Social and spatial foraging patterns of the jackass penguin *Spheniscus demersus*

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The inshore distribution and foraging behaviour of jackass penguins *Spheniscus demersus* were studied between December 1982 and August 1983 in waters close to breeding islands in Saldanha Bay, South Africa. The use of a sail-boat permitted close observation of foraging penguins with minimal apparent disturbance. Penguin numbers at sea were lowest in December, when most birds were confined to islands during moult, and highest during the winter breeding season. Although most penguin group sizes were small (one or two birds), over 44% of penguins occurred in groups of more than 10 birds. Three typical penguin group formations occurred at sea: 'facing-search', 'line-abreast', and 'pointed-ovoid'. Penguins also foraged in association with other seabirds and marine mammals. The importance of large foraging groups suggests that the jackass penguin relies on shoals of similar sizes to those taken by the commercial purse-seine fishery, increasing the potential for competition.

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Die verspreiding en voedselbekommingsgedrag van Kaapse pikkewyne *Spheniscus demersus* is tussen Desember 1982 en Augustus 1983 in die see naby die broeieilande by Saldanhabaai, Suid-Afrika, ondersoek. 'n Seilboot is gebruik om die kossoekende pikkewyne van naby af met minimale versteuring te ondersoek. Die minste pikkewyne is in Desember ter see, wanneer die meerderheid op die broeieilande verveer, en die grootste getalle is gedurende Maart en Augustus, hulle broeipieke, ter see. Alhoewel die meeste voedselbekommingsgroepe klein was (een of twee voëls), het meer as 44% van die pikkewyne in groepe van 10 of meer voorgekom. Drie tipiese groepformasies het voorgekom: 'regoor-soek', 'langs mekaar', en 'spits-eiervormig'. Pikkewyne het ook saam met ander seevoëls en seesoogdiere kos gesoek. Die belangrikheid van groot voedselbekommingsgroepe dui aan dat brilpikkewyne staatmaak op skole vis van 'n gelyke grootte as dié wat deur die kommersiële saknetvissery gevang word. As dit die geval is, kan daar 'n groot potensiaal vir kompetisie tussen die pikkewyne en saknetvissery wees.

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Competition with the commercial purse-seine fishery has been suggested as a major factor responsible for the decrease of jackass penguin populations on the west coast of South Africa (Frost, Siegfried & Cooper 1976; Crawford 1981; Burger & Cooper 1984). The introduction of conservation measures requires an understanding of the foraging behaviour of the jackass penguin and how this overlaps with commercial fishery activities.

This paper examines the foraging behaviour of the jackass penguin based on observations made at sea from a sail-boat between December 1982 and August 1983. I studied the species' spatial pattern of foraging in inshore waters, group size and formation, dive duration and associations between foraging penguins, other seabirds, and marine mammals.

Methods

Study area

Field work was carried out at sea in Saldanha Bay, (33°05'S/17°55'E) South Africa and adjacent waters (Figure 1). The oceanography of the bay is described by Shannon & Stander (1977) and that of waters farther offshore, by Andrews & Hutchings (1980). Saldanha Bay contains three breeding colonies of jackass penguins: Marcus Island (2900 adult penguins and chicks in 1978), Malagas Island (4400 penguins), Jutten Island (3800) (Shelton, Crawford, Cooper & Brooke 1984). A fourth colony, Vondeling Island (304 adults and chicks in 1978) is located 8 km south of Saldanha

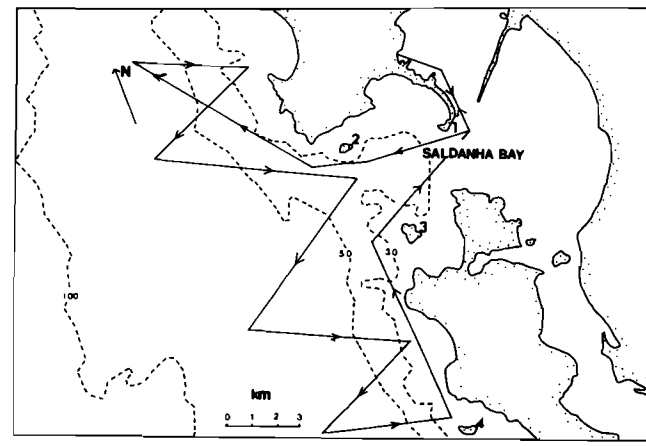

Figure 1 Saldanha Bay area surveyed during transects showing standard transect. Jackass penguin breeding colonies are 1. Marcus Island, 2. Jutten Island, 3. Malagas Island, and 4. Vondeling Island. Depths in metres.

