

Diving patterns of female macaroni penguins breeding on Marion Island, South Africa

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Abstract Despite the large biomass of macaroni penguins *Eudyptes chrysolophus* in the Southern Ocean, their feeding ecology is poorly known at some important breeding localities. We investigated the diving behaviour and diet of female macaroni penguins feeding small chicks on Marion Island (46°52'S, 37°5'E), South Africa, one of the species' most northerly breeding sites, supporting 4% of their global population. We then compared our results with similar studies from other localities. In December 2008, we collected information on 12 foraging trips from 6 individuals using time-depth recorders, as well as diet from 42 individuals. Median trip duration was 22.8 h (5.6–80.8 h). Penguins performed 42.8 ± 15.9 dives per hour at sea, with dive depths averaging 24.6 ± 8.6 m and lasting 40.8 ± 12.1 s, although 74.3% of dives were <10 m. Euphasids dominated their diet (86% by mass),

mainly *Thysanoessa vicina*. A second peak in dive depths at 55–80 m might reflect the 12% of fish in their diet. The substantial proportion of shallow night dives (30% of total dives) suggests some foraging occurs at night. Differences in diving patterns of individual macaroni penguins in this study confirmed the behavioural flexibility of these birds reported from other breeding localities. However, most other studies assumed that dives <3–5 m were commuting dives whereas our study suggests that at least some prey are caught during shallow dives. We highlight how different analytical methods can change the outcome of studies. Despite macaroni penguins' apparent flexibility in foraging behaviour during the breeding season, their numbers are decreasing globally. Further investigations of their foraging behaviour are needed to assess potential competition with other predators and krill fisheries.

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Introduction

Macaroni penguins *Eudyptes chrysolophus* are the most abundant penguin species in the world and are estimated to consume more prey than any other seabird species (Brooke 2004). They rely heavily on Antarctic krill *Euphausia superba* (Croxall and Prince 1987), but also feed on other species of crustaceans, squid and fish (Crawford et al. 2003; Deagle et al. 2008). Their population is estimated to have decreased globally by 30% the last three decades (Kirkwood et al. 2007; Crawford et al. 2009). Although some of these trends have been attributed to differences in count methods (Woehler et al. 2001), some colonies have

decreased steadily (e.g. at Ildefonso and Diego Ramírez Archipelagos, Chile; Kirkwood et al. 2007). The species is currently listed as vulnerable to extinction, with some 18,000,000 individuals (IUCN 2010). Foraging behaviour is more sensitive to environmental change than are life-history traits and thus provides a way to monitor potential population changes (Grémillet et al. 2006). Therefore, to understand the macaroni penguin's recent population trends, it is important to accumulate information on their foraging activity and to determine their role in the Southern Ocean ecosystem. Investigating their diet and their diving behaviour at different colonies may help to determine their ability to respond to environmental changes. Such information is especially important because macaroni foraging behaviour and ecology at sea is unknown at many breeding localities.

Although macaroni penguins are better studied than most other penguins and diving predators, their foraging behaviour has been studied at only three of their 216 known breeding colonies: Heard Island, Australia (53°06'S–73°31'E, Green et al. 1998; Deagle et al. 2008), the Kerguelen Archipelago (49°15'S–69°35'E, Sato et al. 2004) and Bird Island, South Georgia (54°00'S–38°03'W, e.g. Croxall et al. 1993; Barlow et al. 2002; Green et al. 2005; Trathan et al. 2006; Waluda et al. 2010). In this study, we investigated the diving behaviour of macaroni penguins at Marion Island (46°52'S, 37°51'E), South Africa, one of the species' most northerly breeding sites. Marion Island is the larger of the two Prince Edwards Islands, which together support 4% of the global population (Crawford and Cooper 2003). However, the population at the Prince Edwards has decreased by 30% since the mid-1990s, with an estimated 296,000 breeding pairs in 2008 (Crawford et al. 2009). Here, we compare their diving ecology with those of conspecifics from other colonies situated farther south in the core of the species' range. Accumulating information over the long term on the foraging ability of penguins on Marion Island is important in the context of climate change, since the northern position of the colony places them at the forefront of climate warming issues. Our study provides a baseline for future investigation assessing how the population responds to climate change.

Material and methods

Both sexes of macaroni penguins share the care of a single young, but during the early chick-rearing stage, only females forage at sea while males brood and guard the chick (Williams 1982). Between 17 and 23 December 2008, nine female macaroni penguins with small chicks (1–3 weeks old) were weighed and equipped with

