

# Maximum dive depths of common diving petrels (*Pelecanoides urinatrix*) during the annual cycle at Mayes Island, Kerguelen

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## Abstract

Maximum dive depths of common diving petrels *Pelecanoides urinatrix* were measured monthly over > 1 year, from January 1995 to February 1996, with miniature gauges attached to the birds at Mayes Island, Kerguelen Archipelago. Overall, maximum dive depths of 347 diving petrels averaged  $31 \pm 6$  m (range: 8–64 m), with a mode at 30–35 m. Mean maximum dive depths differed significantly over the study period. The lowest value ( $22 \pm 8$  m) was obtained in winter and it was associated with euphausiid crustaceans, suggesting a change in foraging behaviour associated with a shift in the main prey consumed. During the breeding season, birds fed mainly upon the hyperiid amphipod *Themisto gaudichaudii* (66 % of the total number of prey), followed by the large carnivorous copepod *Paraeuchaeta antarctica* (15%) and zoea larvae of the crab *Halicarcinus planatus* (13%). Comparison of the diving capabilities of diving petrels (genus *Pelecanoides*) with those of other diving seabirds suggests that, relative to body mass, diving petrels can dive deeper than penguins and also possibly than alcid, and are thus the most proficient divers among birds.

**Key words:** Alcidae, foraging behaviour, *Paraeuchaeta antarctica*, penguins, *Themisto gaudichaudii*

## INTRODUCTION

Diving petrels (family Pelecanoididae, genus *Pelecanoides*) comprise four species of petrels restricted to the Southern Hemisphere (Marchant & Higgins, 1990; Warham, 1990). Among Procellariiforme seabirds, they present very distinctive and homogeneous morphology and behaviour, being easily recognized by their small size and compact shape. *Pelecanoides* petrels are highly modified for underwater pursuit of food by wing propulsion, a genus forming an ecological analogue of the smallest northern Alcidae, especially murrelets and auklets (Warham, 1990). All diving petrels live in cold or cool waters, most of the breeding colonies being located between the Subtropical Front and the Antarctic Polar Front. Among diving petrels, the common diving petrel *Pelecanoides urinatrix* is the most widespread; it has a circumpolar range and breeds sympatrically with the South Georgian diving petrel *P. georgicus* in remote archipelagos of the Southern Ocean (Marchant & Higgins, 1990; Warham, 1990). At Kerguelen Islands, the common diving petrel is one of the most numerous seabirds, its population being estimated to amount to

500 000–1 000 000 breeding pairs each year (Weimerskirch, Zotier & Jouventin, 1989).

Over the last few decades, the food and feeding ecology of diving petrels has been mainly investigated through the identification of their prey, with little information being available on their foraging behaviour (Ryan & Nel, 1999). At Crozet Islands and South Georgia, the diet of common and South Georgian diving petrels is dominated by pelagic crustaceans, in particular euphausiids and copepods, amphipods being less important (Payne & Prince, 1979; Jouventin, Ridoux *et al.*, 1988; Ridoux, 1994; Reid *et al.*, 1997). In more recent years, the use of capillary-tube depth gauges (Burger & Wilson, 1988) gave a first insight into the diving capabilities of these birds during the breeding season. Depending on the species, diving petrels dive to mean maximum depths of 25–39 m, the deepest dives reaching 49–83 m (Prince & Jones, 1992; Chastel, 1994; Zavalaga & Jahncke, 1997).

Previous works were restricted to the incubation and chick-rearing periods, and they were conducted on only a few individual birds ( $n=6-22$ ) (Prince & Jones, 1992; Zavalaga & Jahncke, 1997), except in one study involving 103 birds equipped with depth gauges (Chastel, 1994). At Mayes Island, Kerguelen

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Archipelago, common diving petrels are present all year round in colonies and feeding behaviour has been observed every month in the vicinity of the island, in the Golfe du Morbihan (Weimerskirch *et al.*, 1989). The aim of the present study was to investigate the diving ability of common diving petrels throughout the year using a significant number of capillary-tube depth gauges each month. Dietary samples were also collected to relate possible seasonal differences in the foraging ecology of the birds to changes in the marine environment.

