Consistent foraging routes and benthic foraging behaviour in yellow-eyed penguins

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ABSTRACT: Yellow-eyed penguins *Megadyptes antipodes* seemingly forage at discrete marine locations over the continental shelf, where they are believed to feed predominantly at the seafloor. Such behaviour would distinguish them from most other penguin species that generally employ pelagic foraging strategies. From 2003 to 2005 we studied the foraging behaviour of yellow-eyed penguins breeding near Oamaru, New Zealand. We used 2 types of data loggers: GPS loggers recorded geographical position and dive depth at set intervals, while time-depth recorders (TDRs) recorded only dive depth. The penguins performed day trips (range: 12 to 20 km from the coast) or shorter evening trips (range: <7 km). Consecutive foraging trips of individuals revealed remarkably consistent foraging routes. Birds travelled along similar — at times congruent — paths, markedly changed course at distinct locations, and revisited certain locations on separate trips, indicating skilful navigation. Three trip stages could be distinguished on one-day trips. During the outgoing (seaward travelling) and incoming (shoreward travelling) stages the birds followed linear courses. These stages were separated by a period of midday activity in which birds exhibited higher dive effort and often tended to stay within confined areas. The diving behaviour revealed an exclusive bottom-foraging strategy, with 87% of all dives being benthic dives; the majority of non-benthic dives occurred during the last 2 to 3 h of the trip, indicating primarily travelling behaviour. Furthermore, yellow-eyed penguins employ benthic dives not only when feeding but also frequently when travelling. We suggest that benthic dives might facilitate navigation and, consequently, account for the consistent foraging patterns of yellow-eyed penguins.

KEY WORDS: *Megadyptes antipodes* · Yellow-eyed penguin · Foraging range · Diving behaviour · Benthic dive · Navigation

INTRODUCTION

Foraging in seabirds often occurs over wide ranges, which is a consequence of the variable marine environment. The pelagic food chain relies mainly on the presence of nutrients in the upper layer of the water column that fuel primary production (Nybakken & Bertness 2005). The distribution of nutrients and, hence, phytoplankton and zooplankton at sea depends mainly on oceanographic parameters such as currents, temperature and mixing (Miller 2004). The result is a patchy distribution of productivity and, ultimately, seabird prey. In response to this, seabirds often need to travel long distances in order to find food.

Penguins are well adapted for a pelagic life and despite their flightlessness are able to cover distances of several hundred km on single foraging trips (Wilson 1995). Although penguins are often described as 'pelagic foragers' (e.g. Williams 1995), some species have adopted an inshore foraging strategy where oceanographic conditions support such a lifestyle (Croxall & Davis 1999). Nevertheless, as consumers of resources that primarily occur in the upper layers of the water column, even inshore foraging penguins must deal with the variability of the marine environ-

ment. As such, they must be able to adjust their foraging behaviour in case of unfavourable prey situations, for example, by extending their foraging ranges or increasing their diving effort (Mattern 2001).

The yellow-eyed penguin *Megadyptes antipodes* is endemic to New Zealand and breeds along the South Island's southeastern coastlines, on Stewart Island and on the subantarctic Auckland and Campbell Islands (see Fig. 1). On the mainland, penguins benefit from oceanic productivity that allows them to stay close to their breeding areas throughout the year (Darby & Seddon 1990). When breeding, the penguins are rarely at sea for longer than 2 d, and after chicks have hatched, the birds leave their nests for only 10 to 15 h at a time (Edge 1996). Accordingly, a telemetry study found that on average yellow-eyed penguins foraged within a 16 km radius from their breeding sites (Moore et al. 1995, Moore 1999).

Interestingly, Moore (1999) also reported that the penguins apparently retained similar foraging patterns on different trips — and seemed to concentrate their foraging to distinct individual centres of activity. However, these individual patterns were only briefly reported and not discussed. Yet the consistency of these patterns (as deducible from data presented by Moore et al. 1995) and the apparently well-defined centres of activity in some birds (see Moore's Figs. 8 & 9 in Moore 1999) warrants a more detailed consideration of individual behaviour in an ecological context. In retrospect, Moore's (1999) data suggests a target-oriented foraging strategy in yellow-eyed penguins that lacks the variability of at-sea movements commonly observed in penguins that find their prey in a pelagic environment (Wilson 1995).

Yellow-eyed penguins primarily feed on benthic fish species (van Heezik 1990a,b, Moore & Wakelin 1997). In comparison with pelagic prey, the distribution of benthic species is less influenced by hydrodynamic processes (e.g. currents) and more related to seafloor substrates and other bottom features such as reefs (Mutch 1983). A feeding strategy that primarily targets benthic species would thus depend mainly on the local benthic environment rather than on oceanographic parameters that usually dictate foraging behaviour in penguins (e.g. Hull 1997, Tremblay & Cherel 2003).

In order to examine whether benthic foraging might facilitate consistent movement patterns, we studied the yellow-eyed penguins' foraging behaviour with GPS dive loggers and time-depth recorders (TDRs). Our aims were to (1) examine in detail at-sea movements and dive behaviour of individual penguins, (2) determine the degree of consistency of foraging tracks within and among individuals, and (3) analyse the observed foraging and diving patterns with regard to the marine areas visited by the penguins, with an emphasis on local seafloor features.

MATERIALS AND METHODS

Study site. Field work was completed in 2 consecutive seasons, 2003–04 and 2004–05, at the Bushy Beach Scenic Reserve, Oamaru, New Zealand (Fig. 1). Here, yellow-eyed penguins breed under dense vegetation on the slope bordering the beach. Bushy Beach represents one of the smaller yellow-eyed penguin colonies on the mainland (1995 to 2004 average: 7 nests; D. Houston unpubl. data) and was chosen for this study primarily because of its accessibility and the availability of observers to monitor the nests. All penguins at Bushy Beach are banded and nests are monitored regularly during the breeding season.