time-depth recorders (TDR, M190-DT, 12 bit resolution, 60 × 15 mm, 15 g; Little Leonardo, Tokyo, Japan). These devices represent 0.3% of the mass of the animals and less than 1.1% of their cross-frontal area (Sato et al. 2004). The loggers monitor depth every second with an absolute accuracy of 0.1 m (see Ropert-Coudert et al. 2003 for details). They were attached with waterproof Tesa tape to feathers on the lower back along the birds' long body axis to minimise drag (Bannasch 1995). Handling lasted <10 min and all birds returned to their nest for 2–12 h before departing on a foraging trip. Their nests were checked every 2 h during daylight (05:00–20:00), and upon return of the instrumented female, the logger was retrieved and mass, flipper length, culmen length and depth were measured. Another 21 breeding pairs were marked without being handled, using a spray of bio-compatible dye, and monitored to estimate their foraging trip durations. Foraging trip durations of control birds were estimated from the first check when the bird was absent until the first check when the bird was back on its nest. For the instrumented birds, a foraging trip was defined from the first to the last dive, and consecutive trips of a single bird were separated when there was a gap in the diving data of >4 h. There were no gaps between dive records between 1 and 4 h. We assumed from our observations on control nests that periods <1 h were too short for birds to get back to their nest to feed their chicks and start a new trip. Diving behaviour was analysed with Igor Pro (Wavemetrics, USA, Version 6.04). Dive threshold was set at 1 m depth (to ignore the effect of wave action and noise when birds were on the water surface), and bottom duration was defined as the period in a dive between the first and last times the dive rate (the difference in depth between consecutive data points) was <0.25 m s⁻¹ (see Kato et al. 2006 for details). A sample of our raw dataset, as well as the corresponding analysis from Igor Pro, is available online as Electronic Supplementary Material (Online Resources 1 and 2). For comparison with other studies on macaroni penguins, we also calculated the average dive depth and duration with dive thresholds of 2, 3, 4 and 10 m, as well as the dive efficiency for dives 2–20 m and >20 m. Dive efficiency (following Dewar 1924) was defined as the ratio of bottom duration (when >0 s) to the dive cycle (=dive duration + post-dive recovery period at the surface) during a foraging bout (i.e. during a succession of more than 5 dives, each dive being separated by surface periods <30 min).

The diet of macaroni penguins was sampled on Marion Island between December 2008 and February 2009 during the chick-rearing period, following CCALMR procedures (Crawford et al. 2003). Forty-two birds were caught when they came ashore, and their stomachs were flushed once with water poured down a tube into the stomach. Logger

birds were not sampled to reduce disturbance to these birds. Diet samples were preserved in alcohol or frozen prior to analysis. In the laboratory, liquid was drained from the samples through a sieve and prey were then identified to species level whenever possible, using fish otoliths and squid beaks for identification when prey were in an advanced stage of digestion. Items were weighed, and we determined the proportion of contribution by mass of different species in the diet of the birds.

The number of foraging trips logged varied between females. To reduce pseudoreplication issues, we calculated the foraging characteristics for each trip and for each bird and then the grand mean for all the birds (i.e. based on the average of each bird). We tested the trip duration of control versus instrumented birds with a Mann–Whitney U test. Data are presented as means ± 1 SD unless stated otherwise.

Results

All nine loggers were recovered but data from three birds were lost due to technical failure of the devices. The remaining six birds logged 17,122 dives during 12 foraging trips ($N = 1$ –5 per bird, Table 1). The average trip duration of equipped birds was 27.5 ± 10.7 h (range 5–80.8 h; Table 1). There was no significant difference between medians of foraging trip durations from equipped and control birds (28.8 h for equipped birds ($N = 6$) and 34.7 h for control birds ($N = 32$, $U = 943$, $P = 0.15$). The observed longer trip duration of control birds might be due to resting times of birds on shore before reaching their nests, although this delay can be highly variable between individuals (pers. obs).

There were marked differences in diving patterns between individuals and between trips of the same individuals (Table 1; Fig. 1), although our sample size was too small to perform formal statistical tests. On most trips, birds performed 30–46 dives per hour (Table 1), but other trips had many short, shallow dives (<10 m) that led to a higher diving rate (95–105 dives per hour) (Fig. 1). Diving rate decreased with increasing dive depth, and there was as much variation among repeated trips of the same individual as there was among birds (Fig. 1). Diving efficiency was nonetheless similar between birds and so was dive duration and depth between individuals and their different trips (Table 1).

Although 74.3% of all dives were <10 m (66.8% <5 m; Fig. 2), dives as deep as 154 m were recorded, with an average dive depth of 24.4 ± 8.5 m (Table 1). Similarly, most of the dives recorded were <10 s, but lasted on average 40.8 ± 12.1 s, with a maximum of 207 s (Table 1). There was a second peak in dive depths at 50–90 m, lasting

140–180 s (Fig. 2). Dive depth and duration were strongly correlated (duration = $35.973 \ln(\text{depth}) - 6.598$; $r^2 = 0.95$, $F = 80.491$, $P < 0.001$). Two diving modes can be identified from our data, with a first mode including shallow short dives with dive duration increasing linearly with dive depth, and a second mode of longer and deeper dives, where dive durations reach an asymptote at around 180 s (Fig. 3). We determine with k-means clustering analysis (MacQueen 1967) that the two modes switched at 15.7 m and 95 s. This threshold between “shallow” and “deeper” dives was similar to that found on Heard Island in 1992/1993 (ca 20 m) by Green et al. (1998).

Birds left the colony irregularly throughout the day and night (Table 1). All birds performed very shallow dives (<5 m) at night (Fig. 4a). They increased the depth of their dives during day time (between civil dawn and dusk, i.e. when the sun is 6° below the horizon, 03:30–19:30 local time), but performed a similar proportion of dives during day and night (Fig. 4b).

