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ORIGINAL PAPER

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Feeding strategies of free-ranging Adélie penguins *Pygoscelis adeliae* analysed by multiple data recording

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Abstract The fine-scale feeding behaviour of free-ranging Adélie penguins (*Pygoscelis adeliae*) during a single foraging trip was investigated by monitoring three parameters simultaneously at a frequency of 1 Hz, these being depth, swim speed and oesophagus temperature. Ingestion events were detected as abrupt drops in the oesophageal temperature and related to the birds' foraging behaviour. Although a high percentage of oesophageal temperature loggers were rejected, 1 complete foraging trip was recorded for all the 3 parameters from 1 bird while 92% and 67% of the foraging trip was recorded for 2 other birds; 12.3% of the temperature drops occurred at the surface but they were mainly small, except 61 of them probably representing snow ingestion while the birds were on land. All other drops were observed during dives, 88% of them during the undulatory (and occasionally the ascent) phase of dives deeper than 40 m. The mean swim speed during non-feeding shallow and exploratory dives was relatively constant throughout the dive, around 2.1 m s^{-1}, whereas during feeding deep dives, swim speed during the undulatory phase was lower (1.71 m s^{-1}) than during the descent and ascent and was characterised by a series of rapid accelerations and decelerations; 42.6% of these accelerations were followed by one or more ingestion events and birds swam upward in 60% of the accelerations. Such multiple data recording opens new paths for the examination of the decision-making processes in foraging penguins.

Introduction

Any assessment of the role of animals within ecosystems should consider feeding habits of primary importance (Collinvaux 1986). Studies on the feeding ecology of air-breathing marine animals are often logistically difficult since direct observation is impossible. Consequently, numerous data loggers have recently been developed to examine various parameters as a function of time (Le Maho 1994). Some of the most promising work using data loggers to assess the role of marine endotherms has investigated the internal temperature of endothermic marine top predators (Wilson and Culik 1991; Wilson et al. 1992; Kato et al. 1996) so as to determine when prey are ingested in tandem with parameters of the animals' foraging behaviour (e.g. Wilson et al. 1993; Weimerskirch et al. 1994). Recently, a logger with particularly fine resolution was introduced for determining feeding activity by monitoring oesophageal temperature (Ancel et al. 1997). This means that, with appropriate complementary data on animal activity, it should be possible to determine those features of foraging behaviour that lead to the successful capture and ingestion of prey.

We present the first data derived from the use of this oesophageal temperature recording system on free-living Adélie penguins (*Pygoscelis adeliae*), simultaneously equipped with depth and swim-speed loggers and recording data with fine temporal resolution. These birds feed mainly on krill *Euphausia superba* and *E. crystallorophias* (Williams 1995), although fish may sometimes be taken (e.g. Ridoux and Offredo 1989). A dietary study conducted on Adélie penguins in Adélie Land showed that euphausids dominate during the first part of the breeding season (Ridoux and Offredo 1989). Although no dietary data were collected during our study,

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we assume that euphausids are the main prey captured by our birds. We consider rates of prey ingestion, and how these are related to water depth and swimming speed. Such analysis of the foraging parameters used by Adélie penguins in relation to a successful or unsuccessful encounter with prey can help elucidate the decision-making process and be used to examine how birds might enhance prey capture and minimise the energy or time expended.

