PENGUINS AND PURSE-SEINERS: COMPETITION OR CO-EXISTENCE?

by

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1. SUMMARY

The relationships between the pelagic purse-seine fishery and Jackass Penguins (*Spheniscus demersus*) were investigated at Saldanha Bay, on the south-western coast of South Africa, between December 1982 and August 1983. The distribution at sea and the foraging behaviour of Jackass Penguins were examined by running standard transects with a sailboat in waters close to the birds' breeding islands. The use of a sailboat permitted close observation of foraging penguins with minimal disturbance. Penguin numbers at sea were lowest in December, when birds were confined to the breeding islands during moulting and were high in March and July during breeding peaks. While most penguin group sizes were small (one or two birds), over 44% of penguins occurred in groups of more than 10 birds. Three stereotypic penguin group formations occurred: 'facing-search', 'line-abreast', and 'pointed-ovoid'. Penguins also foraged in association with other seabirds and marine mammals.

Jackass Penguin breeding biology and chick growth-rate were investigated on Marcus Island (33°S, 17°58'E), Saldanha Bay, between 7 February and 20 June 1983. Chick growth-rate was very variable, but appeared to be greatest in March and April. Penguin nest desertion was highest during early February but decreased thereafter. The rate of nest desertion was not significantly higher in colonial than in non-colonial nesting penguins. Nest desertions were most common during the egg phase and decreased with increasing age of the chick. Heat-stress, depredation by Kelp Gulls, and human disturbance appeared to be the major causes of nest desertion. Sedating adult penguins prior to handling proved an effective method of reducing the
incidence of nest desertion resulting from human disturbance. Incubation shift length was significantly higher in February than in any other month of the study. No significant difference was found in the length of incubation shifts between colonial and non-colonial nesting penguins.

The diet of Jackass Penguins was investigated throughout the study period using a stomach contents sampling device. One hundred and seventy-one stomach samples were collected between 7 February and 20 June 1983. These samples yielded 2,098 food objects, accounting for 11 species, most of which were fish; particularly Cape Anchovy (Engraulis capensis). Fish prey length varied between 40 and 130 mm and mean weight of stomach samples between 80 and 225 g. Stomachs were found to be significantly fuller towards the end of the study period.

The 1983 commercial purse-seine fishing season ran from 1 January until 30 June 1983. Eleven per cent of the fishing fleet effort was concentrated in Saldanha waters (ICSEAF area 8). Sixty-four per cent of fishing effort in Saldanha waters took place during the penguin growth study (7 February-20 June). Fishery catches were atypical for Saldanha waters. Round-herring (Etrumeus teres) contributed 62% to the total catch, Cape Anchovy only 28%, and Cape Pilchard (Sardinops ocellata), Horse-mackerel (Trachurus trachurus) and Lantern Fish (Lampanyctodes hectoris) 9%. Round-herring were more abundant than in recent years, possibly due to the incursion of warm, oceanic water into the fishing grounds. Fishery search-effort for Cape Anchovy was less intense than in recent years, due to confusion among fishermen regarding catch-quotas.

Penguin chick growth showed little correlation with commercial fishery catches. Only mid-age (15-42 day-old) and old
(> 42 day-old) chicks showed a significant positive correlation with fishery catches. Insignificant correlations between chick growth and fishery catches are attributed, in part, to the gross nature of the fishery catch statistics. Fish prey size in penguins overlapped considerably with sizes of fish caught by the fishery. Penguins took a greater proportion of small (30-70 mm) Cape Anchovy than did the fishery. Interpretation of the data combined with circumstantial evidence from purse-seine fishermen suggest that large, commercially exploitable, shoals of Cape Anchovy frequently move close inshore over unfishable grounds. Evidence also suggests that these large shoals may disperse into small, scattered shoals undetectable by conventional echo-sounders. Such phenomena are viewed as potentially beneficial to foraging Jackass Penguins which must rely on a spatially and temporally predictable food supply. However, the implication that both fishery and penguins are, to a large extent, reliant on the same fish shoals, is viewed as a cause for concern in the light of proposed changes in commercial fishing practice.
2. GENERAL INTRODUCTION
2. GENERAL INTRODUCTION


The recent upsurge of interest in the biology of the Jackass Penguin reflects a growing concern over the status of South Africa's only breeding penguin. Jackass Penguin populations have decreased dramatically due to man's activities on and around the breeding islands over the last 100 years (Frost et al. 1976b, Shelton et al. in press). Although penguins are known to have been present in the diet of pre-European inhabitants (Raven-hart 1967), and early seafarers and European settlers used penguins as a source of food and fuel (Thom 1952), it was commercial egg-collectors and guano-scrapers who had a devastating effect on Jackass Penguin populations (Frost et al. 1976b).

Egg collecting began in the 17th Century soon after the Cape of Good Hope area was colonized (Rand 1949, Thom 1952, Westphal and Rowan 1971) and by 1800 Jackass Penguins were extinct on Robben Island (33 48'S, 18 22'E), Table Bay, close to Cape Town. Egg collecting was confined to the Cape islands (Bird Island (Lambert's Bay), Malagases, Marcus, Jutten, Vondeling,
Dassen Islands, Seal Island (False Bay) and Dyer Island. Penguins at Dassen Island (33 25'S, 18 25'E) contributed much of the egg-crop (Cott 1953). Approximately 13 million eggs were collected between 1900 and 1930 (Frost et al. 1976b, Shelton et al. in press). Few attempts were made to develop a rational strategy of egg-exploitation. For example, egg collecting was restricted to certain months of the year, and collecting of eggs was rotated annually among the islands. Both these measures proved ineffectual as a management strategy and a decrease in penguin numbers was reported in many Government Guano Administration reports between 1890 and 1950 (Frost et al. 1976b). The harvest for the years 1930-60 was just over 2.5 million (Shelton et al. in press), a decrease in egg yield of just over 80% in 30 years. As a further attempt to halt the decrease of penguin numbers, egg-collecting was prohibited in 1936-37 in order that the colony could "recuperate" (Cott 1953). Despite this two-year respite, egg yields continued to decrease until commercial egg-collecting finally ceased in 1969, due to increased harvesting costs.

The guano-scraping industry also had severe effects on breeding Jackass Penguins, particularly on the islands off South West Africa/Namibia where guano exploitation was intensive and largely uncontrolled (Eden 1846), as it was also on Malagas Island (33 03'S, 17 55'E) (Burman and Levin 1974). Breeding birds were driven off their nests by gangs of guano workers who removed the deposits of guano into which penguins burrowed. Jackass Penguins then had to nest on exposed bedrock or loose subsoil. On Bird Island, Lambert's Bay, the centre of the island was laid with flat stones to facilitate guano-scraping (Jarvis and Cram 1971). On such open nests, Jackass Penguins and their chicks are subject to heat-stress (Frost et al. 1976a),
predation, (Cooper 1974), and human disturbance (Berry et al. 1974, Hockey and Hallinan 1981), resulting in a reduction of nesting success (Frost et al. 1976b, Cooper 1980). On Dassen Island, the construction of a low concrete wall, believed to have been built to facilitate egg collecting by concentrating breeding birds in sandy burrow areas (D.M. Price pers. comm. to J. Cooper), must have excluded Jackass Penguins from much suitable nesting habitat. Guano-scraping has all but ceased as a commercial concern on South African penguin breeding islands, but still continues on Malagas Island, between March and May, where approximately 160-300 metric tonnes are removed annually (Sea Fisheries Research Institute unpubl. data).

There is concern over another threat to the Jackass Penguin: spillages of petroleum oil from ocean-going tankers. When the Suez Canal was closed in 1967 there was a huge increase in oil-tanker traffic around the Cape coast. Petroleum oil clogs seabird feathers, removing insulating and waterproofing properties. Ingestion of the oil through preening clogged feathers leads to severe inflammation of the digestive-system, such that the bird cannot assimilate food and ultimately dies of starvation (Bourne 1976). Being flightless, penguins are particularly susceptible to oiling at sea and, although only a small percentage of the present population suffers from effects of oiling (Frost et al. 1976b, Morant et al. 1981), there is concern that a major oil spill close to penguin breeding islands could have catastrophic effects.

Despite the effects of commercial egg collecting and guano-scraping and the constant threat of a major oil-spill, dwindling fish stocks due to overfishing by the inshore purse-seine fishery (Davies et al. 1981, Butterworth 1983) present the
greatest threat to the continued existence of Jackass Penguins in the wild (Frost et al. 1976b, Burger & Cooper in press, Shelton et al. in press). The pelagic purse-seine fishery in South Africa began during the 1930's but detailed catch statistics are only available from 1950 (Newman and Crawford 1980). In the early years, the fishery was based on Pilchard and Horse-mackerel and catches increased to a maximum during the early 1960's (Butterworth 1983). However, in 1964 the South African Pilchard industry collapsed (Stander and Le Roux 1968). Pilchard stocks off South West Africa also decreased drastically around this time (Cram and Visser 1973). Decreased Pilchard egg production and a reduction in size-classes suggest that overfishing was a major factor in these stock collapses (Newman and Crawford 1980). Catches of Horse-mackerel have also decreased substantially over the last 20 years (Newman and Crawford 1980).

In response to low Pilchard and Horse-mackerel catches, small-meshed nets (12.7 mm) were introduced in 1964 which allowed Cape Anchovy to be caught (Newman and Crawford 1980). Today, the South African pelagic fishery is largely dependent on Anchovy, which is reduced to fish meal and oil (Butterworth 1983). Many fisheries biologists believe that the Cape Anchovy stock is being overexploited and is in danger of collapse, as occurred with Pilchard and Horse-mackerel stocks (Davies et al. 1981, Butterworth 1983).

During the 1960's, Pilchard was the dominant species in the diet of the Jackass Penguin in the south western Cape (Rand 1960). The collapse of Pilchard stocks resulted in a dietary change by the Jackass Penguin. Currently, the Cape Anchovy forms the bulk of the diet with a frequency of occurrence of 80% (Wilson in press b). Anchovy have an erratic shoaling behaviour
(Crawford et al. 1980) and lower energy content (Batchelor and Ross 1984) than Pilchard and this change to a less predictable, less energy-rich food supply is thought to have contributed to the continuing decrease of penguin populations on the west coast of South Africa (Frost et al. 1976b, Burger & Cooper in press). Changes in the abundance of Anchovy around the breeding islands, caused by over-exploitation by the fishing industry, could have major effects on the population of Jackass Penguins on the west coast of South Africa.

Most studies on Jackass Penguins on the west coast of South Africa have concentrated on the breeding biology, physiology, and behaviour of penguins in the colonies (e.g. Erasmus and Smith 1974, Frost et al. 1976a, Siegfried 1977, Cooper 1978, Eggleton and Siegfried 1979, Cooper 1980, Hockey and Hallinan 1981, Broni 1982, 1983). Less work has been carried out on the distribution and behaviour of birds at sea (e.g. Rand 1960, Siegfried et al. 1975, Cooper 1977b, Wilson in press c) and, in particular, on the nature and extent of the presumed competition between the purse-seine fishery and Jackass Penguins.

The primary aim of my study was to assess the degree of overlap between Jackass Penguins and commercial fishing in the Saldanha Bay area, on the south western coast of South Africa. Do Jackass Penguins compete directly with the fishery, or is the relationship one in which neither party significantly harms the other? I adopted two approaches to this problem: first, I used a sailboat to examine penguin distribution and behaviour at sea in and around Saldanha Bay, between December 1982 and August 1983; I collected data on penguin group size and formation, dive duration and associations between foraging penguins, other seabirds, cetaceans and seals. Secondly, I investigated aspects
of penguin breeding biology, such as nest desertion, length of nest-attendance shifts, diet and, in particular, chick growth at Marcus Island. I examined the effects of commercial fishing on breeding Jackass Penguins by comparing short-term increments in penguin chick growth-rate, incidence of nest desertion, and length of nest-attendance shifts with fishery landings throughout most of the commercial fishing season, which in 1983 ran from 1 January to 30 June.