## MATERIALS AND METHODS

The present study was carried out on Mayes Island (49°28'S, 69°57'E) located in the Golfe du Morbihan, Kerguelen Archipelago, between 3 December 1994 and 17 February 1996. Common diving petrels *P. urinatrix* were captured for 7–21 nights/month, when they returned to their colony. During the breeding period, birds were trapped mainly in burrows, which were marked with numbered wood stakes. In the case of deep burrows, an opening was dug out over the nesting chamber and covered with rock and earth slabs, enabling access to the birds. Outside the breeding period, diving petrels are less faithful to their burrows. We therefore complemented work by mist-netting at night near the colony using 5 nets from dusk to midnight.

The maximum depth reached by common diving petrels was investigated using capillary-tube depth gauges (Burger & Wilson, 1988), following Chastel (1994). Briefly, recorders consisted of 10–12 cm lengths of plastic tube (Tygon brand; internal diameter, 0.8 mm), coated inside with icing sugar and sealed at 1 end. The tube was fitted on the back feathers using waterproof adhesive tape. Each recorder weighed *c.* 0.6 g, i.e. <0.5% of bird body mass. Maximum dive depth was calculated by the equation:  $d = 10.08 [(Ls/Ld) - 1]$ , where *d* is the maximum depth (m), *Ls* is the initial length (mm) of undissolved sugar, and *Ld* the length (mm) on recovery (accuracy ± 0.5 mm). In order to investigate the bird's diving behaviour over an annual cycle, capillary-tube depth gauges were used monthly over the whole study period, except for the first month (December 1994).

Birds were weighed to the nearest 2 g with an electronic balance, and monthly averages in body mass calculated over 1 year. If the same individual bird was captured several times within a given month, its mean value was used to calculate the monthly average in body mass for the population and test statistics in order to avoid potential problems arising from pseudo-replication. Birds with food in their stomach were not considered for the calculations, except during the chick-rearing period when the body mass was measured before they fed their chicks and then calculated apart.

Food samples were collected using a stomach lavage technique similar to that described for diving petrels by Reid *et al.* (1997). A supple plastic tube (2.4 mm

external, 0.8 mm internal diameter) was inserted into the stomach, and water slowly introduced via a syringe. Birds were flushed no more than 3 times, even if water still contained prey items, in order to reduce stress. After lavaging, they were placed in a box to recover and then released at their capture site. Diet samples were drained to remove excess water, immediately frozen at -20°C, and returned to Chizé, France, for analysis. In the laboratory, each sample was thawed, drained for a second time, and placed in a large flat-bottomed tray. Total numbers of common prey were counted from the whole sample mass (Cherel & Ridoux, 1992). Crustaceans were identified from their external features using keys in Baker, Boden & Brinton (1990), Boschi, Scelzo & Goldstein (1969), Razouls (1994), and Schneppenheim & Weigmann-Haass (1986), and by comparison with material held in our own reference collection.

Data were statistically analysed using SYSTAT 7.0 for WINDOWS. Values are means ± SD.