Materials and methods

The study was conducted between mid-December 1998 and mid-January 1999 (guard phase) on breeding Adélie penguins in Adélie Land, Antarctica (66.7°S, 140.0°E). A total of 16 birds were equipped with loggers measuring depth, swim speed and oesophagus temperature. Swim speed and depth of free-ranging penguins were measured every second with 12-bit resolution, 16-Mbyte memory, three channel UWE-PDT loggers (Little Leonardo, Tokyo, Japan). These loggers (102×∅20 mm, 50 g in the air, absolute accuracy for depth and speed: 0.5 m and 0.05 m s^{-1}, respectively) had an anteriorly mounted propeller. Thus, speed was measured by counting the revolutions of the propeller every second, subsequently converted into flow speed (m s^{-1}) using data obtained from calibration experiments in a pool, as well as data obtained from the animal (Fletcher et al. 1993; Blackwell et al. 1999; Ropert-Coudert et al. 2000b). Another logger type, with 12-bit resolution, a 16-Mbyte Flash memory and two channels (UME-TT logger) recorded the oesophagus temperature once a second. In order to maximise the memory usage, only one channel recording the oesophagus temperature was switched on. These devices consisted of a cylinder (68×∅15 mm, 30 g) and a soft plastic cable 27.5 cm long (∅1.2 mm) ending in a temperature sensor (5×3 mm, accuracy: 0.1°C). The cable was attached to a thin filament 50 cm long, both emerging from one end of the cylinder. The filament was composed of several strands to prevent slipping and thus avoid injuries due to friction at the beak rictus. Birds were caught on the shore or directly at the nest prior to their departure to sea and were equipped with loggers. They were induced to swallow the body of the moistened UME-TT with the throat being gently rubbed until the logger reached the stomach. The emerging part of the filament was then glued on the head and neck feathers (see details of the attachment procedure in Ropert-Coudert et al. 2000a). This system ensures that the sensor was held in the oesophagus lumen at the back of the throat. The UWE-PDT loggers were attached in the middle of birds' backs close to the tail to minimize the drag induced by externally attached loggers (Bannasch et al. 1994), with glue (Araldite) and two cable-ties.

After one foraging trip, birds were recaptured either on the shore or at the nest and devices removed, the UME-TT being recovered by pulling gently on the filament until the logger was regurgitated. Data were then downloaded into a computer. Dives were divided into descent, undulatory (two or more undulations >2 m) and ascent phases. Therefore, dives could be separated into those with and without an undulatory component. Moreover, dives were grouped into dive bouts, the end of a bout being defined by a bout end criterion (BEC). The BEC was determined as the point of inflexion of the log-survivor curve of post-dive surface intervals plotted for each individual (Gentry and Kooyman 1986). Drops in oesophageal temperature and abrupt accelerations were treated mathematically using a method that counted the number of markedly decreasing or increasing events over the course of each dive (Ropert-Coudert et al. 2000a, 2000b). This method of determination was successfully tested during feeding experiments performed on captive Adélie penguins in Adélie Land, hand-fed with pieces of shrimps, and on captive penguins in a pool in Japan (see details of the experiments in Ropert-Coudert et al. 2000a). Using this method, 55.3% of isolated ingestion events were detected, although the detection was less than 20% in the case of the ingestion of small prey ranging in length between 20 and 39 mm (Ropert-Coudert et al. 2000a).

Where data were normally distributed, parameters were compared between birds using a one-way analysis of variance (ANOVA) following the procedures recommended by Sokal and Rohlf (1969). Proportions were tested by a χ^2 test. The data were statistically treated using Systat (version 7.0, SPSS) and Statview (version 4.57, Abacus Concepts) softwares. For all statistical tests, the threshold was 5%.

Results

Of the 16 free-ranging birds equipped, 3 regurgitated the oesophagus devices on land prior to departure. Of the 13 birds equipped with both logger types that underwent a full foraging trip, 9 regurgitated the oesophagus logger at sea, 6 of them being retrieved hanging from the bill of the bird. These provided sporadic data. Four birds still had both the oesophagus and speed-depth loggers when recaptured after their foraging trip. One of the UME-TT loggers leaked and, therefore, reliable swim speed, depth and oesophagus temperature data were obtained for three birds, numbered 24, 28 and 07. The three parameters were logged for a full foraging trip in the case of bird 07 (Fig. 1a). The oesophagus temperature was incorrectly recorded due to temporary electrical shunts reversing the polarity of the sensor for three different portions of the trip in bird 28, accounting for 8.8% ($N=83$) of the dives. In bird 24, the oesophagus tem-

