FORAGING ECOLOGY AND DIVING BEHAVIOUR OF MACARONI PENGUINS *EUDYPTES CHRYSOLOPHUS* AT HEARD ISLAND

K. GREEN[1,2], R. WILLIAMS[1] & M.G. GREEN[2]

[1]*Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia*
[2]*Current address: National Parks and Wildlife Service, Snowy Mountains Region, PO Box 2228, Jindabyne, New South Wales 2627, Australia*
(ken.green@npws.nsw.gov.au)

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SUMMARY

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Over the chick-rearing period, Macaroni Penguins *Eudyptes chrysolophus* foraged to the north-east of Heard Island within an approximate 300-km radius, feeding mainly on euphausiids and fish. As the season progressed, the amount of euphausiids in the diet declined by 93% with the diet becoming almost totally composed of the myctophid fish *Krefftichthys anderssoni*. Penguins foraged mainly on the Heard Island shelf area (seas shallower than 1000 m). Penguin dive profiles were complex, unlike the simple 'V' shaped dives recorded elsewhere. Diving was mainly between dawn and dusk to depths of 10–60 m, and the deepest dives were undertaken during daylight hours. The connection between the observed diving patterns and the diet was difficult to elucidate because *K. anderssoni* only migrates vertically into surface waters at night and is believed to be out of the penguins' diving range during the day.

INTRODUCTION

Macaroni Penguins *Eudyptes chrysolophus* on Heard and McDonald Islands are thought to number about two million breeding pairs (Woehler 1991). Of the estimated 521 000 tonnes of prey harvested from the surrounding seas between October and April by vertebrates breeding on Heard Island, Macaroni Penguins take 77% (Woehler & Green 1992). Macaroni Penguins thus make a heavy demand on marine resources from Heard Island between the prelaying period and moulting, a period of about six months, but their major impact is in the two months between hatching and fledging, when their foraging ranges are limited by the necessity of regularly returning to the island with food for chicks. The dietary data available to Woehler & Green (1992) were from a single study conducted in one breeding season covering the period from the return of the females from their first foraging session after egg-laying, and the early period of chick growth (Klages *et al.* 1989). There are no data on the areas in which these penguins foraged. The only other information on the diet of Macaroni Penguins at Heard Island comes from observations by Ealey (1954) which were not quantitative.

Macaroni Penguins are the most abundant penguins worldwide (Woehler 1993). Few studies of diet and diving behaviour have been undertaken, the latter exclusively in the South Georgia area (Croxall *et al.* 1988, 1993) where the diet was dominated by Antarctic Krill *Euphausia superba* (Croxall & Prince 1980, Croxall *et al.* 1993). The present study was designed to examine the foraging ecology and diving behaviour of Macaroni Penguins during the breeding cycle in an area where Antarctic Krill is virtually absent.

METHODS

Diet

Food samples were collected from birds captured on the beach and presumed to have returned from foraging trips. Initially, eight samples were collected at Rogers Head (Fig. 1) on 10 and 14 February 1992. In the following breeding season, 10 samples were collected from the colony at Icicle Gully (Fig. 1) on each of five occasions between 3 January 1993 (after all eggs had hatched) and 15 February 1993 (when the first fledged chicks were seen away from the colony on the beach) (Table 1). Samples were collected using water-flushing techniques (Wilson 1984) with gravity feed (Green & Johnstone 1986, Puddicombe & Johnstone 1988) using multiple flushes. A penguin inverter (Robertson *et al.* 1994) was used both as a restraint for the penguin while introducing the stomach tube and as a means of inverting the penguin to flush out stomach contents. This allowed the operation to be conducted by one person. After stomach flushing, the samples were drained through a 0.5-mm sieve, bottled, and preserved with 100% ethanol for return to the laboratory. Each sample was washed in a sorting tray to settle out otoliths. A subsample (approximately 35%) of the remainder was taken to calculate the composition. Euphausiid eyes, other crustaceans (essentially the amphipod *Themisto gaudichaudii*), and squid were counted in the subsample. All *T. gaudichaudii* and the first 10 measurable carapaces of *Euphausia vallentini* found in the subsample were measured to estimate body size. The carapace measurement for *E. vallentini* was standard length number 5 in Mauchline (1980). Total body length of *E. vallentini* was estimated from carapace