Macaroni penguins from Marion Island generally showed a high diving efficiency of 0.5 (for dives >2 m, Table 2), due to the massive contribution of highly efficient shallow dives. Indeed, there was a progressive decrease in efficiency with increasing dive depth, with maximum diving efficiency attained for dives <30 m, peaking for dives of 5–10 m (Fig. 5). If we separate shallow dives (2–20 m) from deeper dives (>20 m) based on the two modes shown in Fig. 2, there was a marked decrease in average dive efficiency between shallow dives (0.51 ± 0.07) and deeper dives (0.36 ± 0.05 , Table 1). Efficiency of dives >10 m typically was greater for birds from our study than for birds from Bird Island, South Georgia, in 2001–2003 (Green et al. 2005; Table 2).

Between December 2008 and February 2009, the diet of macaroni penguins from Marion Island was dominated by two species, which accounted for >92% by mass: the euphasid *Thysanoessa vicina* (83.0%) and the myctophid *Krefflichthys anderssoni* (9.2%). Overall, breeding birds fed predominantly (86.0% by mass) on crustaceans: 96.5% *Thysanoessa vicina*, 2.9% *Euphasia vallentini* and 0.6% amphipods. Fish comprised 12.1% of the total mass of the diet (81.5% *Krefflichthys anderssoni* and 5.9% *Protomyctophum tension*), with the remaining 1.9% cephalopods (Ommastrephidae and Onychoteuthidae).

Discussion

Diving patterns of macaroni penguins from Marion Island were broadly similar to those recorded from other colonies. Macaroni penguins generally are characterised by flexible foraging behaviour, varying with the type of prey, stage of reproduction, sex and colony location (e.g. Barlow and

Table 1 Diving characteristics during 12 foraging trips from 6 female macaroni penguins raising small chicks on Marion Island, South Africa

Individual	B1 (trip1)	B1 (trip2)	B2 (trip1)	B2 (trip2)	B2 (trip3)	B2 (trip4)	B2 (trip5)	B3	B4	B5	B6 (trip1)	B6 (trip2)
Mass (g)	4,800	4,600	4,600	4,600	4,000	4,800	4,050	4,600	4,800	4,050	4,600	4,600
Start time	2008/12/18 12:52	2008/12/19 07:22	2008/12/19 04:45	2008/12/21 05:15	2008/12/24 21:50	2008/12/26 04:00	2008/12/29 06:47	2008/12/18 15:01	2008/12/19 01:55	2008/12/19 02:23	2008/12/19 02:24	2008/12/20 00:22
Trip duration (h)	5.6	10.3	40.8	80.8	25.0	30.7	8.9	36.2	31.1	25.9	17.7	35.1
Number of dives	253	374	1,908	3,348	922	3,247	369	1,690	1,086	786	1,696	1,443
Mean diving rate (dives h ⁻¹ at sea)	45.3	36.3	46.7	41.4	36.9	105.8	41.5	46.7	34.9	30.3	95.6	41.1
Mean dive depth (m)	17.9 ± 63.8	24.5 ± 66.5	17.5 ± 30.0	20.4 ± 29.9	21.4 ± 28.2	9.2 ± 25.1	27.8 ± 38.3	13.4 ± 26.6	21.0 ± 31.1	16.8 ± 26.0	5.6 ± 14.5	19.3 ± 27.4
Max. depth (m)	76.3	90.6	124.2	154.0	126.0	128.1	102.4	110.8	115.6	105.0	97.9	138.6
Mean dive duration (s)	51.7 ± 26.5	66.3 ± 30.1	42.9 ± 58.5	57.3 ± 58.5	66.1 ± 57.7	18.7 ± 39.7	56.7 ± 72.8	40.1 ± 59.5	58.7 ± 63.8	55.0 ± 54.7	22.1 ± 39.1	66.0 ± 50.2
Max. dive duration (s)	171	190	186	192	183	185	189	200	207	191	200	184
Mean dive efficiency (dives <20 m)	0.48 ± 0.22	0.52 ± 0.19	0.49 ± 0.17	0.56 ± 0.15	0.55 ± 0.13	0.41 ± 0.18	0.40 ± 0.17	0.51 ± 0.18	0.51 ± 0.16	0.55 ± 0.15	0.60 ± 0.16	0.61 ± 0.12
Mean dive efficiency (dives >20 m)	0.44 ± 0.06	0.41 ± 0.08	0.33 ± 0.09	0.30 ± 0.10	0.36 ± 0.12	0.30 ± 0.09	0.29 ± 0.09	0.40 ± 0.09	0.40 ± 0.09	0.41 ± 0.09	0.36 ± 0.11	0.32 ± 0.08
% dives <10 m	71.9	61.8	74.4	63.6	61.9	89.9	65.3	82.0	69.2	71.8	92.9	68.3
Mean depth of dives (>10 m)	57.8 ± 15.4	60.6 ± 15.8	62.8 ± 27.3	51.5 ± 30.6	50.7 ± 26.5	76.7 ± 34.1	76.6 ± 23.8	61.8 ± 29.5	58.5 ± 29.6	50.2 ± 27.1	50.4 ± 26.9	51.1 ± 28.6

Values are average ± SD

Croxall 2002; Green et al. 2005; Deagle et al. 2008). It seems, however, that feeding locations exploited at a particular stage of the breeding cycle may remain consistent over years (Trathan et al. 2006), suggesting that birds rely on predictable resources linked to specific oceanographic features. Although we did not investigate differences between reproductive stages or sex in this study, our birds varied considerably in foraging trip durations, departure times and diving rates (Table 1; Fig. 1), which tallies with the variable foraging ranges (59–303 km) estimated for Marion Island penguins in the 1980s (Brown 1987). The average trip duration in our study was similar to that recorded at Heard Island from birds at a similar breeding stage (23 h, range 4–78 h; Deagle et al. 2008), with both having longer trips than birds at the same stage from Bird Island, South Georgia (<12 h in 1989, Croxall et al. 1993; 15 h in 2004, Waluda et al. 2010).