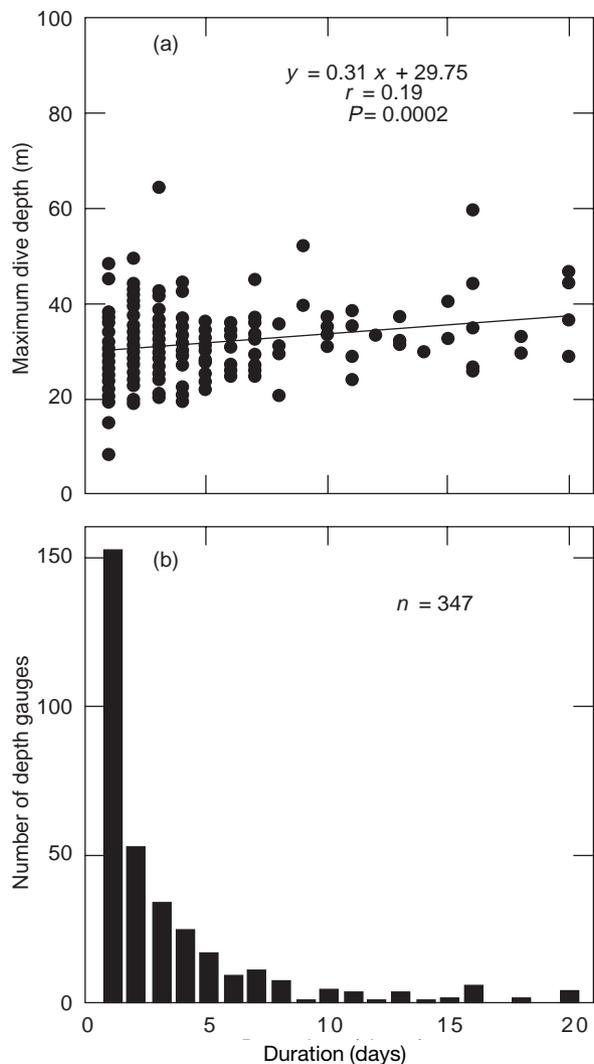
## RESULTS

### General comments

We made 1740 captures of common diving petrels during 182 working nights over 15 months of study; this corresponded to 784 individual birds. The dates of the main reproductive features were similar during the two successive breeding seasons (1994–95 and 1995–96 austral summers). As previously recorded at the Crozet Islands (Jouventin, Mougin *et al.*, 1985), the reproductive cycle was not strongly synchronized at Mayes Island, Kerguelen. For example, the mean laying date in the 1995–96 cycle was 30 November (range 15 November–11 December; *n* = 17). Hatching took place throughout January and fledging throughout March.

Common diving petrels trapped in the reproductive period (*n* = 217) were rarely re-trapped in the following months; only 25 were caught between April and July from 283 individual birds mist-netted at this time, suggesting that most breeding birds left the colonies after the fledging period. Most birds caught in the post-breeding months were therefore probably not successful breeders. They belonged to different age classes as indicated from ringed individuals (*n* = 23) which were 1 to at least 7 years old. Note that the oldest diving petrel captured over the whole study period was at least 9 years old (from 104 ringed individuals).

Diving petrels almost completely deserted their colonies in the middle of winter, with a few birds trapped in July, and only three individuals caught in August. At this time, we also observed few birds foraging nearby, in the Morbihan Gulf, instead of large to very large flocks (hundreds to thousands of birds) commonly encountered during the other months. Common diving petrels returned to their colonies from mid-September, with a maximum of birds occurring in October. They were, therefore, uncommon on land

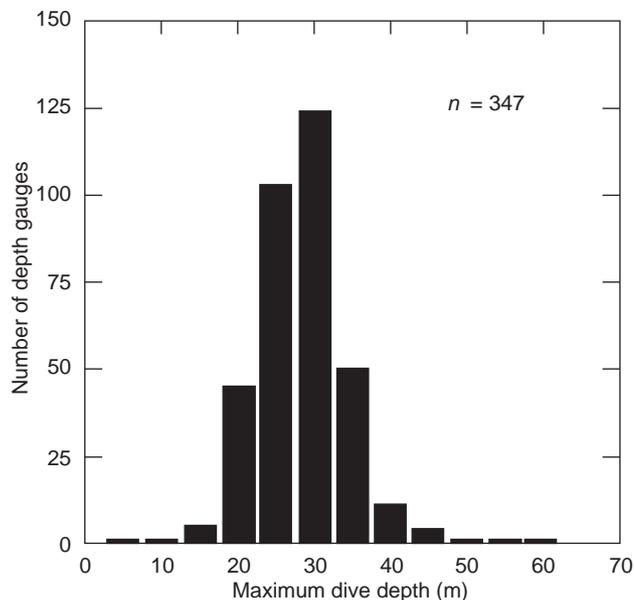


**Fig. 1.** Relationship between maximum dive depth and duration of recorder deployment (a), and frequency distribution of recorders against duration of deployment (b).

during 2–3 months in winter, between a long post-breeding period of 4 months and a shorter pre-breeding period of 1 month, in October.

### Diving behaviour

Of 885 recorders that were attached, 390 (44.1%) were recovered, including 28 that gave non-readable measurements (no clear-cut separation between sugar and air, and/or moisture accumulation), and 15 that were recovered after > 20 days of use and were therefore excluded from the calculation. Common diving petrels were easily re-trapped 1–3 days after being equipped when we worked at burrows. Mist-netting lowered recapture rate, thus inducing a larger range in the duration of deployment (from 1 to > 20 days). A significant correlation was found between time spent at sea and maximum