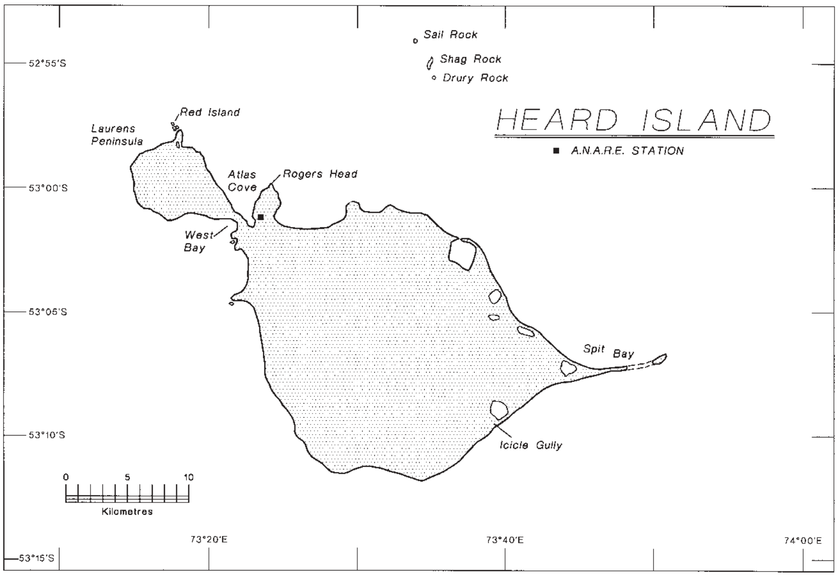

Fig. 1. *Heard Island showing sampling sites used in the present study and by Klages* et al. *(1989).*

measurements by:
Length (mm) = 6.6295 + 2.6048* Carapace, and wet mass (mg) was calculated by Mass = 0.00884*Length $^{2.904}$ (G. Hosie & M. Stolp pers. comm.). Only one *E. vallentini* was measured from the first foraging period so periods 1 and 2 were amalgamated for calculations. After sorting, the sample and subsample were drained and set out in trays spread to equal thickness to dry overnight before weighing. Otoliths were identified by reference to Williams & McEldowney (1990). As with previous studies (Green *et al.* 1989,1991) only otoliths showing little or no signs of erosion were selected for measurement to calculate fish standard lengths from formulae in Williams & McEldowney (1990). The average calculated masses of *E. vallentini* and *Krefftichthys anderssoni* per sample were used to estimate the representation of *E. vallentini* as a proportion of the sum of both.

Diving

Mark 5 Time Depth Recorders (Wildlife Computers, 20 630 NE 150th Street, Woodinville, WA 98072-7641, U.S.A.) were glued to the dorsal midline of penguins with Loctite 401 (Loctite, Welwyn Garden City, Herts AL7 1JB, U.K.). The penguins were held still for 30 s with pressure on the Time Depth Recorder (TDR) before being released. The TDRs were programmed to record depth every three seconds, temperature every 240 s, and each recorder collected light levels for geolocation based on the calculated time of sunrise and sunset. TDRs were deployed on six males and six females during the incubation phase and on 25 females at five intervals spaced throughout the chick-rearing period. Penguins were not banded and were known by their TDR numbers. Where the recorder number is followed by a number in parentheses this number refers to the second, or third deployment of that recorder. Recorders were only deployed once on any individual penguin. On recapture of the penguins, the units were retrieved by prising the plate of glue on the underside of the TDR from the feathers.

Latitude and longitude were calculated using the Geolocation program (Wildlife Computers) which determines the time of dawn and dusk then calculates the location using standard navigational formulae. The general accuracy of the locations were checked by examining the temperature record from the TDRs and comparing the location with the expected temperature from charts of the Southern Ocean. These were Reynolds Blended SST Analysis weekly average sea surface temperatures from the Physical Oceanographic Data Active Archive Centre (NOAA).

The data produced by the program "Dive Analysis" (Wildlife Computers) were sorted by depth and then time. Dives shallower than four metres were considered travelling dives and were termed dive type A. After examination of some hundreds of shallow dives (<20 m) there were few characteristics observed that could be used to differentiate dive types and so all dives deeper than four metres but less than 20 m were classified as type B. The traces of all other dives were then examined. Dives (Fig. 2) were classified as:

A. Dives less than four metres in depth (not illustrated).
B. Dives deeper than four metres but <20 m (not illustrated).
C. Flat-bottomed dives.
D. Two-stage dives in which the deepest part came second.
E. Two-stage dives in which the deepest part came first.
F. Round-bottomed dives.