In Section 3, I describe the study area and include a brief history of the penguin colony on Marcus Island. The foraging behaviour and distribution of Jackass Penguins at sea, in and around Saldanha Bay, are discussed in Section 4. Section 5 presents a comparison between penguin chick growth and fishery catches. I also discuss penguin diet, and factors influencing the incidence of nest desertion and length of nest-attendance shifts. Finally, in Section 6, I assess the implications of the results of my study for the future status of the Jackass Penguin on the south western coast of South Africa and discuss the possible effects of a new commercial fishing season.
3. STUDY AREA
3. STUDY AREA

I carried out my field work in Saldanha Bay (33°03'S, 17°58'E) and adjacent waters (Area 8 International Commission for South-east Atlantic Fisheries (ICSEAF); Fig. 1). The bay is situated about 100 km north of Cape Town and lies in the northward extension of the mediterranean-type climatic belt, which encompasses the coastal areas of the south western Cape Province (Schulze 1965). The mean annual rainfall is c. 300 mm and seasonal temperature fluctuations are small with minimum temperatures normally well above freezing point, and maximum temperatures of 30°C or more (Flemming 1977). In summer, the wind pattern is characterized by a strong south-westerly component, a local derivative of the south-east trade-winds which, in most years, blow persistently during the summer months (September - April) and intermittently during the winter months. The inshore waters respond to the prevailing winds which may affect the water column down to a depth of 50 m or more (Flemming 1977). Upwelling of cold nutrient-rich water has been observed outside Saldanha Bay in summer (Pearce and Smith 1974) and long periods of stable windy conditions in summer result in transport of water to the north, although surface counter-currents occur inshore (Duncan and Nell 1969). In winter, the general direction of water movement varies with the local weather cycle and is controlled by the rate at which cyclonic low-pressure cells pass through the area. There appears to be little direct interchange of water between the sea and the bay (Shannon and Stander 1977). In winter, sea surface temperatures outside Saldanha Bay rarely exceed 15°C, whereas inside the bay the surface temperature may be 16-18°C (Clowes 1950). The salinity of water inside the bay
differs very little from that of open water, being about
34.9 /oo (Flemming 1977). The inshore sea bottom is very rocky,
as is much of Saldanha Bay (Flemming 1977), preventing the
fishing industry from using purse-seines. Farther out to sea,
beyond 15 km, the bottom is smooth or muddy or waters are deep
enough to allow such fishing.

The study area contains four islands with Jackass Penguin
colonies (Marcus, Jutten, Malagas, and Vondeling). Three of
these islands are situated within Saldanha Bay (Marcus, Malagas,
and Jutten). Vondeling Island lies 7 km outside and south of
Saldanha Bay about 1 km from the mainland.

Due to their crepuscular and troglodytic nature, Jackass
Penguins are difficult birds to count accurately on the breeding
grounds (Frost et al. 1976b, Shelton et al. in press). Using
aerial photographic techniques, Rand (1963) estimated a
population of 30 100 breeding adults on the four islands
(Marcus, Malagas, Jutten and Vondeling) in 1956. Furness and
Cooper (1982), using previously unpublished data to supplement
earlier counts made by Rand (1963), calculated a total
population for the Saldanha islands of 21 000 breeding pairs in
1977-78. The latest estimates (based on counts made in 1978)
indicate a total summer breeding population for the Saldanha
islands (including Vondeling) of 11 276 breeding pairs (Shelton
et al. in press). The great discrepancy between the two counts
indicates the problems of accurate censusing.

My work at the breeding islands in Saldanha Bay was
concentrated at Marcus Island, a small (11 ha) former island,
now connected to the mainland at Hoedjies Point by a 2 km
breakwater of sand and rock erected as part of a harbour
development and completed in February 1976 (Cooper et al. in
The Jackass Penguin is the principal breeding seabird at Marcus Island, but many other seabird species breed, or have bred, on the island including Cape (Phalacrocorax capensis), Crowned (P. coronatus), Bank (P. neglectus), and White-breasted (P. carbo lucidus) Cormorants, Kelp and Hartlaub's Gulls (Larus dominicanus and L. hartlaubii), Caspian Tern (Sterna caspia) and Swift Tern (S. bergii) (Brooke and Crowe 1982).

Jackass Penguins nest over most of Marcus Island at low densities but several large and dense colonies occur on the western side of the island (Fig. 1). In one of these colonies ('a' in Fig. 1), the penguins nest predominantly on the surface, whereas in the other ('b' in Fig. 1) they nest under rocks. Elsewhere on the island, penguins occupy a variety of nesting habitats: exposed-surface nests on sand, rock or guano, under bushes, burrows and inside disused buildings.

Since the completion of the causeway in 1976, eight mammal species known to be potential bird predators have been recorded on the island (Cooper et al. in press a). The most frequently recorded species have been Cape Grey Mongoose (Herpestes pulverulentus), Yellow Mongoose or Bushy Tailed Meerkat (Cynictis penicillata), Small Spotted Genet (Genetta genetta), and Cape Fox (Vulpes chama), while Bat-eared Fox (Otocyon megalotis), Domestic Dog (Canis familiaris) and a rat (Rattus sp.) have also been recorded (Cooper et al. in press a).

The bird species most commonly killed by predators were Common Terns (Sterna hirundo), African Black Oystercatchers (Haematopus moquini), Kelp Gulls and Jackass Penguins (Cooper et al. in press a). Small Spotted Genets were probably responsible for most, if not all, of the penguin mortality (Cooper et al. in press a). An anti-predator wall, constructed in 1980-81 and
modified in 1982 has considerably reduced the predation of seabirds by mainland predators (Cooper et al. in press a). Three rodent species have successfully colonized Marcus Island: House Mouse (*Mus musculus*), Striped Field Mouse (*Rabdomys pumilio*), and Vlei Rat (*Otomys unisulcatus*), but they appear to have no adverse affects on resident breeding seabirds, their eggs, or chicks (Cooper et al. in press a, pers. obs).
4. SOCIAL AND SPATIAL PATTERNS OF FORAGING

BY THE JACKASS PENGUIN
4. SOCIAL AND SPATIAL PATTERNS OF FORAGING BY THE JACKASS PENGUIN

4.1 INTRODUCTION

The introduction of measures to conserve the Jackass Penguin requires an understanding of the foraging behaviour of the Jackass Penguin and how foraging overlaps with the activities of the commercial fishery.

This section examines the foraging behaviour of the Jackass Penguin based on observations at sea from a sailboat, between December 1982 and August 1983. In particular, I studied the species' spatial and temporal pattern of foraging in inshore waters, as well as group size and formation, dive duration and associations between foraging penguins, other seabirds, and marine mammals.

4.2 METHODS

4.2.1 ESTIMATING PENGUIN NUMBERS AT SEA

Penguins are difficult birds to study at sea for three reasons: they have very low profiles on the water and thus are difficult to see; they are easily frightened by the noise of an approaching boat and may dive or porpoise away; and they spend a great deal of time underwater either travelling or foraging (Siegfried et al. 1975) which may result in underestimates of numbers present in an area. To minimize these problems, I made my counts from an 11 m sail-boat which had a speed, under sail, of 5-12 km h⁻¹. Slow speed and absence of engine noise enabled me to approach to within 5-10 m of feeding penguins with little apparent effect on their behaviour. Observations were made from a projecting pulpit at the bow of the boat with an observing
height of 2 m. I watched a 180° arc (90° on either side of the boat), extending to a distance of 150 m, recording any penguins observed in this area. On the first two transects, I checked the distance from the yacht to each penguin by means of a handheld optical rangefinder. Of the 40 penguins that I estimated by eye as falling within 150 m of the boat, 80% fell within this range according to the rangefinder. The motion of the sailboat made it impractical to verify every sighting using the rangefinder so, for the remaining period of study, I estimated distances using the naked-eye.

I attempted to run a transect along a set course inside and across the mouth of Saldanha Bay (Fig. 2) during daylight hours between 07h30 and 17h00 hours on 14 days between December and August 1983. The positions of all penguins observed within the transect were plotted on coastal navigation charts by means of triangulation, using a hand-held compass. Plotted locations appeared accurate to within 0.5 km in the inshore waters surveyed. On two days at sea (7 April and 1 July), I terminated the transect early to make observations on intense feeding activity. Data collected during these periods are presented separately.

Transect distance travelled was not equal for all days at sea, hence counts are not directly comparable between transects. To correct for this bias, I first stratified the data with respect to distance from the nearest breeding island (0-1 km, 1-2 km, 2-3 km, 3-4 km, 4-5 km, 5-6 km and > 6 km) and calculated the distance travelled in each of these sectors on each day at sea. I then applied a correction factor to each of the counts as follows:

\[ N_p = \frac{2 \times X}{7Y} \]
where, \( N_p \) = the number of penguins observed had equal distance been travelled in each of the 7 sectors.

\[
Z = \text{Number of birds observed in that sector.}
\]

\[
X = \text{Total distance covered in all sectors on that transect.}
\]

\[
Y = \text{distance travelled in that sector.}
\]

This correction factor results in an estimate of the number of penguins observed had equal transect distance been covered in each of the seven sectors on each day at sea (Table 1a). These data were then summed over all transects for each day at sea and divided by twice the transect distance to give a "corrected mean" number of penguins per 0.5 km for each day at sea (Fig. 3).

To assess the degree of bias imposed on the penguin distribution data by morning and afternoon peaks of departure and arrival at the breeding islands (Frost et al. 1976a, R.P Wilson unpubl. data), I stratified the transect data further, with respect to time of day (08h00-10h00, 10h00-15h00, 15h00-17h00) (Table 1b). I then tested these data using chi-squared test under the null hypothesis that there is no significant difference in the numbers of birds observed at different times of the day, at increasing distance from the nearest breeding island.