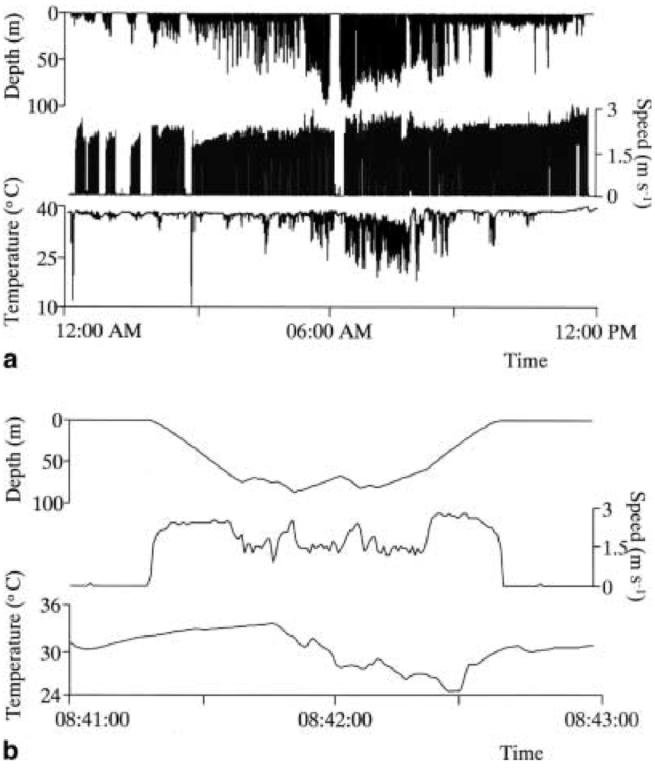


Fig. 1 Depth, swim speed and oesophagus temperature recorded on bird 07 for **a** the full foraging trip (1 day), and **b** detailed for one dive

Table 1 General information on the foraging trip, dives and oesophageal temperature for three equipped Adélie penguins

	Parameters	Bird 24	Bird 28	Bird 07
Bird	Mass (kg)	4.8	4.4	4.9
Trip	Time spent at sea (h)	15	29	22
	Number of bouts (BEC in min)	5 (7.5)	6 (7.5)	6 (6.5)
	Bout duration (h)	2.6 ± 3.5	4.5 ± 5.1	8.2 ± 4.0
Dive	Total number of dives	400	947	877
	Maximum depth (m)	93.2	67.0	58.4
	Mean maximum depth (m)	23.9 ± 26.62	24.8 ± 31.1	18.3 ± 22.3
	Ratio deep/shallow dives	0.31	0.40	0.20
Oesophagus temperature	Basal temperature[a] (°C)	38.3 ± 0.4	39.8 ± 1.1	37.8 ± 1.1
	Total number of drops	269	565	548
	Number of drops per hour	22.1 ± 37.8	22.6 ± 28.7	19.5 ± 24.0
	Minimum temperature (°C)	22.7	18.7	10.2

[a] Temperature recorded before the departure to sea

perature was recorded correctly for the first two-thirds of the foraging trip until the recorded temperature became constant, although the bird continued to dive, indicating a sensor malfunction at this time.

Birds 28 and 07 had longer foraging trips, incorporating more dives than bird 24 (Table 1). Bird 07 dived, on average, significantly shallower than the other birds (ANOVA $F_2 = 14.7$, $P < 0.0001$). The number of temperature drops detected for birds 28 and 07 was similar and greater, respectively, than for bird 24. In penguin 24, the small number of temperature drops was certainly due to the shorter foraging trip duration associated with the fault in the sensor. The occurrence of oesophageal temperature drops per dive bout was extremely variable within birds, temperature drops being concentrated in one or two dive bouts toward the middle of the foraging trip. However, for the three birds, the foraging trip was split into a similar number of dive bouts.