TABLE 1

Average mass and contents of stomach samples from ten individual Macaroni Penguins at five intervals during the breeding season at Heard Island

Date	Av. mass ± SD (g)	Av. no. euphausiid eyes ± SD	Av. no. *Themisto*	Av. no. of otoliths ± SD	*E. vallentini* as a percentage of *E. vallentini* + *K. anderssoni*
3 Jan	66±46	3836±2069	3	116±96	62.8
14 Jan	46±31	3012±2207	3	70±63	78.3*
28 Jan	73±47	2284±2710	3	354±265	35.6
5 Feb	80±55	1459±1596	32	205±189	28.5**
15 Feb	72±68	147±286	7	167±183	5.1

*+ copepod in one sample.
**+*Euchaeta* in one sample, one, two, two and nine squid beaks were found in the last four sampling periods, respectively.

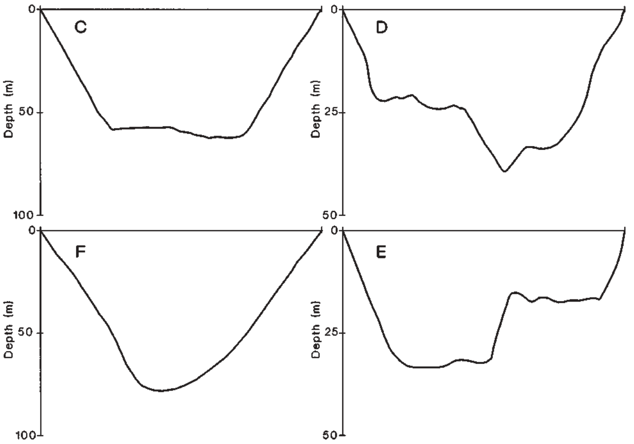

Fig. 2. *Dive profiles of Macaroni Penguins around Heard Island.*

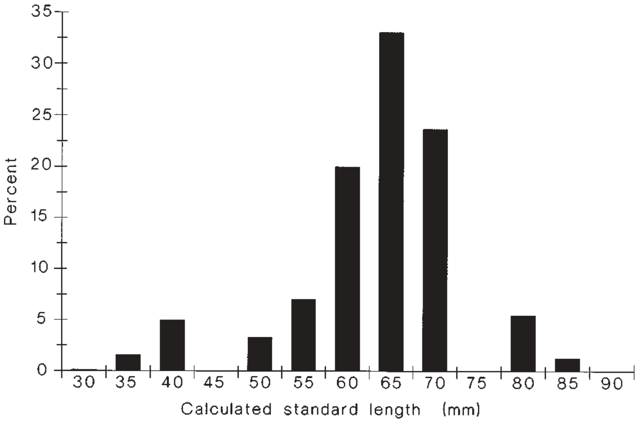

Fig. 3. *Size-frequency distribution of* Krefftichthys anderssoni *in the diet of Macaroni Penguins at Heard Island over the 1993 sampling period.*

RESULTS

Diet

The eight food samples collected at Rogers Head towards the end of the breeding season in 1992 averaged 39.1±33.1 g consisting of 37% *T. gaudichaudii*, 21.6% *E. vallentini* and 41.4% fish by mass. Fifty food samples were collected in batches of 10 over the chick-rearing season of 1993. The mass of these samples averaged 67.1±50.1 g and they normally consisted of a well-digested soup of euphausiids and fish such that the two could not be easily separated with certainty. The amount of euphausiids, mainly *E. vallentini*, as measured by undigested eyes in each sample, fell steadily through the chick-rearing period from nearly 4000 eyes per sample to less than 150. Fish increased proportionately in the diet as *E. vallentini* fell from a high of 78% to 5% by number over the season, however, was no compensatory increase in fish otolith numbers (Table 1) and the difference was made up by an increased proportion of unidentified semi-digested material. Squid beaks were small and were not identifiable.

The size of *E. vallentini* varied little over the breeding season (Table 2). Although the size of *T. gaudichaudii* fluctuated over the season the major difference was between years, with an average size of 17.3 ± 3.3 mm (n = 43) in 1992 compared with 12.2 ± 5.5 mm (n = 28) in 1993, a difference that was significant (*t*-test, $P < 0.001$). The mean carapace length of *E. vallentini* (4.1±1.1 mm, n = 34) in 1992 was less than in 1993 (4.6 ± 1.1 mm, n = 125) but this was not significant (*t*-test, $P = 0.057$).

A total of 8589 otoliths was recovered from stomach samples. All came from one species, the myctophid *K. anderssoni* (Fig. 3), except for a total of 26 otoliths from the myctophid fish *Electrona antarctica*, *E. subaspera*, *E. carlsbergi*, *Protomyctophum normani*, *P. tenisoni* and the Unicorn Icefish *Channichthys rhinoceratus*.