Bay. Dassen Island (16 000 in 1978), located 15 km south-west of Saldanha Bay, may also have contributed birds to the study area. Non-breeding individuals from more distant colonies might also have been present.

Transects

Penguins are difficult birds to study at sea: they have very low profiles on the water and thus are difficult to see; they may be frightened by the noise of power-boats and dive or porpoise away; and they spend a great deal of time underwater either travelling or foraging (Siegfried, Frost, Kinahan & Cooper 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 capable of 5 – 12 km h^{-1} under sail. The vessel was economical to run, stable, and allowed longer trips than did available power vessels. Slow speed and absence of engine noise enabled me to approach to within 5 – 10 m of penguins with little apparent effect on their behaviour.

Observations were made from the bow of the boat at a 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 hand-held 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 sail-boat made it impractical to verify every sighting using the rangefinder so I estimated distances on subsequent transects.

I attempted to run an 80-km transect along a set course inside and across the mouth of Saldanha Bay (Figure 1) during daylight hours between 07h30 and 17h00 on 14 days between December 1982 and August 1983. The transect distance covered was not equal for all days at sea. 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.

I recorded penguin group size and spacing of birds within groups as a function of 'bird-lengths' (one 'bird-length' = approx. 0,5 m). A group was considered to be all birds within ten bird-lengths of each other. I distinguished two types of dive: travelling and foraging. A group which dived as a unit, travelling within 2 – 3 m of the surface, 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 in a dispersed pattern in approximately the same spot was considered to be foraging, because penguins are known to forage routinely at depths of 30 m (Wilson & Bain 1984). I recorded dive-duration using a stopwatch to the nearest 0,1 s. In the case of large groups which dived as a unit but did not surface simultaneously I considered the mean dive duration as the mid-point between the first and last bird surfacing (Ainley 1972). Finally, I noted aspects of the foraging behaviour of jackass penguins, such as shape of groups, formation and dispersal; incidence and synchrony of 'head-dipping' (Siegfried *et al.* 1975); and interactions with other seabirds and marine mammals.

Analysis

Counts are not directly comparable between transects, because of the variable distances covered. 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:

$$N_p = (Z \times X) / 7Y$$

where N_p = the number of penguins observed had equal distance been travelled in each of the seven sectors; Z = number of birds observed in that sector; X = total distance covered in all sectors on that transect and Y = distance travelled in that sector. This correction factor results in an estimate of the number of penguins observed, if an equal transect distance had been covered in each of the seven sectors for each day at sea. 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.

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, Siegfried & Burger 1976; Wilson, Wilson & Hough subm.), I stratified the transect further, with respect to time of day (08h00 – 10h00, 10h00 – 15h00, 15h00 – 17h00). I tested these data using Chi-squared tests with the null hypothesis that there is no significant difference in the numbers of penguins observed at different times of the day, at increasing distances from the nearest breeding island.

Results

Distribution at sea

Although the sail-boat 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. Such windless conditions during the summer are highly anomalous and were associated with a 'warm event' in Benguela waters, with reduced upwelling and changes in the marine fauna and flora (Duffy, Berruti, Randall & Cooper 1984; Shannon, Crawford & Duffy 1984). Numbers of penguins observed per 0,5 km of transect for each day at sea during the study were lowest in December and higher during the rest of the year with apparent peaks in March and August (Figure 2).

At sea, non-breeding adult jackass penguins were indistinguishable from breeders, but immature birds were identified

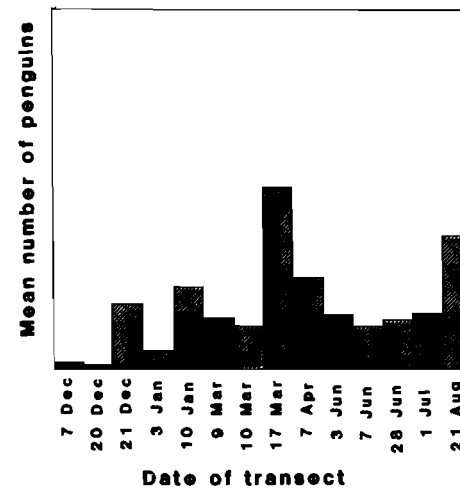

Figure 2 Numbers of jackass penguins per 0,5 km of transect for each day at sea (n = 1 796 birds; 14 transects).

by their brown plumage. A total of 44 immature penguins was observed during the transects, constituting only 2,5% of total penguins seen. I observed immature penguins during all months of the study except March. They were most abundant at sea during December and January and within 3 km of the nearest breeding island (Figure 3).