I recorded penguin group size and spacing of birds within groups as a function of 'bird-lengths' (one 'bird-length' = approx. 0.5 m). I plotted percentage frequency of different group sizes for all days at sea. Inter-bird distance was compared with group size. I recorded dive-duration using a
### Table 1A

**TRANSECT DATA SHOWING DISTANCE TRAVELLED AND JACKASS PENGUIN DISTRIBUTION WITH RESPECT TO DISTANCE FROM THE NEAREST BREEDING ISLAND FOR EACH DAY AT SEA**

<table>
<thead>
<tr>
<th>Distance from nearest breeding island (km)</th>
<th>0-1 km</th>
<th>1-2 km</th>
<th>2-3 km</th>
<th>3-4 km</th>
<th>4-5 km</th>
<th>5-6 km</th>
<th>&gt; 6 km</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td>Z</td>
<td>Y</td>
<td>Np</td>
<td>Z</td>
<td>Y</td>
<td>Np</td>
<td>Z</td>
</tr>
<tr>
<td>------</td>
<td>-----</td>
<td>-----</td>
<td>------</td>
<td>-----</td>
<td>-----</td>
<td>------</td>
<td>-----</td>
</tr>
<tr>
<td>7/12</td>
<td>1</td>
<td>6.25</td>
<td>1.52</td>
<td>2</td>
<td>8.75</td>
<td>1.09</td>
<td>7</td>
</tr>
<tr>
<td>20/12</td>
<td>4</td>
<td>2.25</td>
<td>19.55</td>
<td>4</td>
<td>17.75</td>
<td>2.48</td>
<td>9</td>
</tr>
<tr>
<td>21/12</td>
<td>9</td>
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<td>5.84</td>
<td>33</td>
<td>6.25</td>
<td>11.71</td>
<td>25</td>
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<tr>
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<td>34</td>
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<td>26.24</td>
<td>1</td>
<td>9.0</td>
<td>1.00</td>
<td>2</td>
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<td>7</td>
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<td>7.36</td>
<td>5</td>
<td>4.75</td>
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<td>16</td>
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<td>30</td>
<td>3.75</td>
<td>11.43</td>
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<td>17</td>
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<td>34.10</td>
<td>31</td>
<td>21.25</td>
<td>11.50</td>
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<td>5.38</td>
<td>1</td>
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<td>11.25</td>
<td>12.50</td>
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</tr>
<tr>
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<td>9.75</td>
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<td>4.56</td>
<td>27</td>
<td>10.5</td>
<td>10.74</td>
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</tr>
</tbody>
</table>

**Z** = No. of penguins observed  
**Y** = transect distance covered in each sector  
**Np** = Corrected penguin nos. per sector  
$$Np = \frac{Z}{Y} \times Y$$
### TABLE 1B

DISTRIBUTION OF JACKASS PENGUINS IN AND AROUND SALANHA BAY WITH RESPECT TO DISTANCE FROM THE NEAREST BREEDING ISLAND AND TIME OF DAY

<table>
<thead>
<tr>
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<th>2-3</th>
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<td>888.6</td>
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<td>34.8</td>
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(Excluding two days when I deviated from the transect to investigate feeding behaviour)

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<td>114.7</td>
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<td>12.1</td>
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</table>
Mean number of penguins

Date of transect

7 Dec 20 Dec 21 Dec 3 Jan 10 Jan 9 Mar 10 Mar 17 Mar 7 Apr 3 Jun 7 Jun 28 Jun 1 Jul 21 Aug

n = 2248
stopwatch to the nearest 0.1 s. In the case of large groups which dived as a unit but did not surface simultaneously I took the mean dive-duration as the mid-point between the first and last bird surfacing (Ainley 1972). I plotted dive duration in comparison to group size. Finally, I noted aspects of the foraging behaviour of Jackass Penguins, such as group size, shape of groups, formation and dispersal; incidence and synchrony of 'head-dipping' (Siegfried et al. 1975); and interactions with seabirds such as Cape Gannets (Sula capensis), Cape Cormorants, Sooty Shearwaters (Puffinus griseus), and terns (Sterna spp.), and marine mammals such as Dusky Dolphins (Lagenorhynchus obscurus), Bryde's Whales (Balaenoptera edeni) and Cape Fur Seals (Arctocephalus pusillus).

4.3 RESULTS
4.3.1 DISTRIBUTION AT SEA
Although the sailboat allowed close observation of penguin foraging, its use was dependent on the weather. Lack of wind prevented complete coverage of the transect on 12 of the 14 days at sea. Numbers of penguins observed per 0.5 km of transect for each day at sea were lowest in December when most birds are confined to the breeding islands during moult (Fig. 3; Cooper 1978). Numbers at sea peaked in March/April with a subsidiary peak in July (Fig. 3).

At sea, non-breeding adult Jackass Penguins are indistinguishable from breeders, but immature/juvenile birds can be identified at sea by their brown plumage and partial head moult. A total of 44 immature/juvenile penguins were observed during the transects. This constituted only 2.5% of the total number of penguins observed. I observed immature/juvenile penguins during all months of the study except March, and they
were most abundant at sea during December and January (Fig. 3a).

The comparison between time of day and numbers of penguins observed at different distances from the breeding island yielded a highly significant result ($X^2 = 486.1 > 21.03$, d.f. = 12, $P < 0.001$). If the data from the two days when I deviated from transect line to investigate feeding behaviour (7/4 & 1/7) are excluded in the analysis, the result is still highly significant ($X^2 = 228.5 > 21.03$, d.f. = 12, $P < 0.001$), suggesting that the number of penguins observed was influenced by the time of day.

Penguins appeared to feed close inshore (Fig. 4). In six of the 14 transects where penguins did not occur throughout the transect, the mean distance from shore at which the last foraging penguin was seen was 3.6 km (s.d. = 1.34); however, penguins were still seen foraging to the ends of transects extending 2.5, 2.5, 3.5, 4, 4, 6.2, 6.5 and 7 km from the shore (Fig. 4). In general, penguins occurred in greatest numbers less than 3 km from the nearest breeding island during most of the day (08h00-15h00), although large concentrations of penguins were also encountered in the 4-5 km sector between 15h00-17h00 (Fig. 4a, 4b).

4.3.2 GROUP SIZE AND BEHAVIOUR
Penguin group size at sea during transects ranged from 1 to 50 birds (mean = 2.2, s.d. = 13.1, median = 1, n = 506). However, larger groups of between 50 and 150 penguins occurred on the two days (7 April, 1 July), when I left the transect course to investigate feeding behaviour. Single penguins occurred most frequently (Fig. 5). Three group formations were characteristic of intense feeding activity: 'Pointed-ovoid' formation was most common in groups of more than 10 penguins (mean = 27.7, s.d. =
Distance to nearest breeding island (Km)
Figure 4. Greatest distance from mainland at which Jackass Penguins were seen during 14 transects between December 1982 and August 1983.
Maximum distance from land reached on transect

Range over which penguins were observed

Distance from nearest mainland (km)

Date of transect

7 Dec 20 Dec 21 Dec 3 Jan 10 Jan 9 Mar 10 Mar 17 Mar 7 Apr 3 June 7 June 28 June 1 July 21 Aug
Figure 4a. Distribution of penguins in the study area with respect to time of day and distance to the nearest breeding island, for all days at sea.
Distance from nearest breeding island (Km)

No. of penguins observed (Np)

n = 2248

Distance categories:
- 0-1
- 1-2
- 2-3
- 3-4
- 4-5
- 5-6
- 6
Figure 4b. Distribution of penguins in the study are with respect to time of day and distance to the nearest breeding island, excluding two days (7/4 & 1/7) when deviations from the transect occurred.
Distance to nearest breeding island (Km)
Figure 5. Frequencies of Jackass Penguins in groups of different sizes.
Frequency of foraging groups

Frequency of individuals

n = 435 groups

Group size

Percentage penguins observed
24.6, median= 22.5, n= 12; Fig. 6). The characteristic feature of this formation was the presence of two or three penguins forming a leading apex in the direction of travel just ahead of a main oval-shaped formation of penguins. 'Head-dipping' in these groups was not synchronous. In many cases, only the penguins on the perimeter head-dipped, whereas those in the centre held their heads high and erect. This resulted in a delay of 1-2 s between diving by the birds on the perimeter and those in the centre. 'Line-abreast' formation was most common in groups of 4-5 and 11-20 birds (Fig. 6), but was also observed in larger groups (mean= 12.8, s.d.= 7.52, median= 12, n= 15). These penguins formed a line at right angles to the direction of travel with each bird separated from its neighbour by about 1-2 bird lengths (0.5-1.0 m). All birds head-dipped asynchronously as they swam slowly forward in a line. 'Facing-search' formation was observed in small groups of fewer than five penguins (mean= 2.55, s.d.= 0.68, median= 2, n= 20). During 'facing-search', penguins faced each other at distances of 3-4 bird lengths or more (1.5-2.0 m) and head-dipped while surface-swimming slowly towards each other. Calling between penguins was common.

There appeared to be a relationship between bird-spacing and group size. Comparing groups of 20 penguins with groups of two penguins, bird-spacing within groups of 20 was significantly less at the 10 % level, but not at the 5 % level (t= 1.46, P> 0.05 <0.1, n= 59).

Penguin behaviour at sea changed rapidly. A penguin, preening one minute, might be travelling or diving the next. Similarly, a group in 'pointed-ovoid' formation might then spread out into 'line-abreast' or split into smaller groups and begin 'facing-search'. I also observed small groups coming together to form larger groups, changing from one type of
Figure 6. Frequency of different Jackass Penguin social group formations compared to group size.
formation to another. This continual group formation and dispersal was most evident at times of intense feeding activity. On six occasions during intense feeding activity, I observed solitary penguins calling and coming together to form groups. These groups would then dive and either surface together as a group, having travelled approximately 20 m underwater, or surface asynchronously and dispersed, before calling and coming together again.

Based on group sizes of foraging penguins encountered on the transects, 73% of all foraging groups involved either one or two birds, and only 4.6% involved more than 10 penguins. If the data are included from the two days (7 April, 1 July 1983) when I investigated feeding behaviour off the normal transect line, then groups of 10 birds and over still comprise only 5.8% of all groups observed. However, group sizes of one and two penguins represented only 30% of all penguins observed foraging, while 44% of all penguins observed occurred in groups of 10 birds or more (Fig. 5).

The median dive duration of all penguins observed during the 14 days at sea was 23 s (mean = 26.8, s.d. = 20.2 s, n = 138). Dive duration and group size were significantly correlated (r = 0.18, P < 0.001, n = 143). I distinguished two types of dive: travelling and foraging. A group which dived as a unit and surfaced more than 50 m from its dive position, still as a unit, was considered to be travelling. A group which dived as a unit and surfaced dispersed in approximately the same spot was considered to be foraging. The median dive time of travelling penguins was 26 s (mean = 28.8 s, s.d. = 23.8, n = 53) and of foraging penguins 22 s (mean = 25.8 s, s.d. = 17.3, n = 85). The means were not significantly different (d = 0.78, P > 0.10: 'Student's t-test')
modified for large sample sizes (Bailey 1964).

4.3.3 INTERSPECIFIC FORAGING GROUPS

In 55 out of 129 observations of penguins foraging, I observed Jackass Penguins feeding in association with other species. They fed with Cape Gannets and Cape Cormorants in 46 cases, terns in nine cases, Sooty Shearwaters four cases, and Dusky Dolphins and Bryde's Whales in six cases. Cape Fur Seals were observed on every transect but were most numerous at feeding frenzies.

Mixed-species feeding aggregations appeared to begin with Cape Gannets plunge-diving. Cape Cormorants and Sooty Shearwaters would then join the gannets. Not all species present at a patch fed. Cormorants and shearwaters often sat on the surface making no attempts to dive, while gannets and penguins foraged. Gannets appeared to be the first to cease feeding and to fly to a new patch. Cape Cormorants and Sooty Shearwaters appeared to linger at the old patch until feeding activity by gannets at the new patch was intense.

Penguins travelled for considerable distances underwater, so it was difficult to ascertain when they joined feeding groups. Whenever I approached a feeding aggregation, penguins were already present and actively feeding. Penguins called frequently during these 'feeding frenzies'. Prior to plunge-diving, gannets gave a characteristic call (pers. obs) and on five occasions I observed members of penguin groups visible at the time react to this call by lifting their heads in the direction of the calling gannet and changing their direction of travel towards the gannet, in one case by as much as 90 degrees. On only one occasion did I see a group of penguins swim past a nearby feeding group of gannets, cormorants and other penguins.