Diving

Of the 30 TDRs recovered, one penguin had not gone to sea foraging. Foraging data were therefore available from 10 birds during incubation and 19 birds during chick rearing (Table 3). During the chick-rearing period 132 locations were obtained by units on 18 penguins. Apart from a few outliers to the south of the island most locations were in an arc from north-north-west to east-south-east of the island extending out as far as the shelf break nearly 300 km away (Fig. 4). There did not appear to be any difference in the foraging area between different deployments. The temperatures recorded by the TDRs were generally within the range expected for the sites from geolocation. Thus foraging locations to as far north as 50°S were consistent with sea-surface temperature data. Locations from the Geolocation program require time of sunrise and sunset and are therefore calculated as an average location each day. This fact, combined with difficulties in determining from the recorder when it was at sea and wet or on land and wet made it impossible to calculate how long penguins were away from the colony. However, foraging intervals during chick rearing in excess of three days were confirmed by the time spent by KG waiting at the colony to remove TDRs from returning birds.

TABLE 2

Mean carapace length (mm) of *Euphausia vallentini* and mean total body length (mm) of *Themisto gaudichaudii* in the diet of Macaroni Penguins at Heard Island. Figures are means ± one standard deviation

Date	*Euphausia vallentini*	*Themisto gaudichaudii*
10 Feb 1992	4.1±1.1	17.3±3.3
3 Jan 1993	3.9	–
14 Jan 1993	4.9±1.3	15.5±1.6
28 Jan 1993	4.4±0.6	–
5 Feb 1993	4.1±0.5	10.7±5.2
15 Feb 1993	4.7±0.9	15.2±6.3

Overall, travelling dives (<4 m; type A) only represented 8.4% of dives. Shallow dives (4–20 m; B) , however, comprised 25.8% of dives. Of the deeper dives (>20 m; 65.8% of the total), round-bottomed dives (F) were the most common (37.6%), followed by flat-bottomed dives (C; 16.8%) and two-phase dives (D plus E; 11.4%) (Table 4). The most common dives by females were the shallow B dives or the deeper, round-bottomed, F dives and overall the patterns of diving were consistent throughout the six deployments (Table 4). In males, however, flat-bottomed C dives were second only to round-bottomed F dives in number.

Most dives in November/December were concentrated in the period 03h00–19h00 (dawn about 03h30 and dusk about 20h00) (Fig. 5). In late December to early January, females dived mainly between 02h00–20h00 (dawn 03h30, dusk 20h30) and from early to mid January dives were concentrated between 03h00–20h00 (dawn 04h00, dusk 20h00) contracting to 04h00–19h00 from late January through mid-February (dawn 04h30, dusk 20h00). Throughout the season, therefore, both during incubation and chick-rearing, dives were made essentially during the hours of daylight.

TABLE 3

Summary of dive data for Macaroni Penguins around Heard Island

Sex and number	Start dates	End dates	Max. depth (m)	Max. duration (min)	Number of dives
Males					
M022	20/11	6/12	131	3.7	1621
M027	20/11	8/12	114	3.2	2662
M028	20/11	4/12	113	3.0	1583
M036	20/11	6/12	128	3.1	1488
M047	24/11	6/12	97	3.1	1307
M082	20/11	6/12	117	3.2	1553
Females					
Deployment 1					
F021	2/12	18/12	158	2.6	1482
F029	4/12	18/12	85	2.7	1249
F034	2/12	16/12	92	2.6	1367
F037	2/12	18/12	106	3.2	662
Deployment 2					
F028(2)	29/12	5/1	158	3.4	2215
F036(2)	29/12	5/1	130	2.8	1668
F082(2)	29/12	5/1	112	2.5	217
F027	29/12	6/1	137	3.0	2356
Deployment 3					
F037(2)	5/1	13/1	114	3.3	2929
F034(2)	5/1	13/1	100	3.0	2437
F021(2)	5/1	12/1	141	3.0	1312
F029(2)	5/1	8/1	123	3.0	1270
Deployment 4					
F028(3)	14/1	22/1	125	3.2	2611
F036(3)	14/1	22/1	147	3.4	2838
F031	16/1	22/1	135	3.2	1829
F082(3)	15/1	22/1	157	3.1	2426
F023	14/1	22/1	123	3.0	2281
Deployment 5					
F021(3)	24/1	1/2	122	3.5	1459
F037 (3)	24/1	1/2	111	3.5	2312
F044	24/1	1/2	121	3.0	1492
Deployment 6					
F030	6/2	14/2	120	3.4	2058
F033	6/2	14/2	163	3.5	2326
F041	6/2	14/2	146	3.8	2005
Total number of dives					**53 015**