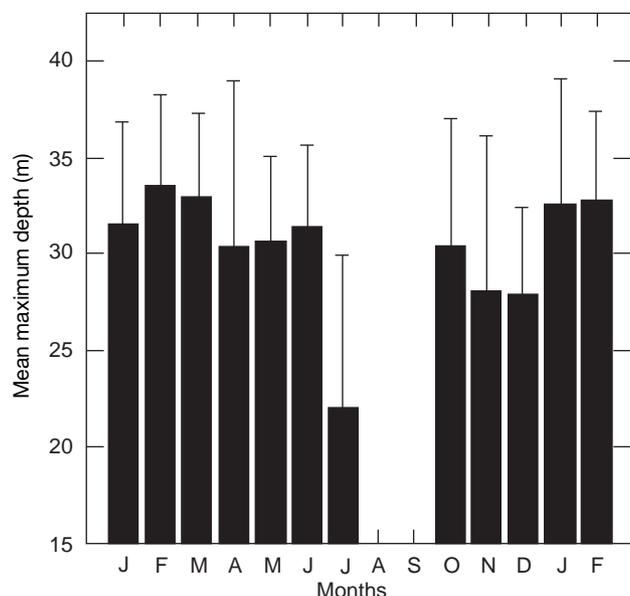


**Fig. 2.** Frequency distribution of maximum dive depths by common diving petrels *Pelecanoides urinatrix* at Mayes Island, Kerguelen.

depth reached ( $F = 14.23$ ,  $P = 0.0002$ ; Fig. 1). The slope of the regression line was, however, low until 20 days, leading us to include in the calculation all the values ( $n = 347$ ) obtained between 1 and 20 days of deployment. Most of the gauges were recovered after 1–3 days (69.7%), 82.4 % and 93.1% being recovered after 1–5 days and 1–10 days of deployment, respectively (Fig. 1).

The maximum dive depths reached by common diving petrels ranged from 7.9 to 64.1 m and averaged  $30.8 \pm 6.0$  m ( $n = 347$ ). The frequency distribution of maximum dive depths was unimodal with a mode at 30–35 m, 92.4 % of the depths being within the 20–40 m range (Fig. 2). Depth gauges were successfully recovered every month ( $n$  range = 6 to 51), except in August ( $n = 1$ ; 14.4 m), and September ( $n = 1$ ; 35.5 m). Maximum dive depths differed significantly over the study period (Fig. 3, one way ANOVA,  $F = 4.52$ ,  $P < 0.0001$ ). Most of the monthly mean maximum dive depths ranged between 30 and 35 m, except values obtained in July, November and December (Fig. 3). The lowest mean maximum dive depth was that from July ( $21.9 \pm 7.9$  m,  $n = 6$ ). It differed significantly from the other means (post hoc Tukey HSD multiple comparison test, all  $P < 0.05$ ), except for those from April, October, November and December. Mean dive depths in November ( $27.9 \pm 8.0$  m,  $n = 31$ ) and December ( $27.7 \pm 4.5$  m,  $n = 30$ ) were significantly lower ( $P < 0.05$ ) than those in February 1995 ( $33.5 \pm 4.7$  m,  $n = 32$ ) and February 1996 ( $32.6 \pm 4.6$  m,  $n = 66$ ). No significant differences ( $P > 0.05$ ) were found when comparing mean dive depths in January 1995 and 1996, and mean dive depths in February 1995 and 1996.

In the second breeding season (austral summer 1995–96), we checked if adult birds which were fitted with



**Fig. 3.** Monthly variations in mean maximum dive depth reached by common diving petrels *Pelecanoides urinatrix* from January 1995 to February 1996 at Mayes Island, Kerguelen. Vertical bars, SD.

depth gauges were attending to an egg or a chick. Common diving petrels rearing chicks dived significantly deeper than those incubating eggs ( $32.5 \pm 4.6$  m,  $n = 73$  vs  $29.5 \pm 6.4$  m,  $n = 37$ ;  $t$ -test,  $t = 2.87$ ,  $P = 0.005$ ).

### Body mass

Most of the birds ( $n = 321$ ) fitted with depth gauges were weighed twice, once when they were equipped, and again when recorders were subsequently recovered. No significant differences occurred between body masses at capture and re-capture ( $143 \pm 11$  g vs  $144 \pm 10$  g,  $t = 1.23$ ,  $P = 0.22$ ), suggesting that the depth gauges did not compromise foraging. The difference in body masses averaged  $+1.2 \pm 9.0$  g.