The role of marine mammals such as dolphins, whales and
seals in the feeding aggregations was not clear. Dusky Dolphins and Cape Fur Seals were present in large numbers on both days when seabird feeding activity was intense. Two Bryde's Whales were also observed on these days. Jackass Penguins have been recovered from the stomachs of Bryde's Whales (Olsen 1913) but this was thought to be atypical. Bryde's Whales are believed to feed principally on small fish and euphausiids (Best 1967). On one occasion I observed a group of 20 penguins porpoising about 100-200 m ahead and away from an approaching Bryde's Whale but it was not clear whether the Bryde's Whale was actually pursuing the penguins. Apart from this one incident involving the Bryde's Whale, cetaceans showed little interest in feeding aggregations of birds but may have been driving shoals of fish inshore. On one occasion I observed a group of approximately 30 terns feeding above a school of Dusky Dolphins. Cetaceans were rarely encountered on days when seabird feeding activity was minimal. Cape Fur Seals which are occasional predators of Jackass Penguins (Cooper 1974) were observed during every transect. Cape Fur Seals were always present at a feeding frenzy but I saw no predation on penguins. On one occasion I observed a group of 10 Cape Fur Seals swim within 10 m of a group of 20 penguins without altering course. The penguins similarly showed no reaction. Only once did I observe a seal capture a penguin and the incident took place away from feeding groups.

4.4 DISCUSSION
Although the use of sail allowed close observations of Jackass Penguins with minimal disturbance, abnormally calm sea conditions during the study period (Walker et al. 1984) hindered completion of transects and thus coverage of the distribution of Jackass Penguins. In normal years or in the Southern Ocean
habitat of other penguins (Watson 1975), winds should be sufficient to allow use of sailing vessels to study penguins at sea. The distributional data were, in any event, sufficient to confirm previous direct (Siegfried et al. 1975, Cooper 1984) and indirect (Wilson in press c) observations that the Jackass Penguin is primarily an inshore forager. Ninety-two per cent of penguins seen were within 4 km of the shore.

The daily variation in the numbers of penguins observed at sea, as shown by transects on consecutive days in December and March, can probably be attributed to variation in the observability of penguins at sea, caused by increased swell height or glare, rather than any real daily variation in the penguin distribution over the study area. The transects of 9/10 March and 20/21 December show only minor differences in the number of penguins observed per 0.5 km.

The numbers of penguins in the study area, based on the transect data, were greatest in March/April and July. A peak of hatching occurred in the first of these periods (pers. obs) so that adults, which must return to feed their young every other day, would have foraging ranges restricted to inshore waters. In July, the peak in numbers of penguins observed at sea coincided with the presence of large numbers of Dusky Dolphins and two Bryde's Whales in the transect area. These cetaceans may have driven fish shoals closer to the breeding islands and concentrated penguin foraging activity, resulting in higher than normal numbers along the transect line.

Jackass Penguins foraged in association with other seabirds. Many of the small penguin groups encountered in foraging areas may be vocally part of much larger groups that coalesce when a food source is found. Alternatively, the three stereotypic foraging groups encountered ('pointed-ovoid', 'line-abreast' and
'facing-search') may facilitate group fishing which, when successful, attract other species. Other seabirds may be using penguins to drive prey to the surface, as tuna (Thunnus spp.) do for tropical seabirds (Ashmole and Ashmole 1967). If the size of the seabird feeding group reflects the size of the patch of prey on which they feed (Duffy 1983a), then the concentration of Jackass Penguins in large foraging groups suggests that they are as dependent on fish shoals as are other group-foraging seabirds such as Cape Cormorants, Cape Gannets and Sooty Shearwaters. The Jackass Penguin is believed to have evolved in the presence of a predictable food supply (Frost et al. 1976b), and Cape Pilchard was probably the archetypal prey species. This assumes that pilchards have always been the dominant fish of the upwelling, in contrast to similar upwellings off California and Peru where anchovy and pilchard have alternated in dominance (Soutar and Issacs 1973, De Vries and Pearcy 1982). If the Jackass Penguin is a Pilchard specialist, it may 'traditionally' have fed in large groups. Data collected prior to the collapse of Pilchard stocks indicate that penguin group size at sea may have been greater than at present. Siegfried et al. (1975) showed that the mean group size of penguins within 12 km of a breeding island was 11 birds. Although their data were collected over a much larger area than my own data, and hence, are not strictly comparable, the frequent, small penguin foraging groups encountered in this study may be a recent foraging adaptation to the unpredictable shoaling behaviour of Cape Anchovy.
5. CHICK GROWTH AND DIET IN RELATION TO COMMERCIAL FISHERY LANDINGS
5. CHICK GROWTH AND DIET IN RELATION TO COMMERCIAL FISHERY LANDINGS

5.1 INTRODUCTION

Seabirds feed near the tops of marine food chains and as 'top' predators they may compete with commercial fisheries which exploit fish species on which birds are dependent. Seabird-commercial fishing interactions have been documented in the North Sea (Furness 1978), and Peruvian (Jordan and Puentes 1966, Schaefer 1970, Duffy 1983b), Californian (Ainley and Lewis 1974, Weins and Scott 1975), and Benguela upwelling systems (Crawford and Shelton 1978, 1981, Furness and Cooper 1982, Abrams 1983, Burger & Cooper in press). Competition with the fishery may have detrimental effects on seabirds such as reduced nesting success (Crawford and Shelton 1978, Duffy 1983b), alteration of normal foraging behaviour and diet (Fisher 1952, Bailey and Hislop 1978, Cooper 1984) and reduced populations (Nelson 1978, Valdiva 1978, Crawford and Shelton 1981).

There may also be beneficial effects. A fishing fleet may provide a predictable food supply in the form of offal (e.g. Fisher 1952, Cooper 1984). Further, by reducing stocks of large predatory species, commercial fisheries increase the availability of small pelagic species on which these predatory fish feed, thereby potentially increasing the food supply for seabirds (Schweigger 1964, May et al. 1979).

Among Benguela seabirds, the Jackass Penguin is one species which appears to have reaped none of the beneficial effects of seabird/fishery interactions. While not 'endangered', the species is now considered to be 'vulnerable' (Brooke in press).

In this section, I investigate the effects of commercial
purse-seine fishing on penguin chick growth-rate and the relationships between penguin diet and commercial fishery catches.

5.2 METHODS
The main approach of my study was a comparison between short-term fluctuations in penguin chick growth-rate and fishery landings. I undertook a five-month chick growth study on Marcus Island between February and June 1983. In 1983, the purse-seine fishing season extended from 1 January to 30 June so I was able to assess chick growth over almost all of the fishing season.

I marked 50 nests with numbered poles. To allow for possible differences in growth-rates between chicks from colonial and non-colonial nests, I chose an equal number of both types of nest: 25 were 'colonial' with three or more other nests within a radius of 3 m and 25 were 'non-colonial' with less than three nests within 3 m. I avoided dense surface-nesting colonies because they are particularly susceptible to human disturbance (pers. obs) but I selected nests over the rest of the island.

At each nest, I marked both adults (one on the head, the other on the chest) using picric acid dye. To minimise disturbance to adult birds on the nest, I marked them using dye-soaked cotton wool tied to the end of a long cane. I determined incubation shifts by visiting nests each morning and noting which adult was present. Chicks were individually dye-marked until they were large enough to flipper-band, using stainless steel flipper bands supplied by SAFRING (South African Bird Ringing Unit) (Cooper and Morant 1980).

Investigator disturbance can be a problem during field studies on densely-nesting seabirds (e.g. Ainley 1974, Anderson and Keith 1980, Hockey and Hallinan 1981). I kept disturbance to
a minimum by using the same route through the colony every day and by visiting each nest only once a day. However, during the early part of the study, desertion of adult birds from nests with eggs and/or small chicks immediately after dye-marking became such a problem that I began sedating adult birds on the nest prior to marking. I used 0.25 ml Ketamine Hydrochloride (trade name, 'Ketalar'), which I injected into the chest muscle of the adult bird as it sat on the nest. In this way I was able to mark the bird and retire from the nest while the bird was still under sedation. In unsedated birds, it appeared to be the action of retiring from the nest which caused some birds to desert. After an initial experimentation period with different doses using non-study birds, I found that sedation was an effective way of preventing particularly nervous birds from deserting the nest.

I made no attempt to mark individual eggs. Hatching dates were considered to be the first days on which chicks were free from their shells. Once a nest was vacated, either because of desertion or departure of young, I marked another nest so that the number of study nests remained constant.

I measured chicks every seven days, before noon, measuring culmen length to ±0.1 mm using vernier calipers and chick mass to ±50 g using a Pesola spring balance. I divided the growth study (7 February-20 June) into 10 two-week 'growth periods' (Table 2) and chicks into three age-classes: (young chicks (less than 15 days), mid-age chicks (15-42 days) and old chicks (older than 42 days)). By dividing chicks into the three age-classes, I hoped to identify the stage at which chicks were most susceptible to fluctuations in fish availability. Growth data were analysed using methods described by Ricklefs et al. (in press). The chicks are divided into size or age-classes (in this
<table>
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<tbody>
<tr>
<td>1</td>
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</tr>
<tr>
<td>2</td>
<td>15-28 February</td>
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<td>3</td>
<td>1-14 March</td>
</tr>
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<td>6</td>
<td>12-25 April</td>
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</tr>
<tr>
<td>8</td>
<td>10-23 May</td>
</tr>
<tr>
<td>9</td>
<td>24 May-6 June</td>
</tr>
<tr>
<td>10</td>
<td>7-20 June</td>
</tr>
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</table>
case three age-classes) and for each of the age groups a regression was calculated (WTI = a + b AGE + c AGE\(^2\)) which takes into account the fact that initial mass (WTI) is related to age. The residuals about this regression (RWTI) were the adjusted initial chick masses summarised in Table 3 which were used to calculate a second regression (DWT = a + b AGE + c AGE\(^2\) + d RWTI) where DWT is the change in mass over a one-week period. Residuals about this regression are the adjusted chick mass increments (RDWT), for which the effects of age (within size group) and adjusted initial mass (indicating recent feeding history) have been removed statistically. The adjusted mass increments were then treated using standard analyses of variance to determine variation among growth periods. The GLM Procedure of the Statistical Analysis System (SAS) was used for the analyses. I used Spearman-rank correlations to test for relationships between fishery landings and growth increments.

For each month of the study (February- June), I calculated the mean incubation shift or nest-attendance period for birds with eggs, young chicks, mid-age chicks and old chicks. I also recorded the incidence of nest desertion for each 'growth period'.

I examined penguin diet by sampling adult birds as they returned to the island in late afternoon or early evening. No diet samples were obtained from birds used in the growth study. Growth-study birds were dye-marked to allow easy identification and avoidance when selecting birds from beach parties for diet sampling. Penguins were stomach-pumped using a water off-loading technique (Wilson in press a). I attempted to collect 10 samples per week during each 'growth period'. Samples were frozen soon after collection and analyzed in the laboratory at the
**TABLE 3**

MEAN INITIAL MASS AND MEAN MASS INCREMENT (g) OF JACKASS PENGUIN CHICKS

AT MARCUS ISLAND FOR EACH 'GROWTH PERIOD' BETWEEN 7 FEBRUARY AND 20 JUNE 1983

<table>
<thead>
<tr>
<th></th>
<th>INITIAL MASS (g) PER CHICK AGE-CLASS PER 'GROWTH PERIOD'</th>
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<tr>
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<td>CHICK AGE</td>
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</tr>
<tr>
<td></td>
<td>Young chicks (0-14 day-old)</td>
<td>Mid-age chicks (15-42 day-old)</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>S.E.</td>
</tr>
<tr>
<td><strong>1</strong></td>
<td>47.0</td>
<td>35.7</td>
</tr>
<tr>
<td><strong>2</strong></td>
<td>52.4</td>
<td>30.9</td>
</tr>
<tr>
<td><strong>3</strong></td>
<td>19.9</td>
<td>12.1</td>
</tr>
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<td><strong>4</strong></td>
<td>24.1</td>
<td>20.9</td>
</tr>
<tr>
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<td>4.3</td>
<td>22.3</td>
</tr>
<tr>
<td><strong>6</strong></td>
<td>30.6</td>
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</tr>
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<td><strong>8</strong></td>
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<td>18.2</td>
</tr>
<tr>
<td><strong>9</strong></td>
<td>3.6</td>
<td>24.3</td>
</tr>
<tr>
<td><strong>10</strong></td>
<td>40.2</td>
<td>61.3</td>
</tr>
</tbody>
</table>
FitzPatrick Institute. I weighed each sample and identified the prey species present, where possible. Otoliths were removed from fish that were too digested to allow direct measurement of length. In such cases, otolith length was used to estimate body length using regression equations developed by the Sea Fisheries Research Institute (unpubl. data). I calculated the mean mass of stomach samples and recorded the number of empty birds sampled during each 'growth period'. I then plotted percentage frequency of all species present in diet samples for each 'growth period'.