The comparison between time of day and numbers of penguins observed at different distances from the breeding islands was highly significant (χ^2 = 486,1; *d.f.* = 12; $P < 0,01$; Figure 4). If the data from the two days when I deviated from the transect line to investigate feeding behaviour are excluded in the analysis, the result is still significant (χ^2 = 228,5; *d.f.* = 12; $P < 0,01$), suggesting that numbers of penguins observed were influenced by the time of day. Jackass penguins feed primarily around mid-day (Wilson 1985b).

Most penguins were seen close inshore. In six of the 14 transects away from land, penguins stopped being seen before the conclusions of the transects. 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 up to the ends of transects extending 2,5; 2,5; 3,5; 4; 4; 6,2; 6,5 and 7 km from the shore (Figure 5). The median distance at which the last penguin was seen, scoring the remaining transects as being > *X*, was 7,0 km.

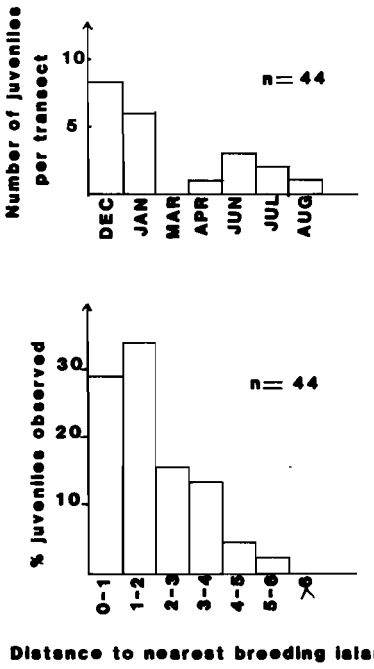

Figure 3 Numbers of immature jackass penguins seen at sea during the study period and their distribution in relation to distance from the nearest breeding site.

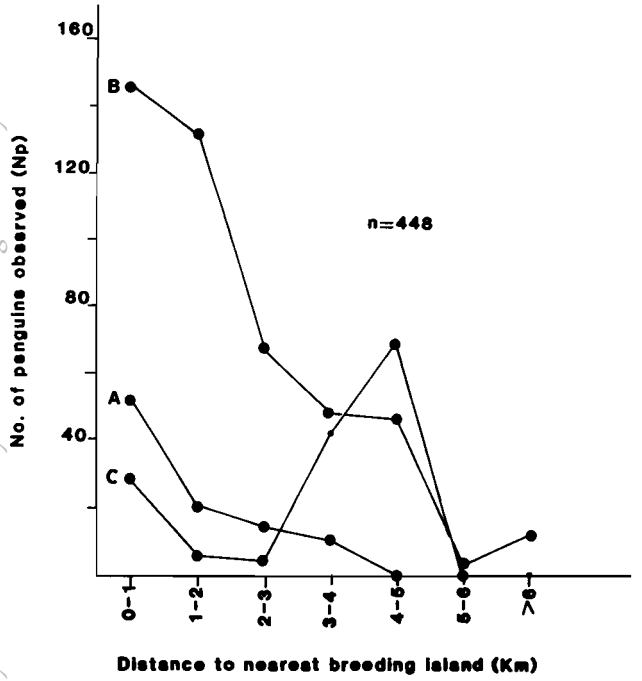

Figure 4 Numbers of penguins observed at different times of day and different distances from breeding islands, corrected for amount of time spent on transect in each zone. A = 08h00 – 10h00; B = 10h00 – 15h00; C = 15h00 – 17h00.

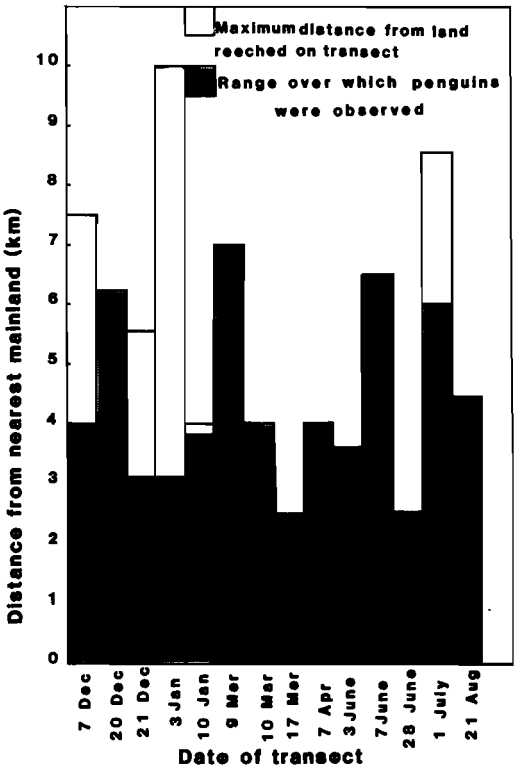

Figure 5 Greatest distance from mainland at which jackass penguins were seen during 14 transects between December 1982 and August 1983.