A total of 264 (16.28%) of the temperature drops occurred when the birds were at the surface. Most of these were small (0.7 ± 0.2°C, $N = 203$) and followed deep dives. However, 61 surface events were considered separately as they showed a greater than average magnitude of drop (4.3 ± 20.6°C, maximum magnitude = 19.5°C) and were only observed during the initial phase of the foraging trip. All other drops occurred during diving (Fig. 1b), most (79.8%) during bouts of dives deeper than 40 m. Deep dives were defined for dives with maximum depth > 40 m, this value representing the trough in the bimodal distribution of the maximum depth frequencies of the three birds (Fig. 2, top graph). The average number of temperature drops per dive was higher for deep dives (4.1 ± 2.1, $N = 310$) than for shallow dives (1.7 ± 1.2, $N = 50$, ANOVA $F_1 = 61.2$, $P < 0.0001$). In addition, the magnitude of the temperature drops during shallow dives (1.6 ± 1.4, $N = 85$) was significantly smaller than that during deep dives (2.4 ± 1.9, $N = 1271$, Student $t_{1355} = -3.9$, $P < 0.0001$). No temperature drops were recorded during the majority (92%) of the dives without undulatory phase, while temperature drops were recorded in 93% of the dives with an undulatory phase. Moreover, the undulatory phase of deep dives started, on average, at 91 ± 11% and ended at 85 ± 18% of the maximum depth (data for the three birds combined). Within undulatory dives, 73% of the drops occurred during the undulatory phase although 23% and 4% occurred during the ascending and the descending phases, respectively (Fig. 3). Single or sometimes multiple drops were occasionally observed between 40 and 50 m during the ascent. However, the

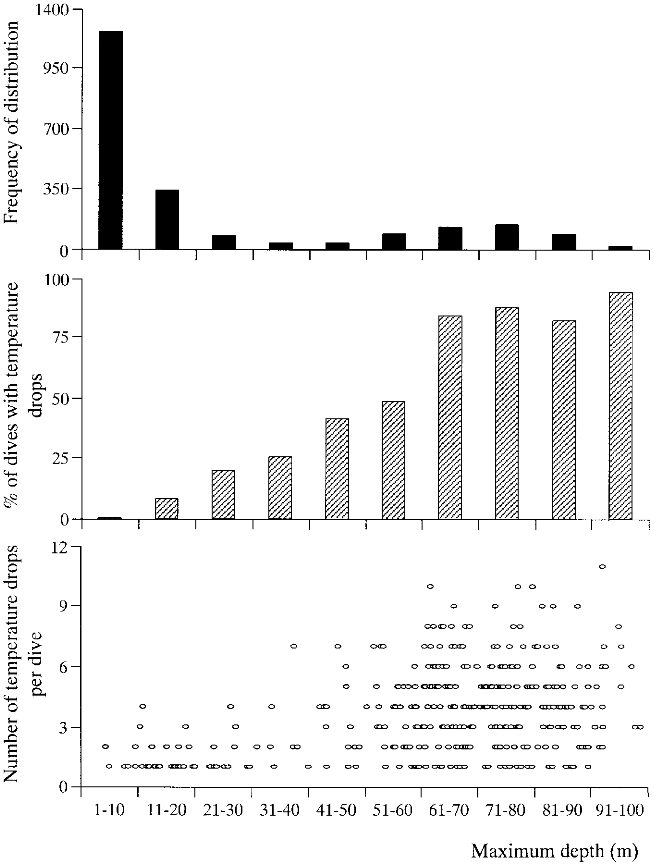
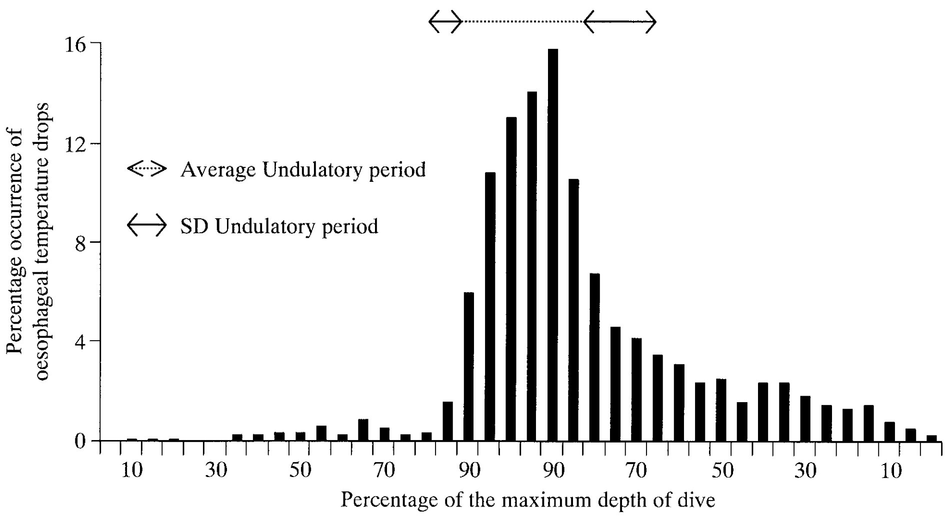