As in other studies (Green et al. 1998, 2003), penguins from Marion Island increased their dive depths during day time (Fig 4a) and performed shallow night dives (<5 m, Fig. 4a; Croxall et al. 1993; Green et al. 2003), suggesting that they follow the daily migration of their prey (Croxall et al. 1993; Green et al. 2003). However, the diving rate of birds from Marion remained similar during day and night (Fig. 4b), which contradicts the findings of other studies. Birds from South Georgia decreased their diving rate at night (Green et al. 2003), when only a small proportion (5–8%) of dives occurred (Croxall et al. 1993; Waluda et al. 2010). The uniform dive rate throughout the day and night for macaroni penguins from Marion Island (Fig. 4b) suggests that they probably feed at night. Their main prey are known to migrate closer to the surface at night at times (e.g. myctophids in oceanic waters or krill in shelf waters, Ichii et al. 2007).

If we follow the criterion of Green et al. (2005) for foraging dives (i.e. dives >10 m), macaroni penguins from Marion Island foraged at average depths of 50.0 ± 15.7 m, which is 35% deeper than the foraging dives of macaroni

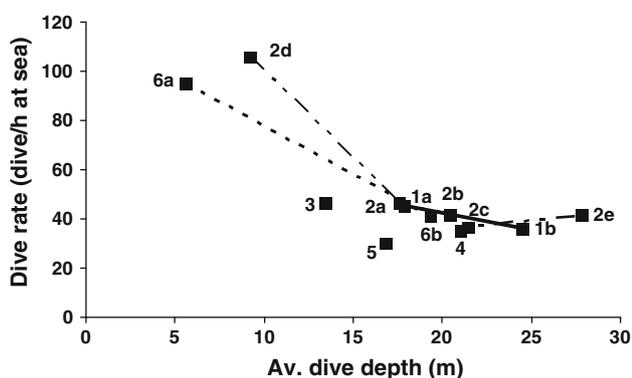


Fig. 1 Average dive depth (m) in relation to dive rate (dive/h at sea) of 12 trips from 6 macaroni penguins from Marion Island

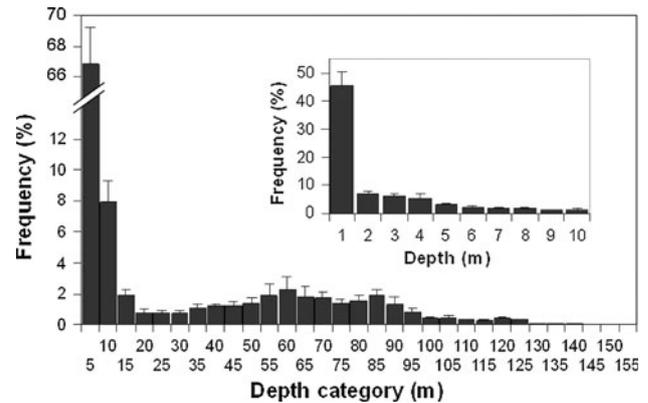


Fig. 2 Frequency of dive depths (dives >1 m, in 5 m classes), with the inset showing dives <10 m in 1 m depth classes, during 12 foraging trips of six macaroni penguins breeding on Marion Island, South Africa (average \pm SE). Note the Y-axis of the main graph has been cut between 14 and 64% to ease the reading

penguins of Bird Island, South Georgia, breeding at a similar stage in 2001/2003 (Green et al. 2005) and on Heard Island in 2003/2004 (Deagle et al. 2008; Table 2). Similarly, if we exclude dives <3 m, the average dive depth from birds of our study was deeper than birds at similar breeding stage from Bird Island in 1998/1999 (Green et al. 2003) and from Heard Island in 2003/2004 (Deagle et al. 2008), only being comparable to the dive depths of incubating birds from Kerguelen Island (Sato et al. 2004; Table 2).

However, comparison of diving patterns between studies is complicated by differences in device accuracy and sampling frequency (e.g. Green et al. 2003, 2005 did not record dives <2.4 m), as well as by differences in the thresholds used to separate commuting from foraging dives (e.g. 4 m in Green et al. 1998; 3 m in Green et al. 2005 and Deagle et al. 2008; see Table 1). Only Sato et al. (2004) used similar data loggers to the ones we used, but they studied incubating macaroni penguins which may use considerably different foraging strategies (cf. king penguin *Aptenodytes patagonicus*, Charrassin et al. 1998). However, few differences were detected between incubating and brooding macaroni penguins on South Georgia in 2001–2003 (Green et al. 2005). Macaroni penguins from Marion Island performed many shallow dives (Fig. 2). Lower sampling frequency in other studies might contribute to this finding: for example, dives <4 m represent 8% of dives by penguins from Heard Island in 1992 when depth was recorded only every 3 s (Green et al. 1998). Also, Deagle et al. (2008) recorded data only every 10 s, thus probably underestimating maximum dive depths (26.4 m on average), among other parameters. However, when encompassing different analytical methods and comparing similar depths, shallow dives of 3–10 m represented a similar proportion of dives from birds across