The body mass of 674 different individuals was recorded during the study (from December 1994 to February 1996). Body mass of common diving petrels ranged from 112 to 184 g and averaged  $145 \pm 10$  g; birds coming back to their burrow to feed their single chick were significantly heavier ( $156 \pm 10$  g,  $n = 96$ ,  $t = 9.95$ ,  $P < 0.0001$ ) than other breeding petrels and non-breeding birds. Body mass differed significantly over the study period (Fig. 4, one way ANOVA,  $F = 5.11$ ,  $P < 0.0001$ ). Most of the monthly mean body mass ranged between 143 and 149 g, except in April when birds showed the lightest mean body mass ( $139 \pm 10$  g; significantly different from average body mass measured in December 1994, May, June, July, September, October and November 1995; post hoc Tukey HSD multiple comparison test, all  $P < 0.05$ ). No significant differences ( $P > 0.05$ ) were found when comparing mean

body mass in December 1994 and 1995, January 1995 and 1996, and February 1995 and 1996.

### Diet

During the study, 259 diving petrels were stomach-flushed, giving only 92 diet samples. Most of the birds had empty stomachs outside the chick-rearing period, thus precluding determination of food habits of common diving petrels throughout the year.

A total of 73 samples was collected during the chick-rearing period in February–March 1995 and 1996. Sample mass averaged  $12.2 \pm 4.7$  g, from 0.8 to 25.1 g. Except for one unidentified fish, all prey items were crustacea that were present in all stomach contents. The main species eaten by common diving petrels was the hyperiid amphipod *Themisto gaudichaudii* which occurred in all samples and represented 66.4% of the total number of prey. Other important items were the calanoid copepod *Paraeuchaeta antarctica* (frequency of occurrence in samples: 49.3%, 14.7% of total prey number), and zoea larvae of the decapod *Halicarcinus planatus* (19.2% and 13.2%). Rare items include calanoid copepods and one species of mysid shrimp.

Only 19 diet samples were collected outside the chick-rearing period. Their mass was generally low, averaging  $1.6 \pm 3.1$  g, from 0.1 to 13.7 g. When the samples were pooled together, *T. gaudichaudii* was again the main prey (frequency of occurrence in samples: 84.2%, 88.6% of total prey number), while *P. antarctica* was a rare item (10.5% and 0.9%). Three stomach contents collected during the winter (July and September) contained only euphausiid crustaceans, namely *Euphausia vallentini* and *Thysanoessa* sp., either *T. macrura* or/and *T. vicina* (the two species were impossible to identify to the species level in food samples).

### DISCUSSION

To our knowledge, this study is the first to investigate the diving ability of a seabird for  $> 1$  year including the non-breeding period. Most seabirds are migrant, being away from the breeding grounds between two reproductive events, thus precluding the recovery of dive recorders outside the breeding season. The common diving petrel therefore offered a unique opportunity to investigate the food and feeding ecology of a diving seabird during most of the bird's cycle.

### Annual cycle

Common diving petrels breed at regular dates each year on Mayes Island, Kerguelen Archipelago. Dates of the main reproductive features were similar during the two successive breeding seasons of the present study and they agree with those previously described for the 1986–87 breeding cycle (Weimerskirch *et al.*, 1989). However,

compared to other localities, diving petrels start laying at Kerguelen Archipelago on average 1 month later than at South Georgia and Crozet Islands (Payne & Prince, 1979; Jouventin, Mougin *et al.*, 1985).

At Kerguelen, common diving petrels are known to be one of the rare seabirds present in colonies all year (Weimerskirch *et al.*, 1989). Colonies are, however, almost deserted in the middle of the austral winter, only a few birds being found on the breeding grounds and observed in the adjacent feeding areas of the Golfe du Morbihan from mid-July to mid-September. Our data also suggest that successful breeders are absent from colonies during the post-nuptial months, only a few ringed birds caught during the reproductive period having been re-trapped between April and July. Unpublished data suggest that most of the non-breeding birds found in colonies after the fledging period are 1-year old individuals (Chastel, pers. comm.). Consequently, although common diving petrels are abundant on breeding grounds for about 10 months, non-breeding birds predominate during the post-nuptial months, most breeders probably being away from late March to mid-September.

The body mass of common diving petrels showed little variation throughout the study (Fig. 4). The lowest mean body mass was recorded in April corresponding to a shift from breeders to non-breeding birds in the colonies (see above). Diving petrels coming from offshore waters may have used energy reserves to go back to the breeding grounds, thus explaining a lower body mass at this time. Small changes in body mass (10 g between the lowest and the highest monthly values, i.e. 7% of the overall mean body mass) are expected for a petrel generally feeding close to its breeding ground, thus allowing a rapid acquisition of energy, in opposition with more offshore species who cyclically build up and use larger amounts of energy reserves (Chastel, Weimerskirch & Jouventin, 1995).