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 (Figure 4).

Penguin foraging group size and behaviour

Penguin group size at sea during transects ranged from 1 to 50 birds ($\bar{x}$ = 2,2; *S.D.* = 13,1; median = 1; n = 506). However, larger groups of between 50 – 150 penguins occurred on two days (7 April, 1 July), outside the transects. Single penguins occurred most frequently (Figure 6). Three group formations were characteristic of feeding activity: 'Pointed-ovoid' formation was most common in groups of more than 10 penguins ($\bar{x}$ = 27,7; *S.D.* = 24,6; median = 22,5; n = 12; Figure 7). 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', which appears to serve both to find food and to co-ordinate diving

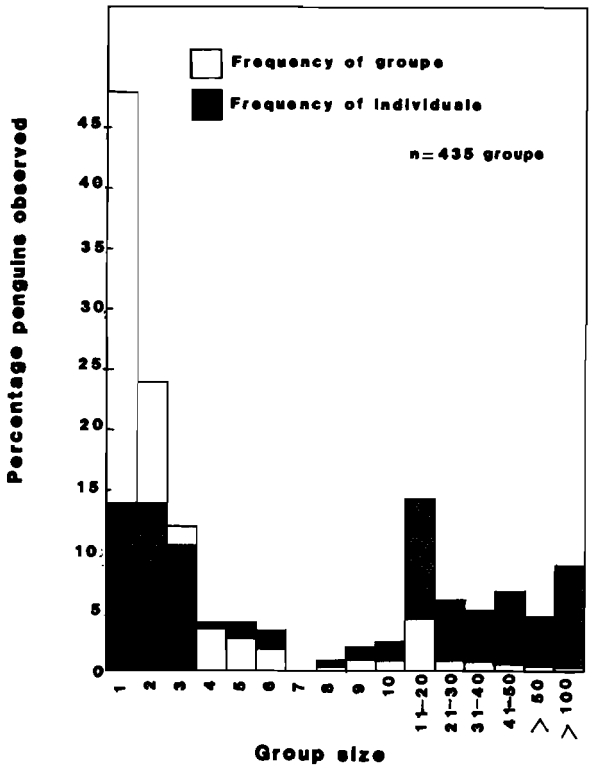

Figure 6 Frequencies of jackass penguins in groups of different sizes.

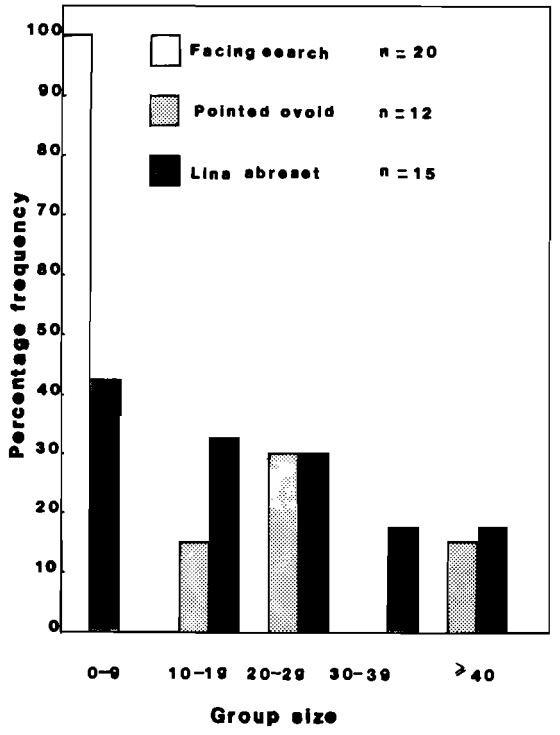

Figure 7 Frequency of different jackass penguin social group formations compared to group size.

(Siegfried *et al.* 1975), 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' formations were most common in groups of 4 – 5 and 11 – 20 birds (Figure 7), but was also observed in larger groups ($\bar{x}$ = 12,8; *S.D.* = 7,52; median = 12; n = 15). The 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 surface-swam slowly forward in a line. 'Facing-search' formations were observed in small groups of fewer than 5 penguins ($\bar{x}$ = 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.