Fig. 3 Relationship between dive depth and dive duration of macaroni penguins from Marion Island. An arrow shows two diving modes switching at 20 m—100 s

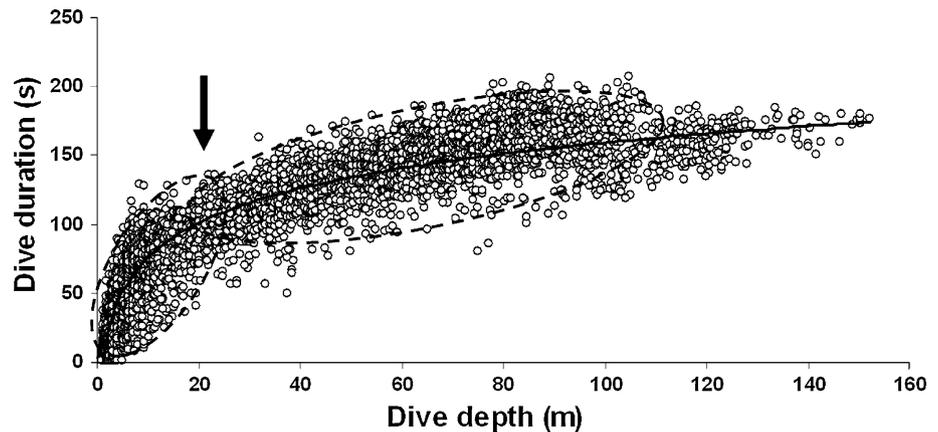
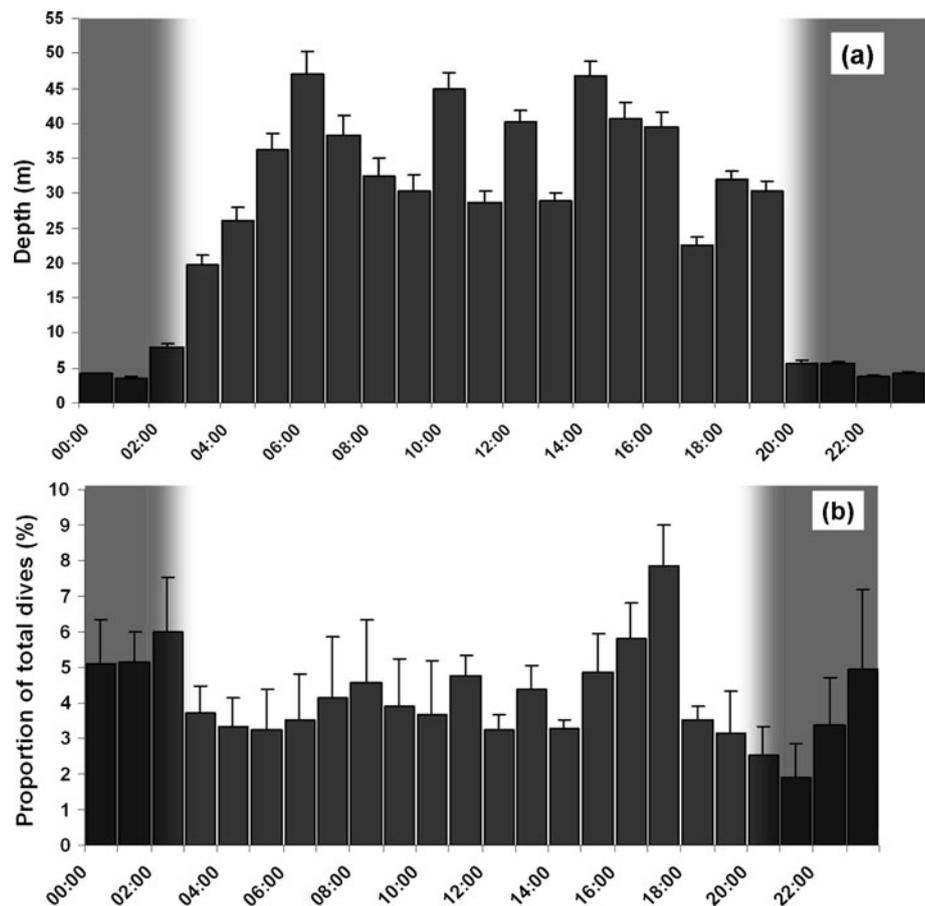


Fig. 4 Distribution of (a) average maximum dive depths and (b) proportion of total dives performed throughout the time of the day during 12 foraging trips of six breeding macaroni penguins from Marion Island, South Africa. Shaded areas represent night time. Values are mean \pm SE



islands: 29% of total dives of macaroni penguins at Bird Island, South Georgia (Green et al. 2005), 27% at Heard Island in 2003/2004 (Deagle et al. 2008) and 22% of dives in our study, even if such proportions may vary between colonies or years with the number of birds sampled, as the data are pseudo-replicated.