#### Food and feeding ecology of common diving petrels

The mean maximum dive depth found in the present study (31 m, mode at 30–35 m) is less than the value (39 m, mode at 35–40 m) obtained in the only previous work performed on common diving petrels (Chastel, 1994). Such differences in mean maximum dive depths can probably be related to differences in the availability of prey in the water column. Unfortunately, however, no dietary data are available in the work of Chastel (1994) to investigate this hypothesis. The deepest dive (64 m) recorded in both studies are nevertheless identical; they could represent dives performed near the physiological limits for the common diving petrel.

Over the 14-month study, most of the mean maximum dive depths ranged between 30 and 35 m. The most noticeable exception in mean maximum dive depth was the value (22 m) recorded in July, during the austral winter (Fig. 2). The few stomach contents collected at this time only contained the euphausiids *Euphausia*

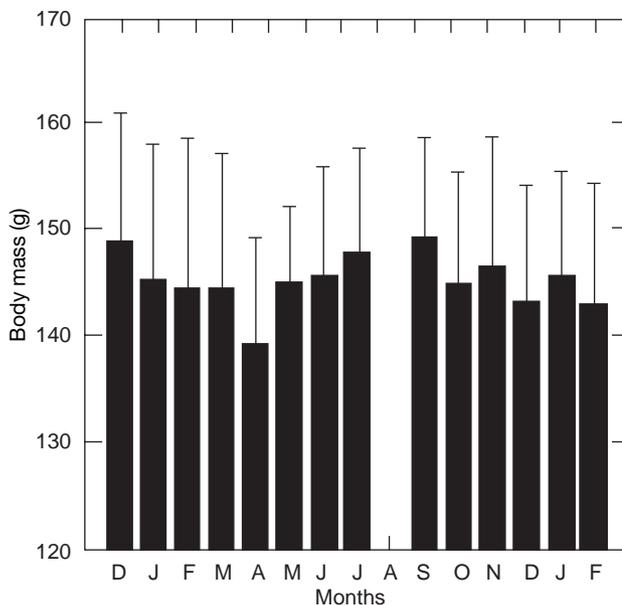


Fig. 4. Monthly variations in body mass of common diving petrels *Pelecanoides urinatrix* from December 1994 to February 1996 at Mayes Island, Kerguelen. Vertical bars, SD.

*vallentini* and *Thysanoessa* sp. which were not found in dietary samples collected in other months. Zooplankton surveys also indicate that euphausiids are abundant in winter in the Golfe du Morbihan (Koubbi, 1992), thus suggesting that the shallower depths reached at this time were linked to a shift in prey species by foraging common diving petrels. Such a relationship between prey types and maximum dive depths has also been suggested from data collected from other diving seabirds, including alcid (Burger & Powell, 1990) and penguins (Tremblay, Guinand & Cherel, 1997).

The diet of common diving petrels has only been investigated in detail at two localities during the breeding season, no data being available outside the chick-rearing period. Birds mainly feed on pelagic copepods at South Georgia (97% of the total number of prey) (Reid *et al.*, 1997), and on euphausiids at Crozet Islands (66%) (Ridoux, 1994). At Mayes Island, by far the main prey item during chick-rearing was the amphipod *Themisto gaudichaudii* (66%), followed by the large carnivorous copepod *Paraeuchaeta antarctica* and larvae of the decapod *Halicarcinus planatus*. Decapod larvae have not been previously found in the diet of common diving petrels (Marchant & Higgins, 1990), while euchaetid copepods are rarely reported (Ealey, 1954; Reid *et al.*, 1997), and *T. gaudichaudii*, together with the other amphipod *Primno macropa*, are either considered as a minor prey (Reid *et al.*, 1997) or a regular food item (Ridoux, 1994). The large inter-locality difference in the dietary items indicates that common diving petrels are opportunistic predators feeding on the most abundant pelagic swarming crustaceans available in the marine environment. At Kerguelen, common diving petrels are frequently seen in summer feeding in large flocks in the vicinity of Mayes

**Table 1.** Comparison of mean maximum dive depths reached by small- to medium-sized seabirds using the maximum dive depth gauge method. Values are means  $\pm$  SD with ranges in parentheses