GPS loggers and dive recorders. We used GPS-dive loggers (GPS-TDlog, earth & OCEAN Technology) that use satellites of the Global Positioning System (www.gps.gov) to record the penguins' at-sea movements and dive behaviour. The GPS-TDlog (L × W × H = 100 × 48 × 24 mm, mass: ca. 70 g) contains a GPS receiving unit that determines its geographical position through an array of global positioning satellites. The interval of position fix acquisition is freely programmable, but reception of GPS signals is inhibited when the device is submerged and is thus only available when the penguin is at the surface (i.e. between dives). For the GPS unit to successfully determine a
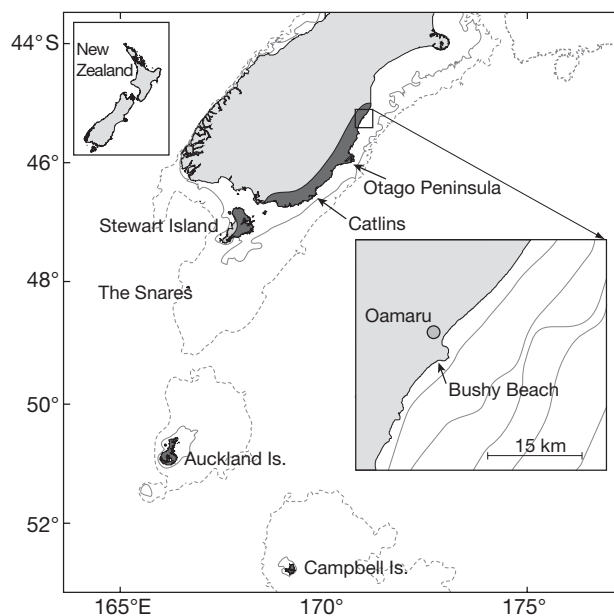

Fig. 1. *Megadyptes antipodes*. Breeding range of yellow-eyed penguins. Main breeding areas are dark grey. Arrows indicate mainland sites with highest nest densities, Otago Peninsula and Catlins, are indicated by arrows. Main figure: solid lines indicate 100 m depth contour; dashed lines indicate 500 m contour. Inset: overview of the study site, Bushy Beach, Oamaru. Here, depth contours given as 10 m isolines

position fix, a penguin needs to stay at the surface for at least 20 s (Mattern 2006). GPS data stored in the memory consist of a timestamp, latitude, longitude, and horizontal travelling speed. Position fixes are highly accurate, with an average error of <10 m for 60% of all fixes and <20 m for 90% of all fixes (Ryan et al. 2004). The GPS-TDlog also features a high-precision pressure transducer (resolution: ~ 0.1 m) and was programmed to record dive depth at 1 s intervals. The GPS unit was duty cycled using the logger's pressure control function so that the GPS receiver was switched off during dives. During periods of inactivity (i.e. when penguins were resting at the surface or on land), GPS data were recorded at 2 min intervals. With this setup, battery life limited the logger's operation period to 3 to 4 d.

In addition to the GPS loggers, we used TDRs (Wildlife Computers MK9). The TDRs are controlled by a saltwater switch (i.e. operate only in water) and record dive depth and temperature over time, but no spatial information. In comparison with the GPS-TDlog, the MK9's sensor resolution is considerably cruder (resolution ~0.5 m). However, the MK9 is only about half the size of the GPS-TDlog (L × W × H = 67 × 17 × 17 mm, mass: ca. 30 g) and battery life is not a limiting factor. As a consequence, we were able to deploy the TDRs over a longer period (7 to 10 d).

The GPS-TDlog's frontal area accounts for approximately 2.0% of a yellow-eyed penguin's cross-sectional area, while that of the TDR accounts for about 1.4%. GPS-TDlogs feature a streamlined Kevlar-housing that reduces drag; we attached streamlined nosecones to the TDRs to enhance their hydrodynamics.

Logger deployments. In the 2003–04 season, we fitted 4 yellow-eyed penguins (2 males, 2 females) with GPS loggers, and a further 3 birds (all males) with TDRs. All birds, representing 50% of the local breeding population, were guarding chicks. Deployments occurred between 12 December 2003 and 11 January 2004. In the following season (2004–05), only 2 nests were still active (chick-guard stage) when field work started due to increased chick mortality that year (see Houston 2005). We fitted both adults from each nest (i.e. 4 birds) with GPS loggers; no TDRs were deployed. All units were deployed between 12 and 22 December 2004. GPS loggers were recovered from penguins after a maximum of 4 d; TDRs were equipped for 7 to 10 d.

All penguins were fitted with loggers at their nest sites. For deployment, a bird was temporarily removed from the nest and weighed to the nearest 50 g using spring balances. Penguins weighing less than 4500 g were considered unfit for deployment. Head and foot length were measured with callipers to determine sex (following Setiawan et al. [2004]) before the bird's head was covered to minimize stress. The devices (i.e. GPS loggers and TDRs) were then attached with industrial adhesive cloth tape (Wilson et al. 1997) to the penguin's lower back. The entire deployment procedure (i.e. capture, measurement, logger attachment, and release) took 10 to 15 min. For device recovery, the birds were intercepted on their way to the nest to avoid unnecessary disturbance at the nest. Device recovery was accomplished without causing any damage to the plumage and usually took less than 5 min.

Data analysis. All data were processed with custom-written software (T. Mattern unpubl. data). Positional data obtained from GPS logger deployments were used to plot foraging tracks of the penguins. Trip length (i.e. distance travelled) was calculated by summing the linear distances between consecutive position fixes of every trip. Dividing trip length and trip duration gave mean horizontal speed. The horizontal speed does not represent a penguin's actual swimming speed because it does not include the bird's vertical movements or any horizontal deviations from the linear distance between 2 fixes. The position fix with the furthest distance from a penguin's nest site was used to determine the maximum foraging distance for each trip. Position fixes that were stored shortly before a bird dived and immediately after it had re-emerged from that dive were used to calculate the linear horizontal dive distance.

Several dive parameters were determined from sensor data, namely: onset and end of a dive event, dive duration, duration of descent, bottom time (i.e. time spent at depths between 95 and 100% of maximum depth), ascent duration, and post-dive interval (i.e. time spent at the surface between consecutive dives). Foraging effort for each dive cycle was calculated as dive time/(dive duration + post-dive interval); diving efficiency was computed as bottom time/(dive duration+ post-dive interval) following Ydenberg & Clarke (1989). Due to the TDRs' depth sensor inaccuracy in the upper 3 m of the water column, dive events could only be accepted when depths >3 m were reached. To maintain comparativeness of the data, GPS-TDlog data was treated the same way, even though the depth sensors in those devices were accurate at depths shallower than 3 m.