I examined the amounts and species composition of all commercial catches made in waters off Saldanha Bay (ICSEAF Area 8; Fig. 1) for each chick 'growth period' using catch statistics supplied by the Sea Fisheries Research Institute. Catch statistics also permitted me to examine catch location and fleet-fishing effort. I plotted the percentage composition of catches for each 'growth period' and the percentage of total fishing season catch of each fish species caught per 'growth period'. I examined species composition and caudal-length frequency of fish taken by penguins and the fishery.

I compared amounts of Anchovy and of all species combined caught by the fishery with penguin chick growth increments for each 'growth period' between February and June 1983.

The 'foraging strategy' of any fishing fleet is dictated by many economic and managerial factors as well as the availability of fish (Idyll 1973), and the South African purse-seine fleet is no exception (Butterworth 1983). I assessed the 'foraging strategy' of the fleet in Saldanha waters by examining fishing effort (standard-boat-days; Crawford 1981b) in Saldanha waters (ICSEAF Area 8) between February and June 1983, and by examining current fishing industry literature (e.g. The South African Shipping News and Fishing Industry Review). Consultation with
fishermen themselves provided valuable insights into the 'behaviour' of the fishing fleet.

5.3 RESULTS

5.3.1 CHICK GROWTH

Despite variability within chick age-classes (Table 3), a number of trends are apparent from the chick growth study (Fig. 7). In February ('growth periods 1 & 2'), young (0-14 day-old) and mid-age (15-42 day-old) chicks gained little weight. No old (> 42 day-old) chicks were present until 'growth period 4' (21 March-3 April).

In early March ('growth period 3'), young chicks gained weight while mid-age chicks lost weight. The first data for old chicks were from 'growth period 4' (late March) and showed a weight gain at this time. In early April ('growth period 5 & 6'), all chick age-classes grew well. By the end of April, young and mid-age chicks were losing weight and the weight gain by old chicks had decreased considerably. In early May ('growth period 7'), all age-classes showed weight losses and this trend continued until the end of May in young and mid-age chicks. Mid-age and old chicks showed a weight gain at the end of May ('growth period 8'). In June ('growth periods 9 & 10'), only young chicks showed a weight gain whereas mid-age and old chicks showed substantial weight losses.

5.3.2. NEST DESERTION AND NEST-ATTENDANCE SHIFTS

Nest desertion was most frequent during the first two weeks of the growth study but decreased steadily thereafter (Fig. 8). Nest desertion was not significantly higher between colonial and non-colonial nesting penguins \((x = 4.53, P > 0.05, d.f. = 7)\). Nest desertion, by both colonial and non-colonial pairs of penguins,
Figure 7. Initial mass and mass increment (g) of Jackass Penguin chicks of different age-classes, for each two-week 'growth period'.
Young chicks (<15 DAYS)

Mid-age chick (16-41 DAYS)

Old chicks (>42 DAYS)

GROWTH PERIOD
Figure 8. Jackass Penguin nest desertion rate for each 'growth period' as a percentage of the total number of study nests active during that 'growth period'.
was most prevalent during the egg phase and decreased with increasing age of chick (Fig. 9). I found no significant correlation between desertion rate of eggs or small chicks and 'total species' fishery catch for each 'growth period' (nests with eggs; \( r_s = -0.28, P > 0.05, n = 9 \); nests with young; \( r_s = -0.43, P > 0.05, n = 9 \); Table 4).

I found no significant difference between length of nest-attendance in colonial and non-colonial nesting penguins (\( d = 1.65, P > 0.05, n = 155 \)), so I combined the data (Table 5). Incubation shifts by adult penguins were significantly longer in February than in any other month of the study (Table 5). Comparing all four months together using the "extension to the median test" also shows a significant different in shift lengths between months (\( X = 58.9 > 7.82, d.f. = 3, P < 0.01 \)).

5.3.3 PENGUIN DIET

I analysed 171 penguin stomach samples containing 2,098 food items of which 68.8\% (by numbers) were Anchovy, 10.6\% squid (Loligo sp.) and 14\% unidentifiable fish remains. The remaining 6.6\% were other species such as Pilchard, Horse-mackerel, Round-herring, Lantern Fish, Sandcord (Gonorhynchus gonorrhynchus), Silverside (Atherina breviceps), invertebrates such as stomatopods (Squilla sp.), and isopods (Table 5a, Fig. 10).

During the study period, the bulk of the diet was Cape Anchovy (Fig. 10). Anchovy were present in the diet of penguins sampled during all 'growth periods', but were least prevalent in 'growth period 1' (early February), and most prevalent during 'growth periods 3-5' (March- early April) and 9 (late May- early June) (Fig. 11). Round-herring appeared in the diet of penguins
Figure 9. Desertion rate of Jackass Penguin nests (colonial and non-colonial) containing eggs, young chicks, and mid-age chicks as a percentage of nests containing that age-class in each 'growth period'. 
% DESERTION

GROWTH PERIOD

- EGGS
  n=64

- 0-14 DAYS
  n=10

- 15-42 DAYS
  n=9


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<tr>
<th>FISHERY</th>
<th>% Desertion from eggs per 'growth period'</th>
<th>% Desertion from young chicks</th>
<th>% Total desertion per growth period</th>
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<tbody>
<tr>
<td>% All species</td>
<td>$r = -0.28$</td>
<td>$r = -0.43$</td>
<td>$r = -0.33$</td>
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<td>catch per 'growth period'</td>
<td>$n = 9, P &gt; 0.05$</td>
<td>$n = 9, P &gt; 0.05$</td>
<td>$n = 9, P &gt; 0.05$</td>
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TABLE 5

NEST-ATTENDANCE SHIFTS OF JACKASS PENGUINS (DAYS) PER MONTH OF GROWTH STUDY FOR EACH CHICK AGE-CLASS, FEB- JUNE 1983

<table>
<thead>
<tr>
<th></th>
<th>Eggs</th>
<th>Young chicks (0-14 day-old)</th>
<th>Mid-age chicks (15-42 day-old)</th>
<th>Old chicks (&gt;42 day-old)</th>
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<tr>
<td></td>
<td>Mean s.d. Range n</td>
<td>Mean s.d. Range n</td>
<td>Mean s.d. Range n</td>
<td>Mean s.d. Range n</td>
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<td>FEB</td>
<td>3.10 2.54 1-16 155</td>
<td>1.24 0.63 1-3 49</td>
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<td>MAR</td>
<td>1.53 1.02 1-16 63</td>
<td>1.73 0.84 1-4 84</td>
<td>1.34 0.15 1-4 101</td>
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<td>APR</td>
<td>1.79 1.43 1-11 122</td>
<td>1.31 0.81 1-6 76</td>
<td>1.38 0.80 1-6 161</td>
<td>1.18 0.43 1-3 60</td>
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<tr>
<td>MAY</td>
<td>2.0 1.34 1-14 53</td>
<td>1.19 0.51 1-3 96</td>
<td>1.15 0.38 1-2 138</td>
<td>1.20 0.60 1-5 59</td>
</tr>
</tbody>
</table>

Incubation shift lengths between months

February vs March  d = 6.46, n = 218, P < 0.001
February vs April  d = 5.64, n = 277, P < 0.001
February vs May   d = 3.68, n = 208, P < 0.001
## TABLE 5A

### ADULT JACKASS PENGUIN DIET DATA FOR EACH GROWTH PERIOD

<table>
<thead>
<tr>
<th>GROWTH PERIOD</th>
<th>ANCHOVY</th>
<th>ROUND-HERRING</th>
<th>PILCHARD</th>
<th>MAASBANKER</th>
<th>LANTERN FISH</th>
<th>NON-COMMERCIAL SP.</th>
<th>SQUID</th>
<th>UNIDENTIFIED FISH</th>
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<tr>
<td></td>
<td>NUMBER</td>
<td>% COMPOSITION</td>
<td>% FREQUENCY</td>
<td>NUMBER</td>
<td>% COMPOSITION</td>
<td>% FREQUENCY</td>
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Figure 10. Jackass Penguin diet and fishery catch (ICSEAF area 8) during the whole study period (February-June 1983) represented as percentage composition by numbers of each species for penguin diet, and as percentage composition by mass of landings of each species for the fishery catch.
Figure 11. Jackass Penguin diet over the study period (February–June 1983) represented as relative abundance and percentage frequency of occurrence of each species in the diet during each chick 'growth period'.
- PILCHARD
- ROUND-HERRING
- ANCHOVY

% COMPOSITION

% FREQUENCY OF OCCURRENCE

GROWTH PERIOD
in small numbers throughout the study period with the exception of 'growth period 8' (10-23 May) (Fig. 11). I found Pilchard in the diet in 'growth periods 3-5' (March- mid-April) and 8-10 (10 May- 20 June), with a peak of occurrence in 'growth period 5' (29 March- 11 April) (Fig. 11). Jackass Penguins took small amounts of Horse-mackerel during 'growth periods 4 & 5' (15 March- 11 April) and 8 & 10 (10 May- 20 June) (Fig. 11). I found only five Lantern Fish, all during 'growth period 4' (15- 28 March), the same period in which the fishery made its only catch of Lantern Fish from Saldanha waters (Fig. 12). Squid occurred in penguin samples throughout the study period (Fig. 11). Finally, non-commercial fish species such as Sandcord and Silverside, and invertebrates such as stomatopods and isopods, occurred in the diet of the penguins in small numbers throughout the study period with the exception of 'growth periods 3-5' (1 March- 11 April) (Fig. 11).

The mean mass of penguin stomach samples ranged from 79 g in 'growth period 1' to 225 g in 'growth period 9' if empty birds are excluded, and from 22.3 g in 'growth period 1' to 156.3 g in 'growth period 9' if empty birds are included (Table 6). I tested for a relationship between stomach sample mass and growth period using the Kruskall-Wallis one-way analysis of variance. The result is highly significant whether empty birds are included ($H = 800.6 > 27.88,$ $P < 0.01$) or excluded ($H = 49.2 > 27.88,$ $P < 0.01$). I then ranked stomach fullness with respect to mean stomach sample mass and compared stomach fullness with chick mass increment for each of the chick age-classes. I found no significant correlation between adult penguin stomach fullness and chick mass increment.

I found a significant correlation between the mean mass of stomach samples and 'growth period' ($r = +0.564,$ $P = 0.05,$ $n = \ldots$)
Figure 12. Total catch of each species by purse-seiners in ICSEAF area 8 for each chick 'growth period' represented as percentage of each species caught during each 'growth period'.
% TOTAL CATCH (AREA 8)

ANCHOVY
n=3610 m tonnes

ROUND HERRING
n=8050 m tonnes

PILCHARD
n=953 m tonnes

MAASBANKER
n=17 m tonnes

LANTERN FISH
n=177 m tonnes

GROWTH PERIOD
<table>
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<tr>
<th>Growth Period</th>
<th>Mean mass of samples (g)</th>
<th>n</th>
<th>s.d.</th>
<th>Range (g)</th>
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<td>(0-423)</td>
<td></td>
</tr>
</tbody>
</table>

(*) Results if empty birds are included in the analysis.
suggesting that stomachs were fuller later in the study period.