Fig. 2 Frequency of distribution, percentage of dives with drops, and number of drops per dive according to the maximum dive depth of dives of free-ranging Adélie penguins

Fig. 3 Percentage of the maximum depth at which oesophageal temperature drops occurred (calculated for all dives and all birds). The depths at which the undulatory period started and ended, averaged for all birds, are indicated by *solid* and *dotted arrows*, respectively. The exact values of the average and standard deviation (*SD*) of the start and end of the undulatory period are given in Results



magnitude of these drops (descent phase 1.47 ± 0.93°C, $N = 60$; ascent phase 1.96 ± 1.44°C, $N = 464$) was significantly less than that observed during the undulatory phase (2.57 ± 2.03, $N = 833$; one-way ANOVA: $F_3 = 83.5$, $P < 0.0001$). The mean number of undulations during undulatory dives was 5.4 ± 2.0 ($N = 122$ dives), 7.4 ± 3.0 ($N = 140$ dives) and 10.8 ± 4.4 ($N = 52$ dives) for birds 07, 28 and 24, respectively. The number of temperature drops per undulatory deep dive was linearly related to the number of undulations ($Y = 0.25 * X + 2.3$, $N = 360$, ANOVA $F_1 = 63.7$, $P < 0.0001$) but the coefficient of determination was poor ($R^2 = 0.15$). Within the undulatory phase of deep dives, drops were separated from each other by a mean of 14.9 ± 12.1 s ($N = 992$).

Although statistically different from each other, the swim speed during shallow dives and non-undulatory deep dives varied little throughout the dive. For undulatory deep dives, the speed during the undulatory phase was significantly slower than the ascent and descent speeds (Table 2). Here, birds decelerated sharply at the point of the first undulation, whereupon the rest of the undulatory period was characterised by low speed with frequent abrupt acceleration and deceleration. The number of abrupt speed changes (Nsc) was linearly related to the number of undulations (Nu) in the undulatory phase ($\mathrm{Nsc} = 0.57 * \mathrm{Nu} + 2.47$, $\mathrm{N} = 316$, $F_1 = 363.5$, $P < 0.0001$, $R^2 = 0.54$). During acceleration that lasted more than 2 s, the values of the depth change were summed in order to determine the preferred direction of swimming. Birds swam upward in 60% ($N = 530$) of the acceleration events and downward in 38% ($N = 330$). Swim depth apparently did not change in 2% of the cases. Summing data for all birds, 42.5% of the abrupt accelerations were followed by one or more temperature drops, while 57.5% were not followed by any drop. In addition, the magnitude of accelerations that were followed by one or more temperature drops (0.77 ± 0.40, $N = 939$) was statistically greater than those without subsequent temperature drops (0.61 ± 0.34, $N = 1224$, ANOVA $F_1 = 111.9$, $P < 0.0001$).