Depth profiles of every dive were analysed with regard to the type of dive, i.e. whether it was a benthic or mid-water dive. From GPS logger data, benthic dives were identified by firstly comparing the measured maximum dive depth with the approximate water depth (as determined from bathymetrical data, Scripps Institution of Oceanography, http://topex. ucsd.edu/cgi-bin/get_data.cgi) at the position of the dive. However, bathymetry data were crude (4 × 4 km raster data) and could not be related to data recorded

by TDRs. The second criterion for benthic dives, which applied to data from both device types, was a trapezoid shape of the dive profile (i.e. steady descent, horizontal bottom phase with little vertical undulation, steady ascent; see Tremblay & Cherel 2000) as well as constant maximum dive depths during a series of dives.

Separate foraging trips were identified from GPS data or from TDR sensor readings. Exact foraging trip duration was determined by calculating the time difference between the onset of the first dive and the end of the last dive of every trip. By projecting dive profiles vertically along foraging tracks, we generated pseudo-3D plots that provided spatiotemporal illustrations of the penguins' dive activity. Although these illustrations do not give true 3D representations of the penguins' dive paths (i.e. no horizontal movements were registered during dives), pseudo-3D plots nevertheless facilitated the analysis of foraging behaviour with regard to environmental features of the visited sea area (e.g. bathymetry, benthic communities).

RESULTS

Data outcome and quality

Table 1 gives an overview of the outcome of logger deployments on yellow-eyed penguins in both seasons. In the 2003–04 breeding season, the 4 GPS logger deployments (2 females, 2 males) at Bushy Beach resulted in GPS data for a total of 7 foraging trips. Complete sets of dive data were obtained for 6 of these trips. The 3 TDR deployments on 3 males yielded dive data for the entire deployment periods and encompassed a total of 17 foraging trips: 2 birds each made 5 foraging trips and 1 bird made 7 trips. In the following season, 2004-05, 4 deployments of GPS loggers on 4 adults from 2 nests resulted in GPS and dive data for 5 complete foraging trips.

In both years, GPS loggers recorded between 69 and 235 position fixes during single foraging trips (mean: 168 ± 60 fixes, n = 11 trips, Table 1). Penguins fitted with GPS loggers performed between 95 and 297 dives per trip (mean: 206 ± 99 dives). The median time inter-

Table 1. *Megadyptes antipodes*. Foraging and diving behaviour of yellow-eyed penguins equipped with GPS loggers and TDRs at Bushy Beach in the breeding seasons of 2003–04 and 2004–05. All foraging and diving parameters given as means ±SD, derived from individual means if birds performed >1 foraging trip during logger deployment. Max. depth represents the mean that derives from the single deepest dives recorded for each bird. Differences in dive parameters determined for short-term and one-day trips in 2003–04 were statistically compared using Student's *t*-test. Similar comparisons were also conducted for one-day trip data recorded in both seasons, but differences proved non-significant and are thus not shown

	2003–04				2004–05
	Evening	One-day	t_8	p	One-day
General parameters					
No. of birds	5	5			4
Total no. of trips	13	11			5
Mean trip duration (h)	4.0 ± 0.9	11.5 ± 2.6	6.15	<0.01	12.9 ± 1.2
Foraging parameters (only GPS)					
No. of birds	2	2			4
No. of trips	3	3			5
Max. range (km)	6.2 ± 0.8	17.5 ± 2.5	–	–	18.2 ± 1.1
Distance travelled (km)	15.9 ± 1.2	47.5 ± 1.8	–	–	46.0 ± 3.0
Horizontal speed (km h^{-1})	4.9 ± 0.7	3.5 ± 0.3	–	–	3.7 ± 0.2
Dive distance (m)	161.1 ± 18.3	166.6 ± 4.9	–	–	162.9 ± 37.9
Diving parameters (all birds)					
Dives per trip	108 ± 15	246 ± 39	7.26	<0.01	286 ± 66
% benthic dives	71.6 ± 6.7	86.6 ± 6.7	0.28	0.79	91.5 ± 2.1
Dive frequency (dives h^{-1})	27.2 ± 2.5	21.6 ± 1.8	–4.11	<0.01	22.2 ± 3.2
Dive duration(s)	85.7 ± 5.8	115.4 ± 9.7	6.37	<0.01	112.6 ± 13.5
Bottom time (s)	47.1 ± 2.9	66.6 ± 8.7	4.75	<0.01	68.1 ± 9.8
Post-dive interval (s)	45.1 ± 7.7	52.1 ± 9.9	1.42	0.19	51.2 ± 10.3
Mean depth (m)	15.8 ± 1.5	25.2 ± 1.7	9.61	<0.01	24.5 ± 2.7
Max. depth (m)	28.1 ± 6.3	41.1 ± 2.9	9.55	<0.01	38.4 ± 8.2
Descent rate (m s^{-1})	0.9 ± 0.1	1.1 ± 0.1	6.15	<0.01	1.1 ± 0.1
Ascent rate (m s^{-1})	0.8 ± 0.1	0.7 ± 0.1	1.77	0.121	0.9 ± 0.1
Foraging effort	0.76 ± 0.03	0.69 ± 0.05	–2.77	0.032	0.68 ± 0.02
Diving efficiency	0.42 ± 0.01	0.40 ± 0.04	–1.16	0.311	0.42 ± 0.02

val between consecutive position fixes averaged 2.7 ± 0.2 min, which corresponds well with the duration of a dive cycle (i.e. dive time + post-dive interval; mean duration: 2.5 ± 0.4 min, see Table 1). This suggests that fixes were recorded after every dive. However, this was only true for the first part of most penguins' foraging trips. In some cases, position fixes became more infrequent when the birds travelled back towards the coast and spent little time at the surface (Table 2). As a result, consecutive fixes were sometimes recorded up to 3 h apart. Consequently, the shoreward portion of some foraging tracks could only be linearly extrapolated from position fixes stored before and after travelling episodes. However, considering the high horizontal swimming speeds determined during shoreward travel (Table 2), it seems likely that the penguins did not deviate far from a straight-line course so that the linear extrapolation was deemed an acceptable approximation to the penguins' true travel paths.