5.3.4 COMMERCIAL FISHERY CATCHES

In 1983 the purse-seine fleet totalled 83 boats and 11% of effort by the fleet occurred in Saldanha waters (ICSEAF Area 8; Fig. 1). Sixty-four per cent of the fishing effort in Saldanha waters took place during the period of the growth study (7 February-20 June). During this period, 12,807 metric tonnes of pelagic fish were removed from Saldanha waters of which 28% were Anchovy and 62% were Round-herring. The remaining 9% was made up by catches of Pilchard (953 metric tonnes), Horse-mackerel (17 metric tonnes), and Lantern Fish (177 metric tonnes) (Fig. 10).

Between 7 February and 11 April ('growth periods 1-5'), landings from Saldanha waters were dominated by Round-herring. Over 85% of the total Round-herring catch was landed before the middle of April (Fig. 12). During the latter part of the study period (12 April-20 June), the fishery switched to Anchovy, landing 97% of the total Anchovy catch between 'growth periods 6 and 10' (Fig. 12). Catches of the three minor commercial species: Pilchard, Horse-mackerel and Lantern Fish, were all made during the first half of the study period (February-April; Fig. 12). The only commercial catches of Pilchard made in Saldanha waters during the study period were made in 'growth period 5', when the frequency of Pilchard in penguin diet was at its highest (Figs. 10 & 11).

5.3.5 COMMERCIAL FISHING STRATEGY

On the west coast of South Africa, most fishing occurs during daylight but purse-seiners from the two Saldanha Bay factories
operate at night (J. Viljoen pers. comm.). Shoals are normally detected using echo-location devices, but purse-seine skippers reported that they relied heavily on visual cues such as water colour, with or without phosphoresence; fur seal and seabird aggregations and bird flight direction (U. Donaggi, fishing boat captain, pers. comm.). Radio reports from other purse-seiners and sightings of other vessels fishing successfully were also important cues in the location of fish shoals (Fishing boat captain, pers. comm.).

Large shoals of Anchovy are traditionally encountered in St. Helena Bay north of Saldanha Bay and boats congregate to 'work' these shoals (Anon 1983c). These southward-migrating shoals frequently disperse as they pass Cape Columbine (32° 50' S, 17° 50' E; Fig. 1), and fishermen believe the fragmented shoals pass very close inshore just north of Saldanha Bay and possibly enter Saldanha Bay itself, because large shoals appear again off Saldanha Bay (Anon 1983c). Fishing effort off Saldanha Bay is directed at the year's nought and one-year old Anchovy, Pilchard, Horse-mackerel and at all age-classes of Mackerel (Scomber japonicus) and Round-herring (Crawford 1980). In South African waters, nought-year-old Anchovy recruits (less than 100 mm; Melo in press) normally first appear in fishery catches in the north-west beyond Lambert's Bay (32° 5'S, 18° 17'E) in February and availability increases throughout the autumn, reaching its highest level in June (Crawford 1980). This trend is illustrated in the length frequencies for both fishery catch and penguin diet (Fig. 13).

In 1983, 48% of fishing effort on the Saldanha grounds was concentrated in the months of March and April, but fishing effort was also intense during the first four weeks of the season (36%) (Fig. 14), prior to the growth study. This early
Figure 13. Caudal length frequencies (cm) of Anchovy caught by Jackass Penguins and those caught by purse-seiners for each month of the study (February-June 1983).
Figure 14. Fishing effort (standard-boat-days) by purse-seiners in ICSEAF area 8 for each week of the 1983 fishing season (January–June) represented as the percentage of total effort in ICSEAF area 8.
GROWTH PERIOD

FLEET EFFORT IN AREA 8 (STD. BOAT DAYS)

n=113.7 std. boat days
effort was directed mainly at Round-herring.

5.3.6 COMMERCIAL FISHERY CATCH VS PENGUIN CHICK GROWTH

Young (0-14 day-old) and mid-age (15-42 day-old) chicks showed non-significant positive correlations with fishery catches in ICSEAF Area 8 ($r_s = +0.47$, $P > 0.1$, $n = 10$; $r_s = +0.27$, $P > 0.05$, $n = 9$; Table 7). Old (> 42 day-old) chicks showed a significant correlation with fishery catches during the study period ($r_s = 0.72$, $P < 0.05$, $n = 7$; Table 7). Young chicks showed an insignificant negative correlation between initial mass and fishery landings in the preceding week ($r_s = -0.34$, $P > 0.05$, $n = 10$), mid-age chicks, almost no correlation ($r_s = +0.02$, $P > 0.05$, $n = 9$); and old chicks showed a low positive correlation ($r_s = +0.30$, $P > 0.05$, $n = 7$). I found little correlation between Anchovy landings by the fishery and growth increment in penguin chicks (Table 7).

To determine whether fishing north of Saldanha Bay might be affecting penguin growth, I compared catches in ICSEAF fishing areas 7 and 8 combined (Fig. 1) with chick growth increment. Once again the correlation coefficients were low for small and mid-age chicks, but I found a significant correlation for old chicks ($r_s = +0.72$, $n = 7$, $P < 0.05$; Table 7). I compared catches in ICSEAF Area 7 alone with chick growth increments and found significant correlations with mid-age and old chicks ($r_s = +0.63$, $n = 9$, $P < 0.05$, $r_s = +0.74$, $n = 7$, $P < 0.05$), but an insignificant correlation with young chicks ($r_s = +0.2$, $n = 10$, $P > 0.05$).

5.3.7 COMMERCIAL FISHERY CATCHES VS PENGUIN DIET

The low occurrence of Round-herring in penguin diet (Fig. 11) despite its apparent availability in Saldanha waters, as shown by fishery catches in ICSEAF area 8, might have been the result
of these large catches made by the fishery (Fig. 10). To examine this, I compared the catch of Anchovy and Round-herring combined with chick growth increment throughout the study period. The results showed a low positive correlation in all chick age-classes (Table 7).

Comparing lengths of Anchovy, the only species abundant in both penguin diet and fishery landings, I found considerable overlaps in the sizes caught by the fishery and by penguins (Fig. 13). The fishery used a mesh-size of 12.7 mm and was thus capable of catching all but very small fish. In February 1983, boats landed fish of similar length to those taken by penguins (80-120 mm) but penguin diet in February also contained a small proportion of young (3-5 cm) Anchovy (Fig. 13). In March, catches by penguin and fishery again overlapped considerably, both taking Anchovy of 80-100 mm. However, penguin diet in March contained a higher proportion of small fish than did the fishery catch (Fig. 13). In April the fishery caught a higher proportion of small fish than did the penguins or than it had in March, but most of the Anchovy caught by both penguin and fishery were still between 80-100 mm in caudal length. In May, penguins caught small Anchovy (40-80 mm) while the fishery catch was primarily the 80-90 mm size class. In June, penguins continued to take predominantly 30-70 mm size fish, while the fishery took almost entirely 60-90 mm Anchovy.

5.4 DISCUSSION

5.4.1 PENGUIN POPULATION TRENDS AND DIET

Even with the cessation of egg-collecting and guano scraping as large scale commercial operations, Jackass Penguin populations on the south western Cape coast, where purse-seine fishing is intense, are still suffering rapid decreases (Shelton et al. in
press). At only three localities are penguin numbers increasing and at these colonies the increases are believed to be related to food availability (Shelton et al. in press). At Dyer Island (34° 41'S, 19° 25'E) off the southern Cape coast, penguin numbers have increased steadily since 1956 (Frost et al. 1976b, Shelton et al. in press). The other localities where penguin numbers are increasing are at Mercury (25° 43'S, 14° 56'E) and Ichaboe (26° 17'S, 14° 56'E) Islands off Namibia. Penguin numbers at St Croix Island, Algoa Bay, on the Cape south coast were, until recently, also thought to be increasing. Aerial photography conducted between 1956 and 1969 (Rand 1963, Ross 1971) indicated an increasing population (Shelton et al. in press). However, more recent estimates indicate that first-year survival is insufficient to support such an increase and the population is currently thought to be decreasing (Randall 1983).

Dyer Island lies close to the Agulhas Bank which is a major spawning ground for Cape Anchovy and large numbers of adult fish are known to occur there between October and January (Crawford 1980). On the South African islands off Namibia, Pelagic Goby (Sufflogobius bibarbatus), a commercially unexploited species, forms the bulk of penguin diet (Crawford and Shelton 1981, FitzPatrick Institute unpubl. data) and large stocks are known to occur in waters surrounding the breeding islands (Cruickshank et al. 1980). Elsewhere throughout the Jackass Penguins' breeding range, Cape Anchovy is the principal prey species. (Furness and Cooper 1982, Randall 1983, Wilson in press b).

5.4.2 COMMERCIAL FISHERY TRENDS AND PREY SPECIES

An increase in fleet hold-capacity and the introduction of echosounders and power blocks to haul nets on many boats resulted in heavy exploitation and the eventual collapse of Cape Pilchard
and Horse-mackerel stocks during the 1960's (Newman and Crawford 1980). Over the last five years Cape Anchovy has been the dominant species in pelagic catches, comprising approximately 80% of the total landings (Butterworth 1983).

However, in 1983 Anchovy landings in the study area (Saldanha Bay; Fig.1) contributed little over 20% of total landings during the traditional fishing period (January- June), (Fig. 10). The major contributor over this period was Round-herring which made up almost 50% of total landings (Fig. 10). There appear to have been two reasons for this switch in emphasis by the fishery. First, there was uncertainty regarding quota levels and a proposal to close the fishery early and reopen it later in the year (Anon 1983a). This led to many factories sending their boats after non-quota species (Anon 1983b). Secondly, the incursion into the fishing grounds of warm, oceanic water, with which Round-herring normally associate, meant that this species was more accessible to the fishery during the early part of 1983 than in recent years (Shannon et al. 1984).

Purse-seiners are capable of 'foraging' over hundreds of kilometres at average speeds 4-5 times those of Jackass Penguins and can 'forage' 24 hours a day. Purse-seiners are, however, primarily offshore foragers (10-30 km from the coast), unable to fish close inshore on rocky or irregular bottoms because of the possibility of damage to nets.

The use of the small-meshed nets by the fishery is thought to have increased the fishing power of individual vessels by as much as 64%, and has resulted in catches with large proportions of nought-and one-year old fish (Newman and Crawford 1980, Butterworth 1983). On average, 72% of anchovy caught since 1980
have been juveniles (Anon 1983c). The industry is therefore dependent, to a large extent, on recruitment strength from year to year (Butterworth 1983).

Jackass Penguins took fish of similar sizes to those taken by purse-seiners, but also took smaller fish (Fig. 13; Wilson in press c) which were not caught by purse-seine nets. Rand (1960), noted a high proportion of juvenile fish in penguin diet samples collected between 1954-56.

Both purse-seiners and penguins rely on the same species of fish and, to a large extent, on the same sizes of fish but the effective foraging range of the Jackass Penguin is much less than that of the purse-seiners. Frost et al. (1976b), hypothesized that the foraging area of individual Jackass Penguins probably does not exceed 40 km, and Wilson and Bains (in press) have shown that the mean round-trip foraging distance for a Jackass Penguin is less than 30 km. Wilson and Bains (in press) also showed that the mean travelling speed of a foraging Jackass Penguin is less than 5 km h⁻¹ and that breeding Jackass Penguins typically spend less than eight hours a day foraging at sea.