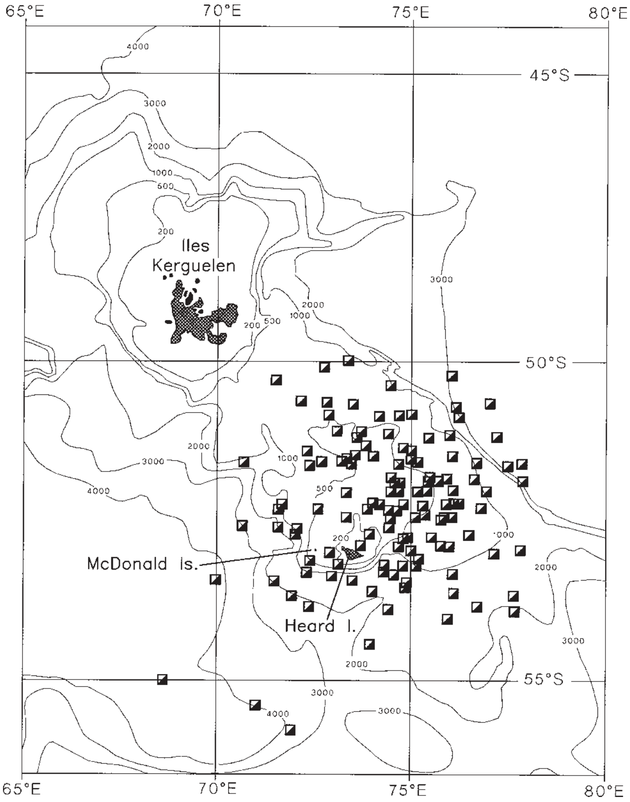

Fig. 4. *Locations of foraging grounds of Macaroni Penguins around Heard Island.*

The most common dives for both sexes and in all time periods were shallower than 10 m (Fig. 6). Dives deeper than 90 m were more commonly made by males than by females (*t*-test, $P < 0.05$, n = 6 and 23). After eggs hatched, females made more dives >100 m than they did before their eggs hatched (*t*-test, $P < 0.05$, n = 19 and 4). However, there were noticeably

TABLE 4

Average distribution of dive types for male and female Macaroni Penguins (deployments 1 to 6) (%) around Heard Island

Dive type	A	B	C	D	E	F
Males	6.9	15.8	22.7	4.7	6.7	43.2
Females:						
Deployment 1	9.8	20.5	12.1	4.9	8.0	44.7
Deployment 2	8.1	26.6	19.3	3.9	10.2	31.8
Deployment 3	7.0	31.0	17.1	4.6	8.2	32.1
Deployment 4	8.1	26.3	22.6	4.5	6.6	31.9
Deployment 5	7.1	31.4	15.9	3.7	6.2	35.7
Deployment 6	11.7	29.1	7.7	3.0	4.7	43.7

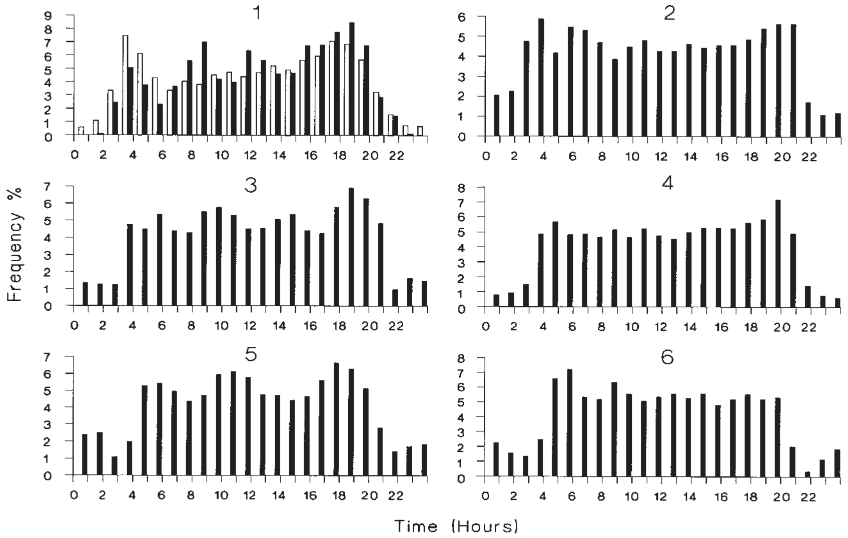

Fig. 5. *Distribution of dives through the day by Macaroni Penguins around Heard Island. Graph 1 has males (open columns) and the first deployment of females; graphs 2 to 6 have the remainder of the deployments on females.*

