer Island to propose possible distribution patterns of juvenile Cape Anchovy around the western Cape. In this thesis, various data sources, including gannet diet, were used to examine the distribution of Saury. The concurrence of Saury with adult Redeye Roundherring in catches and to alesser extent with adult Pilchard suggests that both species are associated with the shelf edge and frontal zone habitats which exist in summer off the western Cape. The use of shelf-edge habitats by older fishes (Armstrong et al. in press) may be a general phenomenon among epipelagic fishes in the western Cape which requires investigation. Factors determining the changes in habitat use by and perhaps shoaling behaviour of epipelagic shoaling fishes as they grow older are not well understood in the western Cape.

The effects of changes in seabird population size on the diet of seabirds must be considered in relation to long-term monitoring. Ashmole (1963) suggested that competition for food in the vicinity of seabird breeding colonies might regulate population size. Hunt et al. (1986) found that one or more measures of reproductive performance (clutch size, growth rate, fledgling mass and breeding success) were inversely related to population size in several northern seabirds, and suggested density-dependent depression of reproductive performance. The causal mechanisms have not been demonstrated, but presumably relate to reduction in the rate and total amount of food delivered to the chicks, perhaps through intraspecific interference on the feeding grounds (Hunt et al. 1986). Furness & Birkhead (1984) suggested that the spacing of seabird colonies around Britain suggested competition for food around colonies. That seabirds are able to consume significant parts of the prey biomass in the vicinity of colonies has not been clearly demonstrated (Hunt et al. 1986), although their impact on fish stocks as a whole may be large (Furness & Cooper 1982; Furness 1982; Furness & Monaghan 1986). In this study, gannet populations remained relatively stable (Crawford 1983c; Chapter 2). Changes in colony size may affect dietary parameters of the Cape Gannet, and any long-term monitoring programme must attempt to separate the effects of variation in resource abundance and density-dependence. Changes in resource abundance have the potential to be large and frequent (Crawford et al. 1980b; Parrish et al. 1981), compared to slower and less variable changes in the demands on the resource by gannets through density-dependent effects (Maccall 1984).

Further investigation is necessary to improve (a) the definition of what constitutes a significant change in the monitored aspects of gannet biology, principally those relating to diet and (b) interpretation of such changes. An adequate analysis of short-term variability in gannet diet is necessary to determine whether changes in diet and other parameters may be attributed to sampling variance or to significant changes in the composition of the resource. This is a complex problem which is being studied by J. Colclough (Port Elizabeth Museum). Improved interpretation of changes in diet will result from an improved understanding of the ecology of predation by seabirds on their prey species, principally with regard to the shoaling behaviour of the prey (the size, timing, duration and location of surface occurrences in relation to the length of the fishes) and their energy content relative to season and length. More data are required on the feeding patterns of gannets, such as how long they search for prey, the relative importance of prey caught singly or in feeding bouts from a single shoal and whether gannets follow distinct strategies such as offshore scavenging versus inshore feeding. It may then become possible to construct a model of the energetic profitability of various feeding strategies which could predict the feeding strategy and hence prey selection of gannets given the shoaling characteristics of the prey and its distance from the colony.

Hydroacoustic estimates of the abundance of fishes in specific areas should be used to assess whether gannets select pilchard ahead of anchovy. Unfortunately, it appears unlikely that direct estimates of Saury abundance will become available in the near future. However, hydroacoustic estimates should not be regarded as the sole test of whether gannets select species preferentially because the abundance of fishes in shallow water cannot be estimated. Elsewhere, studies of predator diets and distribution of their prey determined by hydroacoustics and trawling have not always been in agreement; the size of krill eaten by predators in the Southern Ocean was similar to that caught by research trawls in one area but not in another (Croxall _et al_. 1985). The distribution of murres _Uria lomvia_ and _U. aalge_ was not closely related to the distribution of fish prey detected by acoustics and correlated significantly to the distribution of zooplankton in one of two years only (Woodby 1984). Seabirds respond to changes in prey distribution at various scales of time and distance (Anderson _et al_. 1980; Schneider & Duffy 1985; Chapter 9) in relation to ocean features such as thermal fronts (Schneider 1983; Briggs _et al_. 1984), the presence of predators (Batchelor & Ross 1984; Chapter 7) or weather (Manikowski 1971). Therefore direct surveys of prey populations may not collect data at the correct scale of resolution to assess relationships between the distribution and diet of seabirds and the distribution and abundance of their prey, if such scale-dependent variability is not taken into account.

The use of predators in providing information for fisheries managers has some advantages. Firstly, ongoing monitoring is cheap and inexpensive, although initial research may include costly aerial and ship surveys. Seabirds can be monitored for long periods of the year, and in the case of the gannet, all year. They are most useful in determining changes in fish abundance at low population levels where conventional techniques are at their weakest. Whereas catchability of fishes to purse-seine fisheries is not proportional to their abundance (Ulltang 1980), changes in seabird diet in response to changes in the availability of preferrred prey are likely to be large at low population biomasses (Chapter 9). Seabirds respond rapidly to catastrophic changes (e.g. Schreiber & Schreiber 1984). Again, as a prey becomes more abundant, so do hydroacoustic surveys become more reliable, and the responses of predators are more likely to run into saturation effects where large increases in prey abundance produce small changes in responses.

An increasing number of studies are showing correlations between variables of seabird biology and estimates of fish abundance using catch-based statistics (Crawford & Shelton 1978, 1981; Hislop & Harris 1978; this study) or direct surveys (Hunt & Butler 1980; Anderson _et_ _al_. 1980,1982; Schaffner 1986). However, the use of seabirds in conventional fisheries science will remain peripheral until techniques for using qualitative data are developed. Possible approaches for incorporating such types of data have been proposed by Bradbury _et_ _al_. (1986) and Starfield & Bleloch (1986).

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