5.4.3 AFFECTS OF THE FISHERY ON PENGUIN POPULATIONS
In the presence of a super-abundant food supply, chick growth-rate should vary little from chick to chick. Conversely, a high variability in growth-rate between chicks of similar ages from the same area could indicate that the food supply was variable or unpredictable. A scarcity of food might result in fewer meals, or less food per meal being fed to the chicks. Alternatively, food quality may be low (Batchelor and Ross 1984), perhaps lacking essential trace-elements or nutrients. Slow growth-rate in fish-eating boobies is thought to be due to
a shortage of the essential sulphur-bearing amino acids methionine and cysteine (Ricklefs 1979).

The data from my chick growth study indicate that individual chick mass and chick growth within each age-class were very variable (Table 3). High variability in growth-rate between chicks of the same age has also been documented for Jackass Penguins on St. Croix Island, where it is thought to reflect poor food quality (Randall 1983). In other birds, growth-rates have been found to differ between seasons (Harris and Hislop 1978), areas (Birkhead and Nettleship 1981, Ricklefs et al. in press), brood sizes (Perrins 1965), weather conditions (Lack 1956), and as a result of sibling competition (Ricklefs 1965, Williams and Cooper in press).

While calm, hot conditions associated with the '1983 Warm Event' (Shannon et al. 1984), characterized by the late arrival of strong south-easterly winds and anomalously warm sea-surface temperatures close inshore, probably affected the incidence of penguin nest desertion, any differences in chick growth-rate over the study period is likely to have been related to food availability.

It is, at present, impossible to assess directly 'food availability' for a marine foraging bird such as the Jackass Penguin. Commercial fishery landings are not true indications of fish availability because fishing effort is not constant and is frequently directed at only one species. Penguin chick growth is probably a good indicator of food availability since growth-rate is largely determined by food intake (Lack 1968). The purse-seine fishery removes large quantities of fish species utilized by Jackass Penguins, in particular Cape Anchovy (Figs. 11 & 12). It seemed valid therefore to attempt to correlate fishery
catches with penguin chick growth.

The lack of more statistically significant correlations between penguin chick growth and fishery landings may be due, in part, to the imprecise nature of the fishery catch location statistics. Jackass Penguins forage in only a small part of ICSEAF Area 8 (Fig. 1), and catch data for inshore waters (less than 10 km from the mainland) where most penguin foraging occurs were not available for use in the analyses. However, the penguin diet data do provide some evidence of penguin-fishery interactions. The high relative abundance of Anchovy and Pilchard in the diet of penguins during 'growth period 5' (early April) (Fig. 11) indicates that these species were present close inshore around Saldanha Bay at a time when the fishery made no catches of these species in Saldanha waters (ICSEAF Area 8). Large catches of Anchovy were made by the fishery in 'growth periods 7 and 8' (Fig. 12), and over this period chick growth increments were small and the relative abundances of Anchovy, Round-herring and Pilchard in penguin diet were lowest (Fig. 11), suggesting that fish shoals occurred offshore outside penguin foraging range or that the fishery removed a large proportion of fish before it could be utilized by penguins.

The sharp drop in chick growth between 'growth periods 5 and 6' (Fig. 7) coincided with a decrease in the relative abundances of all major prey items in penguin diet, including Anchovy (Fig. 11). It may also be significant that the low growth-rate of chicks in the latter part of the study period coincided with an increase in the relative abundance of squid. Jackass Penguin chicks have been shown to grow more slowly on a squid diet than on a fish diet (R. Heath unpubl. data). Only young chicks showed a positive growth increment during 'growth periods 9 and 10' when the fishery made its largest catches of Anchovy. Mid-age
chicks (16-42 days-old) in particular, showed very low growth increments over these 'growth periods'. Chicks between 16 and 42 days of age require a relatively large food intake (Cooper 1977a), since it is over this period that penguin chicks build up the reserves which enable them to become thermoregulatory (Erasmus and Smith 1974). Attainment of this capability would demand a large food intake, since the chick, often very mobile at this age (pers. obs), requires maintenance energy plus reserves to lay down substantial fat deposits.

Total species catch in ICSEAF Area 8 and in ICSEAF Areas 7 and 8 combined show significant positive correlations with growth increment of old (> 42 day-old) chicks, and in ICSEAF Area 7 alone significant positive correlations with both mid-age (15-42 day-old) and old chicks (Table 7a). This indicates that both penguin and fishery were utilizing the same fish stocks and may reflect adult birds foraging farther offshore, perhaps to areas utilised by the fishery, in their search for sufficient food to feed both their large chicks and themselves, but, more likely, these significant correlations represent an inshore/offshore movement of fish as they migrate southwards past Saldanha Bay.

The removal of large quantities of fish by the fishery may disrupt events at the breeding colony. A decrease in food availability may result in adult penguins spending longer at sea foraging, or returning with less food for themselves and their chicks. Such a situation could lead to decreased growth-rates, or increases in nest desertion and in the lengths of nest-attendance periods.

However, a number of other factors may cause an adult penguin to abandon its nest, including human disturbance (Frost
et al. 1976b, Hockey and Hallinan 1980), disappearance or injury of one member of incubating pair, infestation by parasites (Duffy 1982), nest-flooding and heat-stress (Randall 1983). Guano Island headmen frequently report cases of breeding penguins deserting eggs or chicks as a result of harassment by Kelp Gulls, but these claims have yet to be substantiated. This wide variety of factors causing nest desertion may explain the lack of any significant correlation between fishery landings and penguin nest desertion rate (Table 4). Nest desertion was highest during the early part of the study when ambient temperatures on Marcus Island were high. At St. Croix Island in Algoa Bay, a high incidence of nest desertion early in the breeding season is thought to be due to heat-stress (Randall 1983). Human disturbance also contributed to the incidence of nest desertion as evidenced by the low incidence of desertion when adult penguins were sedated before marking or handling. Further, since nest desertion rate decreased towards the end of the study period, when commercial Anchovy landings were high, it is unlikely that competition with the fishery can be implicated as the sole factor responsible for the trend in nest desertion throughout the study period.

The mean nest-attendance shift lengths for birds with chicks of all age-classes were one or two days, and did not vary significantly from month to month or from chick age-class to chick age-class, but the variability in shift length within age-classes was high, with shift length ranging from one to six days (Table 5). Since both parents are thought to play equal roles in egg incubation and chick-guarding (Randall 1983), the erratic nature of change-overs may indicate that breeding penguins experienced foraging difficulties during the study period. Nest desertion rates may depend on a combination of fishery
landings and absolute numbers of nesting birds, assuming a finite food availability. There may be a maximum number of breeding birds that the inshore food supply can support at any one time.

During February, incubation shifts were significantly longer than during any other month of the study (Table 5), suggesting that food was scarce and that adult penguins had to spend longer at sea foraging. The mean mass of diet samples collected during February was less than in any other month of the study again suggesting that food availability was low (Table 6). Little fishing effort occurred in Saldanha waters during February (Fig. 14) and only 17 metric tonnes of Horse-mackerel were landed. A large proportion of fleet effort during February was directed at waters north of Lambert's Bay (32°05'S, 18°18'E) (ICSEAF Areas 4 & 5).

It was mid-May before fishermen reported finding Anchovy in Saldanha waters in any quantities (Anon 1983b), yet Anchovy were most abundant in penguin diet samples in April, one month earlier. Fishermen reported that Anchovy appeared from the north (Anon 1983b) and many of the catches in ICSEAF Area 8 during May were made north-west of Dassen Island (Fig. 1), well outside the foraging range of penguins breeding on Marcus Island (Wilson in press c, Section 4). This could explain the very low correlations between growth of penguin chicks on Marcus Island and Anchovy landings by the fishery from ICSEAF Area 8.

The greater proportion of young Anchovy in penguin diets during May and June suggests that young Anchovy passed close inshore as they moved southward past Saldanha Bay, on their migration to the spawning grounds east of Cape Point (34°22'S, 18°30'E).
The erratic shoaling behaviour of Anchovy makes it a less suitable species for the fishery than Pilchard. However, it may be a 'saving grace' for the Jackass Penguin. A fish stock which spends part of its time in small scattered shoals, close inshore in shallow 'unfishable' waters, provides a food supply with a high probable prey-encounter rate for an essentially random (opportunistic?) forager such as the Jackass Penguin. Both the large shoals exploited by the fishery and the small scattered shoals exploited by the penguins close inshore are likely to be from the same stocks and hence both will be subject to fishing mortality and possible collapse. Unfortunately, such fish stocks are very difficult to manage, since the real population size is difficult to determine (Butterworth 1983). The fishery and Jackass Penguins both rely on recruitment strength from one year to the next and a poor recruitment will adversely affect both. The fishery has been operating above catch levels recommended by fishery scientists for the last few years (Davies et al. 1981, Butterworth 1983).
6. SYNTHESIS
6. SYNTHESIS

Jackass Penguins consume pelagic fish, particularly Anchovy (Rand 1960, Furness and Cooper 1982, Randall 1983, Wilson in press b). Other Anchovy consumers include Cape Cormorants, Cape Gannets (Crawford and Shelton 1981, Cooper 1984), albatrosses and shearwaters (FitzPatrick Institute unpubl. data); Cape Fur Seals (Rand 1959); cetaceans (Best 1967) and, predatory fish such as Snoek (Thysites atun) (Nepgen 1979) and Long-fin Tuna (Thunnus alalunga) (De Jager et al. 1963). About 50 years ago, commercial fishing boats were introduced into the Benguela ecosystem. The effect of this 'predator' on pelagic fish stocks has been well documented (e.g. Cram 1977, Newman et al. 1979, Crawford 1980, Butterworth 1983). Its effects on other predators of these pelagic fish stocks are less understood. This study concentrated on the Jackass Penguin whose numbers were severely reduced by man before the arrival of the commercial fishing fleet (see Section 2), and whose continuing decrease has been linked to decreasing food availability resulting from commercial fishing practices.

Jackass Penguins rely on fish that can be found within 15 km of the coast (Siegfried et al. 1975, Frost et al. 1976b, Wilson in press c, Section 4). Cape Cormorants, Cape Gannets, Sooty Shearwaters (Section 4) and, in some areas, purse-seiners may also exploit the inshore shoals of pelagic fish on which Jackass Penguins are dependent. Reliable consumption figures for many pelagic fish predators are not yet available, although initial indications suggest that the combined consumption of Anchovy by marine mammals, predatory fish and squid greatly exceeds that of the fishery (Sea Fisheries Research Institute unpubl. Data).
However, there is no evidence that the consumption by natural predators is significantly greater today than it was in the past when penguin numbers were much higher. The one possible exception to this is the Cape Fur Seal which has increased in numbers in recent years (Shaughnessy 1982). Anchovy forms 15\% (J. David unpubl. data) of the Cape Fur Seal's diet, which also includes fish such as Round-herring, Horse-mackerel (Rand 1959), and demersal species such as Hake which they Scavenge from trawlers. Cape Fur Seals off the Cape west coast occur in large numbers around purse-seiners where they can reduce catches by disturbing fish shoals and damaging nets (Shaughnessy et al. 1981). Although they may consume as much as 75 000 metric tonnes of Anchovy per annum (Sea Fisheries Research Institute unpubl. data) off the Cape west coast, predation by Cape Fur Seals on fish within purse-seine nets is not considered a serious problem (Shaughnessy et al. 1981).