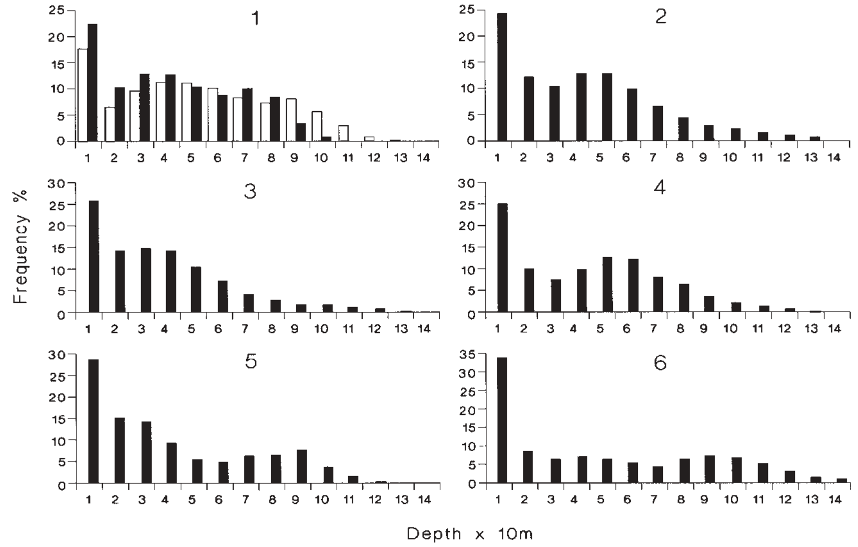

Fig. 6. *Distribution of Macroni Penguin dives by depth. Graph 1 has males (open columns) and the first deployment of females; graphs 2 to 6 have the remainder of the deployments on females.*

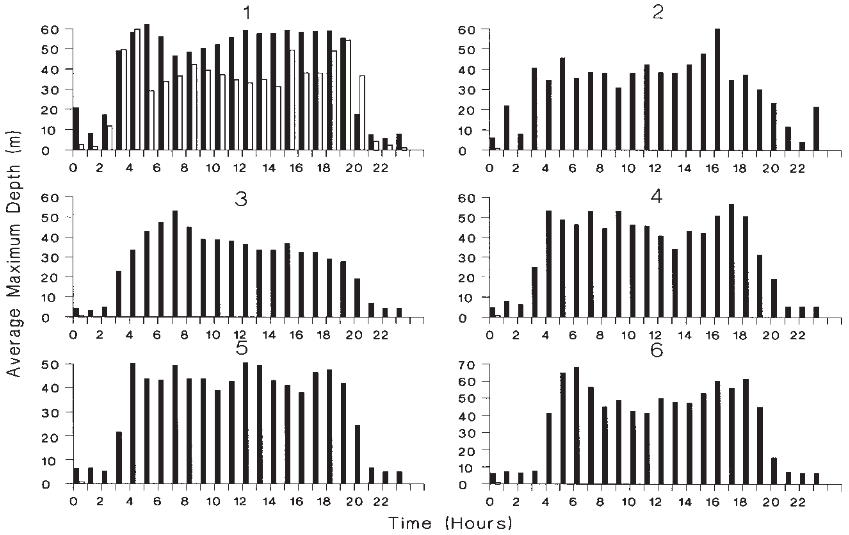

Fig. 7. *Average maximum depth of Macaroni Penguin dives plotted against time of day. Graph 1 has males (open columns) and the first deployment of females; graphs 2 to 6 have the remainder of the deployments on females.*

fewer dives at mid level, particularly around the 50–60 m depth (Fig. 6), with the proportion of dives at 50–60 m significantly fewer in the last two sessions than before hatching (*t*-test, $P < 0.01$, n = 6 and 4). The average maximum depth of dives was greater during daylight hours, when most dives were conducted (Fig. 7).