Trip duration and foraging ranges

In 2003–04, 2 general types of foraging trips were apparent in all penguins regardless of whether GPS or TDRs were deployed: one-day trips and evening trips (Table 1). During one-day trips, the birds left their nests in the morning (generally between 05:00 h and 07:00 h) and returned in the evening of the same day after an average 11.5 ± 2.6 h (range: 9.1 to 15.5 h). One

overnight trip was observed (22.4 h). On evening trips, the penguins left in the afternoon or early evening (between 15:00 h and 18:00 h) and foraged for a mean 4.0 ± 0.9 h (range: 3.1 to 5.0 h) before returning to their nests shortly before nightfall. Evening trips were only observed in 5 males fitted with GPS (2 birds) and TDRs (3 birds). In the 2004–05 season, only one-day trips were recorded (mean duration: 12.9 ± 1.2 h, range: 11.5 to 14.2 h); however, evening trips could have occurred outside of the deployment period. There was little variation in the trip duration of one-day trips in either season (Table 1).

A comparison of GPS data from male (n = 2) and female (n = 4) penguins performing 1 d trips in both seasons revealed no sex-related differences. However, foraging parameters varied greatly with trip type. On evening trips, penguins foraged 6.2 ± 0.8 km away from the coast and covered average distances of 15.9 ± 1.2 km while swimming at an average horizontal speed of 4.9 ± 0.7 km h^{-1}. This was considerably faster than the 3.5 and 3.7 km h^{-1} we determined for penguins on one-day trips in 2003–04 and 2004–05, respectively (see Table 1).

Patterns of at-sea movements

The foraging tracks that were reconstructed from GPS data showed that one-day foraging trips can generally be broken down into 3 stages: (1) the outgoing travelling stage during which the birds maintain a directional course away from the coast, (2) the midday activity period, which was marked by frequent course changes, and (3) the incoming travelling stage, during which the birds again assumed a directional course back towards their colony (Fig. 2). In some instances, the midday activity period was spent in well-defined areas before the birds travelled back towards the land. For further analysis, we divided data from GPS loggers according to trip stage. For this we defined the end of the outgoing stage as the time and position after which a penguin changed its travel bearing at least 3 times by more than 45° within a 15 min interval; similarly, the onset of the incoming stage was defined as the position and time after which course changes of >45° either did not occur or were isolated occurrences that did not affect the linearity of the penguins' travelling trajectory.

Table 2. *Megadyptes antipodes*. Foraging and diving behaviour of yellow-eyed penguins fitted with GPS loggers during different stages of one-day foraging trips recorded in 2003–04 (3 trips, 2 birds) and 2004–05 (5 trips, 4 birds). Trip stages are defined as seaward movement (outgoing), activity at foraging destination (midday), and shoreward movement (incoming). Statistical comparison was performed using 1-way ANOVA

| | Foraging trip stage | | | ANOVA | |
	Outgoing	Midday	Incoming	$F_{2,12}$	p
Distance travelled (km)	17.6 ± 3.4	12.3 ± 7.6	15.9 ± 3.2	1.36	0.29
Duration (h)	4.7 ± 1.2	4.7 ± 2.5	3.3 ± 0.7	1.25	0.32
Horizontal speed (km h^{-1})	3.8 ± 0.4	2.5 ± 0.7	4.9 ± 0.3	32.71	<0.01
Dive distance (m)	191.8 ± 25.3	141.5 ± 28.4	172.3 ± 34.0	3.80	0.06
Dives per stage	84 ± 23	128 ± 48	79 ± 69	2.58	0.11
% benthic dives	91.4 ± 4.2	96.8 ± 2.7	73.9 ± 20.6	5.71	0.01
Dive frequency (dives h^{-1})	18.6 ± 3.1	21.4 ± 3.3	30.1 ± 5.5	10.65	<0.01
Dive duration (s)	124.7 ± 9.9	117.2 ± 14.9	91.8 ± 19.2	6.45	0.01
Bottom time (s)	81.8 ± 13.9	99.4 ± 58.1	69.1 ± 20.1	0.87	0.44
Post-dive interval (s)	76.7 ± 25.9	53.4 ± 13.9	31.4 ± 7.3	8.38	<0.01
Mean depth (m)	22.3 ± 3.2	35.2 ± 9.0	18.6 ± 4.8	10.87	<0.01
Descent rate (m s^{-1})	0.9 ± 0.1	1.4 ± 0.2	0.8 ± 0.2	14.35	<0.01
Ascent rate (m s^{-1})	0.8 ± 0.1	1.2 ± 0.2	0.6 ± 0.2	19.14	<0.01
Foraging effort	0.64 ± 0.06	0.69 ± 0.03	0.74 ± 0.06	5.47	0.02
Diving efficiency	0.33 ± 0.15	0.42 ± 0.06	0.30 ± 0.15	1.19	0.34
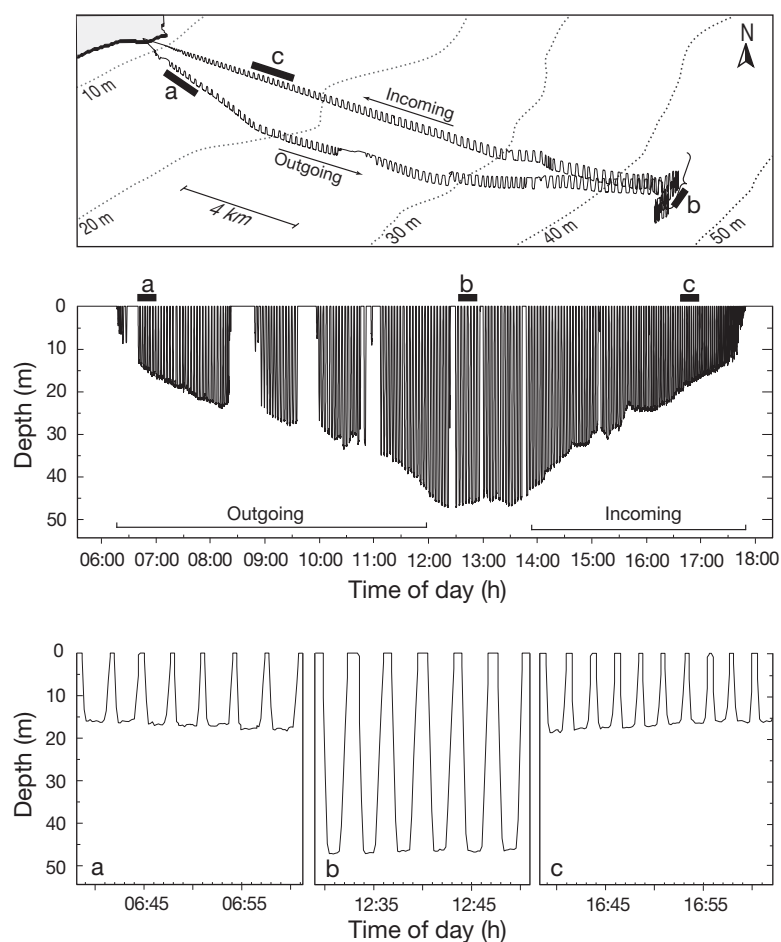
Fig. 2. *Megadyptes antipodes.* Structure of a yellow-eyed penguin's one-day foraging trip (Bird # 3m, trip date 21 December 2004, cf. Fig. 3c). Top: pseudo-3D illustration of the foraging trip. Middle: corresponding dive profile; the majority of dives represent benthic dives so that the overall dive pattern reflects the seafloor's depth profile. Black bars labelled (a–c) alongside the track in the top graph and above the middle graph indicate sections of the dive profile. Bottom: 22 min sections of diving activity during (a) outgoing stage, (b) midday activity and (c) incoming stage. Note differences in dive duration at similar depths between (a) and (c)