Discussion

Device effects

Externally attached loggers have been shown to create additional drag, which affects the swim speed and energy expenditure of captive birds swimming in a water canal (Kooyman 1989; Wilson and Culik 1992). In our study, the cross-sectional area of the logger accounted for 1.6% of the bird's cross-sectional area and we estimate that the external loggers would probably have caused an increase in energy expenditures of less than 2.2%, this value being derived from experiments in a water canal using a logger with a cross-sectional area 1.8% that of the Adélie penguin (Culik and Wilson 1991b), although the loggers used by Culik and Wilson (1991b) were streamlined. The Adélie penguins in our study swam at speeds similar to the birds used by Culik and Wilson (1991b) to derive their estimates.

The effects of the oesophagus device were difficult to assess. No apparent physical injuries were caused to the birds, either by the logger in the stomach or by the cable emerging at the corner of the mouth. There was a high rejection rate of the oesophagus logger that can probably be reduced in future studies by using a retaining system as described in Wilson et al. (1998). Four of the six loggers retrieved hanging from beaks were covered with half-digested food, indicating that birds succeeded in ingesting prey and feeding their offspring.

Surface drops and prey ingestion rate

Substantial drops in the oesophageal temperature occurring in non-diving animals may represent snow ingestion while the birds rested on land or ice outside of

Table 2 Swim speed (m s^{-1}) during the descent, undulatory and ascent phases of Adélie penguins' dives

	Descent	Undulatory	Ascent	One-way ANOVA
Shallow dives	2.16 ± 0.37	2.13 ± 0.42[a]	2.12 ± 0.38[a]	$F_2 = 38.2$; $P < 0.0001$
Deep dives				
Without undulations	2.16 ± 0.28	–	2.00 ± 0.35	$F_1 = 74.0$; $P < 0.0001$
With undulations	2.12 ± 0.29	1.71 ± 0.53	2.04 ± 0.40	$F_2 = 4171.2$; $P < 0.0001$

[a] Within rows, values followed by a superscript were not significantly different by post-hoc tests

the colony (Aoyanagi and Tamiya 1983; Wilson et al. 1989). The small drops between dives may correspond to the cooling of the sensor during breathing events. However, these small surface events were not always recorded and their observation may depend on several factors, such as the air temperature. The high energetic cost of warming ingested water (Wilson and Culik 1991) and results from field metabolic rate studies using double-labelled water (Culik and Wilson 1992) suggest that penguins do not ingest a significant amount of seawater while at sea. Therefore, we assume that temperature drops recorded during diving phases corresponded to prey ingestion.

In our birds, prey were either swallowed directly during, or few seconds after, acceleration. This pattern of capture and swallowing of prey has been observed on several occasions in free-ranging (Zusi 1975) or captive Adélie penguins (Ropert-Coudert et al. 2000b), prey being sometimes gathered in the mouth prior to swallowing. This would lead to an underestimation of the exact number of prey captured when using oesophageal temperature recording. Most of the oesophageal temperature drops were recorded when the bird was swimming in an upward direction, suggesting the use of the backlighting effect to detect and capture prey, as has been observed in Weddell seals (*Leptonychotes weddelli*) (Davis et al. 1999) and king penguins (*Aptenodytes patagonicus*) (Ropert-Coudert et al. 2000a). An eye directed upward in the sea receives about 100 times more light flux than one directed downward (Clarke and Denton 1962), so that marine predators approaching a target from underneath are more likely to be able to visualise its silhouette.