Mean distance between birds was not significantly correlated with group size (r_s = 0,25; n = 15; $P > 0,05$).

Based on group sizes of foraging penguins encountered on the transects, 73% of all foraging groups involved only one or two birds, and only 4,6% involved more than 10 penguins. If the data are included from the two days when I investigated feeding behaviour off the normal transect line, then groups of 10 birds and over still comprised 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 (Figure 4).

The median dive duration of all penguins observed during the 14 days at sea was 23 s (*S.D.* = 20,2 s; n = 138). Dive duration and group size were significantly correlated (r = 0,18; $P < 0,001$; n = 143). The median dive time of travelling penguins was 26 s (*S.D.* = 23,8; n = 53) and of foraging penguins 22 s (*S.D.* = 17,3; n = 850). The means were not significantly different (d = 0,78; $P > 0,01$; n = 138; Student's t test for large sample sizes; Bailey 1964). In contrast, Wilson (1985c) found that travelling birds had mean dive-durations of 22,3 s whereas dives by foraging birds lasted 146 s.

Interspecific foraging groups

In 55 out of 129 observations of penguins foraging, I observed jackass penguins feeding in association with other species: with Cape gannets (*Morus capensis*) and Cape cormorants (*Phalacrocorax capensis*) in 46 cases; terns (*Sterna* spp. in nine cases; sooty shearwaters (*Puffinus griseus*) in four cases; and dolphins and whales in six cases. Cape fur seals (*Arctocephalus pusillus*) were observed on every transect but were most numerous in feeding frenzies.

Discussion

Although the use of sail allowed close observations of jackass penguins with minimal disturbance, abnormally calm sea conditions during the study period (Walker, Taunton-Clark & Pugh 1984) hindered completion of transects. In normal years, winds should be sufficient to allow use of sailing vessels to study penguins at sea. The distributional data appeared to support previous direct (Siegfried *et al.* 1975; Cooper 1984; Wilson 1985c) and indirect (Wilson 1985c) observations that the jackass penguin is primarily an inshore forager: 92% 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 distribution.

The numbers of penguins in the study area, based on the transect data, were lowest in summer and greatest in winter, with greatest numbers observed on transects in March and August. Jackass penguins on Marcus Island are most active reproductively in winter (Duffy *et al.* 1984; Wilson 1985a) and peak numbers of foraging birds would be expected near the

colony at that time. Breeding birds have to forage for their young as well as themselves, increasing the likelihood that they will be at sea. Non-breeding birds are either confined to islands during moult (Cooper 1978) or are free to follow their prey away from the immediate vicinities of the islands, making it less likely that they would be observed on transects.

About half the penguins seen at sea were in groups greater than 10 birds. Many of the small penguin groups encountered in foraging areas may have been parts of much larger groups that coalesce through vocal signalling when food sources are found (Davies 1956). Alternatively, the three typical foraging groups encountered ('pointed-ovoid', 'line-abreast' and 'facing-search') may facilitate group fishing. Other species may also use penguins to drive prey to the surface, as tropical seabirds exploit tuna (*Thunnus* spp.) (Ashmole & Ashmole 1967). If the size of the seabird feeding group reflects the size of the patch of prey on which they feed (Duffy 1983), then the concentration of jackass penguins in large foraging groups and their participation in mixed-species feeding aggregations suggests that they depend on fish shoals as do other group-foraging seabirds such as Cape cormorants, Cape gannets, and sooty shearwaters.

Finally, the commercial purse-seine fishery is also dependent on large shoals, so the penguin and fishery may be in direct competition. 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 in and offshore of Saldanha Bay (Flemming 1977). Farther offshore, beyond 15 km, the bottom is smooth or muddy, or waters are deep enough to allow fishing. Fishing boats rarely operate within 15 km of Saldanha Bay. In contrast, penguins feed inshore. This difference might appear to be an effective natural way of partitioning fish between the industry and the birds. On the other hand, if fish in both areas come from the same populations, commercial over-fishing could diminish the total population and, indirectly, the numbers of fish inshore and thus reduce foraging and reproductive success of jackass penguins.

Conclusions

Despite the frequency of small foraging groups, foraging in large groups appears to be numerically the most important method of obtaining food for jackass penguins around Saldanha Bay. These groups probably depend on the same sizes of shoals exploited by the fishing industry. Rocky, shallow waters prevent fishing by purse-seine vessels in the foraging areas of breeding penguins, and penguins do not forage offshore where the commercial fishery is active, but competition may be severe if fish from both areas are part of the same fish population.

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