DISCUSSION

Diet

The only previous quantitative study of Macaroni Penguin diet at Heard Island was of the contents of 48 stomachs collected in 1986/87 (Klages *et al.* 1989). These were from adult females returning from their first foraging trip, and from adult females during the early part of chick growth; the two phases of foraging were combined (i.e. 15 December to 7 January with chick hatching commencing on 21 December and concluding on 26 December). To make comparison with the present study even more difficult, their data came from three locations at the north-western end of Heard Island (Red Island, Rogers Head and West Bay, Fig. 1). The samples collected by Klages *et al.* (1989) were sufficiently undigested to enable removal of components by taxa for weighing, as were the samples collected in the present study at Rogers Head in 1992, but not the samples from Icicle Gully in 1993. Even at Rogers Head, February 1992 samples differed markedly from those taken in the same region in December 1986/January 1987 by Klages *et al.* (1989). In 1992 fish constituted 41.4% by mass compared with 23.2 % in 1986/87. In 1992 euphausiids constituted less than 22% by mass and no individuals of the euphausiid *Thysanoessa macrura* were found although they were present in 87.5% of samples in 1986/87 (Klages *et al.* 1989). Instead, the amphipod *Themisto gaudichaudii* dominated the crustacean part of the diet. The Mackerel Icefish *Champsocephalus gunnari* occurred in 27% of samples collected by Klages *et al.* (1989) but was absent from samples collected in 1992 and 1993. In both studies squid were relatively unimportant. Marked inter-annual differences in the diets of Macaroni Penguins have been documented at Marion Island (Brown *et al.* 1990) where the status of *T. macrura* also changed from being the dominant crustacean consumed to one of not being found at all. Fish species also varied in importance at Marion Island, with *E. carlsbergi* important in 1983/84, but virtually absent the following year. These results emphasise the need for longer-term studies to determine baseline data on diet and the difficulties in piecing together a reliable picture of prey from studies at different times and localities.

At South Georgia, the amount of fish taken by Macaroni Penguins was negligible (about 2% by mass), and Antarctic Krill was the main prey (Croxall & Prince 1980). In nine years of sampling at South Georgia, on average Antarctic Krill was never less than 90% of the diet by mass (Croxall *et al.* 1993). The situation at Elephant Island (61°S) in a single (partial) season was closer to that at Heard Island with fish constituting about 25% of the diet by mass (Croxall & Furse 1980). At Marion Island, fish was not present in measurable amounts in the diet of Macaroni Penguins in 1983/84, and over three further studies only rose to 16% of the diet (Brown *et al.* 1990). At Iles Crozet, however, Ridoux (1994) found that 28.7% of the diet was fish. At Macquarie Island the analogous species, the Royal Penguin *Eudyptes schlegeli,* had a diet comprising 41.2% fish by mass, mainly *K. anderssoni* (Hindell 1988). The percentage of euphausiids in the diet of Macaroni Penguins at Heard Island fell from a maximum in the second sampling period of 78% by mass to only 5% in the last sampling period, averaging 42% over the season, the remainder being mainly fish. Therefore it would seem that the Macaroni Penguins sampled at Icicle Gully in 1993 were the most piscivorous of all their conspecifics (and the Royal Penguin) and this study further emphasises the importance of fish to predators breeding on Heard Island.

Studies of Adélie *Pygoscelis adeliae*, Chinstrap *P. antarctica*, Gentoo *P. papua* and Macaroni Penguins in the South Atlantic show 'little variation in dietary composition through the chick-rearing period' (Croxall & Lishman 1987). However, Croxall & Prince (1980) recorded fish contributing more to the diet of the normally krill-eating Macaroni Penguin late in the chick-rearing period (although this was only of the order of between two and seven percent). Closer to Heard Island, at Iles Crozet, Ridoux (1994) found a similar result to the present study, with a diminishing predation on euphausiids during chick-rearing. His study recorded a drop in the contribution of crustaceans to the diet from 88% by mass during incubation and 77.5% during chick brooding to 58% during the crèche stage. The greater reduction in reliance on euphausiids in the present study (from 78% by mass to 5%) may be due to concentration on the oil-rich fish *K. anderssoni*, although this was not reflected in the collection of extra otoliths. A similar shift can be seen in the changing diet of Adélie Penguins once their chicks have hatched, from krill (*E. superba* and/or *E. crystallorophias)* to predation on the Antarctic Silverfish *Pleuragramma antarcticum*, which is also high in oil (Williams 1988).

Diving

Only two published studies have examined the diving behaviour of Macaroni Penguins although they are the most abundant penguins worldwide (Croxall *et al.* 1988,1993). These studies were confined to females during the brooding period (Croxall *et al.* 1993) and males rearing crèched chicks (Croxall *et al.* 1988). These data (from just two birds in the 1993 study) came from South Georgia where the majority of the world population of the species exists (Woehler 1993). However, the diet of Macaroni Penguins from South Georgia differs markedly from that at Heard Island.