The mean duration of the stages was similar for outgoing and midday but significantly shorter for the incoming stage (Table 2). During the midday stage, the penguins covered the shortest distances and exhibited the lowest travelling speeds. During the 2 travelling stages we found no differences in the distances covered (outgoing: 17.5 ± 3.4 km; incoming: 15.9 ± 3.2 km; t-test; $t_8 = -0.8$, $p = 0.45$), but travel speeds were significantly higher when the penguins returned to the colony (outgoing: 3.8 ± 0.4 km h^{-1}; incoming: 4.9 ± 0.3 km h^{-1}; $t_8 = 5.18$, $p < 0.01$), suggesting much more travel-oriented behaviour.

Penguins with GPS loggers that performed more than 1 trip during the deployment foraged along similar routes during the different trips and tended to visit the same areas during their midday activity. Further, similarities in foraging patterns were apparent among different birds and between the seasons (Fig. 3). Birds from a pair foraged in the same general areas (Fig. 3c). Some tracks revealed remarkable consistencies both within individuals and among different birds. For example, on 2 consecutive one-day trips in 2003, 1 female (Fig. 3a,d, black solid and dash-dotted lines) travelled along a similar route and concentrated its midday activity in a small area approximately 20 km offshore. Strikingly, another almost identical foraging track to the same area was determined in 2004 for an unrelated male (Fig. 3c,d, grey solid line).

Other remarkable similarities were apparent in the tracks of the 3 evening trips that were recorded with GPS loggers in 2003-04 (Fig. 3b). In this instance, 1 male (solid and dash-dotted lines) performed 2 evening trips on consecutive days. The penguin followed the same route on both days when travelling back towards the coast, with parts of the tracks being virtually congruent with another, which suggests a high degree of navigational specificity. At a distinct location some 4 km offshore, the penguin markedly changed its course towards its breeding colony. A similar course change at the same location was also observed for another male on an evening trip 1 wk earlier (Fig. 3b, dashed line). During a seafloor survey with scuba gear, we found that the location of the course changes coincides with the existence of a small (2 × 50 m) limestone reef protruding ~0.5 m from the otherwise featureless sand bottom, and it seems likely that this feature represented a navigational cue for both birds.