Species	Locality	Status	Body mass (g)	<i>n</i>	Mean maximum depth (m)	Reference
Spheniscidae						
Little penguin <i>Eudyptula minor</i>	Australia	Breeders	1200	32	30 (9–69)	Montague (1985)
Procellariidae						
White-chinned petrel <i>Procellaria aequinoctialis</i>	South Georgia	Breeders	1270	11	6.2 $\pm$ 3 (2.8–12.8)	Huin (1994)
Blue petrel <i>Halobaena caerulea</i>	Kerguelen	Breeders	190	6	4.4 $\pm$ 1.8 (1.0–6.2)	Chastel & Bried (1996)
Thin-billed prion <i>Pachyptila belcheri</i>	Kerguelen	Breeders	150	5	5.5 $\pm$ 1.4 (3.8–7.5)	Chastel & Bried (1996)
Cory's shearwater <i>Calonectris diomedea</i>	Azores Selvagem Is.	Breeders Breeders	779–900 –	19 26	0.3 $\pm$ 0.3 (0–1.4) 2.5 $\pm$ 1.5 (0–5.5)	Monteiro <i>et al.</i> (1996) Mougin & Mougin (1998)
Short-tailed shearwater <i>Puffinus tenuirostris</i>	Tasmania	Breeders–long trips	570–590	8	58 $\pm$ 10.8 (33.5–70.6)	Weimerskirch & Cherel (1998)
Sooty shearwater <i>Puffinus griseus</i>	Snares	Breeders	837–869	35	39 $\pm$ 20 (2–67)	Weimerskirch & Sagar (1996)
Pelecanoididae						
Common diving petrel <i>Pelecanoides urinatrix</i>	Kerguelen	Breeders	147	103	39 $\pm$ 7.4 (14.7–63.6)	Chastel (1994)
Peruvian diving petrel <i>Pelecanoides garnotii</i>	Kerguelen Peru	Breeders/non breeders Breeders	145 202	347 22	30.8 $\pm$ 6.0 (7.9–64.1) 31.6 $\pm$ 3.6 (10.0–83.1)	Present study Zavalaga & Jahncke (1997)
South Georgian diving petrel <i>Pelecanoides georgicus</i>	South Georgia	Breeders	93	6	25.7 $\pm$ 11.4 (17.1–48.6)	Prince & Jones (1992)
Phaethontidae						
Red-tailed tropicbird <i>Phaethon rubricauda</i>	Europa Island	Breeders	800	64	4.6 $\pm$ 2.7 (1–13)	Le Corre (1997)
Sulidae						
Red-footed booby <i>Sula sula</i>	Europa Island	Breeders	900	22	4.9 $\pm$ 2 (2.9–9.7)	Le Corre (1997)
Alcidae						
Cassin's auklet <i>Ptychoramphus aleuticus</i>	British Columbia	Breeders	188	22	28 $\pm$ 12 (6–43)	Burger & Powell (1990)
Rhinoceros auklet <i>Cerorhinca monocerata</i>	California British Columbia	– Breeders	– 520	5 8	32 $\pm$ 7 (24–39) 31 $\pm$ 10 (19–49)	Croll & Carter cited in Burger & Powell (1990) Burger <i>et al.</i> (1993)
Pigeon Guillemot <i>Cephus columba</i>	Vancouver Is.	Breeders	450	2	30	Burger (1991)
Common murre <i>Uria aalge</i>	Newfoundland Norway Scotland	Breeders Breeders Breeders	930 – –	2 22 10	67–138 49.2 $\pm$ 11.5 (34.1–70) 36 $\pm$ 14 (10–52)	Burger & Simpson (1986) Barrett & Furness (1990) Harris <i>et al.</i> (1990)
Brünnich's guillemot <i>Uria lomvia</i>	Norway Northwest Territory	Breeders Breeders	– 1029	20 40	44.2 $\pm$ 13.6 (20.8–70.6) 107 $\pm$ 42 (40–210)	Barrett & Furness (1990) Croll <i>et al.</i> (1992)
Atlantic puffin <i>Fratercula arctica</i>	Newfoundland Norway Scotland	Breeders Breeders Breeders	510 – –	10 5 6	44 $\pm$ 12 (22–68) 26.4 $\pm$ 15.3 (10.3–44.6) 26 $\pm$ 4 (21–33)	Burger & Simpson (1986) Barrett & Furness (1990) Harris <i>et al.</i> (1990)
Razorbill <i>Alca torda</i>	Norway Scotland	Breeders Breeders	– –	18 11	24.6 $\pm$ 6.4 (11.1–38.1) 24 $\pm$ 5 (14–32)	Barrett & Furness (1990) Harris <i>et al.</i> (1990)