Although Cape Fur Seals are known to be occasional predators of Jackass Penguins (Cooper 1974), birds are not a major prey item of Cape Fur Seals. Penguin and seal colonies exist together on some islands, (Shelton et al. in press), although Cape Fur Seals may displace nesting penguins from surface colonies (Shaughnessy 1984).

The commercial purse-seine fishery removes some 200 000-300 000 metric tonnes of Anchovy from the Cape west coast annually (Davis et al. 1981, Butterworth 1983). Anchovy spawn between September and March, with egg production peaking in March (Crawford 1981a). Spawning is concentrated south and east of Cape Point, on the Agulhas Bank. Eggs and larvae drift northwards up the west coast aided by a 'jet current' (Shelton and Hutchings 1982). Juveniles remain on the west coast,
particularly in the region of St. Helena Bay, then move in late winter or early spring towards the spawning grounds in the south (Crawford 1981a). Both the fishery and Jackass Penguins depend heavily on shoals of Cape Anchovy that migrate south from the St. Helena Bay area.

Purse-seiners are dependent on large shoals. Purse-seine fishing nets hang to depths of up to 100 m although most nets effectively fish to only 40 m or so when they are pulled in or 'pursed' to fish. Rocky or foul bottoms prevent the use of nets in shallow (< 100 m) inshore waters. The Saldanha Bay area is rocky out to 15 km, so that fishing boats rarely operate within this limit. In contrast, penguins feed extensively within 5 km of the breeding islands (Section 4). The apparent spatial separation of penguin foraging areas and purse-seine fishing areas apparently partitions the resource between the two consumers. This view rests on several assumptions which are in dispute among those responsible for managing the purse-seine fishery. The fishing industry believes that it harvests less than 25% of the fish that move south. The rest move inshore over foul grounds, in waters too shallow for purse-seining, or disperse into smaller commercially unexploitable shoals (Anon 1983c). The apparent stability of catches in recent years is attributed to the total catch constituting only a small fraction of a much larger stock, most of which emigrates out of the fishing grounds, either offshore or east of Cape Point (Anon 1983d). In contrast, fishery scientists believe that the commercial fishery has been overexploiting the Cape Anchovy (Davies et al. 1981). If fishery scientists are correct, then the fish being exploited by the industry are the same ones being taken by the birds (Section 5.4.3). Further overexploitation by the commercial fishery could then lead to a collapse of the
Anchovy population and a sharp reduction in food availability for penguins.

The presence of a residual fish stock east of Cape Point would explain the rapid increase of penguins on Dyer Island, through increased breeding success, since the cessation of commercial egg-collecting and guano scraping (Frost et al. 1976b, Shelton et al. in press), although some of the increase has been attributed to immigration of birds from other colonies (Shelton et al. in press). At Dyer Island large numbers of Anchovy occur during the spawning season (October-January) (Crawford 1981). Purse-seiners catch large quantities of fish close to Gansbaai, approximately 15 km due west of Dyer Island, but strong currents and foul ground make purse-seining impracticable in waters adjacent to Dyer Island (C. Jeynes, Sea Fisheries Research Institute, pers. comm.). It appears that at Dyer Island a similar situation exists as at Saldanha Bay, where foul grounds prevent purse-seining within 15 km of penguin breeding islands. Yet, Jackass Penguin numbers are decreasing at Saldanha Bay but increasing at Dyer Island. At Saldanha Bay, both fishery and penguins exploit Anchovy as they migrate southwards, and are therefore largely dependent on fish continually appearing out of the north to replace the fish which have migrated to the spawning grounds. At Dyer Island, however, Anchovy gather in warm waters nearby in preparation for spawning, and numbers increase as more fish move down from the north. Spawning is most intense between October and January (Crawford 1981), when traditionally, the fishery is closed.

In contrast, Saldanha Bay penguins must rely on the through passage of recruits during autumn and winter when fishing effort is most intense. If the fishermens' assumption that less than 25
% of the migrating Anchovy are taken by the purse-seiners, then enough fish probably escape the efforts of the fishermen to allow penguins to co-exist with the fishery. However, unless these fish migrate close inshore they will not be available to Jackass Penguins. Fishing boats are believed to disrupt the shoaling behaviour of fish (Anon 1981). If this is so, it could have beneficial effects for foraging Jackass Penguins. Many small shoals would make it easier for Jackass Penguins to find food than would a few, very large shoals. Fishermen frequently report 'losing' shoals they were following because they scattered over rocky foul grounds close to shore (Fishing boat captain, pers. comm.). Such scattering may, in part, be due to the action of purse-seiners themselves. Under such circumstances, there should be a low correlation between fishery landings and penguin chick growth, since the fish available to foraging penguins would largely represent fish that the purse-seiners failed to 'set' a net on. Although the results of my comparison between penguin chick growth and fishery landings (Section 4) are inconclusive, the significant positive correlations obtained for the growth of mid-age (15-42 day-old) and old (> 42 day-old) chicks against fishery landings indicates that penguins are using the same fish stock as is exploited by the fishery. This is further supported by the considerable overlap in the sizes of fish taken by both penguins and purse-seiners. Although the higher proportion of young Anchovy in diet samples from May and June (Fig. 13) may indicate a tendency for young fish to move closer inshore, young fish may simply be slower moving and easier for penguins to catch, or perhaps never form shoals large enough for purse-seiners to catch (Anon 1983d)

During the period of my chick growth study (February-June
1983), the commercial fishery landed large amounts of Round-herring, yet this species was hardly represented in the Jackass Penguin's diet at the time. Round-herring is reported to form shoals very deep during the day time and only occasionally shoals at night (Anon 1983c). The effects of the anomalous weather conditions associated with the 'warm event' in 1983 (Walker et al. 1984) is thought to have increased the abundance of Round-herring in the fishing grounds, but it is unlikely that significant numbers of these fish moved close inshore. Thus, the restricted foraging range of the Jackass Penguin prevented it from exploiting a potential food source. Purse-seiners with their ability to forage over very large areas are equipped to deal with local fluctuations or decreases in fish availability, but Jackass Penguins have no capacity for increasing their foraging range or efficiency, and west coast penguin populations will decrease drastically if Anchovy stocks are allowed to reach very low levels as has happened with stocks of the Cape Pilchard.

In 1983, new changes in fishing seasons and quotas for pelagic shoal fish were introduced as part of a new management policy (Anon 1983a). The new system involved two fishing seasons a year. The first ran from the middle of January until the middle of June, and the second from October until the beginning of December. Thus, for the second season, the fishery caught fish that were spawning or about to spawn (Crawford 1981a). In a fishery dependent on a single year-class, such a strategy could lead to a drastic reduction in fish recruitment strength and, hence, in the food supply of Jackass Penguins on the Cape west coast. The new summer season occurs at a time when most penguins on the west coast are moulting or preparing to moult (Cooper
1978, pers. obs). Jackass Penguins may increase their body mass by as much as 30% in preparation for 18 day moult, during which time the penguin is unable to forage and is confined to land (Cooper 1978). A shortage of food prior to moulting could result in decreased breeding success in the season to follow, or if the food shortage becomes acute, in high mortality of moulting birds. Prior to moulting, Jackass Penguins may stay at sea for as long as 34 days (Randall and Randall 1981), during which time they may forage farther offshore than during the breeding season. In 1983, the summer fishing season began on 15 October and by the end of November, 97 710 metric tonnes of Anchovy had been caught of the Cape west coast. In the Saldanha area, fishermen reported that shoals were less frequent in this season than during the winter season (Anon 1983e). In the south, where large catches were expected, fish were reported to be scarce and catches were low (Anon 1983e). However, in November 1983, Jackass Penguins on Dyer Island fed predominantly on large (100-130 mm) Anchovy (FitzPatrick Institute unpubl. data.). Anchovy must have been present close to Dyer Island, but were possibly too close inshore or too scattered for purse-seiners to catch (Anon 1983d).

The removal of large amounts of pelagic fish at two critical stages in the Jackass Penguin's life cycle (chick-rearing and pre-moult fattening periods) is likely to lead to foraging difficulties and further decreases in breeding success.

It is unrealistic for conservationists to expect restrictions on commercial fishing which may help recovery of penguin populations, when the fishery is already suffering from over-investment (Butterworth 1983). A closed fishing season may do nothing to benefit a species with such a protracted breeding season as that shown by the Jackass Penguin. Another proposal
might be to prohibit commercial fishing close to the Jackass Penguin's breeding islands (Cooper et al. in press b). A natural spatial separation between fishery and foraging penguins already appears to exist off Saldanha Bay, yet there is no evidence to suggest that the decrease in penguin numbers at the Saldanha Bay colonies is less than that at Dassen Island where purse-seining may occur within 500 m of the shore (J. Cooper pers. comm.). Both the industry and the Jackass Penguin would benefit if the fishery broadened the range of fish species it exploited. Lantern Fish is one mesopelagic species towards which the fishery could direct more effort. This species, which presently contributes only 4% to the total catch (Prosch and Shelton 1983), is known to occur over wide areas (Cruickshank 1982) and has a high oil yield. However, Lantern Fish are thought to be important in the diet of young hake (Merluccius spp.) on which the trawl fishery depends (Prosch and Shelton 1983), and more research is needed to determine if an expanding Lantern Fish fishery would have any effects on the demersal ecosystem of the west coast.

The commercial fishery has apparently initiated a dietary change in Jackass Penguins by overfishing Pilchard stocks. This dietary change, from predictably shoaling, relatively energy-rich Pilchard to unpredictable, relatively energy-poor Anchovy, has almost certainly caused foraging difficulties for Jackass Penguins at many localities. Should the Anchovy stock decrease sharply, there appears to be no alternative food source within the foraging range of Jackass Penguins. Only where purse-seine fishery effort is minimal, as at Mercury and Ichaboe Islands off the Namibian coast, or where there appears to be an abundance of fish unavailable to the fishery, as at Dyer Island on the south
coast, are penguin numbers increasing. The nature of the migration and shoaling pattern shown by Cape Anchovy, and the extended breeding season shown by Jackass Penguins (Wilson in press b), means that as long as both fishery and penguins exist, they will compete for the fish resource. Co-existence is still possible, but both fishery management and conservationists will have to compromise their short-term interests for the long-term future of the west coast ecosystem. The fishery must temper its drive for short-term profits and reduce effort and investment in what has virtually become a single-species dependent fishery. A broader fishery base, involving a greater number of fish species, would increase the long-term security of jobs for fishermen and reduce competition with Jackass Penguins.

Conservationists, similarly, must decide what level of recovery they would like to see made by Jackass Penguin populations. A stable population on all the present breeding islands may not be possible while the fishery continues to exploit stocks at current levels. Where purse-seining is intense, as off Saldanha Bay, the carrying capacity of the environment may only be able to support a penguin population much less than exists at present, but even if penguins disappear from some of the present breeding islands, this may be the price the species has to pay for 'co-existence' with the commercial purse-seine fishery. Jackass Penguin numbers at Dyer, Mercury and Ichaboe, appear to be increasing. Jackass Penguins are once more breeding at Robben Island, Table Bay after an absence of some 200 years and, a number of small mainland colonies have been discovered in the last 2-3 years (Broni 1982, Shelton et al. in press, R. Loutit in litt. to J. Cooper). The three increasing colonies at Dyer, Mercury, and Ichaboe Islands would ensure the continued existence of the species at opposite ends
of its present range. However, in such a situation the vulnerability of the Jackass Penguin to possible extinction would be increased, since the survival of the species would be dependent on the populations at only a very few localities. One major oil-spill close to such a locality could effectively destroy a penguin population virtually overnight, and with few colonies remaining elsewhere, the species would very quickly be reduced to 'endangered' status.
7. ACKNOWLEDGEMENTS
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