Diving behaviour

Means of basic dive parameters revealed no significant differences when tested in terms of sex or device type. Accordingly, individual means of dive parameters determined for the respective seasons were pooled with regard to trip type. Dive parameters of birds on evening trips differed from birds performing one-day trips. Overall, the dive frequency on evening trips was significantly higher than that observed during one-day trips (Table 1). The maximum depth was less, which
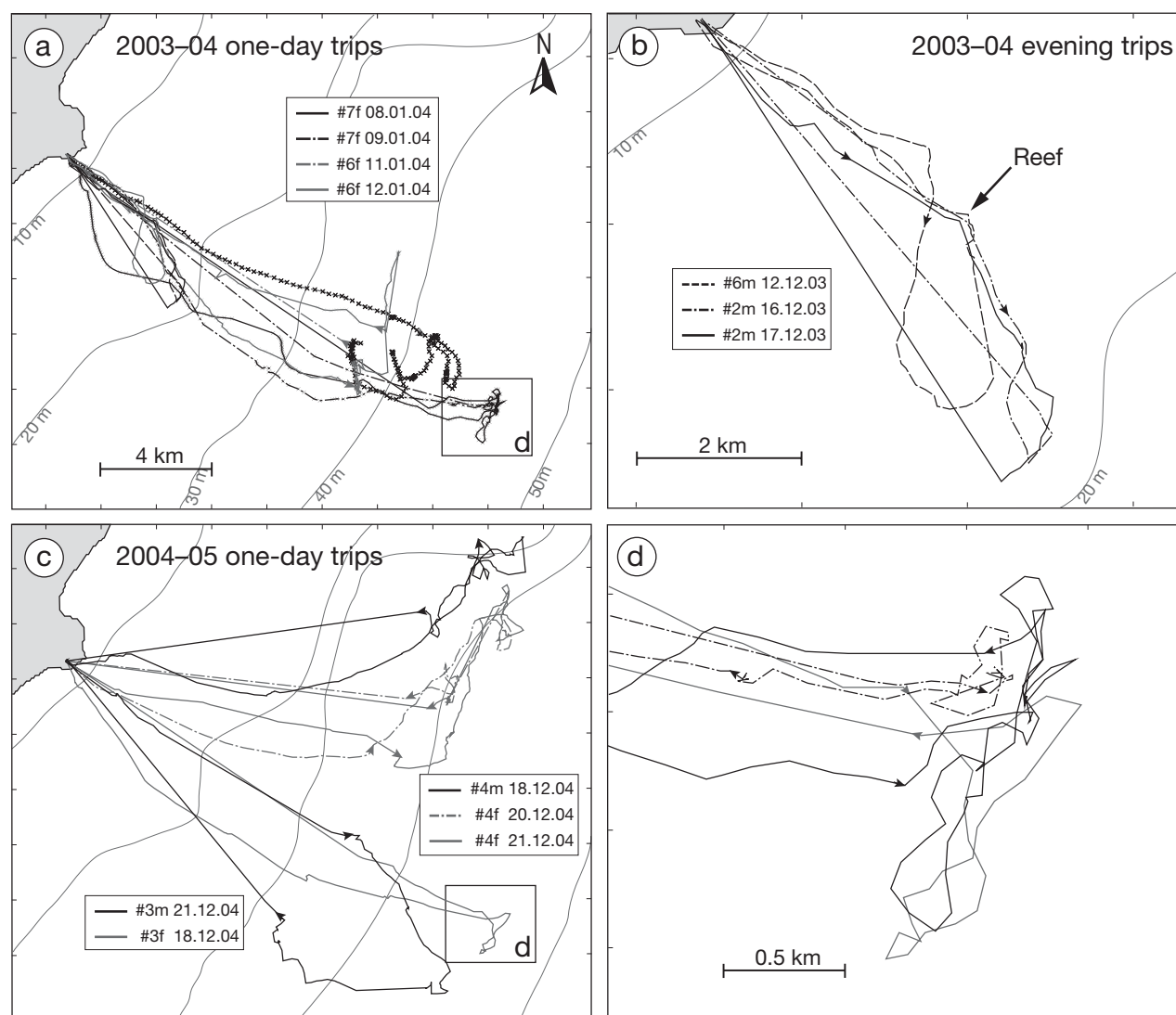
Fig. 3. *Megadyptes antipodes*. Foraging tracks of yellow-eyed penguins in breeding seasons (a,b) 2003–04 and (c) 2004–05. Arrowheads indicate direction of travel and, in the case of one-day trips, mark the onset and end of midday activity for each track. (b) Three evening trips (duration <4 h) by 2 unrelated birds in December 2003; arrow indicates where both birds markedly changed their course towards the colony and marks the approximate location of a 50 m long limestone reef. (d) Detail of track sections from (a, c), showing midday activity of different birds observed in both seasons. Legends: bird identification (nest no. and sex) and date of trip (dd.mm.yy); 10 m depth contours given

was to be expected because the birds did not reach waters deeper than 30 m (Fig. 3b). During evening trips the birds exhibited significantly shorter dive and bottom times, and significantly greater foraging effort (i.e. proportion of time at sea spent underwater), while dive distances were comparable with what we observed for penguins on one-day trips (Table 1).

On one-day trips, the penguins' dive behaviour reflected the 3 foraging stages (Fig. 2). Diving parameters differed significantly among the 3 phases of the foraging trips (Table 2). In all 3 stages, the penguins increased their dive frequency and mean dive duration

decreased accordingly. Bottom times were shortest when the birds were travelling back towards the coast. This was a consequence of the increased frequency of non-benthic dives towards the end of the foraging trips, i.e. during the incoming stage (Fig. 4). Non-benthic dives were usually shallow (<10 m) with low ascent and descent rates (individual means from 6 birds on one-day trips: 0.4 ± 0.1 m s^{-1} and 0.3 ± 0.1 m s^{-1}, respectively). This implies shallow dive angles whereby the duration of descent and ascent is prolonged, which effectively reduced the amount of bottom time.
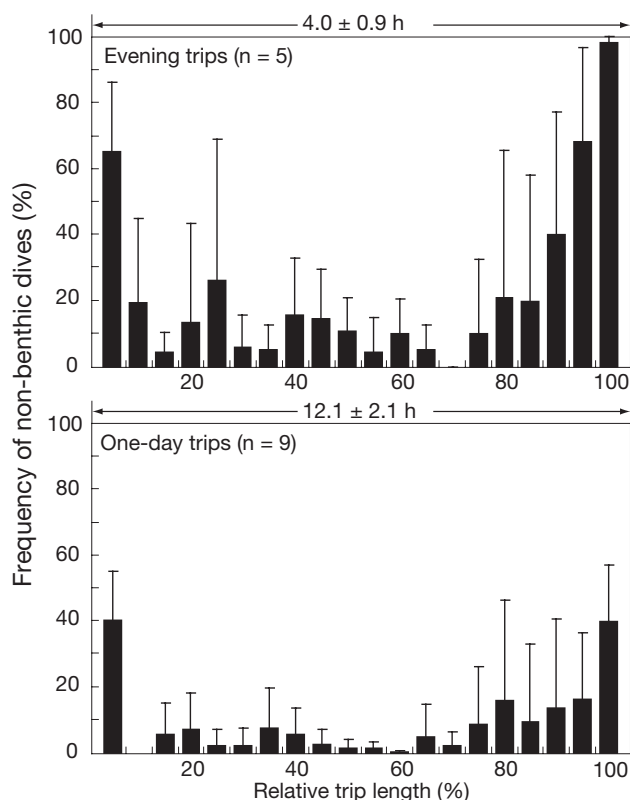
Fig. 4. *Megadyptes antipodes*. Frequency of non-benthic dives during evening and one-day foraging trips performed by yellow-eyed penguins from Bushy Beach, Oamaru. Trip length is given as relative measure (% of total trip length); data is pooled in 5% segments. Average trip length +SD is given above each graph. Note: high frequency of non-benthic dives during the early stage of one-day trips (~40%, lower graph) represents an artefact because penguins tended to perform a series of short, shallow dives during the first 10–15 min after entering the water

DISCUSSION

Logger effects

Externally attached devices on penguins cause additional drag in water and, as such, may affect swimming speed and energy expenditure. The shape and size of the devices are particularly crucial factors of drag (Bannasch et al. 1994).