Macaroni penguins from Marion Island showed a bimodal distribution in their dive depths and durations, switching from shallow short dives to longer deeper dives

at 15.7 m (Fig. 3). This relation between dive depth and duration is similar of incubating birds from Kerguelen, that switched between modes at *ca* 15 m (Fig. 3 from Sato et al. 2004). In our study, the smaller peak of longer, deeper dives occurred at depths of 55–85 m (Fig. 2). This is similar to birds breeding on Heard Island in 1993/1993 that also showed two peaks in dive depths switching at *ca* 20 m, although that second peak varied among individuals and/or time of year, ranging from 40–50 m to 80–110 m (Green

Table 2 Comparison of studies on diving characteristics of breeding female macaroni penguins from different colonies

Location of colony	Study period	Breeding stage	N birds sampled	N dives recorded	Dive threshold (m)	Sampling frequency (s)	Mean dive depth (m)	Max. depth (m)	Mean dive duration (s)	Max duration (s)	Dive efficiency	Reference
Marion Island (46°52'S, 37°51'E)	Dec 2008	Brood guard	6	17,122	1	1	24.6 ± 8.6	154	50.8 ± 12.1	207	0.45	This study
				8,326	2	1	31.2 ± 33.8		87.8 ± 54.2	0.5		
				7,247	3	1	35.5 ± 34.2		98.0 ± 50.6	0.49		
				6,504	4	1	39.2 ± 34.2		105.5 ± 47.7	0.48		
			4,213	10	1	50.0 ± 15.7		133.4 ± 32.4		0.41		
Bird Island, South Georgia (54°00'S–38°03'W)	Jan 1989	Brood guard	2	4,876	1	Continuous	27 (only day dives)	115	92.7 (only day dives)	378	No data	Croxall et al. 1993
				42,054**	2.4	2	17.5 ± 0.8*	94.8	86.6 ± 2.4*	No data	Green et al. 2003	
				97,359**	10	2	37.3 ± 1.9*	132.4**	99.0 ± 1.7*	194.8**		
			23									
Kerguelen Island (49°15'S–69°35'E)	Nov-Dec 2002	Incubating	8	No data	2.4	1	34.9 ± 30	99.2	95.7 ± 51.6	190	No data	Sato et al. 2004
Heard Island (53°06'S–73°31'E)	Nov 1992-Feb 1993	Brood guard	19	No data	4	3	No data	163	No data	228	No data	Green et al. 1998
				31,715	3	10	26.4 ± 8.6	55.2	No data	No data	No data	
			25	18,869	10	10	36.1 ± 13					

Values are average ± SD (* are ± SE)
 ** are data from J.A. Green in litt

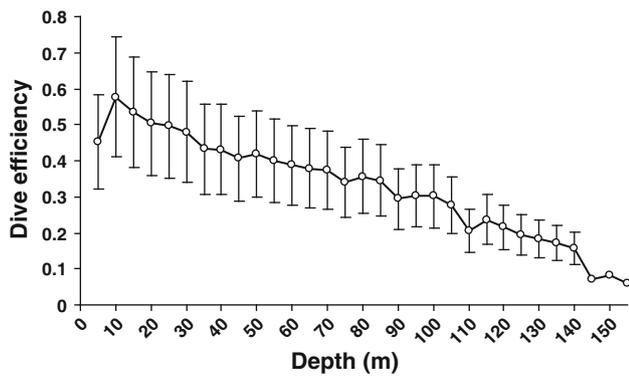


Fig. 5 Dive efficiency (bottom dive as a function of total dive cycle, average \pm SE) in relation to maximum dive depth (>2 m, in 5-m depth classes) of six female macaroni penguins breeding on Marion Island, South Africa

et al. 1998). Bimodal dive depths might correspond to the birds mainly targeting two prey species at Marion Island, with shallow dives mainly targeting crustaceans and deeper dives targeting myctophid fish. This hypothesis is supported by the similar diving structure displayed by birds from Heard Island (Green et al. 1998), where deep foraging dives are performed by birds feeding on myctophids (Deagle et al. 2008). In some years, fish comprise up to 37–52% of the diet by mass of birds breeding on Marion and their chicks survive better when fed on more fish (Crawford et al. 2003). No such bimodal distribution in dive depths was observed in birds from Bird Island, South Georgia (Croxall et al. 1993; Green et al. 2003, 2005; Mori and Boyd 2004), although fish constitute up to 46% of their diet (Barlow et al. 2002; Waluda et al. 2010). This variability in diving behaviour among sites supports the notion that the diving activity of macaroni penguins is flexible, probably linked to differences in the types of prey consumed (Deagle et al. 2008; this study) and in the oceanographic features where foraging occurs (see Chiaradia et al. 2007 for example).

Finally, if we consider shallow (<5 m) dives solely as travelling dives (following Green et al. 1998; Deagle et al. 2008), the trip organisation of macaroni penguins from Marion Island would be extremely erratic: some birds would travel substantially before feeding (with a series of shallow dives at the beginning and end of their trip, independent of the time of day), while others start to feed close to the colony, performing deep dives right at the beginning of their trip. An alternative explanation is that birds feed at shallow depths. Theory predicts a positive correlation between patch quality and patch residence time, so that a diver should stay longer in a better patch (Mori 1998). The diving efficiency of macaroni penguins at Marion Island is high compared to other penguin species (e.g. <0.2 for southern rockhopper penguins *Eudyptes chrysocome*, Tremblay and Cherel 2000), suggesting that feeding

conditions were profitable around Marion Island in December 2008. Macaroni penguins are thought to maximise their energy intake per dive cycle when diving shallower than 30–40 m (Mori and Boyd 2004), which our study confirmed with diving efficiency decreasing for deeper dives (Fig. 4). To confirm that foraging occurs at depths of highest diving efficiency would require a more detailed approach, equipping birds with devices to measure prey ingestion (e.g. Ropert-Coudert et al. 2001; Bost et al. 2007) or jaw movement (Wilson et al. 2002). But our data suggest that shallow dives by macaroni penguins cannot be dismissed as purely travelling dives.