The diversity of dive types recorded here differed markedly from the simple diving patterns recorded by Croxall *et al.* (1993) for Macaroni Penguins from South Georgia. They found that all dives were essentially 'V' shaped and ranged down to 115 m. The range of dives recorded in the present study was more akin to that documented by Williams *et al.* (1992) for Gentoo Penguins from South Georgia. The food of Gentoo Penguins around South Georgia is mainly krill (Williams *et al.* 1992) so it is interesting that there are a number of similarities between the dive types. Williams *et al.* (1992) recorded 'V', 'U' and 'W' shaped dives, the 'W' shaped dives being similar to the D and E dives recorded here. The difference in the diving behaviour was mainly in the distribution of dive types with most deep dives being 'V' (75%) and 'W' (20%). The only dives that had a measurable bottom time ('U') constituted only 6% of deep dives (Williams *et al.* 1992). The similarities in diving may arise as a result of Macaroni Penguins preying on crustaceans around Heard Island. However, dissimilarities such as the importance of flat-bottomed dives around Heard Island probably reflect the fact that Macaroni Penguins were feeding on fish forming scattering layers as they descend during the day (see Perissinotto & McQuaid 1992).

The foraging pattern of Macaroni Penguins at Heard Island was temporally similar to that for krill-eating penguins, with a peak of foraging activity during the day and very little diving during the darkest hours (Williams & Siegfried 1980, Croxall *et al.* 1993). Croxall *et al.* (1993) speculated that overnight diving might develop in Macaroni Penguins as a response to increasing food demands by the chick, possibly during the main period of chick rearing, or the late guard stage. The present study showed the opposite with the proportion of the day when the major diving activity occurred declining with the progress of the season (Fig. 7). This suggests that around Heard Island, light level is a more powerful constraint upon foraging than is demand. The decline in foraging period may, however, be offset by diminishing predation on euphausiids and the increasing predation on the oil-rich *K. anderssoni.*

A maximum foraging range for Macaroni Penguins of about 300 km was found around Heard Island. Calculations of foraging locations to at least 50°S from geolocation software was supported by sea surface temperature data collected by TDRs. In addition, periods spent waiting the return of TDRs at Icicle Gully confirmed that Macaroni Penguins were away from Heard Island for at least three days. The long distance that these penguins travelled to feed indicates either a paucity of prey near the shore or a rich source of food, particularly of *K. anderssoni,* to the north-east of the island. In fact, the seas in this area are highly productive according to studies in 1987/88 to the east and south-east of Kerguelen Island (Ivanchenko 1993, Semelkina 1993). Female Antarctic Fur Seals *Arctocephalus gazella* also travelled similar distances from Heard Island to prey on the same fish species in an area that overlapped the north-easterly extent of foraging by Macaroni Penguins (Green *et al.* 1997).

Around South Georgia both Macaroni Penguins and Antarctic Fur Seals fed on Antarctic Krill. Croxall *et al.* (1985) found a close correlation between diving depth of Antarctic Fur Seals, time of day, and the vertical distribution of krill. One possible reason for this was that seals were minimising the energy costs of foraging by preying upon krill at night when they were closer to the surface. A difficulty with a similar interpretation for Macaroni Penguins around South Georgia was that they foraged during the day (Croxall *et al.* 1993). Around Heard Island, Antarctic Fur Seals also fed on the same prey (*K. anderssoni)* as did Macaroni Penguins (Green *et al.* 1997), and again, as with South Georgia, the two predators fed on this prey at mutually exclusive times of day. At the later part of chick rearing (when the amount of krill taken declined to insignificant levels) mid-level dives (50–60 m) declined in importance for Macaroni Penguins and there was a greater emphasis on the deeper dives between 80 and 100 m. The average diving depth for female fur seals in the same area was similar to this at 80–130 m but at night. Fur seals mainly targeted a smaller size class of fish (25–40 mm) than did Macaroni Penguins (55–70 mm) with the difference being significant (*t*-test, $P < 0.001$).

As with krill, there is a diurnal vertical migration of *K. anderssoni* (Perissinotto & McQuaid 1992). The fish were found in offshore waters of the Prince Edward Islands at 300 to 400 m depth during the day (well out of reach of Macaroni Penguins) rising to 50 to 100 m at night (Perissinotto & McQuaid 1992). Around Heard Island the vertical migration of *K. anderssoni* may not be as pronounced (due to oceanographic changes or due to the higher latitude) or there may be inter-seasonal changes in vertical migration (the data obtained by Perissinotto & McQuaid (1992) were from April, May and August). Latitudinal differences in the depth at which *K. anderssoni* have been caught have been documented by Hulley (1981). Individuals were caught at depths between 50 m and 150 m south of the Antarctic Polar Front whereas in the vicinity of the Subtropical Convergence they were only taken at 1000 m or deeper. It is not clear though whether the trawls were by day or night or whether all data were combined. This then, to paraphrase and amplify on the question posed by Croxall *et al.* (1993), leaves open the intriguing puzzle as to why Macaroni Penguins and Antarctic Fur Seals, despite feeding on the same prey, do so at mutually exclusive times of day and not only that but how it is possible for Macaroni Penguins to feed on the same prey at all.

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