The different sizes of the devices were not reflected in the dive data, i.e. dive parameters of penguins equipped with GPS loggers and TDRs were similar. Thus, penguins with the larger devices were able to compensate for any additional drag. Nest-attendance patterns of equipped penguins did not differ markedly from those observed in unequipped penguins: all birds changed nesting duties on a daily basis. Hence, it seems reasonable to assume that logger data reflect the general foraging behaviour of all yellow-eyed penguins from Bushy Beach.

Foraging ranges and trip types

The foraging ranges, travel distances and trip durations we determined were comparable with those reported for yellow-eyed penguins breeding at the Otago Peninsula (Moore et al. 1995, Moore 1999). According to Moore et al.'s (1995) data, evening trips were also observed during their radio telemetry study; however, these authors did not distinguish between trip types, which might have biased their figures towards shorter foraging ranges. Similar short foraging trips have also been recorded for macaroni penguins *Eudyptes chrysolophus* (Barlow & Croxall 2002) and rockhopper penguins *E. chrysocome filholi* (Tremblay & Cherel 2005).

The high travelling speeds and the increased foraging effort recorded during evening trips suggests that covering large distances in relatively short time was of high priority. In penguins, the likelihood of prey encounter increases with the distance travelled (Wilson & Wilson 1990), so that travelling quickly on evening trips most likely represents a strategy by which to maximise foraging success. Moore et al. (1995) reported that evening trips were exclusively observed during the chick-guard stage, whereas one-day trips dominated in the post-guard stage. This suggests that evening trips do not provide enough food to meet the growing demands of older chicks and implies that the food situation must be better further offshore, i.e. in areas that can only be reached during one-day trips.

In the light of the penguins' benthic diving strategy, a closer inspection of seafloor properties in the areas visited provides clues as to why one-day trips might be more efficient in terms of foraging success. Off Bushy Beach, the benthic environment within range of penguins on evening trips (<7 km from the coast) differs considerably from the mid-shelf areas that penguins visited during one-day trips (12 to 20 km from the coast). The inshore ranges are characterized by a largely uniform sandy bottom that is interspersed by an array of short and shallow limestone reefs. Shingle patches in the vicinity of these reefs were found to be abundant with bottom-dwelling blue cod *Parapercis colias* (G. Loh unpubl. data), a species that occurs frequently in the diet of yellow-eyed penguins foraging close inshore but is believed to be of relatively low nutritional value (van Heezik 1990a, Moore & Wakelin 1997).

In comparison, the mid-shelf areas further offshore are influenced by the Southland Current, which transports nutrients northwards along the coast (Jillett 2003). The current is characterised by high productivity and is an important foraging area for numerous seabird species (e.g. O'Driscoll et al. 1998). The seafloor in the areas visited by the yellow-eyed penguins reflects this productivity. It is colonised with discrete

patches of horse mussels *Atrina zelandica* (G. Loh unpubl. data), which provide substrate for settlement of sponges and soft corals and thus considerably enhance the local benthic biodiversity (Cummings 2001). This in turn is likely to provide yellow-eyed penguins with a wider range of prey species and food of higher nutritional quality than found further inshore (van Heezik 1990b).

Consistent foraging patterns

Foraging tracks compiled from GPS data revealed some remarkably consistent foraging patterns. Yellow-eyed penguins that performed 2 foraging trips during the deployment of GPS loggers all showed very conservative at-sea movements. Regardless of trip type (i.e. one-day trip or evening trip), birds revisited locations on consecutive trips, in some cases travelling along similar, almost congruent routes to and from these locations. This extends the information provided by Moore (1999), who found that yellow-eyed penguins from the Otago Peninsula not only retained foraging ranges and travel directions between foraging trips but also between years.

Moore (1999) raised the question of whether such habitual foraging patterns were a result of the birds favouring certain locations or stemmed from a similar heading that the birds followed each day. Considering the concentration of position fixes in particular areas that we observed for individuals on consecutive trips, it seems that penguins deliberately re-visit certain areas. Presumably, the attraction of these areas is related to prey occurrence and abundance. The fact that different, unrelated birds occupied the same centre of activity in different years suggests that the attractiveness of such locations is not temporary but persistent.

Overall, the conservative routes used by individuals on different foraging trips and the consistency of movement patterns among individuals and between years suggest that yellow-eyed penguins target areas that feature a predictable abundance of prey items. It is unlikely that such a foraging strategy would be viable if these prey species were exposed to the hydrodynamic influence of currents in the middle and top layers of the water column (Wilson 1991). In contrast, the preference of yellow-eyed penguins for bottom-dwelling prey species facilitates a strategy of learned and retained foraging patterns.

Exclusive bottom feeders

Several studies concluded that bottom-feeding behaviour is an important component of the yellow-eyed penguin's foraging strategy (van Heezik 1988, Seddon & van Heezik 1990, Moore et al. 1995, Moore & Wakelin 1997). Our data suggests that benthic foraging is more than just a component. The proportion of benthic dives, particularly on one-day trips (~87 % of all dives), shows that the yellow-eyed penguins from Bushy Beach feed predominantly—if not exclusively—at the bottom. Non-benthic dives occurred mainly during the very early stages and during the last 3 h of the trips (Fig. 4), and as such primarily represent travelling dives during which the birds cover larger distances. In some individual penguins, benthic dives occurred frequently throughout all stages of the foraging trip (Fig. 2). But despite bottom-diving behaviour during the return, these birds covered the distances to their colony in considerably less time than when they headed offshore in the morning, indicating a directional orientation of their dives, primarily consistent with travel.

Moore et al. (1995) used dive recorders to determine dive profiles of yellow-eyed penguins at the Otago Peninsula and from the Catlins. The continental shelf at both locations is considerably deeper than at Bushy Beach (see Fig. 1). Nevertheless, these yellow-eyed penguins seemed to perform mainly benthic dives even though they were foraging in water depths ranging from 80 to 120 m. Furthermore, recent deployments of GPS dive loggers on yellow-eyed penguins from the Otago Peninsula and Stewart Island also revealed predominantly benthic foraging at both sites (Mattern 2006, T. Mattern unpubl. data). Moore et al. (1995) also stated that they observed longer bouts of mid-water dives, and diet studies showed that the penguins occasionally took non-demersal prey species (van Heezik 1990b, Moore & Wakelin 1997). However, from the general prey composition and unpublished dive data available, it appears that mid-water feeding by yellow-eyed penguins is the exception rather than the rule.