Our study is the first description of the diving activity of macaroni penguins from Marion Island. It confirms the variability in diving patterns of individual macaroni penguins (Barlow and Croxall 2002; Deagle et al. 2008) and sets a baseline for future studies to examine changes in diving behaviour seasonally or annually at this site. Marion Island lies at the northern limit of the species range and is therefore expected to be more affected by climate change than more southerly breeding localities (e.g. Chuine 2010). Despite their apparent flexibility in foraging behaviour which helps to compensate for variable feeding environments (Cresswell et al. 2008), macaroni penguin numbers are decreasing globally (Kirkwood et al. 2007; IUCN 2010) including at Marion Island (Crawford et al. 2009). Winter foraging conditions are thought to influence the proportions of birds breeding and their breeding success (Crawford et al. 2006). Conservation of this numerically dominant predator in the Southern Ocean may depend on understanding their at-sea distribution and diet during winter. Studies also are needed to investigate potential competition with other species, such as southern rockhopper penguins, which also have decreased at Marion Island in the last few decades (Crawford et al. 2009). Demand for krill fishing is expected to increase (Kawagushi and Nicol 2007), and existing krill fishing activities overlap temporally and spatially with foraging ranges of breeding land-based predators (Murphy et al. 1997; Croxall and Nicol 2004), including macaroni penguins. Breeding success and survival of some predators are likely to be impacted by krill fishing (Mangel and Switzer 1998). Studies on the foraging behaviour of macaroni penguins in relation to the distribution and abundance of krill catches would help to estimate this potential threat, as well as accurately inform management decisions.