Swim speed during feeding and non-feeding dive

During the descent and ascent phases of the dive cycle, birds swam at ca. 2.1 m s^{-1}, a value that accords closely with the minimum cost of transport (COT_{min}, Schmidt-Nielsen 1972) of 2.2 m s^{-1} calculated on captive Adélie penguins in a swim canal (Culik and Wilson 1991a, 1991b). Under normal circumstances, this should be the optimum speed to travel between the water surface and the preferred foraging depth if birds are to minimise energy expenditure per unit distance travelled but, by the same token, this speed also effectively extends the time that the birds may spend at their preferred foraging depth because less energy (and thus less oxygen reserves) would be wasted in the commuting process. In dives where no prey were ingested, the preferred swim speed during the bottom phase of the dive cycle also accorded closely with that corresponding to the COT_{min}. Again, this allows the birds to travel the maximum distance underwater at minimum cost, a feature which enhances the chances of detecting prey, because the probability that prey will move into the bird's field of vision will be proportional to the distance swum underwater (Wilson et al. 1996).

However, our data suggested that once a prey patch was located, mean penguin swim speed during the undulatory phase decreased substantially. The periods of low speed at the undulatory phase presumably corresponded to prey manipulation by birds and/or search for the next target while acceleration phases probably resulted from the active pursuit of prey. This indicates that the speed at which Adélie penguins effectively process encountered prey is substantially lower than the speed at the COT_{min}. Prey-processing speed in penguins must be put in perspective with prey escape speeds. In species feeding on small prey, such as the pygoscelid and many of the eudyptid penguins (Croxall and Lishman 1987), escape speeds of the prey are essentially negligible compared to those of the penguins. Euphausids, for example, swim at average speeds ranging between 0.13 and 0.15 m s^{-1} (Kanda et al. 1982) up to 0.4 m s^{-1} (Hamner 1984). Occasionally, euphausids can exhibit "tail-flip" escape behaviour where speeds can reach up to 1 m s^{-1} (O'Brien 1987). This difference between prey and predator speeds results from massive differences in body size, which tend to determine the limit of swimming speed (Wardle 1975). Where prey become larger, birds may have to adjust capture speeds to be higher to minimise energetically costly extended chases.

Depth utilisation

The high concentration of capture events in deep dives illustrates the patchy distribution of euphausiids, which aggregate in dense swarms. Investigations of the euphausiids' vertical distribution showed that different stages of euphausiids can be found at various depths in the water column (Marr 1962; Hempel et al. 1979; Hempel 1985; Hosie 1994) with, in some instances, a vertical diel migration that brings the euphausiids close to the surface at night (Everson 1984; Everson and Murphy 1987). Hydroacoustic surveys off Adélie Land in 1996 showed that nearly all of the krill was concentrated in the top 100 m depth zone, with about 80%

being above 75 m (Pauly et al. 2000). This is in accordance with the observation in our study of the oesophageal temperature drops being associated preferentially with dives > 40 m. Hill et al. (1996) compared the size of krill caught by nets with that of krill caught by free-ranging macaroni penguins (*Eudyptes chrysolophus*), and observed that the birds selected prey larger than that caught by net, although this may be biased by other factors such as size-differential net avoidance (Hovekamp 1989). Since gravid females, highly nutritional among euphausiids (Clarke 1984), may be the main target of Adélie penguins (Endo et al. 2000), it is likely that Adélie penguins in our study were also selectively exploiting a category of size among the euphausids that was confined in the depth zone > 40 m.

General features of Adélie penguins' feeding behaviour have been highlighted by the simultaneous recording of depth, swim speed and oesophagus temperature. The results presented here need confirmation with a larger sample size and complete coverage of foraging trips in tandem with the collection of stomach samples. In this respect, it should be noted that the diet of Adélie penguins may change from primarily krill to fish over the second half of the breeding season in Adélie land (Ridoux and Offredo 1989), which may lead to variation in the pattern of capture described above. Diet information will elucidate the capture rate per dive, per bout and per foraging trip and probably provide an estimation of energy intake, a necessary parameter in assessing the role of a major Antarctic predator.

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