Benthic foraging has been observed in penguins that sometimes search for prey in shallow coastal waters, e.g. rockhopper penguins (Tremblay & Cherel 2000), gentoo penguins *Pygoscelis papua* (e.g. Lescroël & Bost 2005), chinstrap penguins *Pygoscelis antarctica* (Takahashi et al. 2003), and emperor penguins *Aptenodytes fosteri* (e.g. Rodary et al. 2000). However, none of these species appear to have developed an exclusive bottom-feeding strategy as have yellow-eyed penguins at Bushy Beach. With the exception of gentoo penguins, these species are offshore feeders that usually forage for pelagic prey in deep waters (Croxall & Davis 1999); thus, bottom foraging seems to be rather opportunistic behaviour.

Gentoo penguins, like yellow-eyed penguins, are considered inshore foragers. Benthic prey is common

in the gentoo penguin's diet at the northern limits of its distributional range, while pelagic prey forms the major part of its diet further south (Claussen & Pütz 2003). This differentiation seems to be a result of the seasonality at higher latitudes, where increased abundance of pelagic prey over the summer makes foraging for such prey a more efficient strategy than targeting a more consistent food source like benthic prey, which is available year-round at lower latitudes (Croxall & Davis 1999). The yellow-eyed penguins' southern distribution limit (i.e. subantarctic Campbell Island, 52°S) is still further north than the northern limit of the gentoo penguins' range in the Pacific Ocean (Macquarie Island, 54°S). Thus, it seems unlikely that prey of southern yellow-eyed penguins is linked to seasonality, so that a specialisation for benthic foraging by all yellow-eyed penguins is imaginable. This would also explain why the species is absent from other subantarctic islands within its latitudinal range that have little continental shelf, such as the Antipodes and Snares Islands (Smith 1987, Fig. 1).

Diving behaviour during different trip stages

In the light of their exclusive bottom-feeding behaviour, the yellow-eyed penguins exhibited surprisingly low overall descent and ascent rates. If all dives during a trip are considered, the penguins spent almost two-thirds of their dive duration transiting between surface and bottom. Theoretically, in order to maximise bottom and consequently feeding time, bottom foragers should attempt to keep the time spent in transit at a minimum, and descent and ascent rates should be high rather than low (Wilson & Wilson 1988). Rockhopper penguins performing benthic dives to depths of 20 to 30 m were found to descend at around 1.5 m s^{-1}, with ascent rates being slightly slower (~1.3 m s^{-1}) (Tremblay & Cherel 2000). Compared with that, the transit rates we observed appear surprisingly inefficient (Table 1). However, mean descent and ascent rates were significantly higher during midday activity, which allowed for longer bottom times and consequently higher diving efficiency at the penguins' trip destinations (Table 2). Thus, yellow-eyed penguins performed the more efficient benthic dives after they arrived in the presumably productive feeding areas that were further offshore. Conversely, during the outgoing and incoming stages of their trips the penguins performed benthic dives that appear inefficient, at least according to the principle of minimised transit times (Wilson & Wilson 1988). However, this principle only applies under the assumption that the primary aim of a benthic dive is to forage for food. The long transit times during the yellow-eyed penguins' outgoing and incoming stages imply shallow descent and ascent angles whereby penguins can cover horizontal distances while transiting to the bottom. Thus, benthic dives during outgoing and incoming possibly serve 2 purposes — to travel and search for prey at the same time.

Interestingly, dive parameters during both travelling stages differ also. It appears as if the penguins were more likely to exhibit 'real' travelling behaviour when returning to the colony: the frequency of non-benthic dives increased markedly (Fig. 4), and horizontal travelling speed was higher, indicating a more linear movement than during the outgoing stage. The differences between outgoing and incoming stages can be interpreted as higher search effort while travelling away from the coast, whereas on return to the coast the penguins' emphasis lies with travelling.

Considering the prevalence of benthic dives during all stages of the trip and the consistency of foraging routes, it is likely that benthic dives are also utilised by the penguins for the purpose of navigation.

Navigation by bottom features?

The occurrence of reefs or similar bottom features triggers behavioural responses in yellow-eyed penguins such as course changes (Fig. 3b). In one case a penguin even followed exactly the same course on separate trips (Fig. 3b, Bird # 2m). This implies a high level of fine-scaled navigation skill.

Little is known about navigation in penguins or seabirds in general. Although olfactory (e.g. Nevitt 2000) and magnetic orientation (Benhamou et al. 2003a) have been considered, it is currently believed that seabirds rely largely on visible cues for navigation (e.g. sun/star compass, wave patterns) (Benhamou et al. 2003b). While the apparent scarcity of visual cues in the offshore oceanic environment suggests non-visual means of route finding, species that forage in coastal waters can use the skyline of landmasses to take their bearings.

In the case of bottom-diving yellow-eyed penguins, the seafloor provides additional features for navigation. The occurrence of reefs and shingle patches (and associated flora such as bladder or giant kelp *Macrocystis pyrifera*) at discrete locations certainly represent underwater landmarks available to yellow-eyed penguins for orientation. Navigation by landmarks has recently been proved to be an important component in the route-finding abilities of homing pigeons (Lipp et al. 2004). Homing pigeons use stereotyped but individual routes over familiar landscapes, and it was suggested that the birds might utilize memorized landscape maps for navigation (Meade et al. 2005). The fact

that yellow-eyed penguins remain resident in their breeding location throughout the year (Darby & Seddon 1990) and, thus, forage in the same sea areas for years on end would allow for the development of navigation skills comparable with those described for homing pigeons.

CONCLUSION

The foraging strategy employed by yellow-eyed penguins from Oamaru is quite extraordinary for a member of the Sphenisciformes. Consistent foraging patterns and exclusive benthic feeding suggest a high level of specialisation that requires a high degree of stability and predictability in the marine environment. Ultimately, this raises the question of whether the yellow-eyed penguins are able to adjust their behaviour to compensate for perturbations in the marine environment as efficiently as other penguin species.

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