Island which is located in a sheltered bay, the Golfe du Morbihan. Both oceanographic samples and the diet of other diving seabirds feeding there (rockhopper and gentoo penguins) also emphasize the abundance of *T. gaudichaudii* in the water column and its major role in the trophic web of near-shore waters at Kerguelen Archipelago (Koubbi, 1992; Bost *et al.*, 1994).

The prey composition of our samples shows that decapod larvae and *P. antarctica* commonly occur in the top 40 m of the water column in coastal waters of Kerguelen Archipelago. This is in agreement with the known vertical distribution of zoea larvae of the only species of crab in Kerguelen waters *H. planatus* (Richer de Forges, 1977). The present study is the first to report *P. antarctica* in the Golfe du Morbihan. Previous zooplankton surveys in the central part of the bay which is free of islands, did not sample the species (Razouls, Koubbi & Mayzaud, 1996), whereas our data together with dietary information from rockhopper penguins indicate that *P. antarctica* is abundant in the western part of the Golfe du Morbihan, which is characterized by deep submarine valleys and numerous islands. Such new biogeographic information emphasizes the use of seabirds as biological samplers of some poorly known pelagic organisms in the Southern Ocean, as has recently been described for cephalopods (Cherel & Weimerskirch, 1995) and mesopelagic fish (Cherel, Ridoux & Rodhouse, 1996).

### Comparison with other diving seabirds

The diving ability of two other species of diving petrels was previously investigated using the maximum depth gauge method (Table 1). Mean maximum dive depth of South Georgian diving petrels (26 m) (Prince & Jones, 1992) and Peruvian diving petrels (32 m) (Zavalaga & Jahncke, 1997) agrees well with the value recorded for common diving petrels in the present study (31 m). Interestingly, however, there is a positive relationship between the deepest dive and the species body mass, the lighter South Georgian diving petrel (93 g) diving to a shallower maximum depth (49 m) than the heavier Peruvian diving petrel (202 g; 83 m), common diving petrels having intermediate values for both body mass (145 g) and maximum dive depth (64 m).

Diving abilities of air-breathing vertebrates are generally related to body mass, larger animals being physiologically capable of longer and deeper dives (Burger, 1991; Schreer & Kovacs, 1997). It is thus interesting to compare our data to the allometric equations relating maximum dive depth to body mass for alcids and penguins, two groups of seabirds well adapted to deep diving (Schreer & Kovacs, 1997). With a mean body mass of 145 g, the predicted maximum dive of common diving petrels is 21 and 11 m, using the equations for alcids and penguins, respectively. These values are much lower than maximum depths recorded for diving petrels (Table 1), thus emphasizing the

greater diving capabilities of diving petrels compared to other wing-propelled diving seabirds, especially penguins. For example, the mean maximum dive depth and deepest dive recorded for the smallest penguin species, the little penguin which weighs about 1.2 kg, are 30 and 69 m, respectively (Montague, 1985).

The diving performance of seabirds having a body mass close to that of diving petrels has only been investigated in three species, two procellariids and one alcid (Table 1). Unlike diving petrels, blue petrels and prions are poorly suited for diving (Warham, 1977) and, accordingly, they only forage in the top few meters of the water column (Chastel & Bried, 1996). The diving capability of the smallest species of alcid investigated so far, the Cassin's auklet (Burger & Powell, 1990), is, however, in the range of that of diving petrels. Clearly, more data are needed on the diving performance of small alcids, such as little auks, auklets and murrelets, to compare their diving characteristics with those of the ecologically closely related diving petrels.

The present study emphasizes the outstanding diving performance of diving petrels when compared to other groups of seabirds (Table 1), except perhaps small alcids. Though the maximum dive depth gauge method only indicated the deepest dives of the foraging trips, it has given a first insight into the diving capabilities and the foraging habitat of diving petrels over > 1 year. A better knowledge of the underwater behaviour of diving petrels requires investigations with more sophisticated devices such as electronic time-at-depth recorders, which at present are too large for small and very small diving seabirds.

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