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References

- Bannasch R (1995) Hydrodynamics of penguins—an experimental approach. In: Dann P, Norman I, Reilly P (eds) *The penguins*. Surrey, Beatty and Sons, Chipping Norton, New South Wales, pp 141–176
- Barlow KE, Croxall JP (2002) Seasonal and interannual variation in foraging range and habitat of macaroni penguins *Eudyptes chrysolophus* at South Georgia. *Mar Ecol Progr Ser* 232:291–304
- Barlow KE, Boyd IL, Croxall JP, Reid K, Staniland IJ, Brierley AS (2002) Are penguins and seals in competition for Antarctic krill at South Georgia. *Mar Biol* 140:205–213
- Bost CA, Handrich Y, Butler PJ, Fahlman A, Halsey L, Woakes AJ, Ropert-Coudert Y (2007) Change in dive profile as an indicator of feeding in king penguins and Adélie penguins. *Deep Sea Res* 54:248–255
- Brooke M de L (2004) The food consumption of the world's seabirds. *Proc R Soc Lond B* 271:s246–s248
- Brown CR (1987) Travelling speed and foraging range of macaroni and rockhopper penguins at Marion Island. *J Field Ornithol* 58:118–125
- Charrassin J-B, Bost C-A, Putz K, Lage J, Dahier T, Zorn T, Le Maho Y (1998) Foraging strategies of incubating and brooding king penguins *Aptenodytes patagonicus*. *Oecologia* 114:194–201
- Chiaradia A, Ropert-Coudert Y, Kato A, Mattern T, Yorke J (2007) Diving behaviour of little penguins from four colonies across their whole distribution range: bathymetry affecting diving effort and fledging success. *Mar Biol* 151:1535–1542
- Chuine I (2010) Why does phenology drive species distribution. *Phil Trans R Soc B* 365:3149–3160
- Crawford RJM, Cooper J (2003) Conserving surface-nesting seabirds at the Prince Edwards Islands: the roles of research, monitoring and legislation. *Afr J Mar Sci* 25:415–426
- Crawford RJM, Cooper J, Dyer BM (2003) Population of the macaroni penguin *Eudyptes chrysolophus* at Marion Island, 1994/1995–2002/2003, with information on breeding and diet. *Afr J Mar Sci* 25:475–486
- Crawford RJM, Dyer BM, Cooper J, Underhill L (2006) Breeding numbers and success of *Eudyptes* penguins at Marion Island, and the influence of mass and time of arrival of adults. *CCALMR Science* 13:175–190
- Crawford RJM, Whittington PA, Upfold L, Ryan PG, Petersen SL, Dyer BM, Cooper J (2009) Recent trends in numbers of four species of penguins at the Prince Edward Islands. *Afr J Mar Sci* 31:419–426
- Cresswell KA, Wiedenmann J, Magel M (2008) Can macaroni penguins keep up with climate- and fishing-induced changes in krill? *Polar Biol* 31:641–649
- Croxall JP, Prince PA (1987) Seabirds as predators on marine resources, especially krill, at South Georgia. In: Croxall JP (ed) *Seabirds feeding ecology and role in marine ecosystems*. Cambridge University Press, Cambridge, pp 347–368
- Croxall JP, Nicol S (2004) Management of Southern Ocean fisheries: global forces and future sustainability. *Antarctic Sci* 16:569–584
- Croxall JP, Briggs DR, Kato A, Naito Y, Watanuki Y, Williams TD (1993) Diving pattern and performance in the macaroni Penguin *Eudyptes chrysolophus*. *J Zool* 230:31–47
- Deagle BE, Gales NJ, Hindell MA (2008) Variability in foraging behaviour of chick-rearing macaroni penguins *Eudyptes chrysolophus* and its relation to diet. *Mar Ecol Progr Ser* 359:295–309
- Dewar JM (1924) *The bird as a diver*. Witherby, London
- Green K, Williams R, Green MG (1998) Foraging ecology and diving behaviour of macaroni penguins *Eudyptes chrysolophus* at Heard Island. *Mar Ornithol* 26:27–34
- Green JA, Butler PJ, Woakes AJ, Boyd IL (2003) Energetics of diving in macaroni penguins. *J Exp Biol* 206:43–57
- Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2005) Behavioural flexibility during year-round foraging in macaroni penguins. *Mar Ecol Progr Ser* 296:183–196
- Grémillet D, Pichegru L, Siorat F, Georges JY (2006) Conservation implications of the apparent mismatch between population dynamics and foraging effort in Northern gannets from the English channel. *Mar Ecol Progr Ser* 319:15–25
- Ichii T, Bengston JL, Boveng PL, Takao Y, Jansen JK, Hiruki-Raring LM, Cameron MF, Okamura H, Hayashi T, Naganubo M (2007) Provisioning strategies of Antarctic fur seals and chinstrap penguins produce different responses to distribution of common prey and habitat. *Mar Ecol Progr Ser* 344:277–297
- IUCN 2010 (2010) IUCN Red List of Threatened Species. <http://www.iucnredlist.org/>
- Kato A, Ropert-Coudert Y, Grémillet D, Cannell B (2006) Locomotion and foraging strategy in foot-propelled and wing-propelled shallow-diving seabirds. *Mar Ecol Progr Ser* 308:293–301
- Kawagushi S, Nicol S (2007) Learning about Antarctic krill from the fishery. *Antarctic Sci* 19:219–230
- Kirkwood R, Lawton K, Moreno C, Valencia J, Shlatter R, Robertson G (2007) Estimates of southern rockhopper and macaroni penguin numbers at Ildefonso and Diego Ramírez Archipelagos, Chile, using quadrat and distance sampling techniques. *Waterbirds* 30:259–267
- MacQueen JB (1967) “Some Methods for classification and Analysis of Multivariate Observations”. *Proceedings of 5th Berkeley symposium on mathematical statistics and probability*. University of California Press, pp 281–297
- Mangel M, Switzer PV (1998) A model at the level of the foraging trip for the indirect effects of krill (*Euphasia superba*) fisheries on krill predators. *Ecol Model* 105:235–256
- Mori Y (1998) The optimal patch use in divers: optimal time budget and the numbers of dive cycles during bout. *J Theor Biol* 190:187–199
- Mori Y, Boyd IL (2004) Segregation of foraging between two sympatric penguin species: does rate maximisation make the difference? *Mar Ecol Progr Ser* 275:241–249
- Murphy EJ, Trathan PN, Everson I (1997) Krill fishing in the Scotia Sea in relation to bathymetry, including the detailed distribution around South Georgia. *CCALMR Sci* 4:1–17
- Ropert-Coudert Y, Kato A, Baudat J, Bost C-A, Le Maho Y, Naito Y (2001) Feeding strategies of free-ranging Adélie penguins, *Pygoscelis adeliae*, analyzed by multiple data recording. *Polar Biol* 24:460–466
- Ropert-Coudert Y, Kato A, Naito Y, Cannell B (2003) Individual diving strategies in the little penguins. *Waterbirds* 26:403–408
- Sato K, Charassin J-B, Bost C-A, Naito Y (2004) Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? *J Exp Biol* 207:4057–4065
- Trathan PN, Green C, Tanton J, Peat H, Poncet J, Morton A (2006) Foraging dynamics of macaroni penguins *Eudyptes chrysolophus* at South Georgia during brood-guard. *Mar Ecol Progr Ser* 323:239–251
- Tremblay Y, Cherel Y (2000) Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. *Mar Ecol Progr Ser* 204:257–267
- Waluda CM, Collins MA, Black AD, Staniland IJ, Trathan PN (2010) Linking predator and prey behaviour: contrasts between

- Antarctic fur seals and macaroni penguins at South Georgia. *Mar Biol* 157:99–112
- Williams AJ (1982) Chick feeding rates of macaroni and rockhopper penguins at Marion Island. *Ostrich* 53:129–134
- Wilson RP, Steinfurth A, Ropert-Coudert Y, Kato A, Kurita M (2002) Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Mar Biol* 140:17–27
- Woehler EJ, Cooper J, Croxall JP, Fraser WR, Kooyman GL, Miller GD, Nel DC, Patterson DL, Peter HU, Ribic CA, Salwicka K, Trivelpiece WZ, Weimerskirch H (2001) A statistical assessment of the status and trends of Antarctic and subantarctic seabirds. Report on SCAR BBS workshop on Southern Ocean seabirds populations, p 43